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ABSTRACT

Grazing animals influence a wide range of plant and soil processes in the world's grasslands. Ecologists have long understood that grazing can stimulate aboveground net primary production (ANPP), although this phenomenon has not been broadly generalizable across grasslands and grazing regimes. The mechanisms underlying grazer stimulation of ANPP are therefore of interest to a wide variety of stakeholders from ecologists to land managers. Three data-supported hypotheses offer differing explanations for the ways in which grazing interacts with resource availability to drive ANPP: the compensatory continuum hypothesis (CCH) implicates background resource availability, the limiting resource model (LRM) considers the direct effects of grazers on resource availability, and the episodic herbivory model (EHM) considers the indirect effects of grazers on resource availability brought about by the removal of standing biomass. No studies have yet compared these three models to measure their relative influence on ANPP. I conducted a paired-plot defoliation experiment in two distinct grassland community types (mesic and dry) in Yellowstone National Park to test how well each model explained variation in ANPP over two months of the growing season. I simulated an average Yellowstone grazing intensity (50% biomass removed monthly) and measured plant-available N and soil moisture as indices of resource availability. I also collected data on ANPP and resource availability in plots grazed by bison to study support for each model under a natural grazing regime. Clipping increased relative growth rates in each grassland type by over 100% but had no effect on N availability or soil moisture. Clipping in June increased ANPP in mesic but not dry grassland, supporting the CCH at the landscape scale. Within mesic grassland there was support for the EHM, LRM_{moist} and CCH_N , but the EHM explained over twice as much variation in the clipping effect on ANPP than the next best model. In dry grassland, the EHM was the only

model with support. The poor predictive power of alternative models in dry grassland may be due to their neglect of resource colimitation, which in a previous study was found to interact with grazing to influence ANPP in this system. Effects of ungulate grazing on ANPP varied between grassland types, and grazer-stimulation of ANPP was accompanied by increases in relative growth rate and N availability, supporting the LRM. Relative growth rate was negatively related to standing biomass in both clipped and grazed plots in accordance with the framework of the EHM. The clipping study empirically demonstrates for the first time a key tenet of the EHM, that herbivory can increase ANPP without any direct effect on resource availability. Both the clipping and grazing studies suggest that the three models considered are not independent and can theoretically operate simultaneously. Considered in full, this thesis highlights the diversity of ways by which grazing by wild, migratory, ungulates can stimulate ANPP.

VARIATION IN HERBIVORE EFFECTS ON GRASSLAND PRIMARY PRODUCTION: A
TEST OF THREE MODELS

Jacob F. Penner

B.A. Goshen College 2017

THESIS

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“Phenomena intersect; to see but one is to see nothing” – Victor Hugo

“But the great fact [is] the land itself” – Willa Cather

Introduction

Grasslands cover over 40% of the Earth’s terrestrial surface and represent the dominant ecosystem in climatic regions with low to moderate rainfall (Dixon et al. 2014). They are among the most productive ecosystems on Earth and support a high density and diversity of the world’s large herbivore species (Olf et al. 2002). Consequently, many grasslands have a large proportion of their plant biomass consumed annually by grazing animals, representing a significant loss of photosynthetic potential (Frank et al. 1998, Augustine et al. 2003). Nevertheless, the long co-evolutionary history of grasses and grazers has resulted in grasslands that are able to sustain biomass production in the face of chronic, intensive consumption (McNaughton 1985, Milchunas et al. 1988), a phenomenon that has been a topic of great research interest to ecologists, ranchers, and land managers for half a century (Noy-Meir 1973, Painter and Belsky 1993, Schwinning and Parsons 1999, Frank et al. 2016).

The grazing optimization hypothesis

A significant topic of debate among grazing ecologists is the validity of the so-called “grazing optimization hypothesis (GOH)” which posits that intermediate levels of grazing can increase aboveground net primary production (ANPP) (McNaughton 1979, Hilbert et al. 1981). An implication of the GOH is that under appropriate management, grazing animals will exert positive feedbacks on their own food supply and sustain their population levels through time. It does not imply that grazing improves the fitness or survival of grazed plants, as plant biomass and productivity are not necessarily representative of fitness (Fridley 2017). The GOH was

developed from the synthesis of multiple field studies in the Serengeti-Mara region of East Africa, where it was observed that ANPP in grasslands grazed seasonally by large, migratory herds of wildebeest (*Connochaetes taurinus*), zebra (*Equus quagga*), and gazelle (*Eudorcas thomsonii*) was a unimodal function of grazing intensity (% biomass consumed) with a peak between 25 and 50% (McNaughton 1979, 1985). Stimulation of ANPP has since been observed in grazing systems around the world including tropical savannas in east Africa and India (Pandey and Singh 1992, Charles et al. 2017), tropical grasslands in South America (Altesor et al. 2005), and montane grasslands in North America (Frank et al. 2002, 2016). Other studies, however, that have attempted to recreate the curve predicted by the GOH have failed to do so (Williamson et al. 1989, Turner et al. 1993, Biondini et al. 1998, Knapp et al. 2012), sparking debate about the generality of the GOH and its relevance in particular to livestock grazing systems (Belsky 1987, Painter and Belsky 1993). Even among wildlife-dominated systems, stimulation may be more the exception than the rule, as syntheses of studies from grasslands around the world have found consistent negative effects of grazing on ANPP, with herbivores optimizing ANPP only under a specific, limited range of conditions (Milchunas and Lauenroth 1993, Ferraro and Oesterheld 2002). This has led many ecologists to caution against the broadscale, general application of the GOH, particularly in both rangelands of the western U.S. with no evolutionary history of grazing and intensively grazed livestock systems that aim to maximize livestock production (Briske 1993, Painter and Belsky 1993, Briske et al. 2008).

While the empirical support for the GOH has therefore been mixed, the wide range of successes and failures in predicting when grazing will increase ANPP offers an opportunity to further study and understand the conditions under which the predictions of the GOH are observed. Such an understanding would help inform conservation efforts in systems dominated

by migratory grazers (which have provided the most support for the GOH) while also generating a framework to assess why the GOH has failed to predict grazing outcomes in more intensively managed systems. The key shortcoming of the GOH is that it does not explicitly consider how grazing interacts with resource limitation to affect ANPP, even though grazing can have dramatic effects on the availability of limiting resources (Bardgett and Wardle 2003). Here I will briefly review three models that invoke distinct interactions between grazing and resource availability as key drivers of the variation in herbivore effects on ANPP.

The compensatory continuum hypothesis

The compensatory continuum hypothesis (CCH) states that plant tolerance to herbivory should be higher in systems with high levels of resource availability (Maschinski and Whitham 1989). While originally developed to model individual plant tolerance of herbivory from a fitness perspective, its predictions have been applied to ANPP in grazing systems as well (Bardgett and Wardle 2003), as ANPP has long been understood to be driven by the availability of limiting resources such as soil moisture and plant-available N (Fay et al. 2015). The CCH therefore ignores potential feedbacks of grazers on resource availability, considering only the background resource availability at the time of grazing. A growth chamber study of the Serengeti grass *Sporobolus kentrophyllus* found that clipping increased production only under high levels of supplemental N (Hamilton et al. 1998). In a Kenyan savanna grazed by both livestock and wildlife, grazing increased ANPP only during wetter-than-average years in habitats with high levels of plant-available N and P (Augustine and McNaughton 2006). Grazing by bison in the grasslands of Yellowstone National Park more frequently increases production at mesic sites with high soil moisture levels than at drier sites (Frank et al. 2018). Other experimental field studies, however, have not supported the predictions of the CCH, finding no or negative effects

of simulated herbivory under high resource levels (Alward and Joern 1993, Leriche et al. 2003, Bagchi and Ritchie 2011). For a grazing system to support the predictions of the compensatory continuum hypothesis, grazing should have increasingly positive effects on ANPP as resource availability increases while having no effects on resource availability (Figure 1). These resource gradients can occur at spatial scales across a landscape as well as temporal scales throughout a growing season.

The limiting resource model

While the CCH does not account for direct, herbivore-driven changes in resource availability, effects of grazing on soil nutrients and their consequences for ANPP are well documented (Ritchie et al. 1998, Augustine and Frank 2001, Pastor et al. 2006, Frank et al. 2018, Marshall et al. 2018), and theoretical models have shown that grazing can increase ANPP by increasing nutrient recycling (de Mazancourt et al. 1998). The limiting resource model (LRM) expands the framework of the compensatory continuum hypothesis to consider how herbivory affects resource availability (Wise and Abrahamson 2005, 2007). It makes multiple predictions that are contingent upon which resource is affected by herbivory and which resource limits plant tolerance to herbivory (Wise and Abrahamson 2005). As with the CCH, the conceptual underpinnings of the LRM are often applied to ANPP in systems grazed by wild ungulates (Bardgett and Wardle 2003, Pastor et al. 2006).

Grasslands around the world are primarily limited by N and water (Fay et al. 2015), two resources on which grazers can have marked effects. Grazing mammals generally increase short-term N availability and speed up rates of N cycling via N-rich dung and urine inputs that decompose much faster than ungrazed vegetation (Frank and Evans 1997, Frank and Groffman 1998, Barthelemy et al. 2018, Veldhuis et al. 2018). Independent of dung/urine inputs, grazing

can also stimulate the exudation of soluble carbohydrates from grass roots that drive increases in microbial biomass, turnover, and N availability (Hamilton and Frank 2001, Hamilton et al. 2008). Grazing can have variable effects on soil moisture among systems: the removal of biomass reduces shading and increases the evaporative demand on plants and soil, but it also can increase soil moisture by reducing the transpirational surface area of the vegetation (Veldhuis et al. 2014, Frank et al. 2018). For the limiting resource model to be supported, positive effects of grazing on the availability of a limiting resource should be associated with similarly positive effects on ANPP. Negative effects of grazing on both resource availability and ANPP should be linked as well (Figure 1).

The episodic herbivory model

The episodic herbivory model (EHM) is a theoretical model that uses classical population dynamics to consider how ANPP in grasslands responds to herbivory (Ritchie and Penner, in review). The EHM is based on the truism that for grazing to increase ANPP, regrowth by grazed plants must exhibit a higher relative growth rate (mass-specific growth rate, or RGR) than similar ungrazed plants (Hilbert et al. 1981). Grasses are particularly well-adapted to regrowth following grazing due to the protected location of intercalary meristems near the soil surface during periods of vegetative growth (Briske 1991, Ferraro and Oesterheld 2002). Leaf tissue that regrows following grazing often has a greater N concentration and photosynthetic rate than immediately prior to grazing as the metabolic energy of the plant is concentrated across a smaller surface area (Painter and Detling 1981, Anderson et al. 2013, Frank et al. 2018). These leaf traits are positively correlated with RGR at individual plant and community scales, demonstrating how grazing can increase RGR simply by altering the phenology of grazed plants (Poorter and Remkes 1990, Garnier et al. 2004, Laliberté et al. 2012).

