THESIS

ECOLOGY OF BISON HERBIVORY IN NORTH RIM GRAND CANYON GRASSLANDS

Submitted by

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ABSTRACT

ECOLOGY OF BISON HERBIVORY IN NORTH RIM GRAND CANYON GRASSLANDS

The American Plains bison (*Bison bison bison*) is a grassland ungulate herbivore that historically played a keystone role in the structure and function of grasslands throughout North America. The mechanisms by which bison influence grassland characteristics are both direct (i.e., via plant consumption and highly nutrient-rich waste deposition) and indirect (i.e., plant community responses), having the capacity to alter entire ecosystems. The ungulate herbivore-grassland relationship has been studied across the globe in a wide range of ecosystems from the tallgrass prairie, montane temperate, and semi-arid grasslands of North America, to the savannah plains of East Africa. My research aims to contribute to this body of knowledge by exploring the effects of bison grazing on the semi-arid, high elevation grasslands of the Southwestern United States in the southern edge of the historic range of the Plains bison in northern Arizona. With recent expansion of Plains bison into the North Rim area of Grand Canyon National Park, I sought to assess the potential effects of bison on grassland structure and function in an ecosystem where this relationship had yet to be assessed. I used a replicated herbivore exclusion experiment in grassland meadow habitats, employing both long-term grazing exclosures (0.40-ha) and temporary grazing exclusion cages (1-m^2) to quantify herbaceous productivity and consumption by free-ranging bison. I established six sites in Grand Canyon National Park (GRCA) in areas

with high bison density, and six additional sites in similar meadow habitat in Kaibab National Forest (KNF) with low to no bison density.

Chapter 1 is largely composed of literature review exploring the importance of grassland ecosystems, bison populations, and the interactive history of the effect of bison across North America. I also provide relevant information regarding the ecological and historical aspects of my study area within the Kaibab Plateau, northern Arizona, including a summary of significant biological and cultural aspects, its history with grazing, and current research goals that include bison management plans. The goal of Chapter 1 is to provide the context for my research as well as to provide background for my research objectives and how I conducted the research, which are described in the following chapters.

In Chapter 2, I conducted an experimental study among meadows of varied bison density to evaluate vegetation offtake, the effect of bison herbivory on aboveground primary productivity and its effect on vegetation ground cover. Using quadrat clipping rings inside and outside of grazing cages, I sampled plant biomass (which I used to calculate offtake and productivity) and measured percent ground cover twice each year in 2021 and 2022, where sampling events occurred in summer and fall to capture peak production of both cool (C_3) and warm (C_4) season plants. I compared the effects of grazing at various intensities on grassland productivity and plant percent cover by taking measurements between treatments (experimental grazed plots vs. exclosure control plots), stratum (high bison use areas in GRCA vs. low bison use areas in KNF), as well as between years (2021 vs. 2022). I calculated aboveground herbaceous production of grazed treatments ($ANPP_g$) and exclosure treatments ($ANPP_{ug}$), as well as total annual offtake of grazed treatments (O_t) using the Sum of Significant Positive Increments (SSPI) method, where only significant ($p<0.1$ due to limited sample size) and positive increments of vegetation biomass change between sampling occasions were summed to the total annual productivity (ANPP) value (measured in g/m^2). I used a linear mixed model to evaluate the influence of treatment, stratum, and year on annual primary productivity.

As expected, GRCA grazed treatments had higher annual offtake and grazing intensity when compared to KNF grazed treatments. Annual aboveground herbaceous production of grazed plots ($ANPP_g$) was significantly higher in GRCA than in KNF and a positive relationship was observed between herbivory utilization and ANPP in GRCA. These results are partially explained by the "Grazing Optimization Hypothesis," which predicts an increase in aboveground production and nitrogen yield of grazed plants compared to ungrazed plants under intermediate grazing; however, my results indicated a continuous increase in aboveground production past intermediate levels of grazing intensity. My results may be better explained by the "Compensatory Continuum Hypothesis," which theorizes that the ability for a plant to tolerate or compensate for losses from herbivory are likely driven by a complex of interactions among the affected plant and its environment (Maschinski and Whitman 1989).

Annual herbaceous production inside exclosure plots ($ANPP_{ug}$) was nearly identical between the two ungulate stratum (high density and low density bison herbivory) and no difference could be detected. When evaluating the relative proportion of ground cover classes, I found no differences between treatments, but differences between strata. Sites within GRCA supported significantly higher coverage of forbs and bare ground, whereas sites in KNF supported significantly higher coverage of graminoids and litter.

Additionally, I deployed a temperature and precipitation gauge at ten sites to collect local climate information. Climate information obtained from weather stations was organized by temperature and precipitation seasonal windows and used in the linear mixed model as predictor variables, where spring temperature was the single most influential weather variable. Twelve motion sensor wildlife cameras (one at each site) were installed to assess herbivore type (bison vs. cattle) and frequency of visits to sites. Results from photos indicated that 1) bison were observed in high proportions throughout GRCA during the growing season, 2) cattle grazing occurred at three KNF sites at low frequencies, 3) bison were observed several times at only two KNF sites, and 4) the camera data was mostly consistent with the data from GPS collared bison that shows seasonal migratory behaviors.

In Chapter 3, I present results of soil conditions between treatments and strata. I took measurements to evaluate soil structure (erodibility) and function (nutrient availability) using soil corers and in-situ soil probes in both grazed and exclosure treatment plots at each of the established twelve sites. Soil condition measurements of stable aggregates and soil nutrients were measured once during the onset of the study in spring of 2021. Additionally, soil probes were deployed after exclosure construction and prior to most bison arriving in my study area, thus, grazing treatment had yet to take effect. Consequentially, soil nutrient measurements were primarily used to assess baseline soil nutrient availability and distribution while also providing insight during the evaluation of spatiotemporal variability in production across the landscape. I used a paired and two-sample t-test to evaluate differences in aggregate stability between treatments and strata, and no difference in the proportion of stable aggregates (erosion potential) was detected at any spatial scale throughout the study area. Soil nutrient analysis using an ANOVA test revealed significantly higher phosphorus concentrations in KNF vs. GRCA and higher nitrate in exclosures vs. grazed plots. When soil nutrients nitrate, ammonium, total nitrogen, and phosphorus (measured in $\mu g/cm^2$) were included in the linear mixed model, soil ammonium was the most influential nutrient predictor variable on ANPP; however, the lack of treatment effect limited my ability to assess the effect of bison herbivory on soil nutrients, and thus, aboveground productivity. Subsequently, I conducted elemental analysis on aboveground clipped herbaceous biomass. This revealed significantly higher nitrogen yield in grazed plants compared to ungrazed plants, consistent with the Compensatory Continuum Hypothesis.

Prior to my research, there was only a single study that explored ecological effects of the bison herd on the Kaibab Plateau; however, that studies' focus was on riparian areas and riparian vegetation. My research provides a novel evaluation of the effect of the Kaibab Plateau bison herd on soil and plant structure and function within grasslands of the North Rim, Grand Canyon. This unique ecosystem has been protected since 1919, when Grand Canyon National Park was established from the surrounding Kaibab National Forest Service lands (Merkle 1962). Its richness in historical, cultural, and biological resources have given this Park its reputation as a natural wonder of the world. With the establishment of Plains bison in this unique ecosystem, my hope is that the results of this study will support resource managers in their efforts to manage and conserve the natural integrity of the Grand Canyon ecosystem while also promoting the welfare and conservation of the American bison, declared the United States' first National Mammal in 2016 (NPS 2016).

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POSITIONALITY STATEMENT

The author, Dana Musto (she/her), is a graduate student based at Colorado State University. This research is being conducted under the natural resource monitoring protocols established within the *2017 Initial Herd Reduction Environmental Assessment* (National Parks Service) and serves to satisfy in part the degree requirements of Master of Science at Colorado State University, Fort Collins. This research also serves to satisfy the management goals of the National Parks Service.

There are 11 tribes with historic connections to the lands and the resources that are now considered Grand Canyon National Park and Kaibab National Forest. According to ethnographic literature, oral history, and shared information between Park and tribe members, the tribes are traditionally connected to the bison in many ways. Bison are used for meat and parts (Hualapai, Zuni, Navajo), are a predominant figure in religious and social ceremonies (Navajo) and have been considered the main livelihood for the food, shelter, clothing, tools, and medicine for Navajos. It is important to recognize and respect the opinions of tribes when conducting research on the land that tribes traditionally lived on.

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CHAPTER 1: INTRODUCTION

Temperate grassland ecosystems once covered nearly half (approximately one billion acres) of the landmass of the United States and sustained 30-60 million Plains bison (*Bison bison bison*), a subspecies of the American bison. Following European settlement (accompanied by the Homestead Act of 1862), conversion of these native grassland habitats to cropland and rangelands surpassed 50%, leading these biologically important ecosystems to become one of the most endangered ecosystems in North America (Samson and Knopf 1994, Knopf 1996, Lott and Greene 2002, Hoekstra et al. 2005). The widespread loss of grassland habitat occurred in tandem with the near extirpation of the Plains bison, when populations were reduced to a nearly a thousand individuals by 1880 (Hornaday 1887, Seton 1929, McHugh 1972, Meagher 1973). The rapid decline of both grasslands and bison populations resulted in a lack of understanding regarding bison-grassland interactions in many of the habitats that sustain Plains bison populations at present (Knapp et al. 1999, Lott and Greene 2002).

Thanks to conservation efforts, the North American Plains bison population has recovered conservation herds to approximately 20,400 and has gained recognition as a keystone species for their ability to drastically alter entire grassland ecosystems and the National Mammal of the United States for their symbolism of resiliency (Knapp et al. 1999, Aune 2017, USFWS 2022). Conservation efforts and the protection of land in areas such as National Refuges, National Parks, and State parks, has paved the way for researchers to study and better understand bison-grassland interactions (Peden et al. 1974, Coppock et al. 1983, NPS 2017). Grasslands are among the most endangered ecosystems in North America (Samson and Knopf 1994), and they are important because they provide ecosystem services such as water supply and flow regulation, carbon storage, erosion control, and pollination, all of which can mitigate the negative effects of global climate change (Bengtsson et al. 2019). In the face of global environmental changes, the role of herbivory on grassland health and sustainability continues to gain urgency and interest to ecologists and natural resource managers. It is the information obtained from such research that informs management and contributes to the conservation of grasslands, rangelands, grazing ecosystems, and bison populations.

The Kaibab Plateau (KP) bison herd presents a unique opportunity to study herbivory effects on the landscape due to a relatively recent change in bison distribution that has restricted this herd since 2010 to concentrated areas within meadows of the North Rim of Grand Canyon National Park (GRCA) boundaries (Terwilliger et al. 2020). GRCA resource managers and biologists have observed landscape alterations since the sustained occupancy of the herd including visibly reduced vegetation structure and abundance, wallows and bison dung scattered across meadows, extensive wildlife trails webbing the landscape, and compromised riparian areas and water sources. However, the effects of bison utilization on grassland conditions have yet to be quantified in this ecosystem.

The National Park Service (NPS) seeks to protect and conserve the historical, archaeological, and biological diversity of natural resources of North Rim, GRCA and is concerned about potential habitat impacts from the newly resident KP bison herd. Given the research needs and overall mission of the NPS, my study was designed to evaluate the potential effects of bison grazing on grasslands of the North Rim, GRCA of the Kaibab Plateau in northern Arizona. My goal was to assess structural and functional properties of vegetation and soil in grassland areas utilized by bison. Evaluating this, and the possible mechanisms of change, may help to understand the optimum grazing dynamics that either facilitates or inhibits grassland productivity, providing insight into how to effectively manage grassland habitats given presence of bison in the GRCA ecosystem.

I conducted this study with the objective of comprehensively evaluating how bison grazing, vegetation, soil, and climate interactively affect the structure and function of the semi-arid, high elevation grasslands throughout the Kaibab Plateau. My first research objective, outlined in Chapter 2, was to evaluate the intensity and pattern of bison herbivory by quantifying vegetation utilization and to measure plant community characteristics such as aboveground productivity and vegetation ground cover to determine plant response to herbivory. Additionally, to provide supplemental information to achieve my first research objective, I sought to assess spatiotemporal variability in local climate conditions and the potential influence of temperature and precipitation on grassland productivity. My second research objective, outlined in Chapter 3, was to assess potential effects of bison on grassland soil quality by measuring soil characteristics such as erosion potential and soil nutrient dynamics to provide baseline soil condition information and to evaluate potential relationships that these factors may have with the quantity and quality of herbaceous vegetation. Lastly, my final objective, which is an accumulation of information included in Chapters 2 and 3, was to evaluate how grazing dynamics interact with both above- (i.e., climate, herbaceous nitrogen yield) and belowground (i.e., nutrient availability) characteristics by constructing a statistical model to allow me to comprehensively assess the ecological variables that either inhibit or enhance herbaceous production, providing insight to a potential grazing optimum.

Study Area

The Kaibab Plateau (KP) is an uplifted mesa of mixed conifer and meadow habitat that sits above the desert shrublands of northern Arizona. The plateau spans 87,000 hectares (ha) and ranges from approximately 1,830 to 2,810 meters (m) in elevation (Plumb et al. 2016, NPS 2017, Rink et al. 2020). Above the desert shrublands are Ponderosa pine forests (*Pinus ponderosa*) at approximately 1,980 to 2,500m, followed by mixed conifer forests of pine, fir (*Abies* spp.), spruce (*Picea* spp.), and aspen (*Populus tremuloides*) at elevations above 2,500m. Open valleys stretch across the top portion of the plateau and support montane meadows and subalpine grasslands where meadow-grasses (*Poa* spp.), fescues (*Festuca* spp.), and sedges (*Carex* spp.) dominate the vegetation community (Halvorson 1972, Rink et al. 2020). These meadows support a vast array of biotic diversity including rare species such as the Kaibab Swallowtail butterfly (*Papilio indra kaibabensis*), endangered species such as Sentry Milk Vetch (*Astragalus cremnophylax*), and endemic plant species such as the Kaibab paintbrush (*Castilleja kaibabenis*) and Kaibab bladderpod (*Physaria kingii* subsp. *kaibabensis*) (Reichenbacher 1986, Spence 2006, 2007, Stevens 2007, Rink 2016, Rink et al. 2020). This high elevation mesa is also home to the Kaibab National Forest (KNF) and the North Rim, Grand Canyon National Park (GRCA), which is rich in cultural resources such as ancestral Puebloan archeological sites (NPS 2014). The study area for this project encompasses approximately 65 square kilometers (km^2) of the KP and includes meadows within KNF (managed by the U.S. Forest Service) and GRCA (managed by the National Parks Service), and ranges in elevation from 2,500 to 2,770m.

This study area is a semi-arid landscape, receiving an average annual precipitation of 65.5 centimeters (cm) (Rink et al. 2020). Most of the annual precipitation falls in the form of snow from October to March, followed by monsoonal rains occurring from June to September.

Early summer on the KP is typically dry, but late summer monsoon storms can provide intense (but often short-lived) bouts of rainfall. These monsoon storms are often patchy in frequency and distribution across the landscape, which may lead to varying grassland conditions. Water sources on the KP are scarce and largely dependent on the snowmelt and precipitation that recharges groundwater reserves. The only perennial surface water sources found in this study area are karstic sinkholes scattered throughout the landscape and one known perennial spring (Reimondo 2012).

Although mainly dominated by cool-season (C_3) plants, the meadows of the KP also support some warm-season (C_4) plants. These two groups have evolved different photosynthetic growth pathways that require different temperature, light, and moisture conditions for optimal growth, revealing distinct ecological functions of each group (Epstein et al. 1997). Warm-season C_4 grasses on the KP such as Blue grama (*Bouteloua gracilis*) require warmer temperatures (ideally >26°C) and have greater nitrogen-use efficiency and photosynthetic potential, affording rapid growth under appropriate environmental conditions (Epstein et al. 1997, Anderson 2006). Warm-season C_4 plants maximize their productivity during these conditions then remain dormant as temperatures cool down in winter and early spring months. Alternatively, the more dominant cool-season C_3 plants on the KP such as Muttongrass (*Poa fendleriana*) and Idaho Fescue (*Festuca idahoensis*) grow best at cooler temperatures (ranging from 15.5-23.8°C). These C_3 plants are typically less resistant to drought and have lower photosynthetic rates compared to C_4 plants (Epstein et al. 1997). Thus, cool-season plants take longer to reach peak productivity and typically achieve maximum growth during spring and fall. Average daily temperatures typically range from -6°C to 7°C in winter; -2°C to 23°C in spring; and 4°C to 25°C in summer (NPS 2023), with an average of 93 growing season days (Merkle 1962).

The meadow habitat throughout GRCA and KNF are ecologically similar and represent ideal grassland conditions for bison. However, bison mostly remain in concentrated areas within GRCA boundaries, spending little to no time in the adjacent KNF. They spend warmer months (typically May-November) wandering throughout meadows of Little Park and the Basin (Figure 1 and 2). Bison avoid harsh winter conditions (typically December-March) by migrating south to areas along (and below) the rim of the Grand Canyon (including Powell Plateau), where warm air from the bottom of the canyon rises to the rim, keeping this area relatively free of snow (Figure 1).

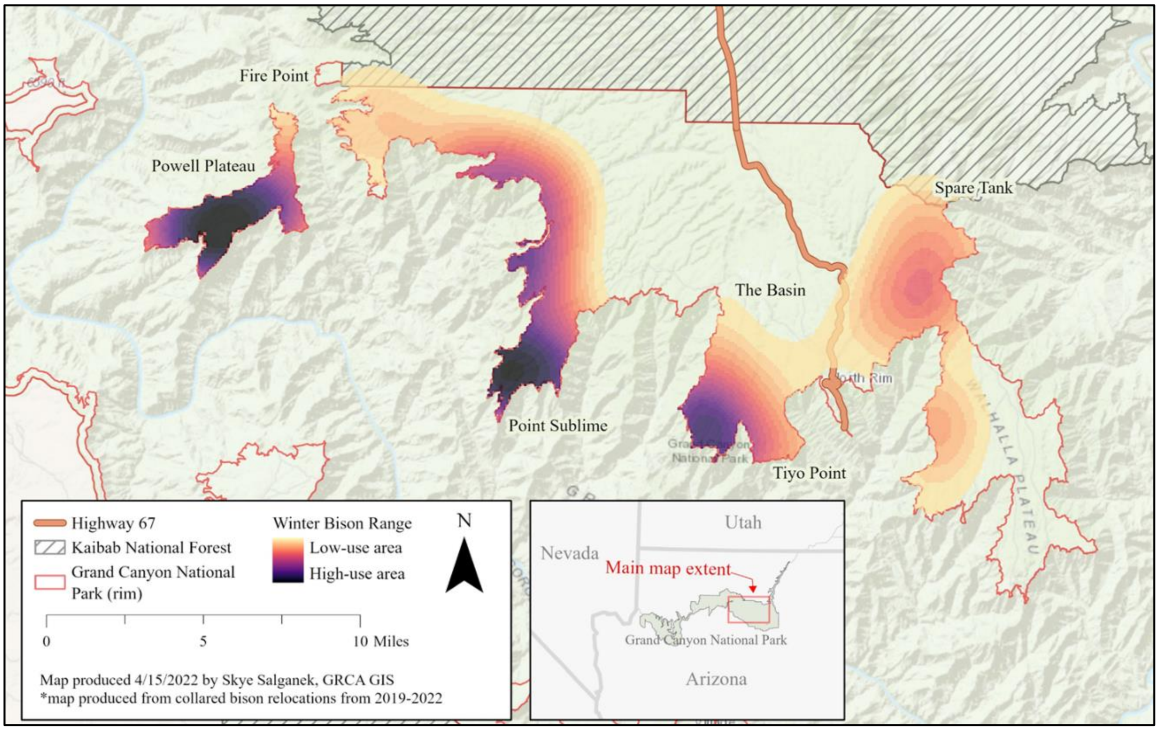


Figure 1. The winter distribution of Plains bison (*Bison bison bison*) across the Kaibab Plateau (KP), Arizona USA. This map was generated using 95% kernel density estimates from GPS location of 31 collared KP bison during 2019-2022. This map depicts the winter range of bison along the rim of the North Rim, Grand Canyon an includes the boundary between the Park and Kaibab National Forest. This map is provided with permission from authors of a manuscript in review (Salganek et al. 2023).

History of Disturbance on the Kaibab Plateau

The KP has a long history of anthropogenic uses, including logging, mining, hunting, and tourism, in addition to a long history of livestock grazing. Historic grazing allotments of the KP supported its highest head of livestock in 1891 (~200,000 sheep and 20,000 cattle and horses), yet was greatly reduced over time, with only 2,200 cattle on the KP in 1962 (USFS 2013). At present day, GRCA is void of livestock; however, KNF currently supports multiple grazing allotments, one of which is the Central Summer Allotment. This allotment consists of two pastures with a rest rotation grazing system where one pasture is grazed each year while the other is rested, and livestock grazing is alternated between pastures each year. The current allotment management plan authorizes 400 head of cattle from 1 June to 30 June and allows 800 head of cattle from 1 July to 15 October (USFS 2013). The portion of my study area in KNF is completely contained within the Central Summer Allotment boundaries. The history of land-use and anthropogenic changes to the KP likely has a direct and significant impact on the biotic communities. Although the KP has a long history of livestock grazing, free-roaming bison grazing is a novel disturbance in this ecosystem.

History of Bison on the Kaibab Plateau

Understanding current grassland conditions on the KP requires the evaluation of recent and historic land-use practices, including the history of bison utilization. Prior to 1905, there was no record of bison presence on the KP (Rink et al. 2020). In 1905, a herd of approximately ten Plains bison were introduced by private landowners to the Grand Canyon Game Reserve in the House Rock Valley (elevation: approx. 914m) of northern Arizona (Terwilliger at al. 2020). This bison herd (which will eventually be known as the KP bison herd) was free-roaming but primarily remained within House Rock Valley throughout the year. The same private landowners attempted to crossbreed bison with cattle; however, attempts were generally unsuccessful. Recent genetic analysis of cattle introgression in the KP bison herd indicated that only 1.6% of the nuclear alleles were of cattle ancestry (Terwilliger et al. 2020). In 1926, the growing herd of 98 bison were sold to the Arizona Game and Fish Department (AZGFD) and managed as huntable wildlife. Public culls and free chase hunting maintained the population under 100 individuals until the late 1990's when the bison began to migrate upland from House Rock Valley through the KP and into North Rim, GRCA (elevation: approx. 2,743m). It is likely that poor range conditions within House Rock Valley were the initial cause of bison migration to higher elevations, followed by a natural fire in GRCA that likely enticed bison to migrate further into the Park in search of fresh and highly nutritious forage. From the 1990's through 2010, the herd spent winters in House Rock Valley and migrated up the KP to spend summers in KNF and GRCA. However, as of 2010, the bison population has not migrated back to their House Rock Valley winter range and now primarily remains within GRCA boundaries throughout the year (Terwilliger et al. 2020). Ungulates such as bison have been shown to use National Parks as refugia to avoid predation by hunters (Davidson 2007) and resource managers believe that this spatial preference limits their migratory routes (AZGFD 2019), which is likely due to the nearly year-round hunting pressure in the surrounding KNF that is encouraging bison to remain in a harvest-free space (Hurley et al. 2020).

Bison in GRCA likely occur in the southernmost extent of their historic range (Cararra and Ballard 2003). Scarce evidence exists that bison historically roamed the KP, and little is known of their habitat interactions in the southwestern U.S. in general. Triggered by the sustained occupancy of bison inside GRCA boundaries and the perceived impacts to natural resources, the *2017 Initial Bison Herd Reduction Environmental Assessment* was developed and approved (NPS 2017). This plan outlines management goals of 1) reducing the KP bison herd to fewer than 200 animals over a 5-year period, and 2) monitoring GRCA natural resources as directed by NPS Management and Monitoring Policies (NPS 2006). The recent sustained occupancy of the KP bison herd in meadows with little evidence of a history of bison grazing presents an unprecedented opportunity to obtain insights into how bison may act as drivers of ecosystem changes over time within high elevation grasslands of GRCA and the KP.

Bison Herd Distribution

In an ongoing companion study, GRCA partnered with the U.S. Geological Survey (USGS) to conduct research to better understanding the size and spatial distribution of the KP bison herd and to determine seasonal and annual habitat selection. In 2019, a total of 25 GPS radio collars (with release mechanisms) were fastened around the necks of adult bison individuals during live capture corralling events. Bison GPS collars record a remote, fixed location every two hours, providing researchers with recent locations and movement patterns that can be assessed spatially overtime. The collaborative information regarding spatiotemporal bison movement via GPS collars will be used alongside my studies' wildlife camera traps and utilization measurements to provide additional insight into the relationship between bison migratory patterns (Figure 1) and grassland patch utilization.

Bison Herd Population Size & Reduction Efforts

Efforts to reduce the KP bison population size have been successful via multiple removal and relocation events, with the goal of reducing herd size to 200 or fewer throughout the span of the 5-year reduction plan (NPS 2017). Each fall since 2019, the Park has partnered with collaborators including the InterTribal Buffalo Council (ITBC) to relocate bison to various Native American tribes across North America. Since the onset of corral operations in 2019, four live capture corral operations have successfully relocated 182 bison to seven different tribes in four different states across North America (Terwilliger 2022). Additional herd reduction efforts were taken in 2021, where GRCA biologists piloted a lethal removal program. Skilled volunteers were trained and accompanied by GRCA biologists and law enforcement to conduct a bison 'hunt' within GRCA boundaries. Five bison were successfully removed as part of this program in 2021. To date, park-initiated herd reduction efforts plus known mortalities and hunting successes in KNF have collaboratively removed a total of 362 individuals from the KP bison herd.

In January of 2020, prior to bison calving, the estimated bison population size ranged from 285-365 individuals with 95% confidence. In January of 2021, the herd was estimated between 269-483 individuals with 95% confidence. Finally, the most recently published population estimate of the herd as of January 2022 was 187-313 individuals with 95% confidence (Terwilliger 2022).

CHAPTER 2: THE SPATIAL AND TEMPORAL VARIATION OF BISON HERBIVORY AND ITS SUBSEQUENT INFLUENCE ON GRASSLAND VEGETATION

Introduction

Natural grasslands are defined by annual climate conditions, in which low precipitation limits forest or shrubby vegetation from establishing and persisting but is sufficient to support well-adapted grasses such as the graminoid family Poacaea (Anderson 2006). Grassland ecosystems, by origin, have specialized adaptations to semi-arid conditions, and the timing of this evolution coincided simultaneously with the rise in large ungulate herbivores such as Plains bison (Stebbins 1972, Raven and Axelrod 1974). Grassland plants evolved certain characteristics to adapt to dry conditions in order to conserve moisture and tolerate potentially stressful environmental conditions. These adaptations include the production of basal meristems, small stature, high shoot density, deciduous shoots, belowground nutrient reserves, and rapid growth (Coughenour 1985). The mechanisms that allow grassland plants to tolerate grazing disturbances are expressed in similar physiological adaptations (Milchunas et al. 1988).

Long-term grassland patch utilization by ungulates can result in morphological and physiological adaptations in plants to resist the defoliation effects of herbivory (Coughenour 1985, Blumenthal and Augustine 2009, Hempson et al. 2015). For example, Hempson et al. (2015) recognized growth switched forms of graminoids with distinct morphological characteristics (such as lateral growth and dwarfed forms) in plants exposed to prolonged grazing. Plants adapted by spreading horizonal stems either above (stolons) or below (rhizomes) the soil surface, which allowed for increased nutrient and moisture uptake and an enhanced capacity to avoid and/or tolerate grazing disturbance. Physiological adaptations due to prolonged grazing disturbance can involve the evolution of mechanisms that facilitate individual plant regrowth, including rapid inherent growth rates, reallocation of stored nutrients, and enhanced photosynthetic rates in regrowing leaves (Anderson and Briske 1995, Strauss and Agrawal 1999, Blumenthal and Augustine 2009).

Plains bison play a critical role in the structure and function of grasslands in many plant communities (Knapp et al. 1999). Herbivory can alter grassland structure such as plant community diversity and composition (Hempson et al. 2015), as well as influence entire ecosystem functions such as nutrient dynamics and interactions among herbivores, plants, and soil microbes (Ellison 1960, McNaughton 1983, Coughenour 1985, Anderson and Briske 1995, Singer and Schoenecker 2003, Blumenthal and Augustine 2009). Although herbivory can reduce vegetation biomass and productivity (Milchunas and Lauenroth 1993, Turner et al. 1993, Chase et al. 2000), it can also have a variety of benefits to grassland communities and ecosystems. For example, bison herbivory can increase local-scale soil nutrient availability, enhance habitat heterogeneity across the landscape (Larson 1941, Milchunas et al. 1988, Knapp et al. 1999), and facilitate entire ecosystem energy flows (McNaughton et al. 1997). However, plant response to grazing and the adaptive tolerance capacity of plants following defoliation varies greatly among individual plants, grassland ecotypes, and across environmental conditions.

Ungulate herbivores and grasslands coevolved spanning ~20 million years (Janis 1989, McFadden 1997) and may be adapted to mutually benefit from each other (Ellison 1960). This symbiotic relationship is, in part, described by the “Herbivore Optimization Hypothesis,” which predicts an increase in herbaceous production and nitrogen yield in areas of intermediate grazing intensities, resulting in a physiological overcompensation in plants and an overall increase in vegetation biomass (Dyer 1975, McNaughton 1979, Hilbert et al. 1981). Compensatory plant responses can be categorized into three outcomes: over-compensation, equal compensation, and under-compensation. Over-compensation occurs when grazed plants are more productive than ungrazed plants, suggesting a mutually beneficial relationship. Equal compensation describes a neutral plant response to grazing, where productivity remains similar between grazed and ungrazed plants. Lastly, under-compensation describes the deleterious effects of grazing, where grazed plants are less productive than ungrazed plants (McNaughton 1983, Maschinski and Whitham 1989).

The effects of herbivory are governed by interactions between the environment and the affected plant (McNaughton 1986) and include the history (both long-term and recent) of grazing (Milchunas et al. 1988), the timing and intensity of grazing, the type of plant eaten (Maschinski and Whitman 1989), the availability of water and nutrients (Turner et al. 1993, Knapp et al. 1999, Schoenecker et al. 2004), and temperature (Wang et al. 2022). Although plant response has been coarsely divided into three potential outcomes, the effect of herbivory on plants is best described as occurring along a “Compensatory Continuum Hypothesis,” where the ability for a plant to tolerate or compensate for losses from herbivory are likely driven by a complex of interactions among the abiotic and biotic factors that influence the environment and plant physiology (Maschinski and Whitman 1989). Thus, it is critical to collectively evaluate the conditions driving herbivory-induced ecological changes and interactions among these factors to better understand the capacity of plants to recover or even thrive in the face of herbivory. This should provide an ecologically comprehensive understanding of the herbivore-grassland relationship and give managers insights into managing the resiliency of grazing ecosystems.

The plant-herbivore relationship and the ability of plants to tolerate and support grazing can be partially ascertained by evaluating the long-term and recent history of grazing in a particular landscape. Morphological and physiological plant growth adaptations that results from grazing disturbance are most prevalent in grasslands with a long history of grazing (Mach and Thompson 1982) and typically exhibit an improved ability to tolerate or compensate for tissue loss at various grazing intensities. In contrast, it is likely that plants in grasslands void of a long grazing history may only be able to tolerate defoliation if grazing is infrequent and at low intensities (McNaughton et al. 1983).

Conflicting evidence exists regarding how individual plant success is affected when grasslands are only exposed to recent grazing (over the span of a few years) (Knapp et al. 1999). Reduced herbaceous production has been observed within the first year of grazing relative to ungrazed areas within the Konza tallgrass prairies of Kansas; however, the grazed areas recovered to their initial rate of production during the second year of grazing, suggesting that in some cases, grazed plants can adapt to grazing disturbance within one year (Knapp et al. 1999). On the contrary, Turner at al. (1999) found that compensatory regrowth of plants following grazing occurred at Konza prairie sites with little history of grazing compared to sites with that were grazed for several years. Plant response to grazing can be very different, and even opposite among different plant communities or between individual plant species (Milchunas et al. 1988). The evaluation of additional, interacting abiotic and biotic factors is critical to better understand the herbivore-plant relationship with different grassland ecosystems.

Along with grazing history (both long-term and recent), the spatiotemporal pattern of grazing (frequency and intensity across the landscape) must be understood to provide insight into how plants and grassland communities respond to grazing and how this response may in turn influence bison movement to access resources. Benefits of herbivory on grassland structure and function tend to manifest when grazing patterns are spatially and/or temporally dynamic across the landscape, where grassland patches are intermittently grazed rather than consistently (Knapp et al. 1999), while also occurring at intermediate intensities (McNaughton et al. 1983).

Intermittent grazing can allow for plants to maintain both above and belowground resource reserves, which is necessary under harsh environmental conditions such as those during the dry season (Hempson et al. 2015). If grazing occurs too frequently, or during a season where plants are more vulnerable (i.e., dry-season or winter), grazing can be a significant factor that drives plant mortality. However, production potential can recover if bison grazing is sufficiently dynamic, either spatially or temporally, such that sites are grazed intermittently, or if the system has a long enough history of grazing to allow for plant resiliency adaptations to have been developed (Knapp et al. 1993, Milchunas and Lauenroth 1993). Intermediate grazing (resulting in partially defoliated vegetation) refers to the amount of herbaceous defoliation and the time left in between grazing occasions allows for the recovery of plant biomass (McNaughton et al. 1983). Increased rates of photosynthesis in partially defoliated individual plants occurs potentially due to an increase in energy demands and increased light penetration to remaining plant meristems (McNaughton 1979, Knapp et al. 1999).

The type of plant consumed is another factor that can influence a plants response to grazing. Bison are short-grass specialists and typically favor fast-growing, dominant graminoids (Fahnestock and Knapp 1994, Knapp et al. 1999, Blumenthal and Augustine 2009). Selective consumption and reduction in the abundance of dominant graminoids incidentally increases available resources (such as space, water, nutrients, and light) to other plant groups such as native forbs or invasive species (Ellison 1960, Fahnestock and Knapp 1994). Forb-rich components of grasslands are important to maintain high levels of biotic diversity (Knapp et al. 1999); however, invasive grassland plant species are often less productive and can reduce habitat quality (Smith and Knapp 1999, Charles and Dukes 2008). Selective foraging of plant types yields varying effects and can both cause and prevent plant invasions (Smith and Knapp 1999, Blumenthal and Augustine 2009), as well as increase or decrease overall plant abundance and diversity (Milchunas et al. 1988, Towne et al. 2005). This depends, in part, on the level of specialization of the grazers.

Highly selective foraging can result in an increased dominance of well-defended, less productive plant species, whereas moderately selective foraging can result in higher proportions of palatable, productive plant species that tolerate some level of grazing disturbance (Blumenthal and Augustine 2009, Hempson et al. 2015). Highly selective grazing could also result in the elimination of plant species that have not adapted to tolerate grazing disturbance (Milchunas 2006). Nonetheless, empirical evidence suggests that a dynamic pattern and intensity of selective and non-selective grazing overtime can create a highly heterogenous landscape with a stronger capacity to support biological diversity in areas that are adapted to grazing pressures (Fahnestock and Knapp 1994, Knopf 1996, Knopf and Samson 1997, Fuhlendorf and Engle 2001).

The availability of water and nutrient resources in the environment directly affects plant productivity (Tilman 1982) and compensatory capacity (Maschinski and Whitman 1989). Plant productivity is particularly limited by the interaction between water and nutrient availability due to its influence on photosynthetic requirements (the mechanism driving plant productivity). Plants absorb soil moisture and available nutrients which supply the energy required for plant metabolic processes such as growth. Empirical evidence shows that precipitation or nutrients alone do not explain changes in herbaceous productivity, rather the interaction between the two, such that precipitation influences plant uptake of soil nutrients by acting on soil microbial respiration, nutrient leaching, and nutrient mineralization (Dijkstra et al. 2012, Gao et al. 2021).

Thus, grazed grassland patches are most productive when soil nutrients and water are both abundant (Augustine and McNaughton 2006).

Temperature has also been recognized as a leading mechanism that drives plant productivity and distribution across the landscape, as it directly affects the capacity for plants to preform enzymatic functions related to photosynthesis (Wang et al. 2022). Many cold-adapted C_3 plants typically perform metabolic function along a temperature gradient between 0°C and 30°C (Regehr and Bazzaz 1976, Mawson et al. 1986, Larcher 2003). While plant metabolic function can operate at 0°C, various studies have detected a sharp increase in high elevation grassland plant growth when mean daily spring temperatures increased from 0°C to 5°C (Peacock 1975, Wingler and Henessey 2016). When winter shifts to spring, low soil temperatures can also limit spring green up. However, cold-acclimated grassland plants have been found to adapt physiological mechanisms that regulate growth during periods of poor environmental conditions (such as harsh winters) by creating underground resource reserves to support winter survival and early growing season temperature fluctuations (Wingler and Henessey 2016).

The ability of ungulate herbivores to influence (and even facilitate) grassland ecosystem functions under varying conditions provides insight into the potential ways that bison may be influencing the North Rim, Grand Canyon ecosystem in northern Arizona. Since little evidence shows that meadows of GRCA were a significant part of the Plains bison historic range and the KP bison herd only recently (as of 2010) became resident and occupied areas within Park boundaries, little information exists regarding their influence in arid or semi-arid southwest regions of the North America. Although a range of research has been conducted on bison herbivory throughout various grassland ecotypes throughout North America (Knapp et al. 1999, Schoenecker et al. 2004, Frank et al. 2016), the effects on grassland structure and function have yet to be assessed within the GRCA ecosystem. This chapter outlines how I assessed plant response to herbivory by evaluating the spatiotemporal dynamics of herbivory, quantifying grassland conditions such as herbaceous utilization, aboveground productivity, and vegetation ground cover, as well as local climatic conditions in meadows throughout the study area.