The EHM modifies a previous theoretical model developed by Hilbert et al. (1981) that also studied the mathematical drivers of variation in herbivore effects at a given grazing intensity. Hilbert et al. (1981) concluded that grazing was more likely to increase ANPP under stressful, low-resource conditions where ungrazed plants would grow well below their maximum relative growth rate (RGR_{max}). When ungrazed plants grow near RGR_{max} it becomes much less likely for a grazed plant to achieve the RGR necessary to surpass the total production of the rapidly growing ungrazed plant. This prediction has empirical support from greenhouse studies of several tropical grasses (Oesterheld and McNaughton 1988, 1991), but it is at odds with the predictions of positive grazer effects at high resource levels made by the compensatory continuum hypothesis (see above). Furthermore, Hilbert et al. (1981) modeled plant growth as an exponential process with constant RGR even though RGR is well-known to decrease as biomass accumulates (Schwinning and Parsons 1999, Paine et al. 2012).

The EHM uses a logistic growth model to explicitly consider the implications of density-dependent resource limitation on the conditions necessary for grazing to increase ANPP (Ritchie and Penner, in review). It shows how grazing can increase ANPP by indirectly increasing resource availability as the removal of grazed tissue relieves limitations on relative growth rate imposed by density-dependence. For a given grazing intensity and frequency, the EHM shows that two parameters, RGR_{max} and initial biomass relative to steady-state, end-of-season peak biomass, determine whether or not grazing increases ANPP. When either parameter is high, the likelihood of grazing stimulating ANPP is high as well. These parameters can themselves be modelled as functions of resource availability using consumer-resource theory in a fashion that accounts for grazing-induced changes in resource supply rate or pool size (Ritchie and Penner, in

review). The EHM therefore predicts that stimulation of ANPP is possible under a wide range of conditions, including no to positive direct effects of grazing on resource availability.

The differing predictions of the CCH, LRM, and EHM offer an exciting opportunity to compare their predictions in the field. The EHM has not yet been tested against other models that attempt to explain variability in herbivore effects on ANPP. The CCH predicts that stimulation of ANPP should be greater at higher levels of limiting resource availability, independent of any interactions with grazing (Figure 1). The LRM predicts that stimulation of ANPP should be greater when grazing directly increases limiting resource availability (Figure 1). The EHM predicts that stimulation of ANPP should be greater when plots have a higher initial relative biomass, thereby indirectly alleviating resource limitations imposed by density-dependent growth (Figure 1). These three predictions can be compared using an herbivore enclosure experiment that is replicated across resource gradients. While these models are not mutually exclusive and could theoretically all operate simultaneously, a direct comparison of their relative influences on ANPP can nonetheless improve our mechanistic understanding of plant-herbivore dynamics in grasslands (Bagchi and Ritchie 2011). I conducted a paired-plot defoliation experiment in the grasslands of Yellowstone National Park to compare these three models and study the mechanisms responsible for grazer-stimulation of ANPP while controlling for defoliation intensity and frequency. I also conducted a small-scale grazing experiment to assess how grazing ungulates influenced the density-dependence of ANPP as predicted by the EHM and to compare the effects of simulated and actual grazing.

Methods

Site Description

This study was conducted in Yellowstone National Park (YNP), an 8995 km² preserve in the central Rocky Mountains of North America that supports large herds of migratory ungulates including bison (*Bison bison*), elk (*Cervus canadensis*), pronghorn (*Antilocapra americana*), bighorn sheep (*Ovis canadensis*), and mule deer (*Odocoileus hemionus*). Grazing pressure in YNP has shifted from elk-dominated to bison-dominated over the last 40 years, resulting in an increase in annual grazing intensities in areas where bison concentrate (Frank et al. 2016). YNP ungulates track the seasonal green-up of forage from low-elevation winter range to high-elevation summer range each year (Frank and McNaughton 1992, Middleton et al. 2018), stimulating several ecosystem processes such as N mineralization (Frank and Groffman 1998) and net primary production (Frank et al. 2002). Other processes such as litter decomposition are unaffected by grazing and are driven instead by climatic variability (Penner and Frank 2019).

My study examined two types of grasslands in YNP: mesic, productive grasslands on the core summer range of YNP bison, and dry, unproductive grasslands grazed transitionally during ungulate migration (Geremia et al. 2014). Mesic grasslands have deep soils with higher levels of soil C and N than the shallow, rocky soils of dry grasslands (Frank et al. 2018). Plant communities at mesic grasslands are dominated by non-native, sod-forming pasture species such as the grasses *Poa pratensis*, *Agrostis stolonifera*, and *Phleum pratense*, along with the forbs *Trifolium repens* and *Taraxacum officinale*. Dry grassland communities are dominated primarily by native bunchgrasses such as *Poa secunda*, *Hesperostipa comata*, and *Festuca idahoensis*, as well as a native sedge, *Carex duriuscula*.

Clipping Experiment

Twenty 2.5 m x 2.5 m exclosures were established prior to snowmelt in 2018 across four sites in mesic and dry grassland on YNP's Northern Range (10 replicates in mesic grassland distributed across 2 sites, 10 replicates in dry grassland distributed across 2 sites). Within each exclosure I paired two 0.5 m² plots with a similar vegetative composition and randomly assigned treatments of clipped or unclipped. There was no difference in standing biomass between paired plots prior to treatment application at the end of May ($t = 0.07$, $df = 19$, $p = 0.94$). For clipped plots, I removed approximately half of the standing biomass of each shoot present twice over the course of the growing season: once during late May/early June and again one month later during late June/early July. This simulated grazing intensity of 50% mirrors observed grazing intensities by bison in YNP (Frank et al. 2016). All experimental plots were watered weekly following treatment application to reduce moisture limitations on ANPP. Each plot received five liters supplemental water per week for six weeks, a rate equivalent to the long-term precipitation average for the region during June (NOAA Climate Data Online).

I used the canopy-intercept method (Frank and McNaughton 1990, Frank et al. 2018) to nondestructively estimate standing biomass throughout the experiment, quantifying pin-hits at the species level and converting hits per pin to biomass per m² using previously determined calibration curves (C. Geremia, unpublished data). Biomass was estimated in each plot over two months (late-May/early-June to late-July/early-August), a period that included peak standing biomass at each site. Growth intervals were between 24 and 32 days in June and between 22 and 31 days in July. In clipped plots, I estimated biomass immediately before and after clipping the vegetation on each sampling date to quantify the simulated grazing intensity. Daily ANPP was calculated for each plot as the difference in standing biomass between sampling dates for each

month-long interval. Daily RGR was calculated as the difference in log-transformed (base e) biomass estimations between sampling dates. The monthly clipping effect on ANPP and RGR was calculated as the difference in ANPP or RGR between clipped and control plots.

I indexed plant-available soil nitrogen concentrations using ion-exchange resin bags (Binkley and Matson 1983). Two level tablespoons (29.6 mL) of Dowex Marathon mixed-bed resin (Sigma Aldrich, St. Louis, MO) were placed into 4 x 4 x 1 cm nylon bags. Resin bags were buried in the top 10 cm of the soil immediately adjacent to each sampling plot to avoid soil disturbance in the sampling plot. Because resin bags were buried in the rooting zone and competed with roots for N uptake, total N adsorption to each bag represents the size of the available N pool and represents the steady state balance between supply rate and plant uptake. In clipped plots, the clipping treatment was applied to the vegetation surrounding the resin bag to ensure that the soil supplying nitrogen to the resin bags was under clipped conditions. Resin bags were left in the field for approximately one month following the first clipping treatment in late May, after which they were replaced with fresh bags in the same location for the subsequent clipping treatment in late June. Once collected, all bags were washed with DI water to remove soil and roots before being air-dried. All bags were stored in sealed containers at room temperature prior to lab extractions. I extracted the resin bags by shaking each bag in 125 ml of 2 M KCl for one hour. Resin bags sat in solution for an additional hour, after which I collected 15 ml KCl from each sample in a plastic vial. Vials were kept at -20°C prior to analysis for extractable NH_4^+ and NO_3^- on a SEAL Autoanalyzer3 colorimetric analyzer (SEAL Analytical, Mequon, WI). Total N adsorption rate (N availability) was calculated on a per day basis over the same growth intervals used to measure ANPP. Volumetric soil moisture was measured in each

plot at each sampling date with a Hydrosense II soil-water sensor (Campbell Scientific, Logan, UT).

Grazing Experiment

ANPP and RGR were calculated during June and July in grazed grassland using 1 m² moveable exclosures (n = 5 for each grassland type) (Frank et al. 2002, 2018). Exclosures were randomly relocated each month. Grazing intensity was calculated as the proportion of biomass removed in randomly located grazed plots relative to temporarily protected plots. In ungrazed grassland, ANPP and RGR were calculated each month in 5 plots distributed across three 3 x 3 m fixed exclosures established after snowmelt. Standing biomass was estimated at the beginning and end of each month using the canopy-intercept method, and daily ANPP and RGR were calculated as previously described for the clipping experiment. Soil N availability and soil moisture were also measured as previously described. Grazed plots were not paired with ungrazed plots, allowing for only mean comparisons between grazed and ungrazed treatments. Plots in the grazing experiment did not receive supplemental water.

Statistical Analysis

Realized clipping intensities were calculated as the proportion of standing biomass removed by clipping. I used 2-way ANOVA with Tukey's HSD post-hoc test to analyze the effects of grassland type and clipping or grazing treatment on ANPP, RGR, N availability, and soil moisture in each month. To test the biomass dependence predicted by the episodic herbivory model, I plotted RGR as a function of biomass at the beginning of the growth period (post-clipping) for each grassland in each month. The EHM predicts that this relationship is linear and negative, with a y-intercept of RGR_{max} and an x-intercept of K (peak biomass). I used

standardized major axis (SMA) regression in the R library ‘smatr’ (Warton et al. 2012) to minimize error in both x and y while estimating these parameters and testing the slope of the line.

I used Bayesian multiple linear regression to compare the relative effect sizes of each model at each grassland with ΔANPP (clipped – control) as the response variable. Month was modeled as a random intercept to account for repeated sampling across months while increasing statistical power. I modelled mesic and dry communities separately because previous work has shown that grazing had different ecological effects on soil resources between these two communities (Frank et al. 2018). Terms modelled for the compensatory continuum hypothesis were N availability and soil moisture in clipped plots. Terms added for the limiting resource model were ΔN availability and Δsoil moisture. Interaction terms between N availability and soil moisture were not significant for the CCH and LRM and were not included in the final model. The term added for the episodic herbivory model was a function of the biomass in the control plot relative to peak biomass (K) for the grassland type in the given month, referred to hereafter as “initial relative biomass”. The final regression model, run separately for mesic and dry sites, combined these five terms standardized to the Z distribution (eqn 1).

$$\Delta\text{ANPP}_{\text{mesic}} \sim \beta_{\text{CCH,N}} * \text{N}_{\text{clip}} + \beta_{\text{CCH,moist}} * \text{moist}_{\text{clip}} + \beta_{\text{LRM,N}} * \Delta\text{N} + \beta_{\text{LRM,moist}} * \Delta\text{moist} + \beta_{\text{EHM}} * \text{initial relative biomass} + (1|\text{month}) \quad (1)$$

I assessed the collinearity of model predictors from all others with Pearson correlation. I then ran the full model in JAGS (Plummer 2003) using ‘R2jags’ (Su and Yajima 2015) and compared posterior distributions for each coefficient: for a model to be supported, coefficients needed to be > 0 . Prior distributions were non-informative: priors for fixed effects were normally distributed with mean zero and variance 10^5 and priors for random effect standard deviations

were uniformly distributed (0,100). The final model was run as three concurrent Markov chain Monte Carlo (MCMC) chains for 50,000 iterations, the first 10,000 of which were thrown out as burn-in. I used the Gelman-Rubin diagnostic (<1.1) to confirm that models converged (Gelman and Hill 2007).