Methods

Study Design

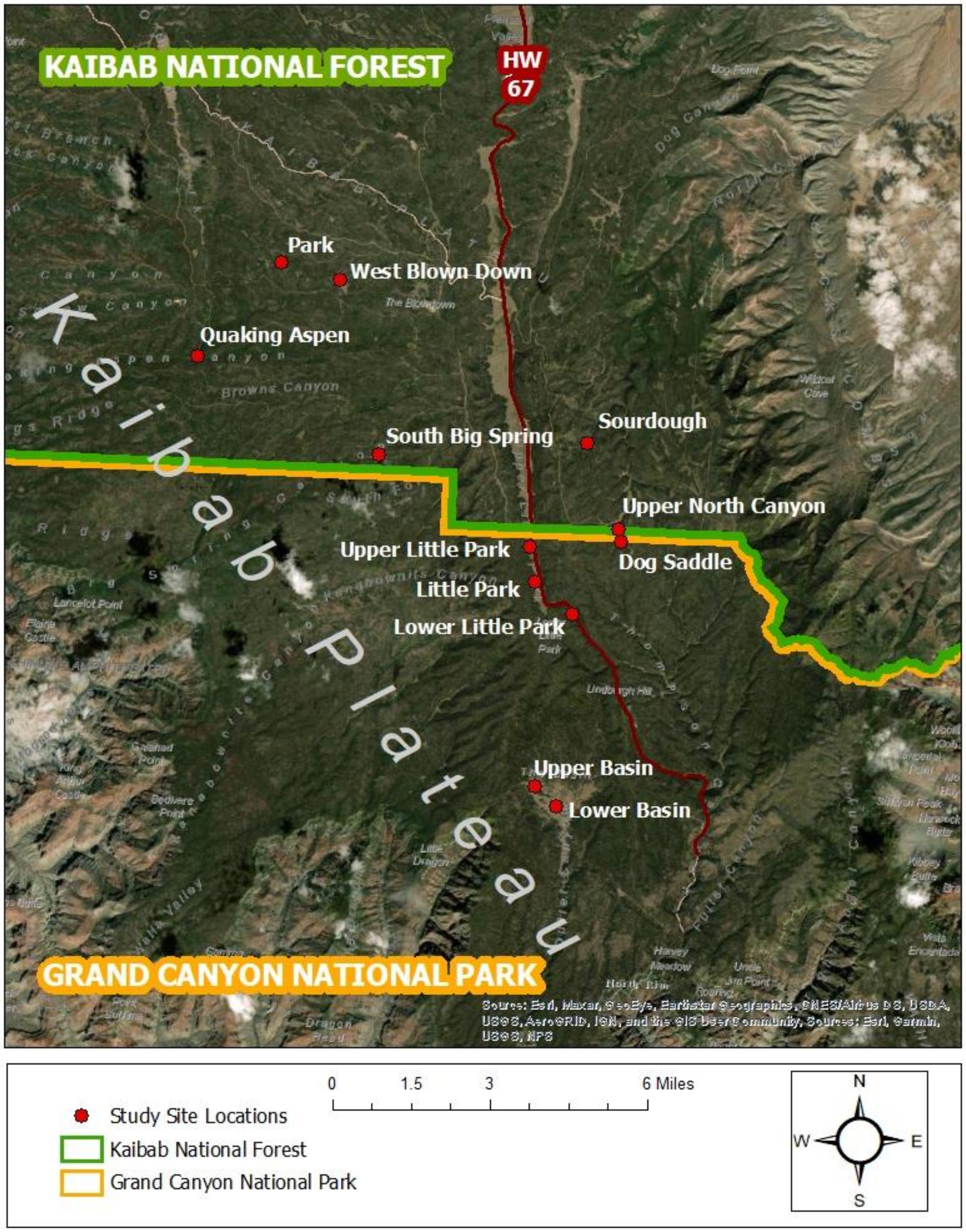
Preliminary Grassland Study

In summer of 2019, I assisted GRCA staff and members of the Southern Colorado Plateau Inventory and Monitoring Network, the Grand Canyon Conservancy, and the U.S. Geological Survey in a preliminary vegetation survey throughout KP grasslands to assess plant diversity, abundance, height, and relative percent ground cover using point-intercept and belt transects. Results from this pilot effort to assess grassland conditions as it relates to bison utilization showed no difference in overall species richness (mean number of species recorded) between GRCA meadows and KNF meadows. However, in areas with bison grazing (GRCA meadows), mean height of graminoids was >10cm shorter, relative percent cover of graminoids was ~20% lower, relative percent cover of forbs was ~10% higher, and relative percent cover of bare ground was ~5% greater, compared to KNF meadows without grazing. These preliminary results indicated that bison grazing may have influenced grassland community composition and abundance and was the impetuses for my larger grazing exclosure experiment which is described in following sections. These results were conducted concurrently with the onset of the *2017*

Bison Herd Reduction Plan, and although results were insightful, further information was required to assess the range of potential bison influences and grassland condition.

Site Selection

In my study, twelve sites were selected using spatial analysis and randomly generated plots within ecologically homogenous communities that exhibited varying rates of bison utilization. I identified two "stratum" which refers to the land management agency that is associated with differing bison densities: Grand Canyon National Park (GRCA) and Kaibab National Forest (KNF). Six study sites were established in GRCA meadows with varying ranges of bison occupancy and six study sites were established in KNF (of homogenous meadow habitat), which have little to no bison occupancy (Figure 2; Table 1). The number of study sites was selected to provide a sample size large enough to represent key areas of grazing, account for natural variability within and among plots, and to maintain a large enough sample size in case of attrition of any sites. The Grand Canyon National Park-Grand Canyon/Parashant National Monument vegetation classification and mapping project (Kearsely et al. 2015) was used to identify Montane-Subalpine Grassland areas, then study sites were selected from a group of randomly generated areas within montane meadow grassland habitat using ArcMap (ESRI, ArcGIS Version 10.7.1). Generated study sites that were located >350m away from access roads were eliminated due to difficulty in transporting fence-building materials from vehicles to exact site coordinates. Study sites were then filtered from this pool to represent homogenous grassland habitat that contained similar elevation, soil order and type (from USDA data) (Lindsay et al. 2003), aspect, slope, distance to roads, and distance to water (Table 1). Sites were then surveyed using GPS to ensure that each location could contain a 0.40-hectare "grazed" plot (with five ~1-m^2 grazing cages) as well as an adjacent 0.40-hectare fenced "exclosure" plot of similar meadow habitat. Site selection surveys included eliminating any sites with relatively frequent livestock grazing in KNF (as determined by remote wildlife camera traps) to maintain the focus of the study on bison grazing. NPS compliance requirements were completed and approved by the GRCA superintendent for all related research activities at each six sites within the Park. Separate compliance was required for KNF sites under the advisory of U.S. National Forest Service (USFS) monitoring protocols. NPS and KNF compliance protocols were completed, and no adverse effects were determined to result from proposed research activities.



Source: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community, Sources: Esri, Garmin, USGS, NPS

Figure 2. Map of designated study sites within Grand Canyon National Park (GRCA) and Kaibab National Forest (KNF) throughout the Kaibab Plateau. Study sites above the yellow line are within KNF, where bison are thought to avoid, and sites within GRCA are below the green line. The GRCA portion of this map encompasses much of the herds known summer range, while Figure 1 depicts the herds winter range. This map was created using ©ArcMap (Version 10.7.1).

Treatments: Grazed vs. Exclosure Plots

Twelve sites were selected throughout the study area, each comprised of one ~0.40-hectare "grazed" treatment plot and one 0.40-hectare "exclosure," or control, treatment plot, where each grazed plot was established adjacent (<60m) to a paired exclosure plot. Five grazing cages were placed throughout each grazed treatment plot in similar meadow habitat (similar in the abundance and composition of plants). Each cage consisted of a protected (caged) subplot inside and a paired, unprotected (grazed) subplot directly outside the cage. With five cages, this allowed for five pairs of caged and grazed subplots. Each paired subplot is dependent based on each individual grazing cage, whereas pairs of subplots are independent due to the randomness of cage deployment throughout the plot. Five grazing cages were placed within each grazed treatment plot to suitably capture variation and minimize within-plot and among-plot variability (Schoenecker 2012). Each of the twelve grazed treatment plots have the potential to be exposed to a range of bison grazing intensities. Each of the twelve study sites also contained long-term, fenced ungulate exclosures. These exclosures protect ~0.40-ha of meadow from ungulate grazing and served as control treatments to provide reference information for this research to evaluate and compare conditions in the adjacent grazed treatment plot.

In fall of 2020, construction began on the twelve long-term exclosures at each study site. Construction was contracted out and funded by GRCA and partners (GCC and USGS) and completed by Taylor Made Fencing, LLC (St. George, Utah). Each exclosure is comprised of galvanized steel posts and braces to support all corners. To avoid using cement to install posts, each steel post was installed ~1m in the ground, for a ground-up total heigh of approximately 2.4m. Galvanized steel woven wire (fixed-knot pattern) was wrapped around each post to enclose the area inside. The installment of all twelve exclosures was completed by winter of

2020. These long-term exclosures were constructed initially to monitor meadow resources for my study; however, National Park, Forest Service, and biologists alike anticipate utilizing them for future research (for example) pertaining to climate change or landscape-level grassland changes overtime.

Table 1. Designated study sites within the study area including site number, name, central coordinate location, and site characteristics. Sites 1-6 are within Grand Canyon National Park (GRCA) and sites 7-12 reside within Kaibab National Forest (KNF). All sites were often utilized by deer. All KNF study sites overlap with a livestock grazing allotment; thus, all KNF sites have the potential for some cattle grazing to occur. Additionally, hunting for various game and fowl is permitted throughout KNF; therefore, all KNF sites can potentially be affected by hunting activities. "Average Bison Days" and "Average Cattle Days" represents the proportion of days that a bison or cow was observed via motion sensing cameras relative to the total number of days the camera was operating.

Site Number	Site Name	Location (Lat/Long)	Elevation (meters)	Soil Order, Soil Type	Distance to road (meters)	Distance to water (meters)	Avg. Bison Days (%)	Avg. Cattle Days (%)	Visual Evidence of Other Activity
1	Upper Little Park	36.26239, -112.10373	2,498	Alfisols/ Entisols, mixed-loamy	306	604	18.9	0.0	Pocket gopher, coyote
2	Middle Little Park	36.26786, -112.11103	2,512	Alfisols/ Entisols, mixed-loamy	280	303	19.5	0.0	Pocket gopher
3	Lower Little Park	36.31551, -112.10160	2,666	Mollisols, mixed-loamy	7	604	8.9	0.0	Pocket gopher
4	Upper Basin	36.32331, -112.11482	2,681	Mollisols, mixed-loamy	177	253	34.7	0.0	Coyote
5	Lower Basin	36.33321, -112.11697	2,699	Mollisols, mixed-loamy	107	885	24.1	0.0	Coyote
6	Dog Saddle	36.33641, -112.08642	2,749	Mollisols, mixed-loamy	405	2,221	9.3	0.0	Pocket gopher, Mountain lion

Table 1. continued.

Site Number	Site Name	Location (Lat/Long)	Elevation (meters)	Soil Order, Soil Type	Distance to road (meters)	Distance to water (meters)	Avg. Bison Days (%)	Avg. Cattle Days (%)	Visual Evidence of Other Activity
7	Park	36.40901, -112.20601	2,645	Mollisols, mixed-loamy	291	574	0.0	1.2	Cattle, coyote
8	West Blown Down	36.40505, -112.18558	2,681	Mollisols, mixed-loamy	355	386	0.0	6.5	Cattle, Hunting
9	Quaking Aspen	36.38231, -112.23329	2,463	Mollisols, mixed-loamy	34	1,028	0.0	2.5	Cattle, Pocket gopher, coyote
10	South Big Spring	36.35691, -112.17014	2,642	Mollisols, mixed-loamy	53	1,244	3.9	0.0	Hunting salt lick
11	Sourdough	36.36258, -112.09903	2,716	Mollisols, mixed-loamy	105	1,223	0.0	0.0	Pocket gopher
12	Upper North Canyon	36.22867, -112.08739	2,742	Mollisols, mixed-loamy	78	2,780	5.0	0.0	Pocket gopher, Hunting

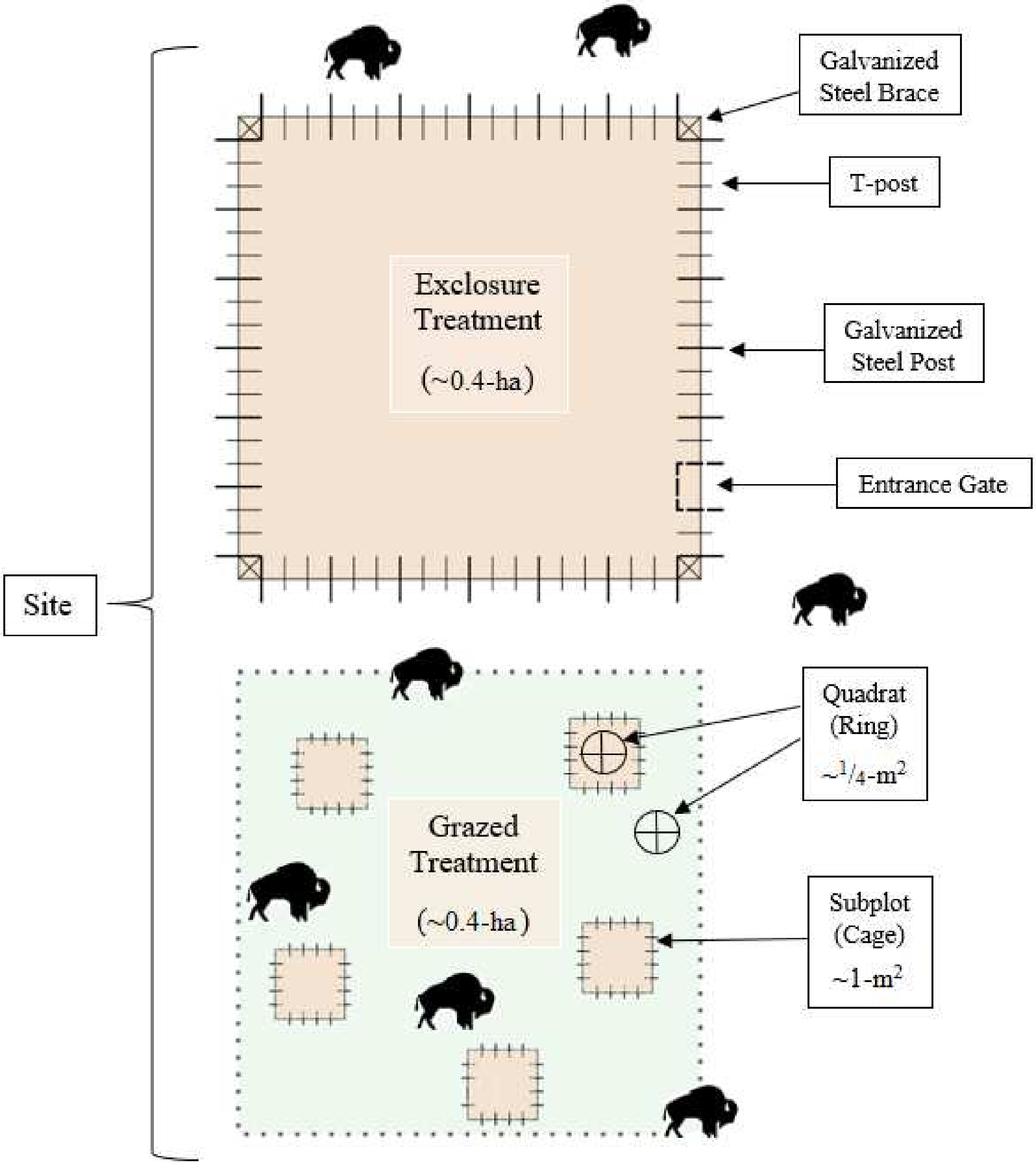


Figure 3. Schematic of an individual site, which depicts the general experimental study design, including relative placement and size of treatment plots, grazing cages, and quadrat clipping rings. Exclosure treatments were constructed to exclude the entire ~0.40-ha meadow area from ungulate utilization. Each exclosure treatment has an adjacent, paired grazing treatment, which consisted of an ~0.40-ha unfenced area of grassland entirely exposed to grazing except for the 1-m^2 area within grazing cages. Five grazing cages were randomly placed throughout the grazed treatment to exclude bison grazing within the enclosed 1-m^2 area. One quadrat clipping ring (~¼-m^2) was placed inside and outside of each of the five grazing cages in grazed treatments, and five quadrat clipping rings were randomly placed within each exclosure treatment to collect vegetation measurements. No grazing cages were placed inside exclosures.

Field Methodology and Data Collection

Annual Aboveground Herbaceous Production, Offtake, and Grazing Intensity

Aboveground herbaceous biomass was harvested (clipped) in areas of varying bison use to assess vegetation offtake (utilization) rates, annual aboveground primary production, and grazing intensity. Grazing cages were installed while bison occupied their winter range (Figure 1) and remained in place until the summer data collection occasion of each year (July 2021 and 2022). One ¼-m^2 circular quadrat clipping ring was placed inside and outside of each grazing cage, where each quadrat represents a subplot (subsample). Quadrats were placed in similar meadow habitat that encompasses homogenous plant species composition and abundance. All herbaceous biomass was clipped within quadrat rings close to the ground using scissors and plants were separated by functional group (graminoids vs. forbs) and labelled with site number, site name, date, and quadrat (subplot) placement (inside vs. outside grazing cage). Once subplots were clipped, each grazing cage was relocated and secured with T-posts and rebar to a different, random location within the grazed treatment plot, where it remained until the second (and final) clipping occasion in the fall of that same year (October in 2021 and September in 2022). Cages were once again re-located to a random location within the grazed plot and secured in place until the following years' (2022) data collection. Randomization was determined using a list of generated random azimuth directions from 0° to 160° and the relative number that the second-hand fell on a hand watch was used as the number of steps, allowing anywhere from 0 to 60 forward steps. A total of five quadrat rings were also placed randomly inside of each exclosure using the same randomization method and clipping protocol as described above. Summer and fall clipping events were scheduled to capture peak production of both cool and warm season plants within meadow habitat while bison were in their summer range. The entire ~65-km^2 study area is located solely on bison summer range; therefore, no winter offtake was measured.

Once clipped and bagged, plant biomass samples were transported to USGS Fort Collins Science Center where they were dried in a scientific drying oven at 55°C for 48 hours then weighed. Separation of standing dead (last year's growth) from live plant material (this year's growth) occurred in the lab and only current year's plant material was used in the calculation of utilization (offtake) and annual aboveground production. Each sample of dry weight clipped biomass (inside cage, outside cage, and inside exclosure) were used in the calculation of aboveground primary production, offtake, and grazing intensity.

Weather Stations

Weather stations (Onset HOBOware® data logging temperature and rain gauges [Version RG3]) were deployed at the center of exclosures at each study site except for Upper North Canyon (KNF) and Upper Basin (GRCA) for a total of ten weather stations. These battery powered systems use a HOBO® event logger to collect remote, site-level climate information including precipitation and temperature. Weather stations were programmed to collect temperature readings every 30-minutes and collect all measurements of precipitation events. Measurements of precipitation were recorded using a tipping-bucket mechanism, where a single "tip" represented 0.01 millimeters (mm) of precipitation. Solar radiation shields were also installed on each station to enhance reading accuracy. These weather stations have the capacity to collect a total of 4,000mm of precipitation and can collect up to 127mm of precipitation per hour (Onset Computer Corporation 2010).

In addition to collecting climate information throughout the duration of the study, it was important to collect precipitation information from the winter months leading up to the following years' spring season green up since annual production may be largely influenced by winter precipitation in this ecosystem. Since weather stations were not deployed until late September of 2021, supplementary data were needed during the timeframe of October 2020 to September 2021. Additionally, select weather stations experienced failures throughout their deployment and were found to be inconsistent (and unsuccessful) at capturing winter precipitation in the form of snow accumulation (Appendix A: Figure A1). Thus, I externally sourced supplemental data to fill in climate data gaps and to augment the winter months when data were missing from the Hoboware weather stations, when required.

Climate data from each weather station was remotely offloaded from the logging device to the Onset HOBOware Pro Software (Version 3.7.21) and various climate variables were recorded including daily minimum, maximum, and mean temperatures, precipitation events, and daily cumulative precipitation. Data from the remote logger was offloaded during each succeeding sampling occasion and the logger was returned to its secured location affixed within the solar radiation shield, where it remained until the next sampling occasion.

Percent Ground Cover

As an additional means of measuring grassland structure and function, relative percent of ground cover was measured and analyzed to evaluate the potential influence of bison grazing on the relative proportion of functional plant group composition and potential overall differences across the landscape. Paired quadrat clipping rings were placed on the inside and outside of each of the five grazing cages, which had previously been installed in a random location throughout the grazed treatment plot. Five quadrat clipping rings were also randomly distributed throughout each exclosure treatment and relative percent ground cover was estimated by using an ocular estimation technique in increments of 5% to estimate the relative proportion of various cover classes prior to clipping (McCune and Grace 2002). Cover classes were separated into the following structural groups: graminoids, forbs, litter, bare ground, rock, bison scat, crown (dormant bunch grass), moss, gopher disturbance, and other. Since it is possible for multiple cover classes to overlap with vertical structure (i.e., rocks under graminoids, forb growing out of a bison pie, etc.), percent ground cover values either equaled or exceeded 100%. Once percent ground cover was estimated and recorded for each subplot (inside cage, outside cage, and inside exclosure), herbaceous biomass was clipped. After percent ground cover measurements were taken within subplots of grazed treatments, grazing cages were moved to a random location within the 0.40-ha grazed plot and remained in place until the next sampling occasion.

Wildlife Sensing Camera Traps

Motion-triggered wildlife camera traps were installed at each of the twelve study sites to monitor study site utilization, including herbivore type and relative frequency. Cameras deployed at KNF sites were initially utilized to distinguish whether herbivory effects were from cattle or bison during the site selection process to best avoid areas frequented by cattle and were subsequently utilized to monitor overall site utilization throughout the remainder of the study. The six cameras in KNF sites were deployed with a lock box to prevent any interference with KNF visitors. The cameras deployed throughout GRCA sites provided information regarding the timing and frequency of bison utilization. Each camera was installed on nearby trees and were able to capture the entire range of each 0.40-ha grazed plot. All cameras were in place by 28 August 2020. These motion sensor Bushnell cameras have a 12MP lens with a 0.3-second trigger and an illuminating range of 25m. The cameras were programmed to capture photos and videos, where three consecutive photos were captured every 10-seconds and 30-second videos were recorded when triggered by motion. The 32MB memory card of each camera was collected and replaced with a new one during each sampling occasion and contents were reviewed.

Data Analysis

Annual Aboveground Herbaceous Production, Offtake, and Grazing Intensity

Selecting a Method for ANPP and Offtake Calculations (SPNI vs. SSPI)

Two different methods for estimating annual aboveground productivity (ANPP) and total offtake (O_t) were applied to the data and results were statistically compared. The first method, described by Bonham (1989), determines total annual herbaceous production by summing both positive and negative incremental changes in vegetation biomass between sampling occasions (summer and fall for this study). This method, referred to as the Sum of Positive and Negative Increments (SPNI), uses the following calculation to estimate grazed productivity:

$$ANPPg = P_{cs} + \sum (P_{cf} - P_{us})$$

where $ANPP_g$ is total annual aboveground net primary production in the presence of grazers, P_{cs} is the average caged biomass at initial summer sampling occasion, P_{cf} is the average caged biomass at the second clipping occasion in fall, and P_{us} is the average uncaged biomass during summer. Averages are based on the five replications of subplot (inside vs. outside cage) during each sampling occasion. Total annual aboveground production inside exclosures ($ANPP_{ug}$) was calculated as the average biomass clipped from five quadrat rings during the first sampling occasion, plus any differences in biomass in the succeeding sampling occasion. Using both positive and negative increments of change avoids overestimation and accounts for potential user error while still capturing small increments of biomass growth. Significant plant senescence from one clipping occasion to the next could result in an underestimation of production values (Schoenecker et al. 2022); however, field observations of local plant phenology dismiss this possibility. For each sampling occasion, offtake (utilization) was calculated by averaging the difference in caged versus uncaged biomass, using the equation below:

$$O_s = \sum (P_{cs} - P_{us})$$

where O_s is summer biomass offtake, P_{cs} is the average caged biomass during the summer sampling occasion, and P_{us} is the average uncaged biomass in the summer. Fall offtake (O_f) was determined using the same calculation as summer offtake. Total growing season offtake (O_t) was then calculated as the sum of summer and fall offtake $O_t = O_s + O_f$ and includes both positive and negative values (Bonham 1989)

The second method avoids user error entirely in its estimation of $ANPP_g$, $ANPP_{ug}$, and O_t by only adding increments of biomass change that are statistically significant ($p \leq 0.1$ due to a limited sample size). This method, referred to as the Sum of Statistically Positive Increments, will be hereafter be referred to as the SSPI method (Augustine and McNaughton 2006, Frank et al. 2002, 2016, Schoenecker et al. 2022). Here, for $ANPP_g$, the average caged biomass in summer was statistically compared to the average uncaged biomass in the fall; for $ANPP_{ug}$, the average exclosure biomass in summer was statistically compared to the average exclosure biomass in fall; and for O_t, the average difference in biomass from inside versus outside grazing cages in summer was statistically compared to the average difference in biomass from inside versus outside grazing cages in fall. Since the SSPI method only accounts for statistically significant increases in biomass and avoids random sampling error, this method is a more conservative estimation of annual herbaceous production and total growing season offtake. However, the SSPI method neglects increments of biomass change below the statistically significant p-value ($p \leq 0.1$), failing to account for small incremental change that could be attributed to growth or consumption rather than sampling error.

Total annual offtake (O_t) values were used in a proportion over the total annual grazed herbaceous production ($ANPP_g$) to calculate Grazing Intensity (GI) for each site. Grazing Intensity is defined as the percent of the current year's aboveground production that is consumed (or destroyed) by grazing using the difference method described by Bonham (1989) using the calculation below:

$$GI = (O_t/ANPP_g) * 100\%$$

This measurement, which represents the biomass utilized by bison relative to the biomass produced at a particular site, was used to evaluate the intensity of grassland patch use and to help determine spatial patterns of vegetation use, providing insight regarding bison distribution across the landscape.

The number of observations (n) for $ANPP_g$ (n=12) and for $ANPP_{ug}$ (n=12) were calculated for each year in 2021 (n=24) and 2022 (n=24), for a total of n=48 observations of aboveground herbaceous production collected throughout this study.

All statistical analyses were performed using RStudio (Version 2022.07.0). Under the SSPI method, I constructed a linear model for $ANPP_g$ and $ANPP_{ug}$ to determine if there was a statistically significant increase in biomass from summer to fall for each year. I used stratum, interval (sampling season), and site as covariates in a 3-way interaction. This model was used to determine whether there was a significant increase in biomass production that was dependent on bison presence (represented by stratum).

Using the same model structure as above, a separate linear model was constructed for Total Annual Offtake (O_t) to determine if there was a statistically significant increase in herbaceous offtake (consumption by herbivory) between summer and fall for each year. If a statistically significant biomass increase was observed from summer (O_s) to fall (O_f), the values were summed in the calculation of total annual growing season offtake (O_t). Under the SSPI method, only statistically significant increases were included in annual calculations; thus, if the difference in biomass from summer to fall was insignificant, the values were not summed, and total annual offtake was simply represented by the summer offtake value.

Finally, I conducted a paired t-test to evaluate potential differences in the herbaceous productivity and offtake values produced by the SPNI method versus SSPI method, and whether those differences were dependent on year or stratum.

Annual Aboveground Herbaceous Production, Offtake, and Grazing Intensity

I used a paired t-test to compare the treatment effect on the productivity within each site and whether productivity and offtake values differed between strata. The t-test used the average ANPP and offtake values (based on two years of measurements) across all sites within their respective stratum. An additional Welch two-sample t-test was employed to determine if there were differences in $ANPP_g$, $ANPP_{ug}$, O_t, and GI between years 2021 and 2022.

Additionally, a simple linear regression was employed to determine the relationship between annual grazed production and total annual offtake ($ANPP_g$-O_t relationship), parsing out GRCA and KNF. I assessed the strength of the production-offtake relationship based on the slope (beta estimate) and 95% confidence intervals (CI) and used R^2 values to assess variance explained by the model for each stratum.

Weather Stations

Precipitation

Climate data were organized into temporal windows associated with annual climactic changes expected to contribute to plant phenology throughout KP grasslands. Plants are typically classified by photosynthetic pathway (C_3 vs. C_4) related to their physiological growth dynamics which are based on environmental conditions. The cool-season C_3 plants are largely reliant on winter precipitation and cooler spring temperatures, whereas warm-season C_4 plants rely on summer monsoonal rains and warmer temperatures for growth (Epstein et al. 1997). Daily minimum and maximum temperatures, as well as daily precipitation values were compiled into temporal windows based on climate and seasonality, where October-March represented winter, April-June represented spring, and July-September represented summer. Daily values were summed for each month, then each month was added based on its respective seasonal window. Total annual precipitation was an accumulation of precipitation captured from October, November, and December of the previous year, until September the following year, to capture the comprehensive effects of snowfall's influence on the proceeding spring green up. Winter, spring, summer, and total annual precipitation values (measured in millimeters) were each used as an independent covariate in the candidate linear mixed model, described in the section below (Chapter 2: Data Analysis; Candidate Model Selection).

Temperature and Growing Degree Days

I calculated Growing Degree Days (GDD) for each site to evaluate the potential influence of temperature on site productivity. Although a large portion of the literature on GDD focuses on agricultural applications such as estimating crop harvest time or predicting pest growth (Onset Computer Corporation 2010), GDD provides a measure of the number of days during each annual growing season that the daily temperatures fall within a range of suitable conditions to either sustain or enhance vegetative growth.

A single growing degree day is equivalent to a one degree increase above a minimum threshold temperature for a period of one day and is calculated for each full calendar day (Onset Computer Corporation 2010). I chose to calculate GDD using the "Average Method", which calculates the average of the maximum and minimum temperatures for the day (adjusted to the lower and upper thresholds, if necessary), then subtracts the minimum threshold to compute the GDD. The equation for GDD incorporates the daily minimum and maximum temperatures, and a base temperature for this specific region of the minimum base threshold (1.6667°C) and the maximum base threshold (29.444°C). The equation for calculating Growing Degree Days (using the Average Method) is given below:

$$GDD = \left[\frac{T_{max} + T_{min}}{2}\right] - T_{base}$$

Where T_{max} is the daily maximum temperature in degrees Celsius, T_{min} is the daily minimum temperature in degrees Celsius, and T_{base} is the lower or upper temperature threshold (0°C and 30°C, respectively). GDD values were accumulated for months in spring (April-June), and summer (July-September), and the summation of spring and summer GDD values (total annual GDD) were utilized as three separate covariates that were added to the candidate linear mixed model as described in a following section.

Supplemental Climate Data - Daymet

To fill in any gaps in climate data when Hoboware weather stations had yet to be deployed or had malfunctioned, precipitation and temperature data were downloaded from Daymet, a long-term (since 1980), continuous data product (Thornton et al. 2022). Daymet is supported by NASA through the Earth Science Data and Information System and the Office of

Biological and Environmental Research within the U.S. Department of Energy's Office of Science (Thornton et al. 2022). Daymet consists of interpolated and extrapolated meteorological observations that produce 1km x 1km resolution grids of daily weather parameters.

Daily precipitation and temperature values were downloaded from Daymet using the central, longitudinal, and latitudinal coordinates for each site. I summed daily precipitation values (in mm) from data sources (Daymet vs. Hoboware) by month and categorized data into common seasonal temporal windows (winter, spring, and summer). I used a linear model for each seasonal precipitation window to test how well daily Daymet and Hoboware precipitation values fit. I constructed a separate linear model to test the similarity (or differences) among daily minimum and maximum temperatures obtained via Daymet and Hoboware weather stations. To determine whether data sources produced statistically similar values, assessed the strength in similarity of values produced by each data source based on the slope and used R^2 values to assess variance explained by the model for each stratum (Appendix A). For any site that did not have a complete set of values for each month day, mean daily values for each month were imputed to fill in values for those days. As an additional means of comparison, I ran a paired t-test to test for statistical similarity ($p>0.05$) in values between data sources. Finally, once a completed set of temperature and precipitation values were established and values separated into temporal windows, I ran an ANOVA test to evaluate potential spatial variability in climate between stratum (GRCA vs. KNF) and temporal variability between years (2021 vs. 2022).

Percent Ground Cover

I used an ANOVA comparison to test for differences in the percent ground coverage between uncaged quadrats within grazed treatments and the relative percent cover inside quadrats within exclosure treatments to test for potential relationships that bison may have with the relative percent of different ground cover classes. Analysis of percent cover data were focused on graminoids, forbs, bare ground, and litter. Each cover class was compared between treatment (exclosure vs. grazed), stratum (GRCA vs. KNF), year (2021 vs. 2022), and sampling season (summer vs. fall). Average percentages of cover classes were compared at the treatment level (grazed treatment vs. exclosure treatment) and the landscape/stratum level (GRCA vs. KNF) to identify differences in ground cover related to bison use.

Wildlife Sensing Camera Traps

Wildlife camera photos from each SD card of each camera were downloaded and organized by site, month, and year. All photos were evaluated for animal use, with emphasis on determining the frequency and duration in which bison and cattle utilized each site. For each site, the number of days an herbivore was captured by a camera was put in a proportion to the total number of days recorded, which I define as "trap days." A summary of herbivore type and relative frequency is provided in the Results section of this Chapter.

Linear Mixed Model

My small sample size (n=48) limited my ability to assess all possible covariates in one complex model (i.e., global model), so I first developed a linear mixed model structure to capture my overall experimental design based on *a priori* inferences (hereafter referred to as the 'Base Model'), considering the effect of treatment (grazed vs. exclosure), stratum (GRCA vs. KNF), and year (2021 vs. 2022) on annual herbaceous production. The Base Model was constructed with a two-way interaction between treatment and stratum, year as an additional main fixed effect, and site as a random effect. A common slope was produced for each site based on the assumption that variability was similar among sites. Although each site produced unique intercept values, my small sample size caused limitations in the number of predictor variables I could include in the mixed model without inducing overparametization; thus, intercept values were averaged across all sites. I included the interaction of treatment and stratum because I expected the effect of treatment to depend on stratum, since high utilization was expected in GRCA grazed treatment plots, whereas little to no utilization was expected in KNF grazed plots. This Base Model will provide the foundation for further evaluation of additional, measured predictor variables, which will be discussed in the “Candidate Model Selection."

I used the lmer() function in RStudio (Version: 2022.07.0) to conduct linear mixed model analysis. I diagnosed model assumptions through the interpretation of residual versus fitted value plots, a normal Q-Q plot, and Shapiro-Wilks test to determine whether my herbaceous production data satisfied the assumption of a linear mixed model (equal variance, linearity, and normally distributed, respectively). Herbaceous production data violated the assumptions for the mixed model and were therefore log-transformed; however, interpretation of results are based on non-transformed data.

Candidate Model Selection

Once the entire set of additional environmental predictor variables (covariates) were calculated (i.e., Growing Degree Days, Precipitation, Total belowground Nitrogen, etc.), I employed an iterative process of adding individual environmental covariates into the Base Model to assess which factors may best explain variation in herbaceous production in the presence and absence of bison. This exploratory phase of covariate selection was based on specific *a priori* hypotheses regarding what I considered to be important variables to avoid ‘fishing expeditions’ that result from researchers seeking significant predictor variables among a large pool of contenders (Anderson and Burnham 2002, Grueber et al. 2011).

These candidate models were compared using recommendations and guidelines from Anderson and Burnham (2002). I had seven climate covariates representing variants of temperature and precipitation. These included winter, spring, summer, and total annual precipitation (measured as the accumulation of both rain and snow water equivalent precipitation) for each respective seasonal time frames, and temperature variables included spring, summer, and total annual Growing Degree Days. I had four soil nutrient covariates which included Phosphorus (P), Ammonium (NH_4^+), nitrate (NO_3^-), and total below ground Nitrogen (measured in micro grams/10cm^2), which will be described in more detail in Chapter 3.

I used information from Pearson's Correlation to determine (and eliminate) any environmental covariates that were strongly correlated. Collinearity among predictor variables may lead to issues in result interpretation since correlated predictor variables explain some of the same variation in the response variable because their effects cannot be estimated independently (Quinn and Keugh 2002, Graham 2003). Estimation of regression coefficients can be precise at moderate levels of collinearity ($r=0.5$) but becomes less reliable as collinearity increases (Freckleton 2011); thus, I chose to use ($r\leq0.7$) as my maximum threshold to detect collinearity and determine which predictor variables should not be used together in the same model (Dormann et al. 2013).

With a small sample size of $n=48$ observations of ANPP (12 in summer 2021, 12 in fall 2021 and 12 summer 2022, 12 in fall 2022), I was limited in the number of covariates (and therefore model complexity) for any given candidate model. To allow for the addition of various combinations of covariates while avoiding overparametization, Harrison et al. (2018) suggests an approach of $n/k\leq10$ where n= number of observations and k= number of covariates. With an $n=48$, I elected to limit the total number of main predictor variables (including random effects and interaction terms) to $k \leq 8$ for any candidate model to improve the accuracy of parameter estimation and model predictability.

Covariates were individually added to the Base Model and compared using Akaike's information criterion (AIC_c) to determine the relative importance of each and their ability to explain the variation in ANPP. I used delta AIC_c (the change in AIC_c value relative to the top model) to identify the top three most competitive candidate models, considering models with a delta AIC_c between 0 and 2 as competitive (Anderson and Burnham 2002). Additionally, Akaike weights (w_i) and log-likelihood values were reported for each candidate model and used to quantify the importance of the accumulated set of variables selected for that model and its respective estimate of maximized fit (Grueber et al. 2011).

Results

Annual Aboveground Herbaceous Production, Offtake, and Grazing Intensity

Selecting a Method for ANPP and Offtake Calculations (SPNI vs. SSPI)

Linear regression results indicated that ANPP and O_t values produced by the SPNI versus SSPI method were similar (p=0.628). I found no significant interaction between method and year (p=0.654) or between method and stratum (p=0.592). Results from the analysis for comparing and selecting which method to employ for production and offtake calculations, including values produced by each site for each year, and results from the linear model (including p-values) are presented in Appendix B. Since results from the paired t-test indicated that values for herbaceous production and offtake were statistically similar between methods (p=0.9386), I further only report on results using the more conservative SSPI method.

SSPI: Annual Aboveground Herbaceous Production, Offtake, and Grazing Intensity

Based on paired t-test results, I found a significant increase in productivity of grazed treatment plots at all sites in GRCA (t=2.9336, df=11, p=0.0136), where average $ANPP_g$ was estimated to be 25.65g/m^2 higher than average $ANPP_{ug}$. Enhanced $ANPP_g$ values occurred at all sites in GRCA, ranging from 9.3% to 33.8%, for an average increase of 23% (Table 3). ANPP did not differ between treatments for sites within KNF (t=-0.08, df=11, p=0.9359). On average, aboveground herbaceous production of grazed plots ($ANPP_g$) was higher in GRCA (105.0g/m^2) than in KNF (79.4g/m^2), though variability was greater in GRCA (Table 4; Figure 4). Average $ANPP_{ug}$ was similar between strata (t=-0.077931, df=21.969, p=0.9386), where GRCA exclosures produced 78.9g/m^2 (±8.73) of herbaceous biomass and KNF exclosures produced 79.9g/m^2 (±8.4) (Table 4; Figure 4). Results from the Welch two-sample t-test that evaluated potential differences in $ANPP_g$, $ANPP_{ug}$, and O_t between years 2021 and 2022 indicated that measurements of total annual production and offtake remained relatively consistent between years in both GRCA and KNF (no significant difference was detected; p=0.46836). Since no statistical difference could be detected between years, some additional analyses and interpretation of results uses an average of measurements collected from 2021 and 2022.

Although I found no difference in average annual herbaceous offtake (O_t) between years based on the Welch two-sample t-test, the paired t-test indicated that offtake differed between stratum where average O_t was significantly higher (p=0.0058) in GRCA (53.39g/m^2± 6.9) compared to sites in KNF (3.88g/m^2± 1.2) (Table 4). Additionally, the greatest O_t values were captured at the most productive sites (4 and 5) located in GRCA (Tables 2 and 3; Figure 4). In GRCA, average grazing intensity values ranged from 28.9% (site 6) to 63.4% (site 4). In KNF, average grazing intensity ranged from 0% (sites 8 and 11) to 18.1% (site 12) (Table 3). On average, grazing intensity was higher in sites within GRCA (46.2%) compared to sites in KNF (4.9%) (Table 4).

Table 2. Result estimates in the presence ($ANPP_g$) and absence ($ANPP_{ug}$) of bison grazing, total growing season herbaceous offtake (O_t), and the proportion of annual biomass growth to consumption (Grazing Intensity) for 2021 and 2022 using the SSPI method. Sites 1-6 are located within Grand Canyon National Park and sites 7-12 in Kaibab National Forest. $ANPP_g$, $ANPP_{ug}$, and O_t are measured in g/m², and grazing intensity is given as a percent.