Finally, I used non-metric multidimensional scaling (NMDS) to determine if clipping had systematic effects on species composition that were related to Δ ANPP, standardizing species composition by plot biomass to account for material removed by clipping and assessing compositional similarity between plots using Bray-Curtis dissimilarity. In the grazing experiment I analyzed the effects of grassland and grazing on ANPP, RGR, N availability, and soil moisture with 2-way ANOVA. I didn't perform post-hoc analyses in the grazing experiment due to small sample size ($n = 5$) and limited statistical power. Plots were not paired in the grazing experiment, so I tested only the assumption of resource-limited, density-dependent growth from the episodic herbivory model. I used SMA regression to determine if there was a negative relationship between RGR and standing biomass for each grassland in each month and compared estimates of RGRmax and K to those from the clipping experiment.

Results

Clipping Experiment

Mesic sites were more productive than dry sites in June ($F = 56.50$, $df = 1,36$, $p = <0.001$) and July ($F = 34.92$, $df = 1,36$, $p = <0.001$) (Figure 2). ANPP at mesic sites was dominated by two introduced grasses, *Poa pratensis* and *Agrostis stolonifera*, along with the introduced legumes *Trifolium repens* and *Taraxacum officinale* (Figure 3, Table 2) while ANPP at dry sites

was dominated primarily by a suite of native bunchgrasses including *Poa secunda*, *Hesperostipa comata*, *Pseudoroegneria spicata*, and *Festuca idahoensis* (Figure 4, Table 2). Soil moisture was greater in mesic grassland than dry grassland in June ($F = 38.10$, $df = 1,35$, $p = <0.001$) and July ($F = 33.07$, $df = 1,36$, $p = <0.001$), but there was no difference in N availability between grasslands in either month (Figure 5).

Clipping treatments simulated moderate grazing intensities slightly below the intended 50% grazing intensity (mean \pm SD, 42 ± 11 %). Species composition varied across plots within each grassland at the beginning and end of the experiment but was not affected by clipping (Figure 6). There was an interaction between clipping and grassland type during June such that clipping increased ANPP at mesic grassland but not dry ($F = 4.05$, $df = 1,36$, $p = 0.05$) (Figure 2). There was no effect of clipping on ANPP at either grassland in July ($F = 0.97$, $df = 1,36$, $p = 0.33$) (Figure 2). RGR was similar between mesic and dry sites in June ($F = 0.09$, $df = 1,36$, $p = 0.77$), but was slightly greater in mesic sites during July ($F = 3.74$, $df = 1,36$, $p = 0.06$) (Figure 2). Clipping increased RGR by over 100% at all sites in June ($F = 32.13$, $df = 1,36$, $p = <0.001$) and July ($F = 17.08$, $df = 1,36$, $p = <0.001$) (Figure 2). There were no effects of clipping on plant N availability or soil moisture in either June or July (Figure 5).

RGR was negatively related to standing biomass at both communities in each month (Table 1, Figure 7). The relationship between standing biomass and RGR was strongest at mesic sites in June and was weaker at dry sites (Table 1). Estimated maximum growth rate, RGR_{max} values decreased from June to July for both communities, while estimated peak biomass, K, values increased (Table 1).

N availability and Δ N availability were correlated in dry grassland, but no other model predictors were collinear in either grassland (Pearson correlation coefficient < 0.52 , Table 3). In

mesic grassland, initial relative biomass, as predicted by the EHM, had the strongest positive effect on Δ ANPP (>99% of posterior distribution > 0, Figures 8, 9), more than two times the effect size of the next best model. Δ moisture (LRM) and N availability (CCH) had weaker positive effects on Δ ANPP in mesic grassland (97% and 84% of respective posterior distributions > 0), while soil moisture (CCH) and Δ N (LRM) were not positively related to Δ ANPP (< 18% of posterior distribution > 0) (Figure 8). In dry grassland, initial relative biomass (EHM) had the strongest positive effect size on Δ ANPP (95% of posterior distribution > 0), soil moisture (CCH) had a very weak positive effect (65% of posterior distribution > 0), and no other model was likely to have a positive effect (< 39% of posterior distribution > 0) (Figures 8, 9).

Grazing Experiment

Grazing intensities were moderate but extremely variable in both grasslands (mean \pm SD, mesic: $32 \pm 22\%$, dry: $18 \pm 25\%$). Grazing increased ANPP and RGR in June but had no effect during July (Figure 10). Grazed plots had higher N availability than ungrazed plots in each grassland during both months (Figure 11), while there was no effect of grazing on soil moisture (Figure 11). RGR was significantly negatively related to standing biomass in mesic grassland during June, and weakly related during July (Figure 12). At the dry grassland, RGR and standing biomass were weakly related in June and had no relationship during July (Figure 12, Table 1).

Discussion

The goal of this study was to compare three models that attempt to explain the variation in herbivore effects on grassland aboveground net primary production (ANPP). While not explicitly independent of each other, the three models tested are built on distinct underlying

mechanisms and invoke as the key driver either background resource availability (compensatory continuum hypothesis, CCH), grazer effects on resource availability (limiting resource model, LRM), or resource limitation imposed by density-dependence (episodic herbivory model, EHM) (Figure 1).

A key component of the EHM is that grazing reduces the degree of density-dependent resource limitation, allowing grazed communities to grow at a higher relative growth rate (RGR) and surpass ungrazed communities in total ANPP. I found that clipping increased RGR in each month by over 100 % (Figure 2). This stimulation of RGR was negatively related to standing biomass following clipping as predicted by the EHM (Figure 7), strongly suggesting that RGR was limited by biomass accumulation. This finding supports previous greenhouse studies of tropical grasses that found greater increases in RGR following clipping when plants initially grew at a low RGR (Oesterheld and McNaughton 1988, 1991, Oesterheld 1992). The tightness of this RGR ~ biomass relationship affects the confidence in estimates of maximum growth rate (RGR_{max}) and peak biomass (K) and therefore the ability of the EHM to predict Δ ANPP. R² values decreased from June to July in mesic communities, suggesting that factors such as species composition and resource availability could become increasingly important drivers of RGR_{max} and K later in the season. Species composition, though unaffected by clipping, did vary within each grassland type (Figure 6), and is a well-documented driver of ANPP (Tilman et al. 1996, 2001). Alternatively, a decrease in soil moisture from June to July could have limited RGR and ANPP more strongly than biomass accumulation. Moisture availability is a strong regulator of other ecosystem processes in this system, including the decomposition of litter and organic matter (Risch et al. 2007, Penner and Frank 2019).

In mesic grassland, the EHM was more effective at predicting clipping effects on ANPP than the CCH or LRM. Plots with a higher initial relative biomass were more likely to have ANPP stimulated by clipping. Clipping had no effect on N availability or soil moisture, yet a range of positive growth responses to clipping was observed. While rarely reported in the literature, this finding supports theory from the EHM that shows that herbivory can increase ANPP without directly impacting soil resource availability (Ritchie and Penner, in review). Biomass removal increases light availability and reduces the nutrient demand of the vegetation that remains, improving resource availability even if the absolute size of the resource pool does not change.

There was also support for the limiting resource model in mesic grassland when soil moisture was the resource considered: in plots where clipping increased soil moisture, ANPP was likely to be stimulated as well. This is likely due to clipping reducing the transpirational surface area of the vegetation and conserving soil moisture, a well-documented effect of grazers in Yellowstone (Frank et al. 2018). In plots where clipping decreased soil moisture, ANPP tended to decline. This could be an effect of increased solar radiation to the soil surface that in turn increases soil evaporation and water loss, which has been observed in grazing lawns in African savanna (Veldhuis et al. 2014). The EHM more accurately predicted Δ ANPP in June while the LRM_{moist} was more effective during July (Figure 9), indicating that the mechanisms by which grazing influences ANPP can change throughout the growing season. This could be due to the decline in soil moisture discussed above that may have limited RGR and ANPP more strongly than biomass accumulation, highlighting the impacts of interactions between herbivory and seasonal shifts in resource availability. Alternatively, it could be partially due to differences in initial biomass between paired plots at the start of the second growth period. This difference

occurred because clipped and control plots grew differently following the first clipping treatment. Future tests of the EHM should avoid repeated sampling over the course of a single growing season to ensure that the initial biomass in paired plots is similar.

Δ ANPP in dry grassland was best predicted by initial relative biomass and the EHM (Figure 8), although support for the EHM in dry grassland was weaker than in mesic grassland. The failure of the CCH and LRM in dry grassland could be due to their shared assumption of single-nutrient limitation that ignores more complex interactions between grazing and resource limitation. Previous work in Yellowstone grasslands suggests that grazing can shift the resource most limiting growth from N in ungrazed conditions towards colimitation between N, moisture, and potentially P in grazed conditions (Frank et al. 2018). Furthermore, resin bags measured N availability as steady-state pool size and not as supply rate. Pool size and supply rate are distinct aspects of resource availability and are expected to have different effects on the outcome of grazing episodes (Ritchie and Penner, in review). Alternatively, watering of the experimental plots could have relieved moisture limitation and lessened the probability of support for the CCH_{moist} and LRM_{moist}.

While there was limited statistical support for the CCH within each grassland type, there was support for the CCH at the larger landscape scale. Clipping stimulated ANPP in June in mesic grassland but not at dry grassland. The two grasslands had similar N availability during this period, but soil moisture was much higher in mesic grassland. This suggests that at large landscape scales, positive responses of ANPP to grazing may be limited to areas of high water availability (Knapp et al. 2001, Augustine and McNaughton 2006). In these wetter grasslands, the mechanisms of the EHM and LRM may be more often observed. This interpretation, however, is confounded by significant changes in species composition between mesic and dry

grasslands. An alternative explanation for this pattern is that the perennial bunchgrasses growing in dry grassland are more conservative in their allocation to aboveground growth following defoliation than species in the mesic grassland, instead choosing to invest carbon assimilated after grazing into roots (Augustine et al. 2011). The evolution of large belowground nutrient reserves that can support growth during windows of high resource availability has been proposed as an adaptation to grazing and drought simultaneously, and may explain why dryland species rarely show strong positive responses to grazing (Coughenour 1985, Milchunas et al. 1988).