	2021 *Sum of all significant positive increments (SSPI)*				2022 *Sum of all significant positive increments (SSPI)*			
Site	$ANPP_g$ (g/m^2)	$ANPP_{ug}$ (g/m^2)	O_t (g/m^2)	Grazing Intensity (%)	$ANPP_g$ (g/m^2)	$ANPP_{ug}$ (g/m^2)	O_t (g/m^2)	Grazing Intensity (%)
1	58.60	38.86	25.40	43.3%	101.57	71.43	47.93	47.2%
2	59.05	44.04	35.58	60.3%	69.88	72.66	23.06	33.0%
3	74.47	64.50	37.74	50.7%	123.45	77.50	45.18	36.6%
4	221.85	144.54	156.19	70.4%	146.21	99.03	82.33	56.3%
5	89.32	116.97	34.71	38.9%	141.58	92.66	84.60	59.7%
6	110.86	57.94	72.09	65.0%	58.14	67.08	-4.15	-7.1%
7	68.64	42.94	20.96	30.5%	76.54	71.78	-3.07	-4.0%
8	43.02	48.25	-3.87	-9.0%	79.99	47.14	13.29	16.6%
9	98.95	103.55	4.59	4.6%	91.55	141.96	-10.26	-11.2%
10	66.53	70.57	8.50	12.8%	91.94	95.58	4.00	4.4%
11	70.32	82.63	-16.81	-23.9%	113.72	109.38	2.68	2.4%
12	69.06	78.16	16.98	24.6%	82.58	66.90	9.62	11.6%

Table 3. Results estimates of average $ANPP_g$, $ANPP_{ug}$, O_t, and Grazing Intensity based on two years of measurements (2021 and 2022 pooled) including 1 standard error in parentheses. Sites 1-6 are located within Grand Canyon National Park and sites 7-12 in Kaibab National Forest. All values were calculated using the SSPI method. $ANPP_g$, $ANPP_{ug}$, and O_t are measured in g/m², and grazing intensity is given as a percent.

Stratum	Site	Avg. $ANPP_g$ (±SE)	Avg. $ANPP_{ug}$ (±SE)	Avg. Annual Offtake (O_t) (±SE)	Avg. Grazing Intensity (±SE)
Grand Canyon National Park	1	80.1 (21.5)	55.1 (16.3)	36.67 (11.3)	45.3 (1.9)
	2	64.5 (5.4)	58.4 (14.3)	29.32 (6.3)	46.6 (13.6)
	3	99.0 (24.5)	71.0 (6.5)	41.46 (3.7)	43.6 (7.0)
	4	184.1 (37.8)	121.8 (22.8)	119.26 (36.9)	63.4 (7.0)
	5	115.5 (26.1)	104.8 (12.2)	59.66 (24.9)	49.3 (10.4)
	6	84.5 (26.1)	62.5 (4.6)	33.97 (38.1)	28.9 (36.1)
Kaibab National Forest	7	72.6 (4.0)	57.2 (14.6)	8.95 (12.0)	13.3 (17.3)
	8	61.5 (18.5)	47.7 (0.6)	4.71 (8.6)	3.8 (12.8)
	9	95.2 (3.7)	122.8 (19.2)	-2.84 (7.4)	-3.3 (7.9)
	10	79.2 (12.7)	83.1 (12.5)	6.25 (2.3)	8.6 (4.2)
	11	92.0 (21.7)	96.0 (13.4)	-7.07 (9.7)	-10.8 (13.1)
	12	75.8 (6.8)	72.5 (5.63)	13.3 (3.7)	18.1 (6.5)

Table 4. Comparison of average $ANPP_g$, $ANPP_{ug}$, O_t, and Grazing Intensity results based on compiled site values separated by stratum (Grand Canyon National Park and Kaibab National Forest) and averaged across two years of measurements using the SSPI method. $ANPP_g$, $ANPP_{ug}$, and O_t values are measured in g/m^2, and grazing intensity is given as a percent. Twelve observations were included in these averages for each variable, for a total of n=48 observations.

Stratum	Avg. $ANPP_g$ (±SE)	Avg. $ANPP_{ug}$ (±SE)	Avg. Annual Offtake (O_t) (±SE)	Avg. Grazing Intensity (±SE)
Grand Canyon National Park	105.0 (14.0)	78.9 (8.7)	53.39 (6.9)	46.20% (8.6)
Kaibab National Forest	79.4 (5.3)	79.9 (8.4)	3.88 (1.2)	4.90% (1.7)

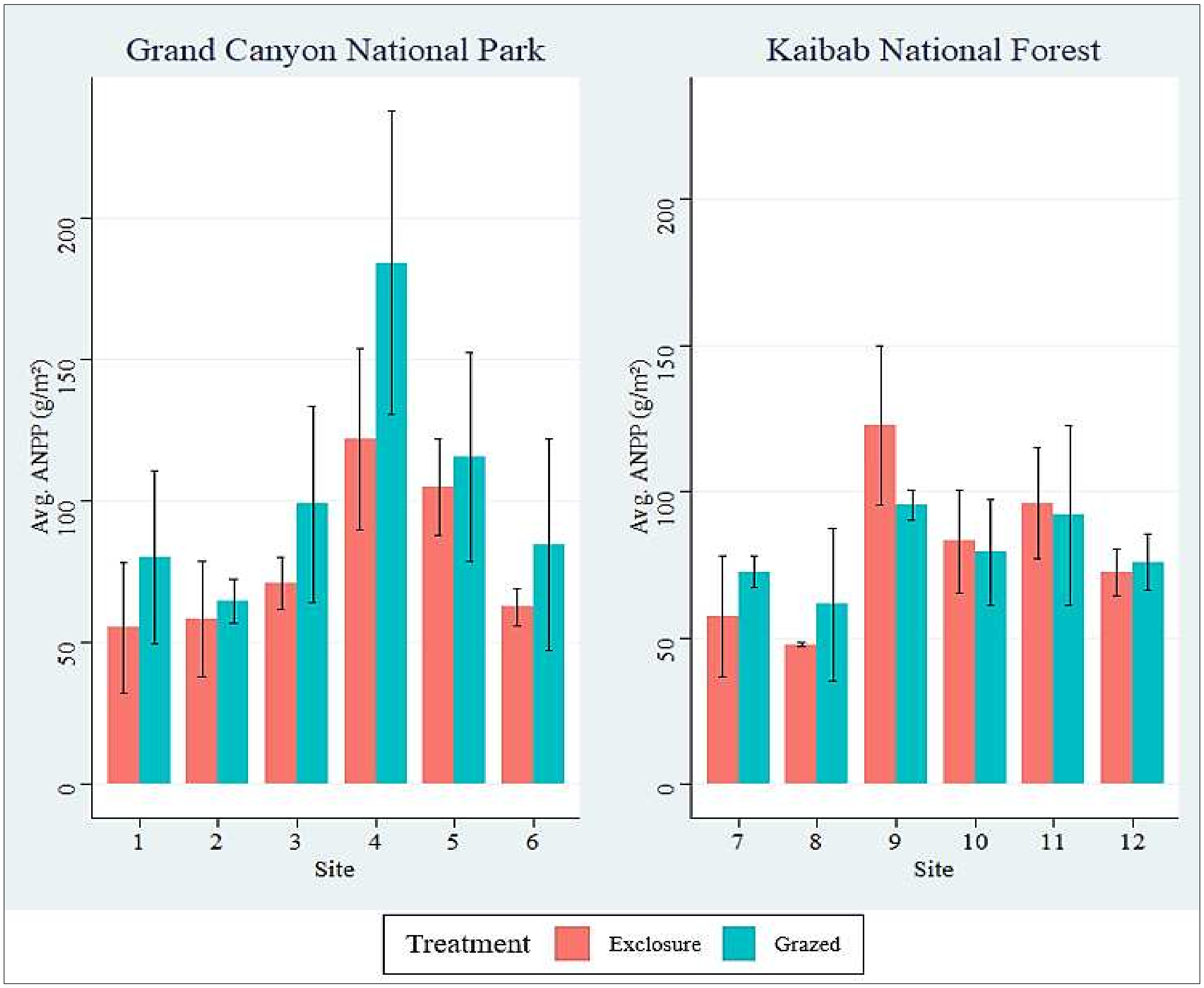


Figure 4. A comparison of average annual herbaceous production (ANPP) measured in exclosures versus grazed treatments in Grand Canyon National Park (left) and Kaibab National Forest (right). Values are given in g/m^2 and standard errors are based on two years of measurements (2021 and 2022).

Results from the linear regression analysis showed that total annual offtake increased linearly with total annual herbaceous production in GRCA but decreased linearly in KNF ($\beta_{GRCA}=0.808$; $\beta_{KNF}=-0.017$) indicating a stronger positive relationship between herbaceous offtake and productivity of grazed plots in GRCA (Figure 5). Approximately 90.4% of the variance could be explained by the GRCA linear regression model, with little variation explained within KNF (0.08%) (Figure 5).

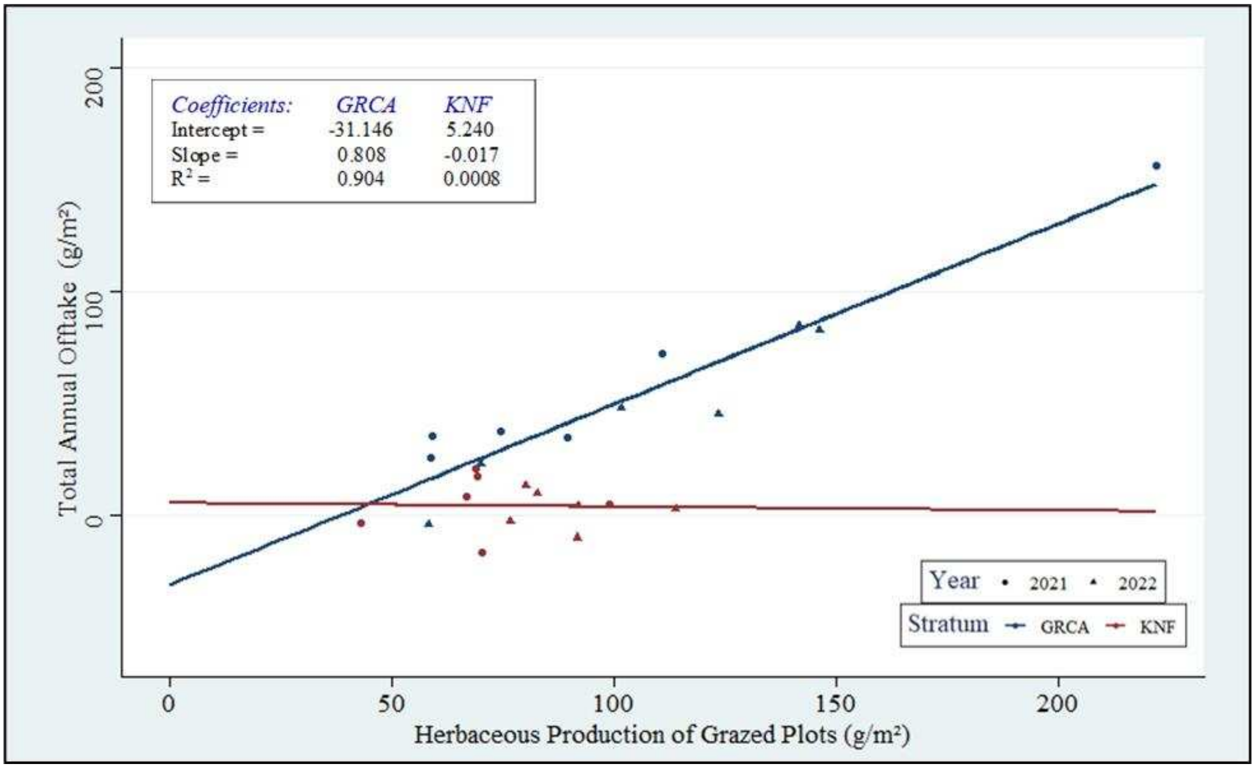


Figure 5. Results from the linear regression analysis demonstrating the relationship between annual herbaceous production of grazed treatments (ANPPg) and total annual offtake (Ot) measured in g/m^2 in Grand Canyon National Park (GRCA) and Kaibab National Forest (KNF) during 2021 and 2022, including regression coefficients. The blue line represents the slope of the relationship in GRCA and the slope in red line represents to relationship in KNF. R^2 values represent the proportion of variance in productivity explained by offtake, where this variation is 90.4% explained in GRCA but 0.08% explained in KNF. The slopes of this graph demonstrate a positive linear relationship with total annual offtake and annual grazed production in GRCA, but little to no relationship in KNF.

Weather Stations

Supplemental Climate Data - Daymet

Results from linear models comparing precipitation values from each data source (Daymet vs. Hoboware) provided minimal evidence that Daymet could accurately predict Hoboware winter month precipitation (β_{winter}=0.0579, R^2=0.0144) (Appendix A: Figure A1); however, stronger predictive ability was observed from the linear model for spring (β_{spring}=1.4265, R^2=0.557) (Appendix A: Figure A2) and summer precipitation (β_{summer}=1.2653, R^2=0.363) (Appendix A: Figure A3).

Results from the paired t-test provided evidence that Daymet produced significantly higher precipitation values during winter (t=-2.8844, df=54, p=0.005) with an estimated increase of 21.7mm compared to Hoboware. Spring values were nearly identical (t=1.6493, df=40, p=0.1096) and summer values were estimated to be 44.75mm lower from Daymet than Hoboware (t=7.301, df=41, p<0.001).

Although the proportion of variance in Hoboware values was only somewhat explained by Daymet values (based on spring R^2=0.557 and summer R^2=0.3629), I used these models to predict monthly summed precipitation values when Hoboware data were missing during any spring and summer months. The regression coefficients that I extracted from the spring and summer linear models were used in a predictive equation, which is provided in Appendix A: Tables A2 and A3. Given that the winter linear model provided weak predictive ability (R^2=0.014), but indicated significantly higher Daymet estimates for winter precipitation, I concluded that the Hoboware stations were insufficient at capturing precipitation in the form of snow compared to rain. Thus, I used raw Daymet values to replace all winter precipitation values collected from the Hoboware stations.

Results from the linear models comparing Daymet and Hoboware values for daily temperatures indicated that daily minimum temperatures ($\beta_{minimum}$=0.97323 (±0.01546), and R^2=0.7462) and daily maximum temperatures ($\beta_{maximum}$=0.94841 (±0.003652), and R^2=0.9804) had strong predictive power. With this strong predictive power, I extracted regression coefficients from the linear model for each minimum and maximum temperature to fill in any gaps in my Hoboware temperature data (Appendix A: Figures A4 and A5).

Precipitation

Total annual precipitation ranged from 452.0mm to 769.8mm in 2021 and from 545.2mm to 800.3mm in 2022 (Table 5) and was significantly greater in 2022 during all temporal windows except spring but including total annual precipitation (*p*=<0.0001; Table 7). Spatial differences in precipitation were observed, where KNF showed higher precipitation during summer and total annual windows (*p*=0.022 and *p*=0.023, respectively; Table 7).

Table 5. Precipitation values (in mm) where winter values are a summation of raw Daymet values, spring and summer are a summation of Hoboware values, and in any case of missing data, winter raw values were used, and spring/summer predicted values were used.

Site	*Year*	*Winter Precip. (Oct.-March)*	*Spring Precip. (April-June)*	*Summer Precip. (July-Sept.)*	*Total Annual Precip.*
1	2021	198.3	20.6	240.6	459.6
	2022	278.5	26.9	239.6	545.1
2	2021	197.5	20.6	243.7	461.7
	2022	281.3	28.2	241.0	550.6
3	2021	199.3	20.4	243.8	463.5
	2022	277.5	37.1	456.5	771.1
4	2021	189.6	20.3	245.0	454.8
	2022	300.2	38.5	299.3	638.0
5	2021	188.7	20.1	243.3	452.1
	2022	261.2	20.6	300.6	582.3
6	2021	202.1	45.5	240.6	488.1
	2022	329.5	44.9	295.0	669.3
7	2021	191.9	18.1	248.0	458.0
	2022	282.4	18.3	373.0	673.6
8	2021	201.1	25.5	310.6	537.3
	2022	331.3	20.8	342.8	694.9
9	2021	187.4	99.6	282.7	569.7
	2022	317.1	27.7	352.7	697.5
10	2021	194.0	184.9	391.0	769.8
	2022	324.3	42.2	433.9	800.3
11	2021	198.1	20.3	248.7	467.1
	2022	271.0	21.1	304.0	596.0
12	2021	202.1	20.3	240.6	463.0
	2022	321.9	40.6	305.6	668.0

Temperature and Growing Degree Days

Total annual GDD ranged from 2,544.97 to 3,071.62 in 2021 and from 1,917.40 to 2,272 in 2022 (Table 6). ANOVA results indicated significantly higher GDD in 2021 compared to 2022, where total annual GDD values were estimated to be 414.4 GDD units higher in 2021 compared to 2022 (all $p<0.0001$) (Table 7). No evidence of a spatial difference in GDD values was observed for any temporal windows when comparing stratum (all $p\geq0.7866$) (Table 7).

Table 6. Results from Growing Degree Day calculations during the annual herbaceous growing season (April through September) for each site (1-12) and year (2021 and 2022). Using the Average Method, daily maximum and minimum temperatures (°C) were used in a calculation that produces a temperature threshold relative to temperature conditions suitable for plant growth and respiration.

Site	*Year*	*Spring GDD (Apr.-June)*	*Summer GDD (July-Sept.)*	*Cumulative Annual GDD*
1	2021	1,179.86	1,365.11	2,544.97
	2022	691.22	1,226.18	1,917.40
2	2021	1,188.26	1,646.08	2,834.34
	2022	819.17	1,246.67	2,065.84
3	2021	1,182.31	1,639.93	2,822.24
	2022	795.61	1,210.08	2,005.69
4	2021	1,128.25	1,588.39	2,716.64
	2022	1,092.65	1,546.13	2,638.79
5	2021	1,296.61	1,775.02	3,071.62
	2022	884.15	1,289.85	2,174.00
6	2021	1,163.54	1,619.66	2,783.20
	2022	861.48	1,148.70	2,010.18
7	2021	1,178.13	1,648.18	2,826.31
	2022	790.74	1,198.98	1,989.72
8	2021	1,186.55	1,643.10	2,829.66
	2022	789.73	1,185.83	1,975.56
9	2021	1,267.74	1,728.04	2,995.78
	2022	899.09	1,372.90	2,271.99
10	2021	1,187.63	1,645.35	2,832.98
	2022	813.62	1,286.64	2,100.26
11	2021	1,194.62	1,652.04	2,846.66
	2022	801.65	1,171.63	1,973.28
12	2021	1,014.48	1,470.46	2,484.94
	2022	981.048	1,426.34	2,407.39

Table 7. Mean values (±1 SE) for measured climate variables for temperature and precipitation. Each climate variable were categorized by season based on plant phenology in this study area associated with temporal changes throughout the year. Precipitation is measured in millimeters and temperature (demonstrated by Growing Degree Days) is measured in °C. The table includes results from ANOVA comparison to test the difference between year and stratum for each climate variable.

Mean values (±1SE)				
Climate Variable	Year		Stratum	
	2021	2022	GRCA	KNF
Precipitation (mm)				
Winter	195.84 (1.07)	297.99 (5.09)	241.97 (10.1)	251.87 (12.2)
p-value	<0.0001**		0.5385	
Spring	43.01 (10.0)	30.56 (1.91)	28.62 (2.02)	44.95 (9.9)
p-value	0.2349		0.1188	
Summer	264.87 (9.0)	325.46 (13.9)	274.08 (12.5)	361.25 (12.6)
p-value	0.0007*		0.02171*	
Total Annual	503.72 (18.3)	654.8 (16.8)	542.25 (20.7)	616.26 (23.8)
p-value	<0.0001**		0.02321*	
Temperature (GDD)				
Spring	1180.66 (13.7)	851.68 (20.8)	1023.59 (39.8)	1008.75 (37.7)
p-value	<0.0001**		0.7866	
Summer	1618.45 (21.5)	1275.83 (23.6)	1441.82 (43.0)	1452.46 (41.6)
p-value	<0.0001**		0.8595	
Total Annual	2799.11 (32.4)	2127.51 (42.8)	2465.41 (80.6)	2461.21 (78.7)
p-value	<0.0001**		0.9704	

Percent Ground Cover

ANOVA results indicated that there was no difference in the proportion of cover classes between treatments the effect of year and sampling season varied depending on cover class; however, each cover class was significantly different between strata (Table 8; Figure 6). In 2021, relative ground cover exhibited lower percent cover of graminoids (*p*<0.001), and higher percent cover of litter (*p*<0.001) and bare ground (*p*=0.0266) overall, whereas no difference was found between years relative to forb coverage. Seasonal differences in ground cover was observed by the lower cover of graminoids (*p*=0.0036) but higher cover of litter (*p*<0.001) in summer, whereas no difference in forbs or bare ground was observed between seasons. When comparing ground coverage classes between strata (Figure 6), sites within GRCA supported higher relative coverage of forbs and bare ground (*p*<0.0001), whereas sites within KNF supported higher relative coverage of graminoids and litter (*p*<0.0001) (Table 8; Figure 6).

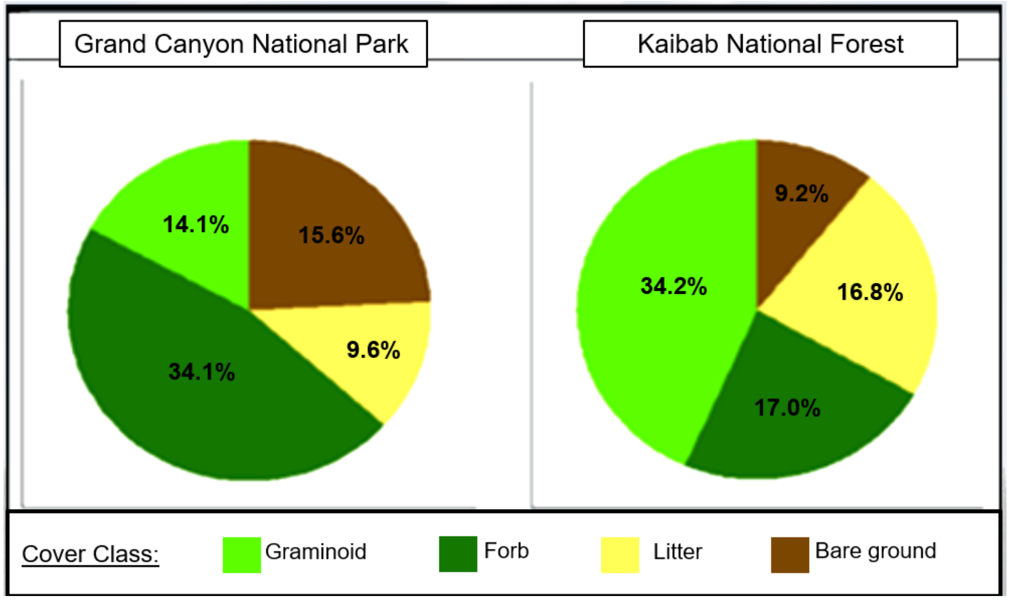


Figure 6. Total percentage of each ground cover class (pooled by treatment since no statistical difference was found between treatment) from Grand Canyon National Park (left) and Kaibab National Forest (right) averaged across all sites for all sampling occasions during 2021 and 2022 (n=120 observation per cover class).

Table 8. Average percent of ground cover (and standard errors) of Graminoids, Forbs, Litter, and Bare ground compared between year (2021 vs. 2022), season (summer vs. fall), stratum (Grand Canyon National Park vs. Kaibab National Forest), and treatment (grazed vs. exclosure plot) and their respective p-values obtained by the ANOVA comparison.

Average % Ground Cover (±1SE)								
	Year		Season		Stratum		Treatment	
Cover Class	2021	2022	Summer	Fall	GRCA	KNF	Grazed	Exclosure
Graminoids	21.3% (1.25)	27.0% (1.25)	22.1% (1.22)	26.2% (1.30)	14.1% (0.92)	34.2% (1.23)	23.3% (1.23)	25.0% (1.03)
p-value	<0.001**		0.0036*		<0.001**		0.1758	
Forbs	26.2% (1.08)	24.8% (1.07)	25.6% (1.08)	25.5% (1.07)	34.1% (1.09)	17.0% (0.71)	25.9% (1.03)	25.2% (1.12)
p-value	0.2764		0.9720		<0.001**		0.5720	
Litter	15.8% (1.06)	10.6% (0.77)	15.5% (0.97)	10.9% (0.88)	9.62% (0.80)	16.8% (1.01)	13.4% (0.95)	13.0% (0.93)
p-value	<0.001**		<0.001**		<0.001**		0.8778	
Bare ground	9.73% (0.92)	15.1% (1.25)	14.1% (1.24)	10.7% (0.95)	15.6% (1.22)	9.20% (0.94)	12.9% (1.15)	11.9% (1.07)
p-value	0.0266*		0.0939		<0.001**		0.6101	

Wildlife Sensing Camera Traps

Although all twelve motion triggered wildlife cameras were deployed during winter of 2020 at each site, several issues including user error, lost or stolen cameras, and device malfunction resulted in several gaps in camera trap data from the time of initial deployment to the time of camera collection at the completion of the study. The table below (Table 9) summarizes the number of days throughout each year and from each site that cameras successfully operated and captured herbivore presence.

Table 9. Wildlife camera trap results from 2021 and 2022 for each site including total number of camera days, number of days bison were captured, number of days cattle were captured, and the proportion of days an herbivore was captured (% Bison Days and % Cattle Days).

Remote Wildlife Camera Days and Herbivores Captured											
Year	2021						2022				
Stratum	Site	Total Camera Days	No. Bison Days	% Bison Days	No. Cattle Days	% Cattle Days	Total Camera Days	No. Bison Days	% Bison Days	No. Cattle Days	% Cattle Days
Grand Canyon National Park	1	60	12	20.00%	0	0.00%	90	16	17.78%	0	0.00%
	2	100	20	20.00%	0	0.00%	28	19	67.86%	0	0.00%
	3	24	4	16.67%	0	0.00%	91	1	1.10%	0	0.00%
	4	24	6	25.00%	0	0.00%	18	8	44.44%	0	0.00%
	5	62	12	19.35%	0	0.00%	122	35	28.69%	0	0.00%
	6	100	15	15.00%	0	0.00%	112	4	3.57%	0	0.00%
Kaibab National Forest	7	62	0	0.00%	0	0.00%	41	0	0.00%	1	2.44%
	8	140	0	0.00%	1	0.71%	114	0	0.00%	14	12.28%
	9	121	0	0.00%	2	1.65%	91	0	0.00%	3	3.30%
	10	100	7	7.00%	0	0.00%	142	0	0.00%	0	0.00%
	11	121	0	0.00%	0	0.00%	140	0	0.00%	0	0.00%
	12	120	8	6.67%	0	0.00%	122	4	3.28%	0	0.00%

Wildlife cameras recorded the highest proportions of bison trap days at sites within GRCA during my study, with no evidence of cattle at any sites within GRCA in 2021 or 2022 (Table 9; Figure 7). On average, the highest proportion of bison trap days within GRCA were observed at sites 4 and 5 (both within the Basin meadow) and the lowest average bison trap days were recorded at GRCA site 3 (lower Little Park) (Figure 7). Camera traps also detected minor bison presence in KNF during both years at the sites 10 and 12. During the study, low proportions of cattle (≤7%) were captured at three sites within KNF sites 7, 8, and 9 (Figure 7).

Results from wildlife camera traps showed that bison rarely (if at all) occupied my study area during winter months. The cameras detected that bison left the study area in December of 2020, returning to the study area in April of 2021. In 2021, bison remained within my study area until December of 2021 and returned to the study area again in April of 2022. Since cameras were removed from the study area in September of 2022, I relied on internal NPS/USGS monthly bison location maps (*unpublished data*) to determine that bison left the study area in December of 2022.

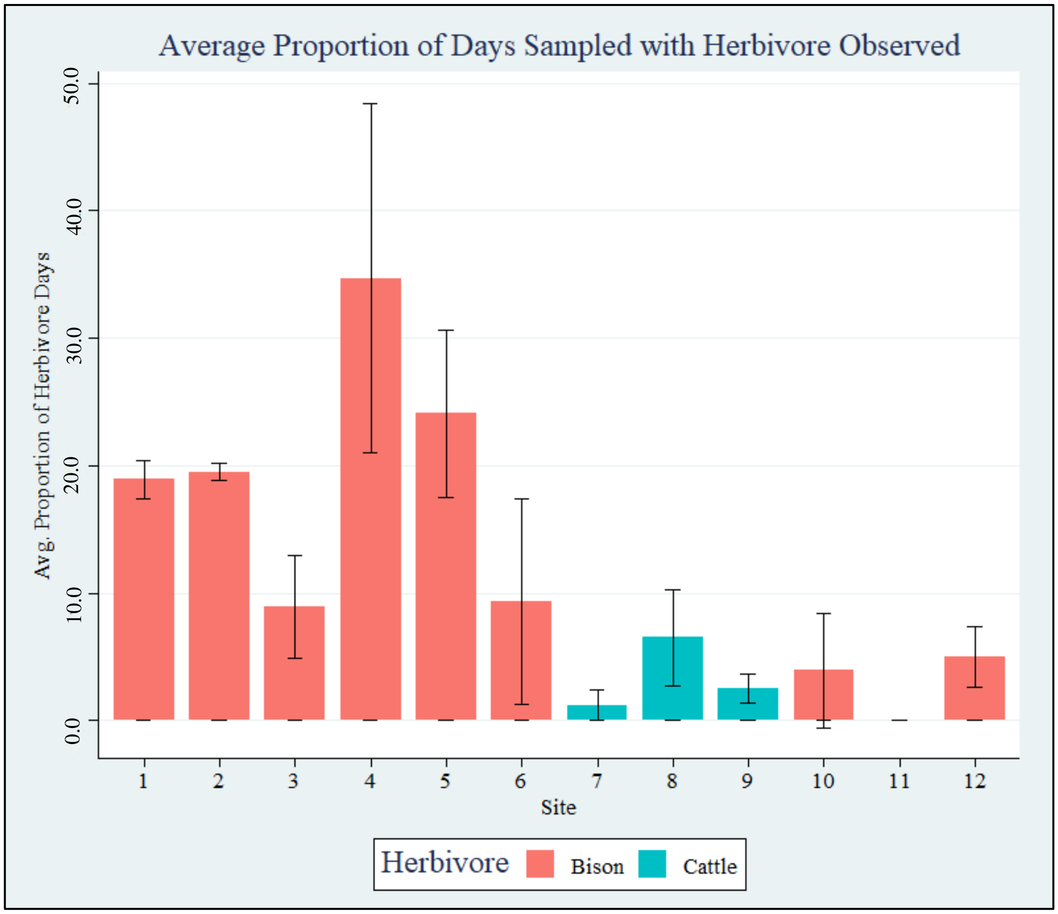


Figure 7. The Average proportion of days sampled between 2021 and 2022 (±1SE) via motion triggered wildlife cameras that bison or cattle were observed at each site. Sites 1-6 within Grand Canyon National Park show high proportions of bison observations and sites 7-12 within Kaibab National Forest show minimal observations of bison or cattle.

Linear Mixed Model

The Base Model suggested annual herbaceous production varied depending on treatment (p=0.00577) and year (p<0.01); however, was not influenced by stratum (p=0.5472), nor was there evidence of a significant interaction between stratum and treatment (p=0.0724). Since little to no bison grazing occurs in KNF, there was little if any 'treatment' effect in KNF, which may have led to the insignificance of stratum on ANPP in the linear mixed model. To evaluate this potential discrepancy, I re-fit the Base Model to parse out ANPP values by stratum, and ran separate, individual model analyses to determine whether the effect of treatment (grazed vs. exclosure) was only detectable in areas with bison grazing (GRCA).

When considering only GRCA sites, treatment had a significant effect on herbaceous production, where ANPP was significantly higher (p=0.0211) in grazed treatment plots compared to exclosure treatment plots. Evidence for a significant difference in ANPP between years was no longer apparent in GRCA (p=0.2531). In contrast, the model that included only KNF sites indicated that differenced in ANPP between treatment was no longer significant (p=0.6833); however, year was significant (p=0.0023). Parsing out areas of high bison grazing (GRCA) from low to no bison grazing (KNF) and running separate models suggested that the effect of treatment and year were likely influenced by the lack of grazing in "grazed" treatment plots in KNF, and the relationship among year and treatment were in fact dependent on stratum. Additionally, site was included in the mixed model and although each site produced unique intercept values, my small sample size caused limitations in the number of covariates I could include in each candidate model without inducing overparametization. When intercept values were averaged across all sites, they equaled to 0 and were thus removed as a covariate in the Base Model as well as any candidate model.

Candidate Model Selection

With a small sample size of n=48 observations of ANPP, I reduced the Base Model and individually added environmental covariates to produce a set of candidate models, which were used to evaluate and make inference regarding which factors were most influential in affecting the spatiotemporal variability in aboveground herbaceous productivity during my study. Repetitive or unnecessary covariates in candidate models were removed to avoid overparametization and increase potential model predictability. Year was removed in any candidate model that also included a climate variable since all climate variables represent measurements over time and intrinsically would account for changes between years. Additionally, the negligible use of bison grazing occurring in KNF grazed treatments contrasts the strong treatment effect apparent in GRCA; thus, adding stratum may add more variation, obscure the accuracy of parameter estimates, and reduce predictive ability. Consequently, some candidate models were constructed without stratum included as a predictor variable since treatment was better able to ascertain grazing effects on ANPP. Lastly, if no significant interactions were found ($p \geq 0.05$) between variables, models were reduced and re-fit without interactions.

The table below (Table 10) offers a summary of the Base Mixed Model (denoted by *italicization*) as well as the top three most competitive candidate mixed models. A full table including results from all 17 constructed candidate models is provided in Appendix C. The top model affirming change in ANPP included treatment, spring growing degree days, and soil ammonium, though two other candidate models were competitive ($\Delta_i \, AIC_c \leq 2$) (Table 10). Table 11 shows the top candidate models and their relative relationship with ANPP (as described by the beta estimates/slopes). Methods on data collection and analysis for covariates related to soil nutrients are provided in the following chapter (Chapter 3).

Table 10. Summary of the top 3 candidate models and The Base Model, which is represented by italicization. Note: K= the total number of estimable parameters; log-likelihoods= natural logarithm of the maximum likelihood for model i; AIC_c= the information "score" of model i given a small sample size; (Δ_i AIC_c)= [AIC_c – min(AIC_c)]; w_i (Akaike weights)= probability that the sum of individual covariates in model i represent the best fit model. The top model is demonstrated by Δ_i AIC_c= 0.0 and the highest w_i value of 0.36.

Candidate Models - with environmental covariates					
Model	**K**	**log-Likelihood**	**AIC_c**	**Δ_i AIC_c**	**w_i**
Trt+spring_GDD+NH4	6	-2.69	19.42	0.00	0.36
Trt+spring_GDD+Total_N	6	-3.31	20.67	1.25	0.19
Trt+Stratum+spring_GDD+NH4	7	-2.21	21.22	1.81	0.14
*Trt*Stratum+Year*	7	-5.81	28.41	8.99	0.00

Table 11. Parameter estimates (±1SE) for the top 3 candidate models and the reduced Base Model (denoted by italicization), including the environmental covariates that were the most influential in explaining variation in aboveground production in addition to the covariates that describe experimental design (as demonstrated in the Base Model). Note: Trt= Treatment; Stratum= Grand Canyon National Park vs. Kaibab National Forest; spring_GDD= cumulative GDD during spring months; NH4= soil available ammonium concentration (µg/cm^2); Total_N= the sum of soil ammonium and soil nitrate concentration (µg/cm^2).

Model	Parameter values (±1SE)							
	β_0	β_{Trt}	$\beta_{Stratum}$	β_{Year}	$\beta_{Trt*Startum}$	β_{spring_GDD}	β_{NH4}	β_{Total_N}
Trt+spring_GDD+NH4	5.2910 (±0.20)	-0.1675 (±0.06)	NA	NA	NA	-0.0007 (±0.0002)	-0.0084 (±0.0036)	NA
Trt+spring_GDD+Total_N	5.2992 (±0.21)	-0.1028 (±0.06)	NA	NA	NA	-0.0007 (±0.0001)	NA	-0.0024 (±0.001)
Trt+Stratum+spring_GDD+NH4	5.3766 (±0.22)	-0.1690 (±0.06)	-0.1507 (±0.15)	NA	NA	-0.0007 (±0.0001)	-0.0089 (±0.004)	NA
*Trt*Stratum+Year*	4.4721 (±0.13)	-0.2587 (±0.09)	-0.2142 (±0.17)	0.1803 (±0.06)	0.2306 (±0.12)	NA	NA	NA

Discussion

Bison herbivory dynamics varied across the landscape but appeared to influence various aspects of grassland vegetation function based on analysis of herbaceous production, offtake, grazing intensity, and percent ground cover. I found that the effect of herbaceous offtake by bison herbivory had a positive, linear effect on herbaceous production in my study. Overall, total annual offtake and grazing intensity were 53.39g/m^2 and 46.20% (respectively) in GRCA, compared to 3.88g/m^2 and 4.90% (respectively) in KNF (Table 4), equating to a 92.7% increase in total annual offtake and an 89.4% increase in grazing intensity in GRCA compared to KNF. Regardless of this stark difference between strata, the increased offtake in GRCA was associated with an average 24.9% increase in productivity values of grazed treatments compared to exclosure treatments, whereas no difference was found between treatments in KNF (Table 4). The consistently higher rates of ANPP within grazed treatment plots, particularly those in GRCA with higher offtake rates and grazing intensities, indicates that there is a positive relationship between ANPP and utilization. This provides evidence that grazed plants in this ecosystem have the capacity to not only tolerate but overcompensate for tissue damage from grazing defoliation.

When evaluating the range of grazing intensities that may have correlated with plant response throughout my study, I expected areas of intermediate grazing may response by over-compensation, based on the Grazing Optimization Hypothesis, predicts an increase in aboveground herbaceous productivity and overall vegetation biomass in plants that are grazed at intermediate intensities (McNaughton 1979). However, I observed a continuous increase in ANPP relative to herbaceous offtake, even at grazing intensity levels ranging from ~50-70% (Table 2) and a decline in herbaceous production relative to increased herbaceous offtake was never observed (Figure 5). Interestingly, the highest ANPP$_g$ values were found at the two sites that experienced the highest total offtake values (sites 4 and 5; Table 2), suggesting that grazing pressure even at these relatively high levels that occurred were not detrimental to herbaceous production during my study.

Additionally, the Compensatory Continuum Hypothesis states that a plants response to disturbance falls along a continuum of responses based on myriad abiotic and biotic factors in addition to grazing, but a plants tolerance to herbivory defoliation (both at the species and landscape scale) is predicted to be higher in systems with high resource availability (Maschinski and Whitman 1989). However, I found that grazing enhanced grassland site productivity regardless of grazing intensities, and despite below-average precipitation. My study recorded a total annual precipitation value that was 23.3% lower than the expected average (NPS 2023) were a 23.1% decline; however, reduced precipitation and increased grazing intensity did not appear to have a detrimental effect on herbaceous production. For example, the highest grazing intensities were observed in GRCA in 2021; 65.0% and 70.4%, and were associated with 34.8% and 47.7% enhanced ANPP, respectively (Table 2).

The positive relationship between offtake and productivity suggests that an increase in utilization is related to an increase in productivity, and an increase in productivity is related to an increase in utilization. When evaluating the production-offtake relationship, it was apparent that total annual offtake was higher in areas with higher herbaceous production, and the degree of this relationship was really an effect of the presence of grazing (Figure 5). For example, there was a positive relationship between O_t and $ANPP_g$ in GRCA (β_{GRCA}=0.808) with higher offtake rates, but little to no relationship was observed in KNF (β_{KNF}=-0.017), where bison grazing (or utilization) was minimal (Figure 5). Evaluation of the relationship between offtake and productivity provides further evidence that grazed plant either tolerated or overcompensated for defoliation.