Species composition varied within each grassland type, but there was no effect of clipping on composition over the duration of this experiment. There are several possible reasons for this. While grazing can have substantial effects on composition, these are often documented over many years or under severe grazing intensities (Frank 2005, Derner et al. 2018), not the single season of relatively moderate clipping in my study. Additionally, all plots, controls included, were protected from grazing during the year of the study but have been intensively grazed for years prior to this experiment. It is possible that decades of prior grazing have already removed grazing-intolerant species from the community, resulting in a community composed of grazing-tolerant species. The mesic grasslands of Yellowstone are in fact composed almost entirely of non-native European pasture species that have a high RGR_{max} and can rapidly regrow after being grazed.

Bison were the most abundant grazer at each grassland type for the duration of the grazing experiment (J. Penner, personal observation). Average grazing intensity was nearly twice as high at mesic grasslands than at dry grasslands. Bison rarely graze dry grassland as intensively as mesic grassland in Yellowstone, as dry grassland occupies transitional range during seasonal migrations to and from summer range on mesic grassland (Geremia et al. 2014). While the

design of the grazing study prevented a direct comparison of all three models as was done in the clipping study, I found some evidence for mechanisms proposed by the LRM and EHM. During June, grazing stimulated both ANPP and N availability in agreement with the framework of the LRM, and these plots also exhibited the density-dependence predicted by the EHM. Positive feedbacks of ungulate grazing on N availability and productivity have previously been documented in migratory grazing systems (McNaughton 1985, Augustine and McNaughton 2006, Frank et al. 2018), as has density-dependent growth (Ritchie and Penner, in review), but this is the first time, to my knowledge, that multiple mechanisms have been shown to operate simultaneously. This relationship decoupled in July however, as grazing stimulated N availability but had no effect on ANPP. That grazing, but not clipping, had a positive effect on N availability is likely due to substantial N inputs from urine and feces in grazed plots that were not present in clipped plots (Barthelemy et al. 2018).

These experiments indicate that the recently developed episodic herbivory model can explain variation in herbivore effects on ANPP as well or better than alternative, commonly considered models. The success of the EHM in mesic and dry grassland supports the claim that migratory/rotational grazing behavior is essential to the long-term sustainability of ANPP. Per the EHM, grazing is most likely to stimulate ANPP when initial relative biomass is high, meaning that a grassland must have enough rest time between episodes of herbivory for vegetation to grow and reach this critical biomass threshold. In systems such as the Serengeti where grazer migrations are increasingly impeded by human activity, high grazing intensities and short rest intervals have triggered declines in ANPP and other ecosystem processes like soil carbon storage (Veldhuis et al. 2019). Grazing systems, whether natural or agricultural, that mimic migratory behavior by allowing episodic herbivory will likely maintain higher ANPP than

similar non-migratory/non-rotational systems. To confirm this prediction and investigate its broader utility, the episodic herbivory model needs to be experimentally tested in systems beyond Serengeti and Yellowstone that span a wide range of migratory/rotational behavior.

The relative utility of all three models seems to also vary with the scale of observation. The applicability of the CCH or LRM at small plot or patch scales may depend on whether grazing changes which resource most limits ANPP and thereby violates a model's assumption of single-resource limitation. In these circumstances, the EHM is likely more useful as a null model (in the absence of direct feedbacks of grazing on resource availability) for grazer effects on ANPP. As scale increases and differences in resource availability become more drastic between patches, the CCH and LRM become effective as well.

Conclusion

North American grasslands are expansive, species-rich ecosystems, and most of them share a long evolutionary history with grazing mammals that provide a wide array of cultural and ecosystem services to human society (Milchunas et al. 1988, Naidoo et al. 2008, Wallen et al. 2015). My work illustrates the wide range of effects that grazing can have on plant growth, showing how different theoretical models can explain why grazing sometimes increases plant productivity at different scales. This research also adds to a body of work showing that grazing regimes produced by migratory herds of ungulates can and do increase primary productivity. My theoretical approach to this study can and should be replicated across grazing systems to further strengthen our understanding of the mechanisms by which grazing animals influence this important ecosystem process.

Tables

Table 1: Parameter estimates for testing of the episodic herbivory model. R^2 and p-values are calculated from SMA regression shown in Figures 4 (clipping, $n = 20$) and 12 (grazing, $n = 10$).

Grassland	Month	Experiment	RGRmax ($\text{g g}^{-1} \text{day}^{-1}$)	K (g m^{-2})	R^2	p
Mesic	June	Clipping	0.036	321.80	0.61	<0.001
		Grazing	0.047	292.55	0.54	0.015
	July	Clipping	0.031	347.39	0.43	0.002
		Grazing	0.043	418.65	0.36	0.066
Dry	June	Clipping	0.041	83.94	0.29	0.014
		Grazing	0.049	65.21	0.35	0.070
	July	Clipping	0.024	98.30	0.29	0.015
		Grazing	0.034	79.51	0.21	0.180

Table 2: Species names for codes given in Figures 3 and 4

Code	Scientific Name	Code	Scientific Name
ACHMIL	<i>Achillea millefolium</i>	FESIDA	<i>Festuca idahoensis</i>
AGOGLA	<i>Agoseris glauca</i>	fuzzy Erigeron	Unknown Asteraceae #1
AGRSTO	<i>Agrostis stolonifera</i>	HESCOM	<i>Hesperostipa comata</i>
ANTMIC	<i>Antennaria microphylla</i>	JUNBAL	<i>Juncus balticus</i>
ARANUT	<i>Arabis nuttallii</i>	KOEMAC	<i>Koeleria macrantha</i>
ASTMIS	<i>Astragalus miser</i>	LUPSER	<i>Lupinus sericeus</i>
Carex sp.	<i>Carex sp.</i>	PHLPRA	<i>Phleum pratense</i>
CARDUR	<i>Carex duriuscula</i>	POAPRA	<i>Poa pratensis</i>
CERARV	<i>Cerastium arvense</i>	POASEC	<i>Poa secunda</i>
CHRVIS	<i>Chrysothamnus viscidiflorus</i>	PHLHOO	<i>Phlox hoodii</i>
CIRARV	<i>Cirsium arvense</i>	PSESPI	<i>Pseudoroegneria spicata</i>
CREOCC	<i>Crepis occidentalis</i>	smooth Erigeron	Unknown Asteraceae #2
DRANEM	<i>Draba nemorosa</i>	TAROFF	<i>Taraxacum officinale</i>
EQULAV	<i>Equisetum laevigatum</i>	TRILON	<i>Trifolium longipes</i>
ERICOR	<i>Erigeron corymbosus</i>	TRIREF	<i>Trifolium repens</i>

Table 3: Pearson correlation coefficients between predictors for the CCH, LRM, and EHM.

Values for mesic grassland are reported in upper right panel and for dry grassland in lower right panel. See text for full model descriptions.

	CCH _N	CCH _{moist}	LRM _N	LRM _{moist}	EHM	
CCH _N		0.50	0.51	0.10	-0.33	
CCH _{moist}	0.19		0.07	0.15	-0.24	Mesic
LRM _N	0.74	-0.10		0.12	-0.37	
LRM _{moist}	-0.39	-0.17	-0.07		-0.33	
EHM	0.07	-0.29	0.17	0.12		
Dry						

Figures

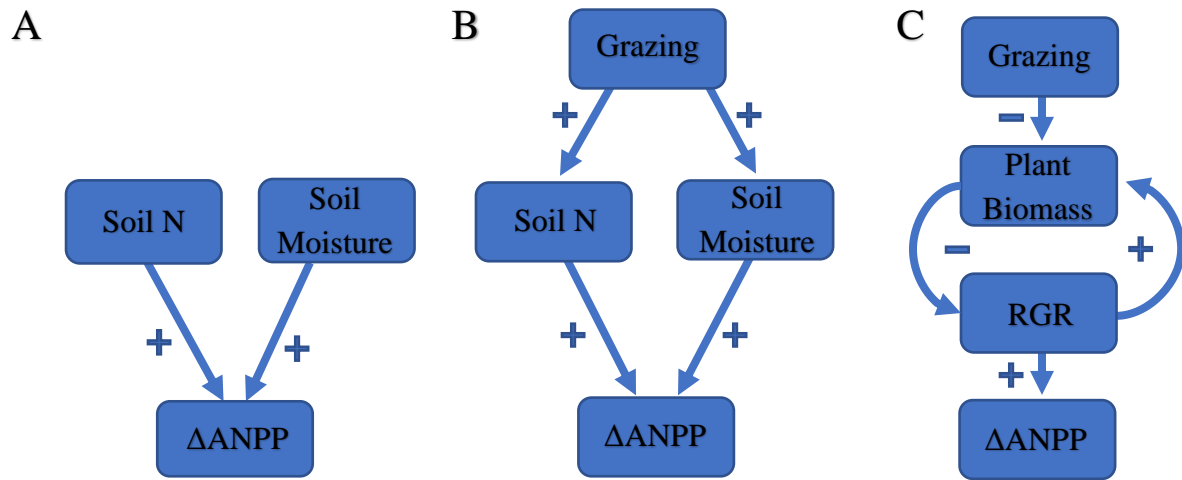


Figure 1: Conceptual model of how grazing in Yellowstone interacts with resource limitation to influence grassland primary productivity (Δ ANPP) according to the compensatory continuum hypothesis (CCH, panel A), the limiting resource model (LRM, panel B), and the episodic herbivory model (EHM, panel C).