Other studies using a similar ungulate herbivore experimental exclusion design have found a positive effect of herbivory offtake on grassland production. This has been shown in the East African savannah (McNaughton 1979, Augustine et al. 2003), Yellowstone National Park (YNP) in Wyoming (Frank and McNaughton 1993, Frank et al. 2002, Frank et al. 2016), and in Great Sand Dunes National Park (GRSA) in Colorado (Schoenecker et al. 2022). Among the first instances of ungulate-enhanced herbaceous production were observed in East Africa, where wildebeest, zebra, and antelope were found to increase production two-fold in areas of intermediate grazing (GI= 25-50%) and sufficient moisture (McNaughton 1979, 1985). Results found in the temperate grasslands of YNP indicated that measurements of production in areas of abundant bison and elk grazing increased ANPP by 43% in 1989 (Frank et al. 1989), 47% in 1993 (Frank and McNaughton 1993), 22% in 2001 (Frank et al. 2002), and by 34% in 2016 (Frank et al. 2016), in which the additive effect of grazing plus moisture availability on plant response varied among these studies. In the 2016 study in YNP, researchers found that herbaceous biomass increased by 34% and peaked at a grazing intensity of 40% before declining. These studies evaluating the positive ungulate consumption-ANPP relationship found in global grasslands commonly observed peak production at intermediate grazing intensities, which was not observed in my study. More comparable results were found in the semi-arid grasslands of GRSA, where Schoenecker et al. (2022) observed a similar capacity for grazed plants to overcompensate for herbivory damage regardless of the level of grazing intensity. However, the ability for grazed plants to overcompensate for defoliation was dependent on soil moisture in that system (Schoenecker et al. 2022).

Precipitation has been shown to largely control the spatiotemporal variation in grassland productivity across landscapes (Henry et al. 2018). The weather stations I deployed throughout my study area allowed me to estimate potential spatial variability, or patchiness, in precipitation. When precipitation values from this study were compared to historic GRCA precipitation records, I found that values were below the expected average (23.23% lower) in 2021 but were similar in 2022 (NPS 2023). During my study, total annual precipitation was higher in 2022 compared to 2021 and higher in KNF compared to GRCA (Table 7). It was expected that this temporal and spatial variability in precipitation may, in part, explain variability in ANPP; however, despite evidence of significantly higher annual precipitation in 2022, no difference was found in the average $ANPP_g$ or $ANPP_{ug}$ for either stratum between 2021 and 2022 (Table 6). Additionally, despite higher annual precipitation throughout KNF sites (Table 6), my results show overall higher rates of productivity in GRCA (Table 4). It is possible that precipitation was less of a driving factor in ANPP during this study compared to other factors such as grazing intensity, temperature, or soil nutrient availability.

When comparing differences in relative percent ground cover between stratum, analysis revealed significantly higher percent cover of forbs and bare ground in GRCA but higher graminoids and litter in KNF. On average, GRCA sites supported approximately 50.1% higher percent cover of forbs and 41.0% higher bare ground coverage when compared to KNF; however, on average, KNF sites supported 58.8% higher percent cover of graminoids and 42.7% higher litter coverage (Table 8; Figure 6). The differences in the ground cover of forbs and graminoids found between stratum in my study were consistent with the "Preliminary Grassland Study" conducted in 2019, which also found a greater proportion of forbs in GRCA and graminoids in KNF when cover classes were compared between strata. This finding is consistent with observations found throughout bison exclusion experiments conducted in the Konza Prairie in Kansas, where a higher coverage of forbs and a lower coverage of graminoids were observed in grazed meadows compared to exclosed meadows following a six year bison exclusion experiment (Catchpole 1996).

In 1962, a vegetation ground cover experiment was conducted throughout meadows of North Rim, GRCA and KNF in some of the very meadows that I conducted my research using similar estimation techniques. This provided an opportunity to compare my results (post-sustained bison occupancy) to percent ground cover conditions recorded prior to the sustained occupancy of bison. In all North Rim meadows, Merkle (1962) reported that average total vegetation coverage (graminoids plus forbs) was 42% and bare ground constituted an average of 50% or greater. During my study, average total vegetation coverage (graminoids plus forbs) was 48.2% and bare ground averaged at only 15.6% across North Rim meadows (Table 8). This comparison of ground coverage overtime suggests that that bare ground coverage has been reduced in GRCA meadows within my study area since 1962, and were likely not caused by bison, but rather, were pre-existing and may be better explained by other factors such as the legacy of grazing in this ecosystem or other variables I did not measure.

In my study, the average total vegetation coverage (graminoids plus forbs) was similar between stratum (GRCA=48.2% and KNF=51.2%); however, there was an observed shift in the dominance of forbs in the presence of herbivory versus dominance of graminoids in areas void of herbivory. The increase in overall percent forb cover in GRCA provides evidence of preferential selection of graminoids and purposeful avoidance of forbs, suggesting that bison grazing may have altered plant community composition. However, localized patches of forbs have been attributed to maintaining higher levels of biotic diversity and are considered an important component of grasslands (Knapp et al. 1999). My results of percent ground cover also revealed higher overall coverage of litter in KNF, which also exhibited lower ANPP values, which may be partially explained by the absence of grazing, such that an accumulation of litter has been found to inhibit aboveground primary production, likely caused by a shading or "litter-choking" effect that limit vegetation growth and photosynthetic capacity (Knapp and Seastedt 1986). Since bison herbivory appears to reduce presence of litter this may contribute to the higher levels of ANPP in areas that have bison grazing.

It should be noted that the ocular estimation technique utilized for vegetation ground cover analysis has its limitations as it is not a precise measurement. Studies that have tested the repeatability of this method show variability under in results based on factors such as plant structural traits, and observer bias and ability (Daubenmire 1959, Mueller-Dombois and Ellenberg 1974, Jukola-Sulonen and Salemaa 1985, Elzinga et al. 1998, McCune and Grace 2002). However, information obtained from the ground cover analysis provide useful information that can also be used to evaluate potential indirect effects of bison herbivory on grassland structure, and this information can be useful future research on grassland ground cover in this ecosystem. The proximity in time in which herbivore exclosures were constructed relative to my measurements of percent ground coverage months revealed no significant differences in any cover class between treatments during the duration of this research (Table 8). However, these long-term herbivore exclosures provide an opportunity to evaluate future changes in ground overage and grassland structure over time, especially if bison are to persist on this landscape.

Linear Mixed Modelling allowed me to determine which predictor variables were more influential in explaining variability in ANPP during my study. The Base Model provided additional evidence that bison grazing (as demonstrated by the treatment main effect) was a strong predictor variable that explains the variation in aboveground herbaceous production values across the landscape (Table 10). When I considered other environmental factors that could influence aboveground herbaceous production based on the renditions of the Base Model, such as climate and soil nutrients, I found that the addition of spring growing degree days and available soil ammonium best explained variation in productivity (Table 10). [Note that Chapter 3 will discuss in detail the methods for data collection and analysis regarding soil nutrient data]. Nonetheless, I move on in the interpretation of my top ranked candidate models to determine which environmental covariates provided the best explanation for variation in herbaceous production.

Justification in the top model is provided by AIC, and although the second and third ranked models were competitive, they were effectively subsets of the top model. Model 2 simply replaces soil ammonium with total belowground nitrogen (Total N), which represents the sum of ammonium soil nitrate. However, when soil nitrate and ammonium were added separately to the Base Model, nitrate availability showed little to no effect whereas ammonium exhibited a strong effect, indicating that Total N is largely influenced by the effect of ammonium. Model 3 simply included stratum; however, the lack of grazing in KNF grazed treatment plots resulted in a negligible treatment effect, obscuring the realized effect of bison grazing treatment in GRCA. In summary, I found that the inclusion of covariates explaining the structural design of the experiment (treatment and startum) in addition to spring growing degree days and belowground nitrogen (particularly ammonium) best explain variability in ANPP based on the accumulated Akaike weights of 0.69 (Table 10).

Since grassland plants generally reflect their greatest growth potential when cold temperatures shift to warmer temperatures in spring (Wingler and Hennessy 2016), it was expected that higher values for spring Growing Degree Days would increase ANPP; however, I found a slightly negative response in ANNP to an increase in spring GDD (β_{sp_GDD}= -0.0007±

0.0001) (Table 11). This relationship could inversely be interpreted as: higher temperatures may inhibit productivity, particularly in the spring. Our findings contrast the large body of literature regarding the relationship between temperature and grassland productivity in that temperatures below thermal optimums are typically associated with inhibited plant growth (Hochachka and Somero 2002, Sage and Kubien 2007, Wingler and Hennessy 2016). The relationship found in my study may be explained (in part) by the dominance of cool-season C_3 plants in my study area (Rink et al. 2020), that grow best in colder temperatures, particularly during spring (Milchunas 2006). With the dominance of C_3, it is possible that herbaceous production is limited by warmer spring temperatures. Our results are substantiated by findings across various grassland types, including arid and semi-arid ecosystems, where an increase in growing degree days is associated with a decrease in C_3 plant production (French 1979). Many plant species can physiologically adapt to changes in preferred growth temperatures (Atkin et al. 2006); however, fluctuations in temperature can influence competition between C_3 and C_4 plants (von Fisher et al. 2008), which has been found to induce shifts between C_3 and C_4 dominance (Sage and Kubien 2007) in grasslands throughout North America (Teeri and Stowe 1976, Epstein et al. 1997, Ehleringer et al. 1997, Jump et al. 2006, Menzel et al. 2006, Mouthon and Daufrense 2006).

Spring growing degree days demonstrated a stronger influence than any precipitation covariate (as illustrated in the top mixed model), indicating that precipitation may not have as strong an effect as other study design elements or environmental variables. Although only two years of climate data were analyzed, temperature is a principal control over plant enzymatic function and overall productivity (Ehleringer et al. 1997) and these results provide important information about the potential effects of temperature may have on plant production in the Grand Canyon ecosystem.

My research, although only conducted over the duration of two years, provided insightful information regarding the factors that can influence grassland productivity and plant response to bison grazing. Empirical evidence suggests that dynamic grazing, sufficient environmental conditions (i.e., climate), and available resources (i.e., soil nutrients) can allow plants to overcompensate for herbivory damage and result in increased rates of productivity and an increase in overall biomass in semi-arid ecosystems like that of Grand Canyon (Schoenecker et al. 2022). Future long-term environmental monitoring would help researchers better understand the mechanisms that drive the physiological plant responses to bison grazing as well as other environmental changes. My research provides evidence that the grasslands of the Grand Canyon ecosystem exhibited enhanced productivity along a gradient of grazing and environmental conditions. It is my hope that my results will inform management practices that maximize grassland productivity while also sustaining bison populations.

CHAPTER 3: THE INTERACTIONS BETWEEN BISON AND SOIL DYNAMICS

Introduction

Soil is a dynamic natural resource (Blanco and Lal 2008), which is essential to sustain all life on Earth and is only renewable on centennial to millennial timescales (Parton et al. 1987). Soil is comprised of structural and functional properties that provide the environment for plant growth and the security of food, fuel, feed, and fiber (Blanco and Lal 2008). The belowground structural (i.e., aggregate stability, porosity) and functional (i.e., nutrient dynamics, microbial activity) properties of soil directly act on aboveground ecosystem processes such as primary productivity (Augustine and McNaughton 2006) and the dynamic interactions among the physical, chemical, and biological processes occurring both above and belowground effects the resiliency of grasslands to tolerate disturbance. However, this vital resource is susceptible to alterations in land-use practices including both human-induced and natural, environmental changes.

Grazing by large ungulate herbivores such as Plains bison has the capacity to alter various grassland soil properties and processes and the ability for soil (and consequently, plants) to tolerate these changes varies depending on interacting factors such as grazing intensity, climate conditions, resource availability, and plant tolerance (Blanco and Lal 2008, Gass and Binkley 2011, Schoenecker et al. 2022). The interaction of these factors dictates the direction and degree of soil and plant response, where herbivory effects on ecosystem properties can range along a continuum of degrade and enhancement (Maschinski and Whitman 1989). The outcome of herbivory-induced habitat alterations reflects the overall stability, resiliency, and sustainability of the grazing ecosystem. Thus, evaluating herbivore-soil-plant interactions is critical for researchers to understand how to maintain an equilibrium among herbivores, grassland soils, and the plants they support (Briske 1996).

Ungulate herbivory and associated behaviors (i.e., migration, trampling, wallowing) can have profound effects on the structural propoerties of soil including soil bulk density and porosity (Daniel et al. 2002), the proportion of vegetation versus bare ground (Blanco and Lal 2008), and the stability of soil aggregates (Seybold et al. 1999). These physical alterations in turn effect properties and processes required for plant growth (Niell 1979), including water holding capacity (Chirwa et al. 2004), nutrient availability (Sparling et al. 2003, Bremer and Ellert 2004), and rooting success (Tian et al. 2000, Akhter et al. 2004). Many propoerties of soil act as indicators for soil and grassland health; however, aggregate stability has been widely recognized as one of the key indicators influencing soil health in grasslands including grazing ecosystems (Seybold et al. 1999).

Soil aggregate stability is a critical component of soil health and stability as it provides a measure of the soil's capacity to withstand erosion (Pierson and Blackburn 1994), which in turn reflects overall ecosystem sustainability (Blanco and Lal 2008). Stable aggregates fall within a range of values relative to their size in diameter and is typically between 0.25mm (fine aggregates) and 2.0mm (coarse aggregates). Stable aggregates that fall within this range typically bind together to resist erosion. High proportions of stable aggregates indicate high quality soil structure, especially as reflected by having a diverse mixture of stable aggregate sizes that preform different soil ecosystem functions. For example, fine stable aggregates support water storage and retention, whereas coarser stable aggregates allow for enhanced water movement and aeration (Nimmo 2004, Six et al. 1998). The heterogenous space between stable aggregates also allows for a range of microhabitats in which a diversity of plants may establish (Tisdall et al. 1978, Tisdall 1996).

Light grazing has been found to promote the formation of coarse aggregates, which are more able to withstand erosion and allow for water infiltration compared to finer soil particles (Wang et al. 2020), even within semi-arid grassland ecosystems (Steffens et al. 2011). However, prolonged, heavy grazing can reduce soil stable aggregates and result in degraded aggregate stability and increased erosion (Seybold et al. 1999), especially in more arid ecosystems (Milchunas and Lauenroth 1993). Erosion can impair land productivity and further impact ecosystem services such as carbon sequestration, nutrient cycling, and water provisioning (Herrick and Whitford 1995), which are all crucial for ecosystem sustainability. Aggregate stability varies widely across a variety of temporal and spatial scales (Pierson et al. 1994) and soil types; however, an evaluation of potential variation in a particular region may provide insight into soil and grassland condition as it relates to ungulate herbivore activity (Herrick and Whitford 1995).

Along with ungulates potential effects on soil structural properties like aggregate stability, ungulates can also have significant effect on soils' functional properties such as ion exchange capacity (Bremer and Ellert 2004), biological and microbial activity (Wander et al. 1994, Sun et al. 2017), and decomposition rates (Tisdall 1996). These changes can manifest from direct habitat alterations such as deposition of fecal waste or can occur indirectly via the interactions among the physical, chemical, and biological properties of soils. There are various functional propoerties of soil that provide indication of ecosystem health and sustainability; however, plant growth capacity is largely determined by soil nutrient dynamics (Maschinski and Whitman 1989). Additionally, herbivore-plant-soil interactions are a critical factor driving the distribution, availability, and conservation of nutrients such as nitrogen and phosphorus within individual plants and across the landscape (Gibson et al. 1993, Hamilton and Frank 2001, Singer and Schoenecker 2001, Schoenecker et al. 2004, Blumenthal and Augustine 2009).

Nitrogen is a critical nutrient required for plant growth and the availability of nitrogen is directly related to soil structure and function and thus, grassland condition. Bison uptake (remove) nitrogen from the environment via consumption of relatively recalcitrant plant tissue and litter, while simultaneously depositing nitrogen back to the environment via nitrogen-rich urine and feces (Augustine and Frank 2001, Schoenecker et al. 2022). Plants and soil microbes uptake nitrogen from the soil in the form of ammonium (NH_4^+) or nitrate (NO_3^-) ions (Ricklefs et al. 2014) and bison waste (composed largely of urea) can be easily broken down (mineralized) to these ions at a faster rate than nitrogen turnover via plant litter decomposition (Reuss and McNaughton 1988). Therefore, bison contribute readily available, growth-limiting nutrients to plants and soil microbes in areas they utilize (Hamilton and Frank 2001, Singer and Schoenecker 2001, Hempson et al. 2015).

An increase in soil nitrogen has been found to mitigate the damaging effects of defoliation by herbivores (Wieder et al. 2015) and improve a plants ability to compensate for tissue damage in multiple ways (Maschinski and Whitman 1989, Schoenecker et al. 2022). Higher nitrogen turnover rates can also stimulate soil microbe activity in the rhizosphere (Hamilton and Frank 2001, Hempson et al. 2015). Enhanced plant nitrogen uptake during the growing season can lead to enhanced leaf tissue nitrogen in grazed plants, which allows for increased and prolonged photosynthetic activity and plant growth (Geremia et al. 2019). Since a scarcity of nitrogen often limits plant productivity (Ricklefs et al. 2014), and bison herbivory can alter nitrogen dynamics, it is important to understand how bison interact with grassland nitrogen cycling to determine the effects that large ungulates such as bison may exert on grasslands.

Soil phosphorus (P) is also a critical soil nutrient for its role in plant energy transfer (Baldarelli et al. 2021). As a critical element required for plants and microorganisms, phosphorus is closely tied to ecosystem functions such as nitrogen fixation, decomposition, and photosynthesis (Walker and Syers 1976, Delgado-Baquerizo et al. 2013). Phosphorus is mainly derived from the weathering of soils' parent material and its availability depends on soil pH (Frank 2008); however, phosphorus is often limited in most terrestrial ecosystems, especially grasslands (Lui et al. 2023). Empirical evaluations of herbivory's effect on phosphorus dynamics and its relationship with herbaceous plant productivity is lacking. Many studies have determined that the effect of grazing on phosphorus availability and plant uptake capacity is largely determined by microbial activity occurring in the rhizosphere (Lui et al. 2023). For example, grazing induces plants to release excess carbon to the rhizosphere, stimulating microbial and extracellular enzyme activity activities that regulate phosphorus transformations and plant nutrient uptake (Sun et al. 2017). The importance of microbial activity in nutrient cycling is relatively well documented; however, the relationship between grazing and the regulation of soil microbial communities is complex and still unclear.

The influx of available resources required for plant growth in labile forms of nitrogen (via bison waste) and the plants physiological pathway of nitrogen reallocation following defoliation can lead to an increase in aboveground net primary productivity (Frank and McNaughton 1993), resulting in higher biomass in grazed plants compared to plants that are void of grazing (Anderson and Briske 1995). When herbivory enhances nutrient cycling and productivity rates, this can enhance the quantity and quality of the vegetation biomass that directly supports those herbivore populations, resulting in a series of feedbacks referred to as the *accelerating effect* of herbivory (Singer and Schoenecker 2002, Blumenthal and Augustine 2009, Geremia et al. 2019). This is typically observed in ecosystems that have a relatively long co-evolutionary history that has resulted in plant tolerance adaptations. Alternatively, intense, prolonged, or highly selective herbivory in regions with little herbivory/disturbance history can deplete underground nutrient and biomass reserves past the point of tolerance. This can inhibit primary productivity, and consequently, herbivore populations, resulting in a *decelerating effect* of herbivory on ecosystem processes (Milchunas and Lauenroth 1993, Blumenthal and Augustine 2009) in which herbivory can cause long-term degradation of grassland soil and plant structure and function (Schoenecker et al. 2022).

It is likely that the relationship that bison have with belowground soil properties has profound effects on aboveground grassland properties such as productivity within the Grand Canyon ecosystem (Boyer 1982, Knapp and Smith 2001). Since plant response and tolerance capacity depends largely on resource availability (Maschinski and Whitman 1989), it is critical to evaluate how bison influence the plant-limiting growth resources such as nitrogen and phosphorus to determine whether grassland plants may be able to compensate for loss due to herbivory defoliation by facilitating growth. This evaluation may provide insight into the potential mechanisms that drive grassland patch utilization and migratory patterns of bison across the landscape and over time.