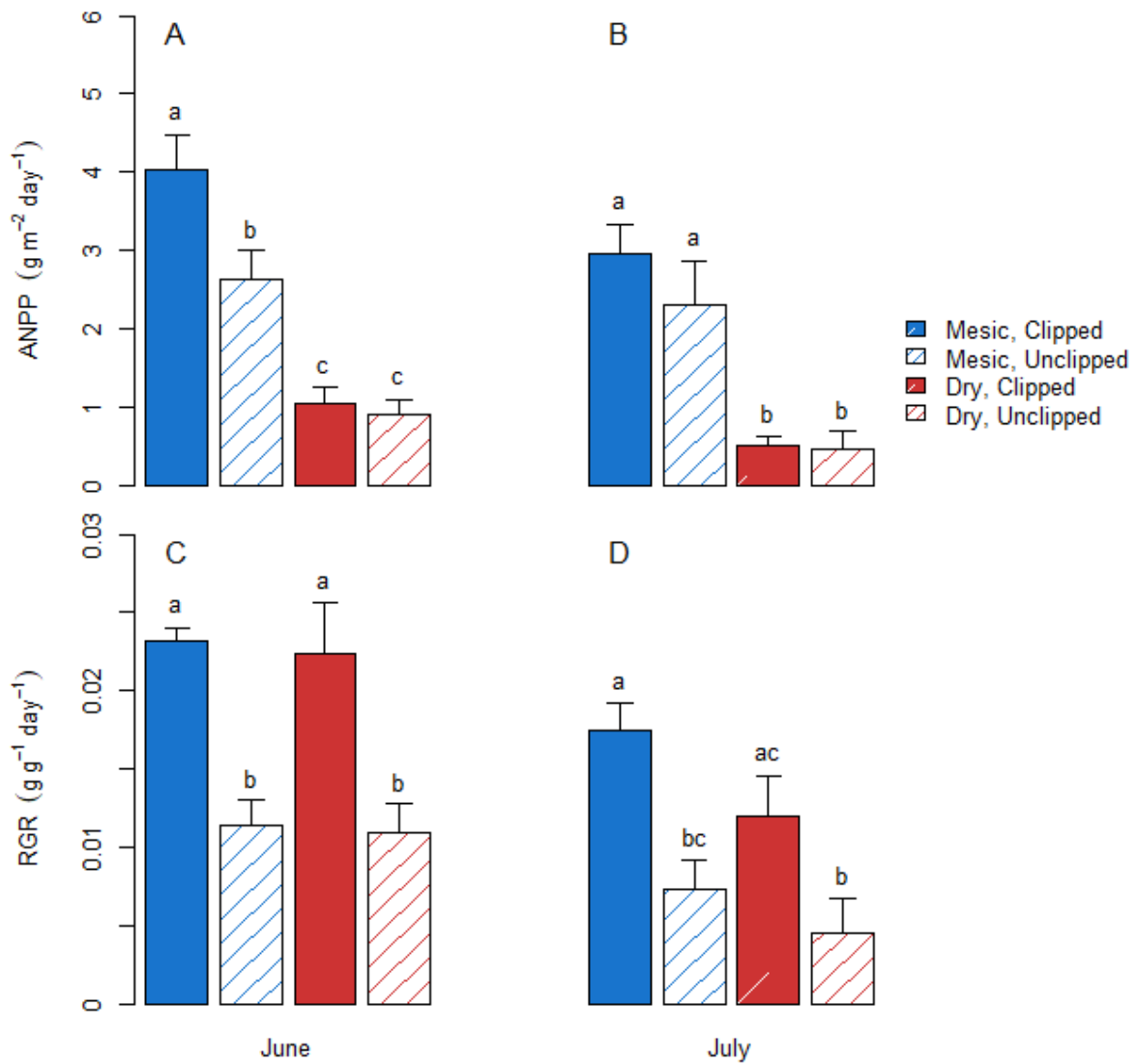


Figure 2: Effects of grassland type, clipping, and month on ANPP (A, B) and RGR (C, D).

Different letters represent significant differences between all treatments in each month ($n = 10$ for each treatment). Error bars represent standard error.

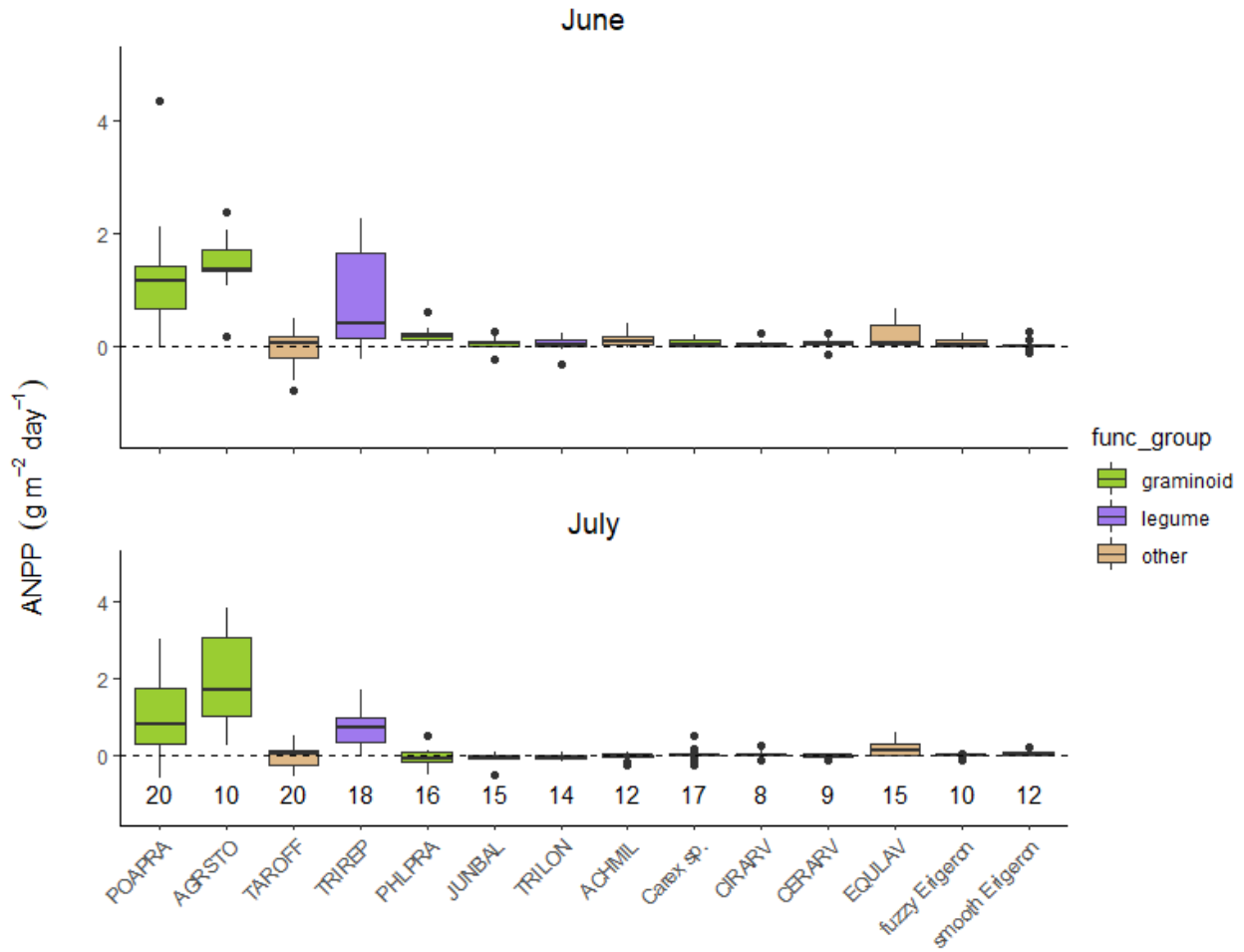


Figure 3: ANPP of plant species in mesic grassland during clipping experiment. Control and clipped treatments are pooled. Species are listed by initial abundance at the start of the experiment in late May (i.e. POAPRA = most abundant). Color represents plant functional group (see legend). All species present in 8+ plots (of 20) are shown, with actual number of plots shown above species code.

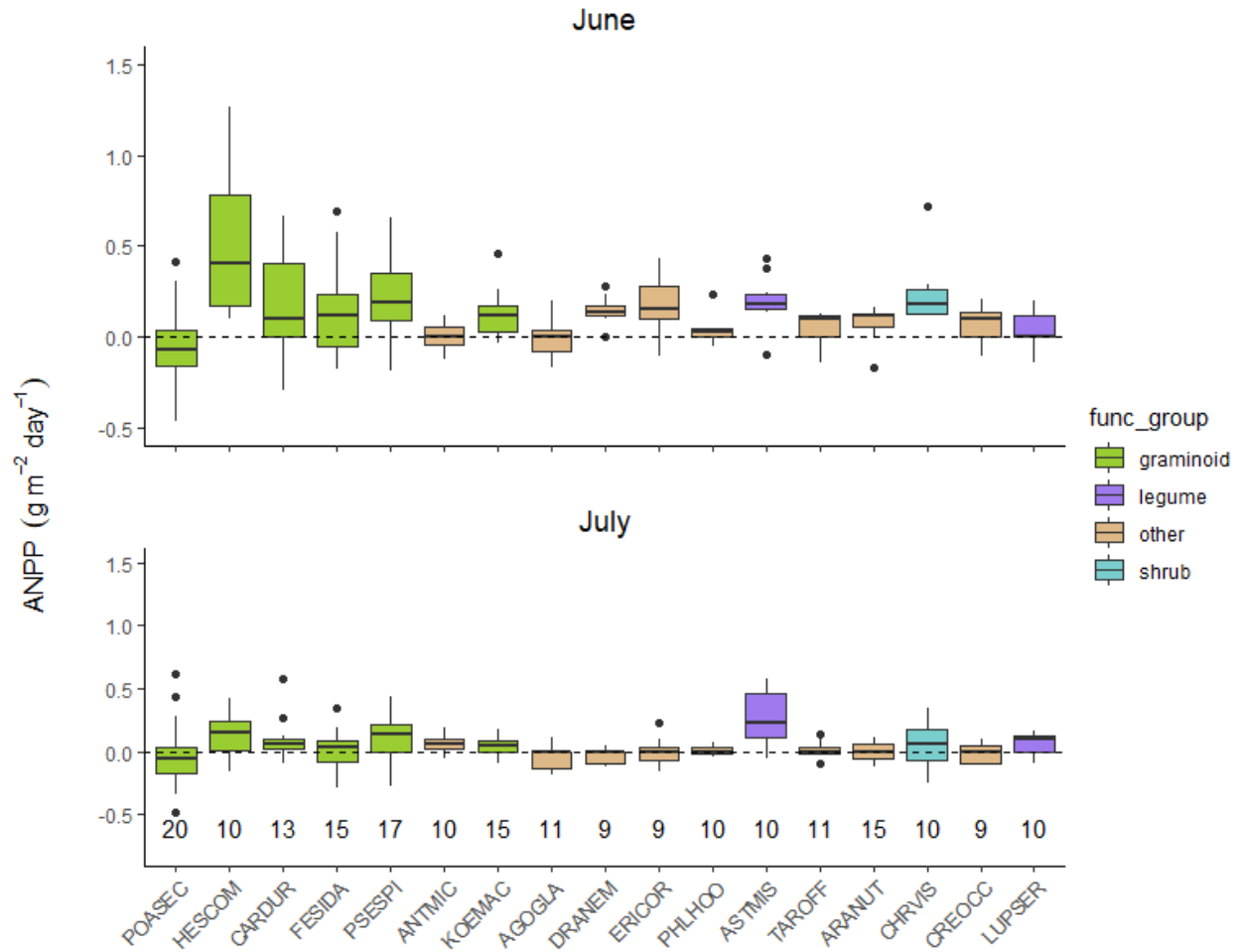


Figure 4: ANPP of plant species in dry grassland during clipping experiment. Control and clipped treatments are pooled. Species are listed by initial abundance at the start of the experiment in late May (i.e. POASEC = most abundant). Color represents plant functional group (see legend). All species present in 8+ plots (of 20) are shown, with actual number of plots shown above species code.

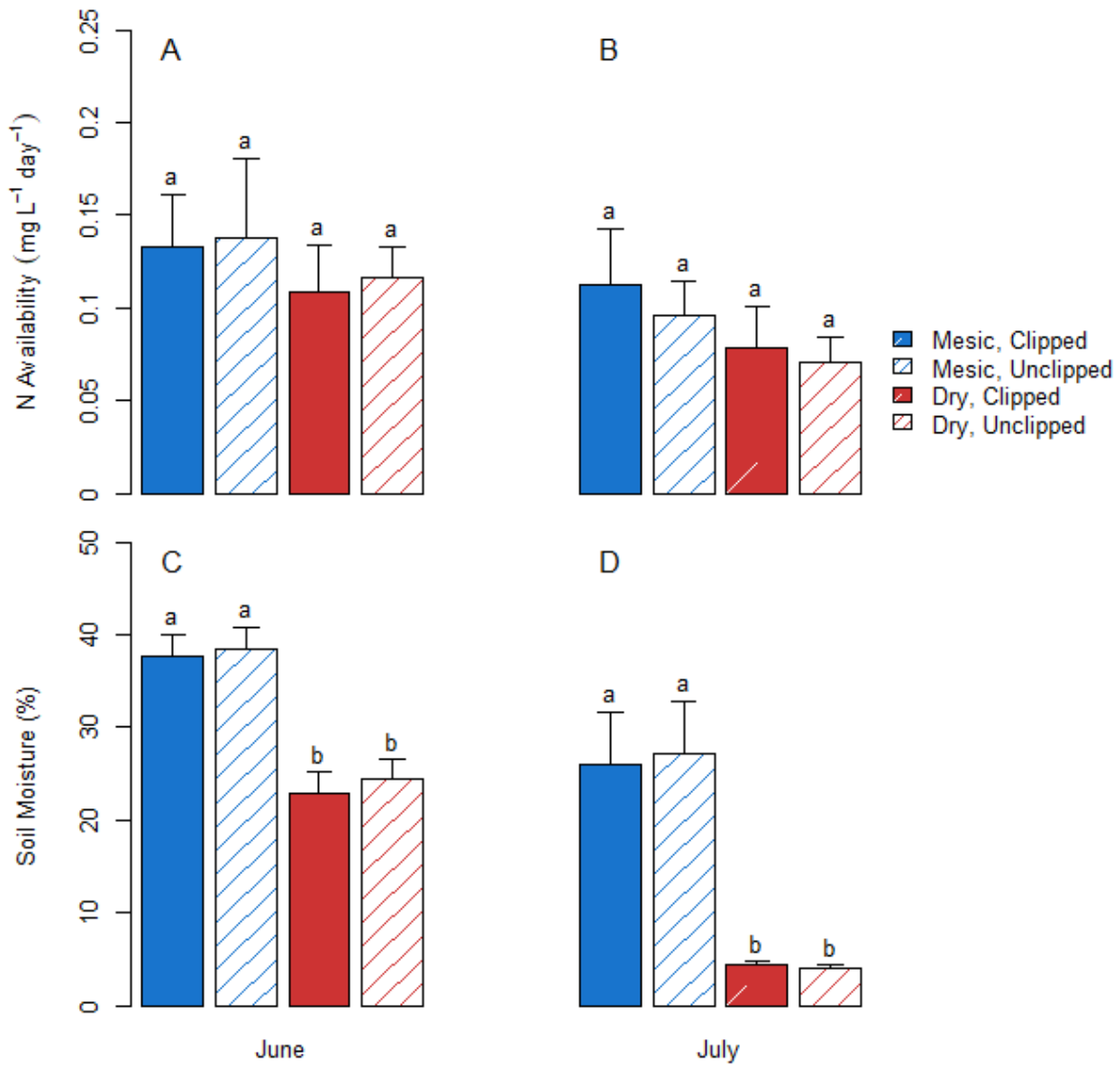


Figure 5: Effects of grassland type, clipping, and month on soil N availability rate (A, B) and soil moisture (C, D). Both soil resource measurements represent a steady-state pool size. Different letters represent significant differences ($p < 0.05$) between all treatments in each month ($n = 10$ for each treatment). Error bars represent standard error.

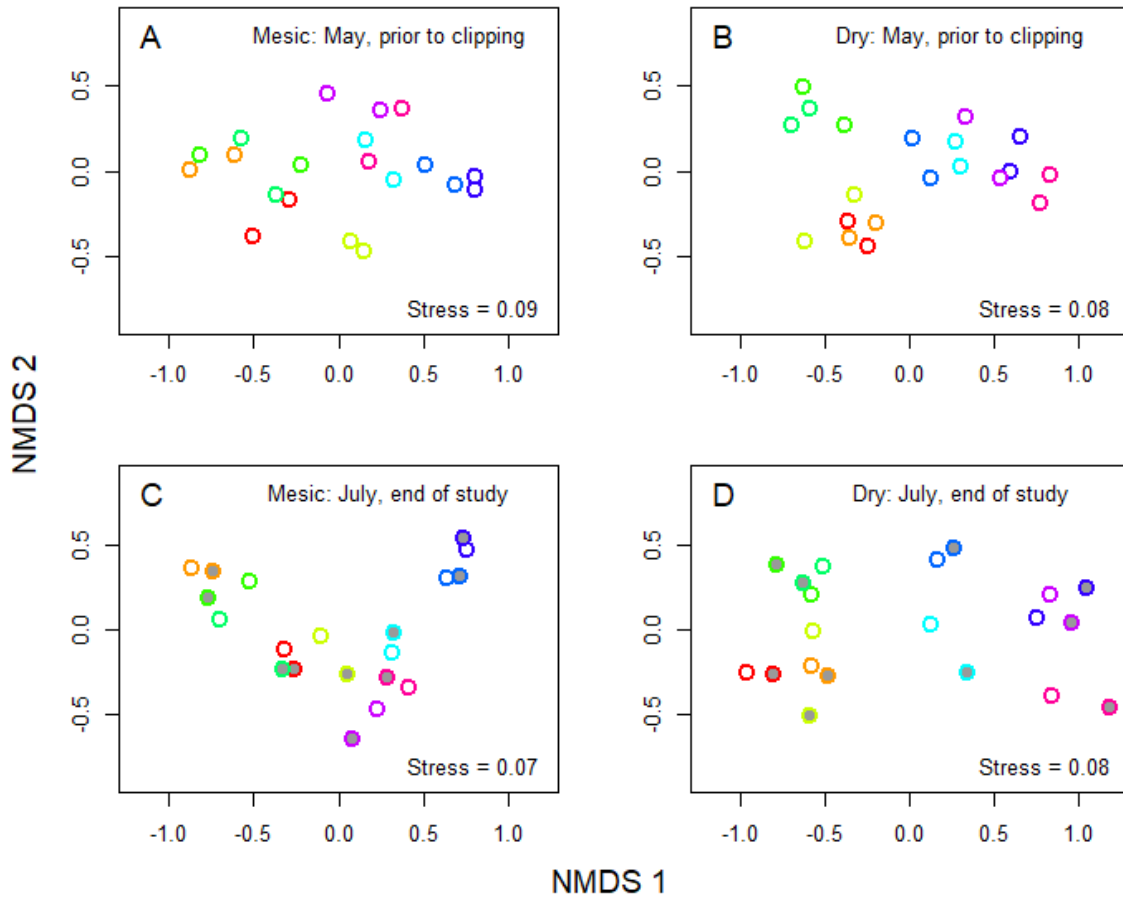


Figure 6: Nonmetric multidimensional scaling (NMDS) over two axes of compositional similarity of species before study began (A, B) and after study ended (C, D), scaled by total plot biomass. Within each panel, a single color represents one set of paired plots. Points with white fill represent control plots, and points with gray fill represent clipped plots.

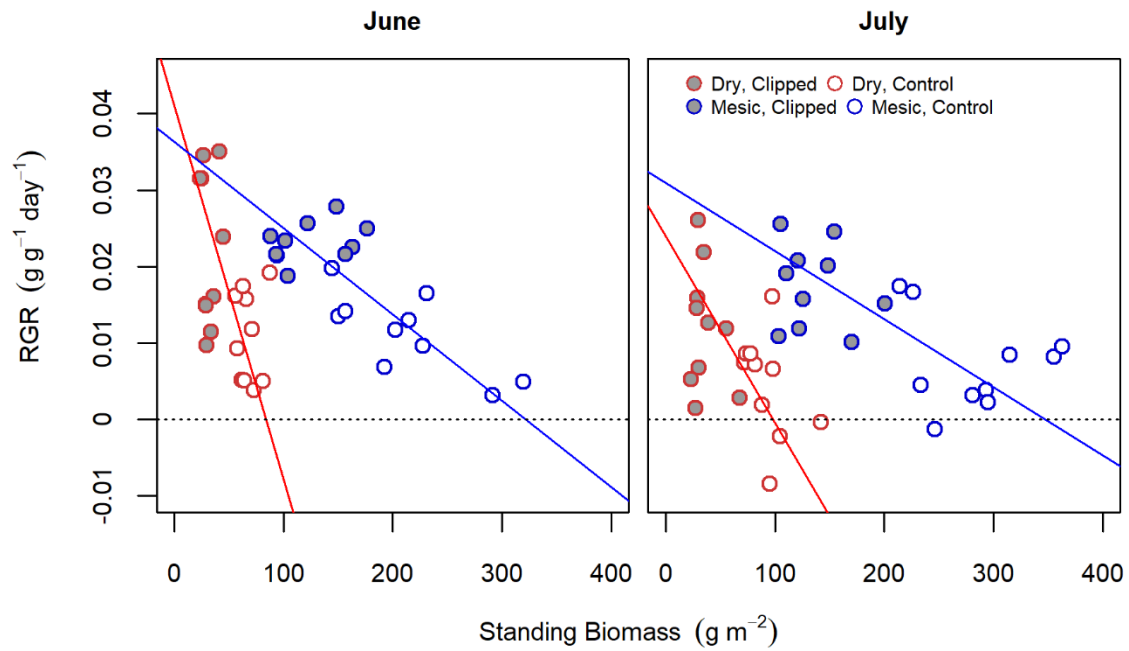


Figure 7: Density-dependent growth in clipped mesic and dry grassland over two months. Standing biomass of clipped plots was measured immediately after clipping. Solid lines represent significant negative slope of SMA regression ($p < 0.05$). Estimates of y-intercept represent RGRmax, while estimates of x-intercept represent K. See Table 1 for estimated parameter values.

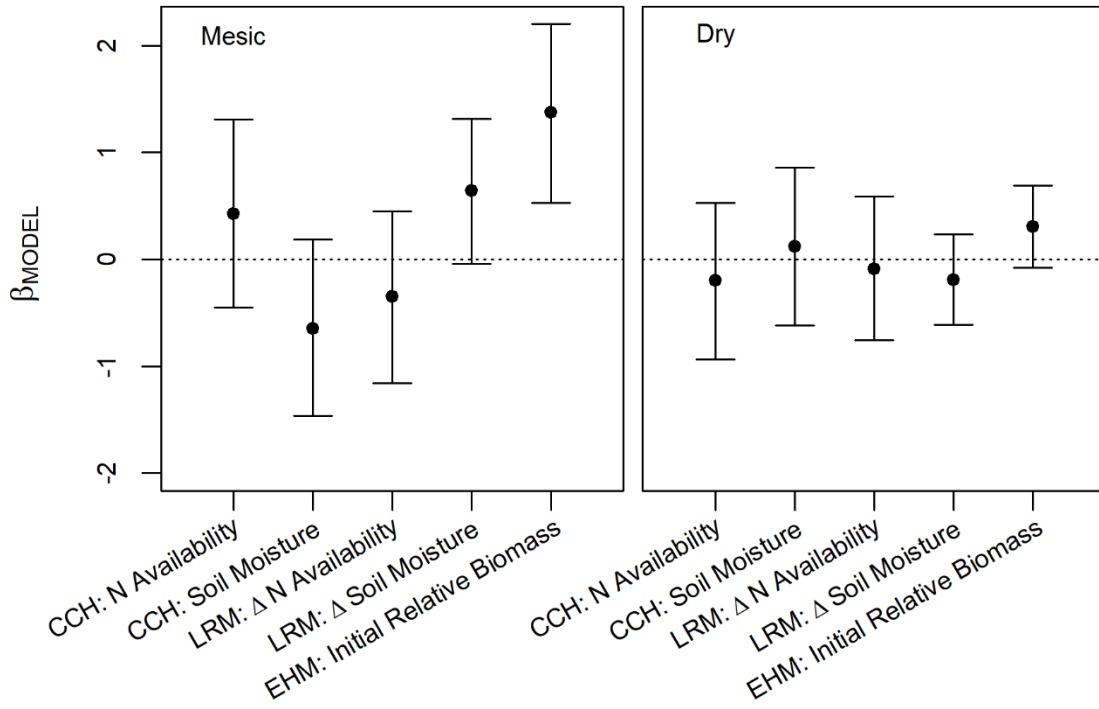


Figure 8: Standardized model slope estimates (\pm 95% credible intervals) from regression of clipping effect on ANPP (Δ ANPP) for mesic and dry sites.

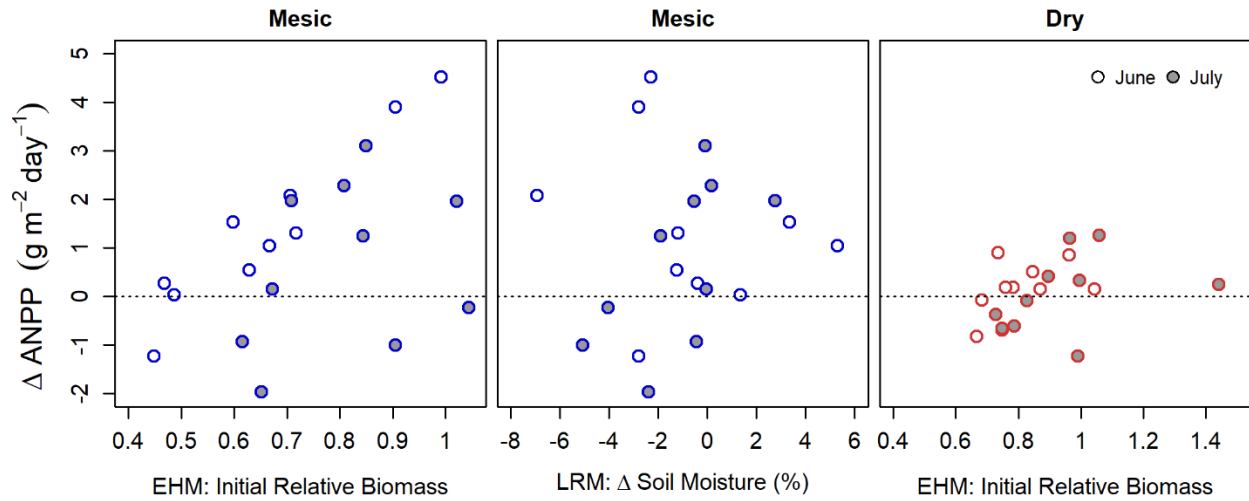


Figure 9: Relationship between clipping effect on ANPP and models with the most support (>90% probability of positive effect, see Figure 5). Initial relative biomass is calculated as the fraction of pre-clipping biomass relative to the K-value estimated from Figure 4 and Table 1. Initial relative biomass > 1 is due to scatter around the regression line in Figure 4.

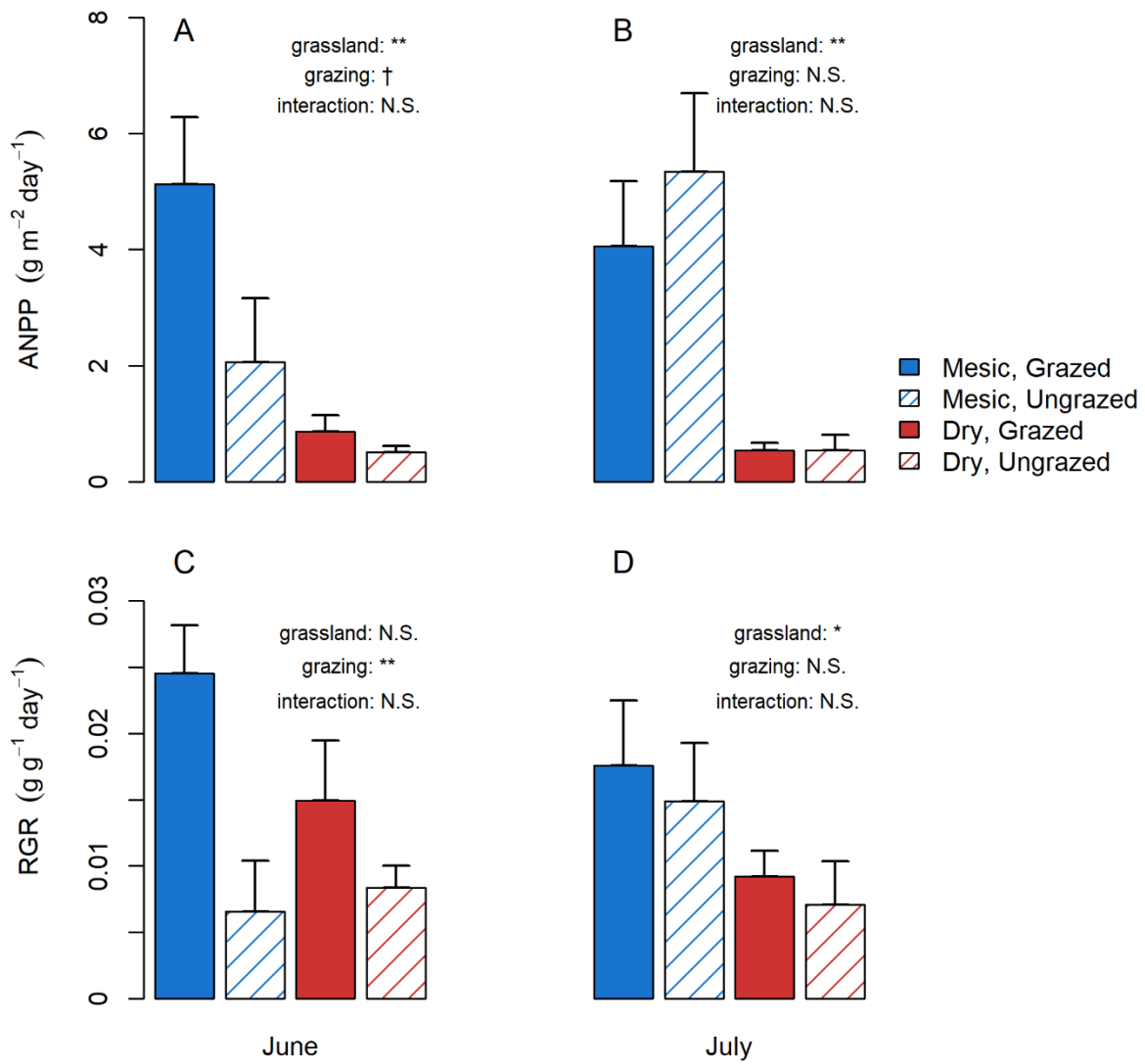


Figure 10: Effects of grassland type, grazing, and month on ANPP (A, B) and RGR (C, D). Two-way ANOVA results are summarized in each panel (** = $p < 0.01$, * = $p < 0.05$, † = $p < 0.10$, N.S. = $p > 0.10$). Error bars represent standard error, $n = 5$ for each treatment.

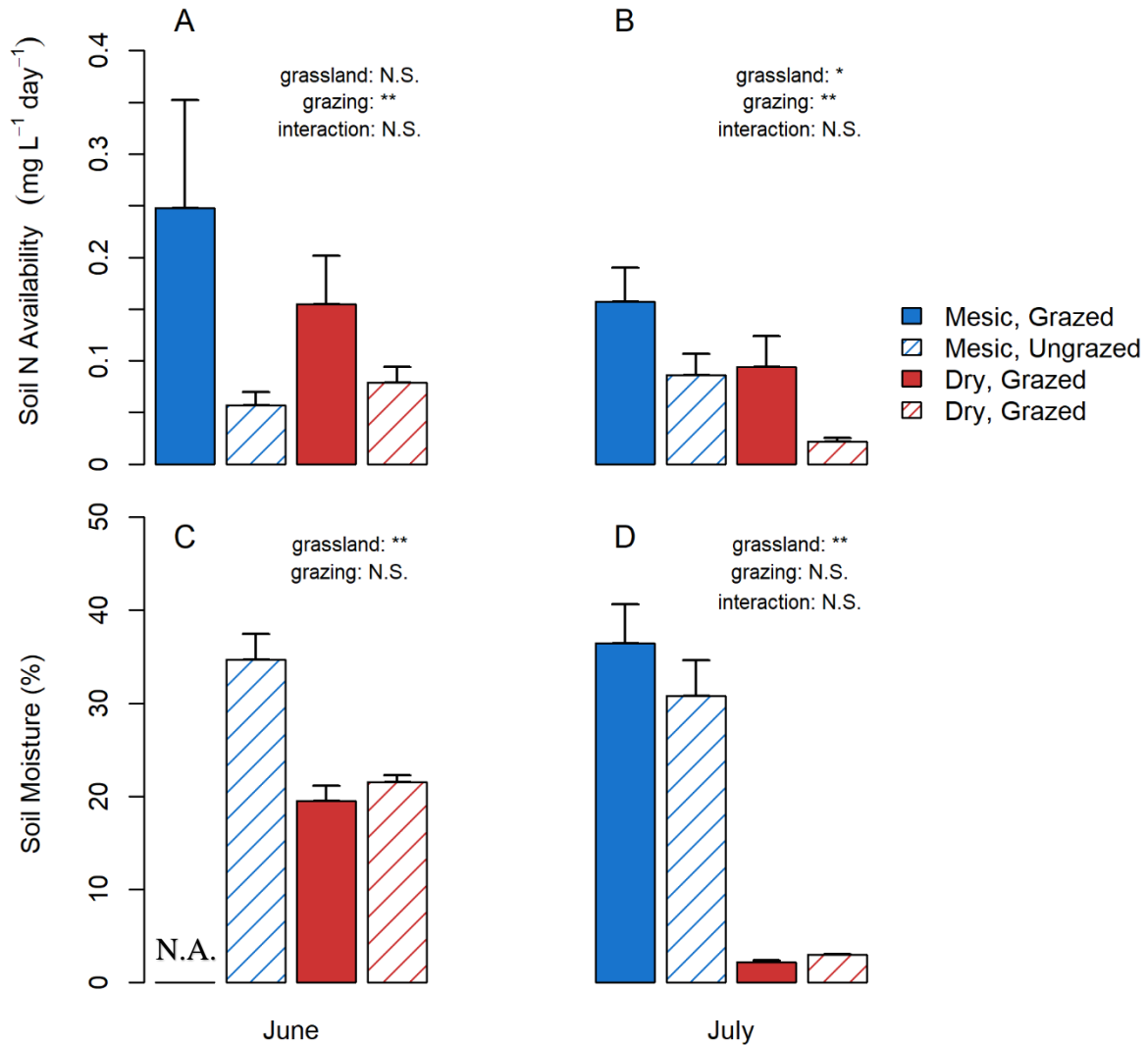


Figure 11: Effects of grassland type, grazing, and month on soil N availability (A, B) and soil moisture (C, D). Both soil resource measurements represent steady-state pool size. Two-way ANOVA results are summarized in each panel (** = $p < 0.01$, * = $p < 0.05$, † = $p < 0.10$, N.S. = $p > 0.10$). Error bars represent standard error, $n = 5$ for each treatment. No soil moisture data was collected from grazed, mesic grassland in June (N.A.).

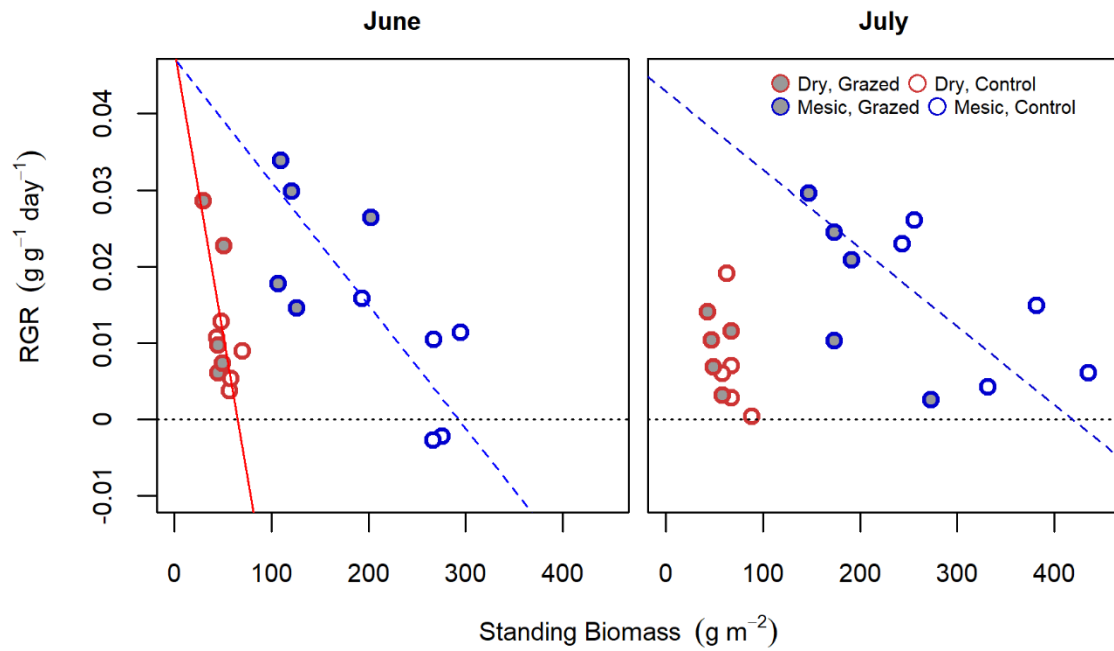


Figure 12: Density-dependent growth in grazed mesic and dry grassland over two months. SMA regression lines are fit separately for each grassland type. Solid lines indicate $p < 0.05$, dashed lines indicate $p < 0.10$, and no line indicates no significant relationship.

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VITA

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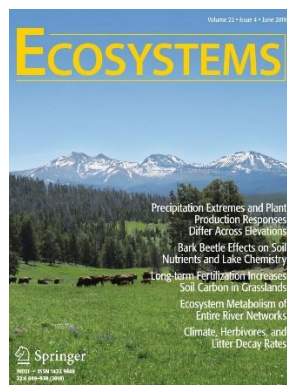
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EDUCATION

- M.S. Syracuse University – Biology Anticipated graduation – Dec. 2019
Advised by Dr. Doug Frank
- B.A. Goshen College – Environmental Science, *Summa Cum Laude* 2017
Advised by Dr. Ryan Sensenig

PUBLICATIONS

- Ritchie ME, **JF Penner**. In review. Episodic herbivory, resource-limited density dependence and stimulation of plant production.
- Penner JF**, DA Frank. 2019. Litter decomposition in Yellowstone grasslands: The roles of large herbivores, litter quality, and climate. *Ecosystems*, 22, 929 – 937. (with cover image)
- Jacobson FE, GE Garrison, **JF Penner**, JC Zecchini Gebin, MA Eifler, DA Eifler. 2016. Escape behavior in the leopard lizard (*Gambelia wislizenii*): Effects of starting distance and sex. *Amphibia-Reptilia*, 37, 320 – 324.
- Garrison GE, JC Zecchini Gebin, **JF Penner**, FE Jacobson, MA Eifler, DA Eifler. 2017. Intraspecific variation in habitat use and movement in long-nosed leopard lizards (*Gambelia wislizenii*) from the Alvord Basin, Oregon. *The Southwestern Naturalist*, 62, 187 – 192.



RESEARCH PROJECTS

- 2017 – Pres. Grazer Stimulation of Grassland Production: Understanding Species-Specific Responses. Fieldwork in Yellowstone National Park. Data analysis at Syracuse University, advised by Dr. Doug Frank.
- 2016 Factors Affecting Generalist Insect Herbivory on a Chemically Defended Plant (*Asclepias eriocarpa*). Research Experience for Undergraduates. Fieldwork at Bobcat Ranch, CA. Data analysis at UC Davis, advised by Dr. Louie Yang.
- 2015 – 2017 Behavioral and Chemical Ecology of the Long-nosed Leopard Lizard (*Gambelia wislizenii*). Fieldwork in Alvord Basin, OR. Data analysis at Erell Institute, advised by Drs. Doug and Maria Eifler.
- 2014 – 2017 Effects of Elephant Browsing and Fire on an Acacia-Ant Mutualism. Fieldwork at Mpala Research Centre, Kenya. Data analysis at Goshen College, advised by Dr. Ryan Sensenig.

TEACHING EXPERIENCE

- 2019 **Teaching Assistant**, Integrative Biology, Syracuse University
- 2018 **Teaching Assistant**, Animal Behavior, Syracuse University
- 2017 **Teaching Assistant**, Marine Biology, Goshen College
- 2014 – 2016 **Tutor**, Ecology and Evolution, Goshen College
- 2015 **Tutor**, Pollinators in Peril, Goshen College
- 2014 **Teaching Assistant**, Ecology and Evolution, Goshen College

Topics lectured on to undergraduates: Behavioral ecology, food webs/trophic cascades, introduction to statistics, mangrove ecology

OTHER FIELD EXPERIENCE

- 2017 **Volunteer**, Yellowstone Bison Project, Yellowstone National Park.
- 2016 **Student**, Sustainability in India. Hanifl Centre, Uttarakhand, India, with Goshen College.
- 2016 **Student**, 3-month Study-Service Term in Peru, with Goshen College.
- 2016 **Volunteer**, Frog Population Monitor, Junin National Reserve, Junin, Peru.
- 2016 **Volunteer**, Fundo San Jose Parque Ecologico and Lodge, Chanchamayo, Peru.
- 2014 **Student**, Conservation and Research Methods in Savannas. Mpala Research Centre, Kenya, with Goshen College.
- 2013 **Intern**, Dyck Arboretum of the Plains, Hesston, KS.

PRESENTATIONS

- Penner, JF**, ME Ritchie, DA Frank. 2019. Grazers of mass production: stimulation of grassland production by episodic herbivory. Poster. Ecological Society of America Annual Meeting.
- Penner, JF** 2018. Consumer versus environmental control of litter decomposition in Yellowstone grasslands. Poster. International Association of Vegetation Science Annual Symposium.
- Penner, JF** 2017. Visual and ultraviolet absorbance in femoral gland secretions of two desert lizards. Senior Biology Research Symposium. Goshen College.
- Penner, JF** 2015. Behavioral and chemical ecology of a sexually dimorphic desert lizard. Goshen College Science Speaker Series.
- Penner, JF**, P Meyer-Reimer. 2015. Synergistic effects of fire and elephant browsing on *Acacia drepanolobium* nutrient quality. Goshen College Student Research Symposium.
- Sensenig, RL, **JF Penner**, P Meyer-Reimer, J Davila. 2015. Ants, fire, and elephants: ecological synergies. Goshen College Science Speaker Series.
- Penner, JF** 2014. Ecological research in Kenya. Celebrate Summer Science. Goshen College Science Speaker Series.
- Penner, JF**. 2014. Stories, slides, and science from Kenya. Community Presentation. Dyck Arboretum of the Plains, Hesston, KS.

FELLOWSHIPS AND SCHOLARSHIPS

2018 – 2019	Teaching Assistantship , Syracuse University Department of Biology (\$29,000)
2017 – 2018	Graduate Research Fellow , Syracuse University Graduate School (\$30,000)
2013-2017	Menno Simons Scholar , Goshen College (\$48,000)
2016	Research Experience for Undergraduates (REU) Grant , National Science Foundation through UC Davis (\$5,500)

OUTREACH AND SERVICE

2018	Member , Social Committee, Syracuse University Biology Graduate Student Organization.
2018	Member , Outreach Committee, Syracuse University Biology Graduate Student Organization.
2015, 2017	Volunteer , Science Olympiad Regional Tournament, Goshen College.
2015, 2017	Volunteer , Rocky Mountain Mennonite Camp, Divide, CO.
2013	Volunteer , Mennonite Disaster Service, Northern Cheyenne Nation