It was expected that differences in soil aggregate stability may not be evident between treatments since there was a negligible treatment time and effect; however, I predicted to observe differences between strata because of the relatively longer time frame of bison density differences between GRCA (high bison density) and KNF (low to no bison density). I predicted that soil aggregate stability would be influenced by bison utilization relative to stratum. However, the relationship between aggregate stability and herbaceous production is still unclear because little empirical evidence exists on this topic. Additionally, I expected enhanced soil nitrogen in areas frequented by bison, and that this enhanced nitrogen availability would improve plant nutrient uptake and its capacity to not only tolerate but overcompensate for tissue losses due to herbivory. It was expected that differences in ANPP across the landscape may partially be explained by the relative availability of soil nutrients, where an increase in soil nitrogen and phosphorus would have a positive relationship with ANPP and this relationship would depend on bison presence. Finally, I predicted that areas grazed by bison (treatment= grazed; stratum= GRCA) would exhibit higher aboveground nitrogen yield and higher total belowground nitrogen concentration due to the enhanced availability of nutrient supply from bison waste.

Methods

Study Design

A brief description of study design is provided here; however, the research conducted in this Chapter utilized the same overall study design, which is described in full detail in Chapter 2. This study defined two strata: GRCA (high bison density) and KNF (low to no bison density) and selected six sites within each strata of similar meadow habitat, for a total of twelve sites. Each site consisted of a meadow area large enough to establish two treatment plots: one 0.40-ha unfenced "grazed" treatment plot and an adjacent one 0.40-ha fully fenced "exclosure" treatment plot that was completely protected from bison. Five movable grazing cages (~1-m^2) were randomly installed throughout each grazed treatment, and measurements were taken using quadrat clipping rings (¼-m^2) placed inside cages, outside cages, and inside exclosures, representing subplots. Vegetation ground cover and biomass were measured in each subplot twice per year, and clipped biomass samples were dried and weighed. These weights were used in calculations of $ANPP_g$, $ANPP_{ug}$, O_t, and GI. These dried, weighed herbaceous biomass samples (separated by forbs and graminoids) were stored until Chapter 3 analysis was ready. Using this experimental exclusion design, I was able to assess bison effects on soil structural properties (aggregate stability) as well as soil functional properties (plant-soil interactions and plant nitrogen uptake).

Field Methodology and Data Collection

Soil Aggregate Stability and Soil Cores

To evaluate physical soil condition, I used an Impact Driven Soil Corer to extract six soil core samples from each treatment plot within each twelve sites (for a total of 144 soil core samples) to a depth of 10cm in the summer of 2021. I randomized locations for soil core collection within each treatment plot by using a randomly generated azimuth (0-160°C) and pacing forward whichever number the clocks second-hand lands on (0-60 seconds or steps). After collection, soil samples were stored in pre-labeled ziplock bags labelled with site name and number, treatment plot (grazed or exclosed), stratum, and date. Soil samples were preserved in a dark cooler and transported to the EcoCore lab at Colorado State University for processing of aggregate stability.

Soil Nutrient Availability and PRS Soil Probes

Western Agricultural ion-exchange membrane probes (IEM; Plant Root Simulator™-probes) were used to quantify potential differences in soil nutrient availability among sites and to account for baseline soil nutrient availability conditions prior to sampling. Each soil probe sample composed of one anion probe and one cation probe that was buried underground. The anion probe is a positively charged resin membrane that attracts and absorbs negatively charged ions such as nitrate and sulfate. The paired cation probe is a negatively charged membrane that attracts and absorbs positively charged ions such as phosphorus, magnesium, potassium and ammonium (Western Agricultural Innovations 2018). The absorption of anions and cations gives an index of the nutrients available to plants during the burial period (Hangs et al. 2004). This absorption is a function of the size of the nutrient pool and the rate of transformation of the element such as Nitrogen to its anion (i.e., NO_3^-) or cation (i.e., NH_4^+) form in which it is available for plant uptake. Thus, these measurements are important indications of nutrient supply rates and mineralization rates among sites (Millet and Edmunson 2015).

Six pairs of soil probes were deployed synchronously (using the random azimuth-hand watch technique) throughout each treatment plot in all twelve study sites (for a total of 144 soil probe pairs) by vertically inserting each membrane into the topsoil layer. Probes were buried in early May 2021 and remained buried for 8-weeks to capture sufficient ion activity. Soil probes were deployed in early spring to assess potential relationships with spring soil nutrient availability and ANPP, since burial prior to the period of rapid nutrient uptake by plants can provide a measure of the nutrient supply that is likely to influence plant growth (Western Agricultural Innovations 2018). Flagging tape was affixed to each soil probe for easier retrieval after the 8-weeks. After the 8-week burial period, soil probes were collected by hand, scrubbed with a brush, and washed with de-ionized water to dislodge any sediment from the resin membrane. Probes were placed in pre-labeled ziplock bags and kept moist and cool until being sent to ShangriLab (Moscow, Idaho) for processing.

Soil probes were deployed after exclosure construction and prior to the arrival of most bison in their summer range (my study area) in early spring 2021. Thus, grazing treatment had not taken effect. The information obtained from soil probe measurements was subsequently used to account for pre-existing soil nutrient availability and distribution as well as to provide information to assist in the evaluation of spatiotemporal variability in productivity measurements, which are described in detail in Chapter 2.

Aboveground Nitrogen in Plant Tissue

Aboveground herbaceous nitrogen content was measured using the clipped herbaceous biomass from ¼-m^2 circular quadrat clipping rings inside and outside of grazing cages. A detailed description of these methods can be found in Chapter 2.

Data Analysis

Soil Aggregate Stability and Soil Cores

Soil core samples were air dried and combined at EcoCore lab (CSU), representing a subsample of the soil throughout the entire treatment plot of each site. The combined samples from each treatment were then weighed to approximately 100.0g. Each soil sample was processed using a Yoder Apparatus (Yoder 1936), a machine which consists of a series of four different sized sieves stacked from smallest sieve size (0.25mm) on the bottom, to the largest (2.0mm) sieve on top. Each 100.0g soil sample was placed on the top 2.0mm sieve and the machine was turned on. The machine separated soil particle size classes from each sample by dipping the stack of sieves in a bucket of clean water for a total of 30 strokes or dips. Sieved soil samples were then removed from the water bucket, rinsed into pre-labelled tins, and placed in a drying oven until all water content was evaporated. Once completely dry, the total dry weight of the tray and soil were weighed. Each 100.0g sample was then passed through a final 2.0mm sieve to remove any rocks (soil particles >2.0mm in diameter). The remaining soil sample consisting of soil particles between 0.25mm and 2.0mm in size was considered the total water stable aggregates. Water stable aggregates were weighed a final time and divided by the initial weight of the soil sample (including rocks). The amount of water stable aggregates per sample was calculated as a proportion of the initial weight and the weight of water stable aggregates alone. I used a paired t-test and a Welch two-sample t-test was used to determine whether there was a difference in the proportion of stable aggregates between treatment and strata. Values for wet stable aggregates were compared using thresholds provided by EcoCore Lab, Colorado State University shown in Table 12.

Table 12. Thresholds of percent of wet stable aggregates indicating soil condition quality provided by EcoCore Lab, Colorado State University.

% Wet Stable Aggregates	Soil Condition Quality
<25%	poor physical quality
30 to 50%	low to medium physical quality
50 to 75%	medium to good physical quality
>80%	excellent physical quality

Soil Nutrient Availability and PRS Soil Probes

Although PRS soil probes detected various ions, Nitrate (NO_3^-), Ammonium (NH_4^+) and Phosphorus (P) were specifically chosen for analysis due to their well-studied influence on grassland plant productivity (Ricklefs et al. 2014, Baldarelli et al. 2021). Analysis of soil nutrient availability was outsourced by Western Agricultural Innovations Inc., where soil probes were sent to ShangriLab (Moscow, Idaho) for processing. Sample results were sent back to me in an excel document, where the availability of each nutrient was measured in $\mu g/cm^2$.

An ANOVA analysis was used to determine whether there was a difference in the concentration of soil NH_4^+, NO_3^-, Total Nitrogen ($NH_4^+ + NO_3^-$), and P between treatment and strata. Values of NO_3^-, NH_4^+, and P represent an average of the four replicate samples obtained for each treatment (grazed or exclosed) at each site. Measurements of each of these nutrient concentrations were also used as individual covariates in the candidate liner mixed modeling process as described in Chapter 2 to determine the relative influence of each covariate on variability in herbaceous production. Results from the linear mixed model and candidate model selection were also considered as part of this analysis and interpretation to provide insight into potential patterns of belowground nutrient concentration as it relates to variability in aboveground primary production.

Aboveground Nitrogen in Plant Tissue

Samples used for aboveground plant tissue nitrogen yield analysis were selected from all twelve grazed treatment plots during the summer sampling occasion from both 2021 and 2022. Each sample was separated based on the plant functional group (graminoids and forbs), site (1-12), and stratum (GRCA vs. KNF). I selected a portion of plant material from each subplot outside of a grazing cage to create a representative subsample. Each subsample was then grinded using a Wiley Mill and a 20-mesh gauge to ensure homogeneity for nitrogen content analysis. Each grinded, composite plant sample was then run through a VELP C/N Elemental Analyzer (CN 802), using a 0.90g-1.0g aliquot of each subsample. This elemental analyzer uses combustion and Helium (an inert gas) to reduce the nitrogen dioxide to its molecular form, where the concentration of nitrogen is then precisely detected using a Thermal Conductivity Detector. To ensure the elemental analyzer was running quality tests, I conducted three “blanks” prior to processing; one blank after every 12 samples, and one blank at the end, for a total of seven quality analyses (quality assurances) tests and no discrepancies were observed. I calculated Nitrogen Yield (%N) by multiplying $ANPP_g$ site values by the corresponding nitrogen concentration for each graminoid and forb subsample. The effect of bison herbivory on aboveground nitrogen availability was examined by comparing nitrogen yield in grazed areas of GRCA with areas with little to no bison grazing in KNF using a Welch two-sample t-test to determine potential differences between the two strata.

Results

Soil Aggregate Stability and Soil Cores

Aggregate stability was similar across the landscape. T-test results showed no evidence of a statistical difference in the proportion of stable aggregates between treatments (p=0.4265) or stratum (p=0.4443). In grazed treatments, values ranged from 20.50% to 60.80% in GRCA and from 49.17% to 62.34% in KNF. The variation in values was higher in GRCA compared to KNF based on standard deviations (Figure 9). As an additional means of evaluation, data were parsed by stratum to see if a treatment effect could be detected in areas that specifically exhibit bison utilization (sites in GRCA). Results from this subset analysis continued to show no statistical difference (all p>0.18) in the proportion of stable aggregates when comparing grazed sites to exclosure sites in GRCA.

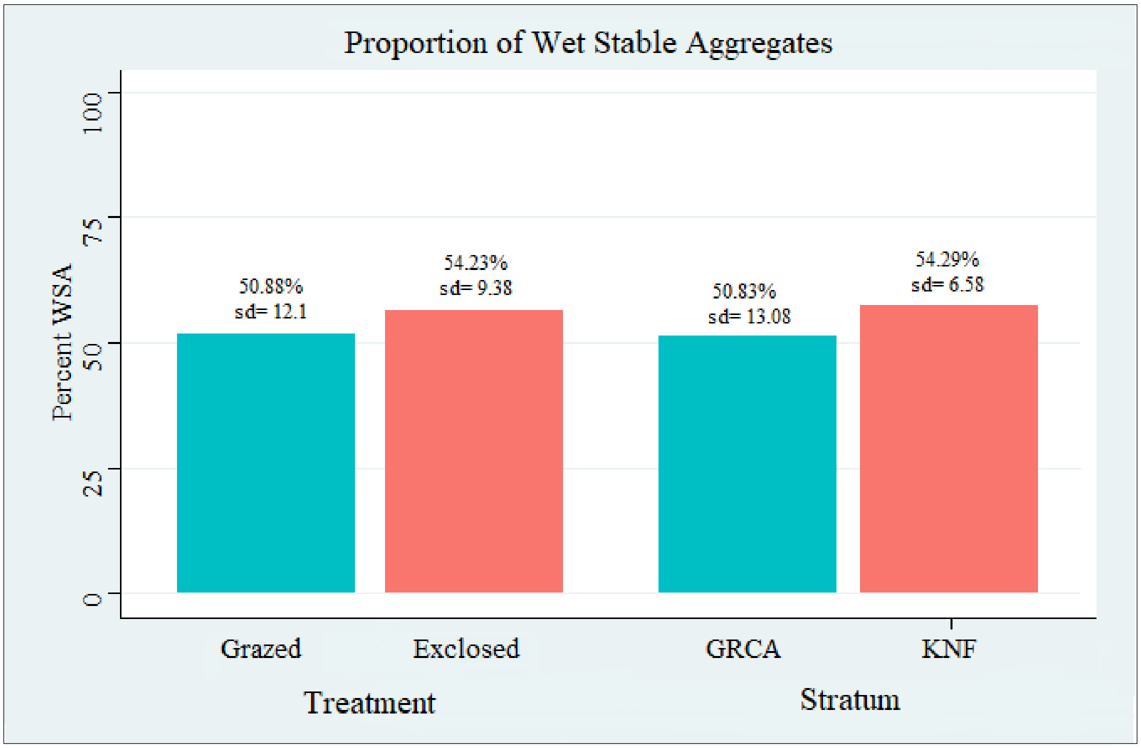


Figure 8. Measures of mean value of stable aggregate percentages, with standard deviations, from soil core samples collected from 2021 from all 12 sites and each treatment: grazed vs. exclosure (left) within stratum: GRCA vs. KNF (right).

Soil Nutrient Availability and PRS Soil Probes

Some soil probes were never retrieved, either lost in the soil or trampled and broken by bison. A total of 288 soil probes (or 144 pairs) were deployed across the study areas and 259 were recovered successfully. The largest loss in soil probes never exceeded 2 pairs, so each treatment plot had at least 4 pairs of soil probes worth of data for each treatment in each site. These data, which were measured in µg/cm^2, were averaged for analysis and interpretation. Soil ammonium values ranged from 0.72µg/cm^2 (site 4; treatment=grazed) to 107.2µg/cm^2 (site 1; treatment=exclosure) (Figure 9); soil nitrate ranged from 42.8µg/cm^2 (site 7; treatment=grazed) to 278.52µg/cm^2 (site 4; treatment=exclosure) (Figure 10); soil phosphorus ranged from 1.24µg/cm^2 (site 1; treatment=grazed) to 32.08µg/cm^2 (site 10; treatment=grazed) (Figure 11);

and total soil nitrogen ranged from 42.8µg/cm^2 (site 7; treatment=grazed) to 278.52µg/cm^2 (site 4; treatment=exclosure) (Figure 12).

Based on ANOVA results, the only significant differences in soil nutrient concentration could be observed between treatments for nitrate and between stratum for phosphorus, where nitrate concentration was significantly higher in exclosure treatments (77.2µg/cm^2 ±7.46) compared to grazed treatments (57.4µg/cm^2±3.62) (*p*=0.0227), and phosphorus was higher in KNF (7.42µg/cm^2 ±0.661) than in GRCA (4.54µg/cm^2 ±0.567) (*p*=0.00186) (Table 13).

Table 13. Summary of results from ANOVA statistical comparison of the concentration of select soil nutrients including ammonium, nitrate, total belowground nitrogen, and phosphorus between treatments (grazed vs. exclosure) and stratum (GRCA vs. KNF). Values are presented as average values (±1SE) in µg/cm².

Mean Nutrient Availability in µg/cm² (±1SE)					
		Stratum		Treatment	
Nutrient		GRCA	KNF	Grazed	Exclosure
Ammonium		22.20 (±3.36)	17.50 (±2.46)	21.30 (±2.83)	18.40 (±3.09)
	p-value	0.2615		0.4979	
Nitrate		72.02 (±7.48)	62.60 (±4.41)	57.40 (±3.62)	77.20 (±7.46)
	p-value	0.2853		0.02274*	
Total belowground Nitrogen		94.30 (±7.63)	80.11 (±5.18)	78.70 (±4.25)	95.65 (±8.08)
	p-value	0.1331		0.0719	
Phosphorus		4.54 (±0.567)	7.42 (±0.661)	6.74 (±0.87)	5.22 (±0.363)
	p-value	0.001857*		0.1178	

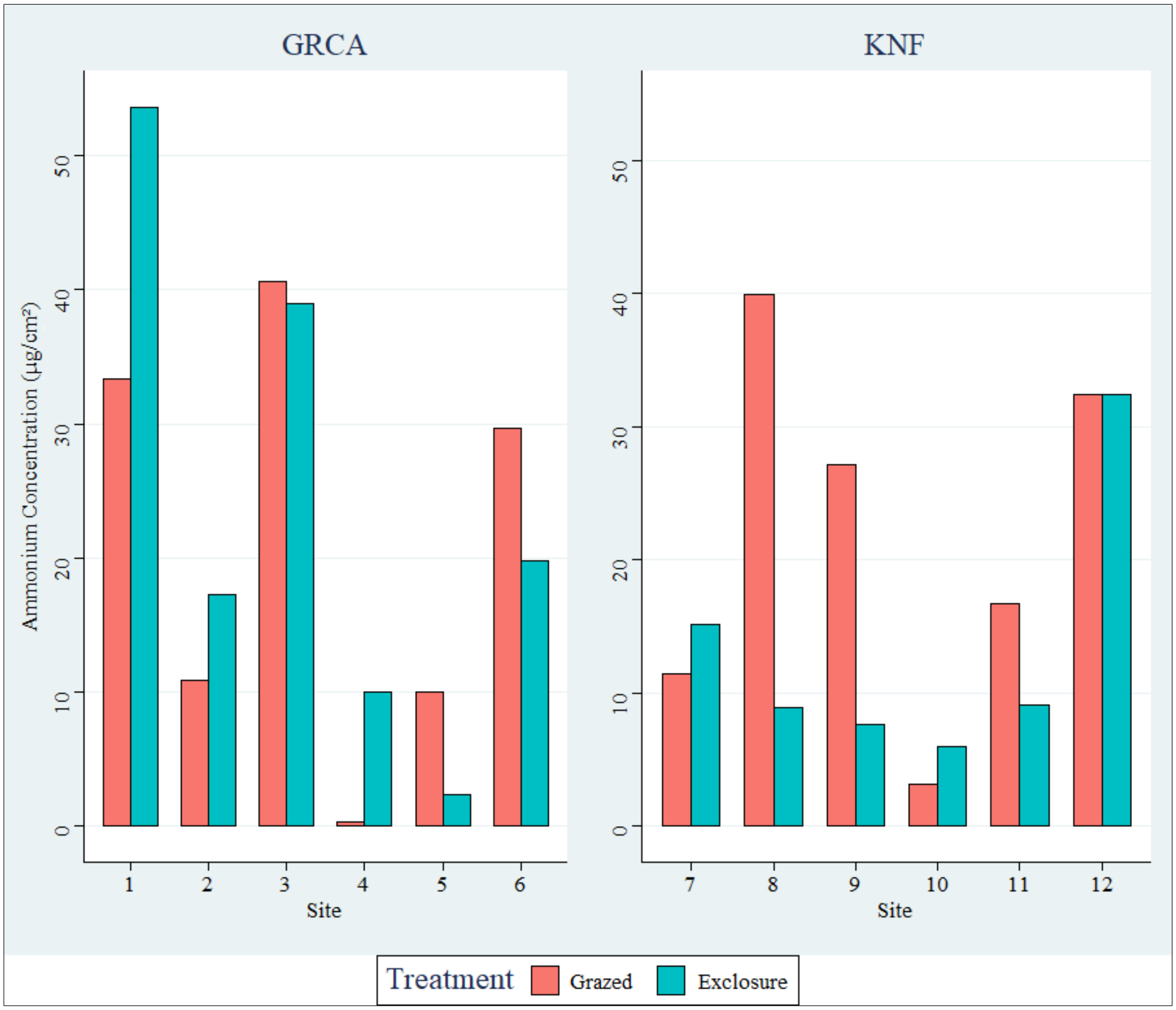


Figure 9. Average ammonium concentration, based on measurements collected from four to six pairs of PRS Soil Probes for each site during 2021, separated by treatment: grazed vs. exclosure, and stratum: Grand Canyon National Park, GRCA (left) vs. Kaibab National Forest, KNF (right).

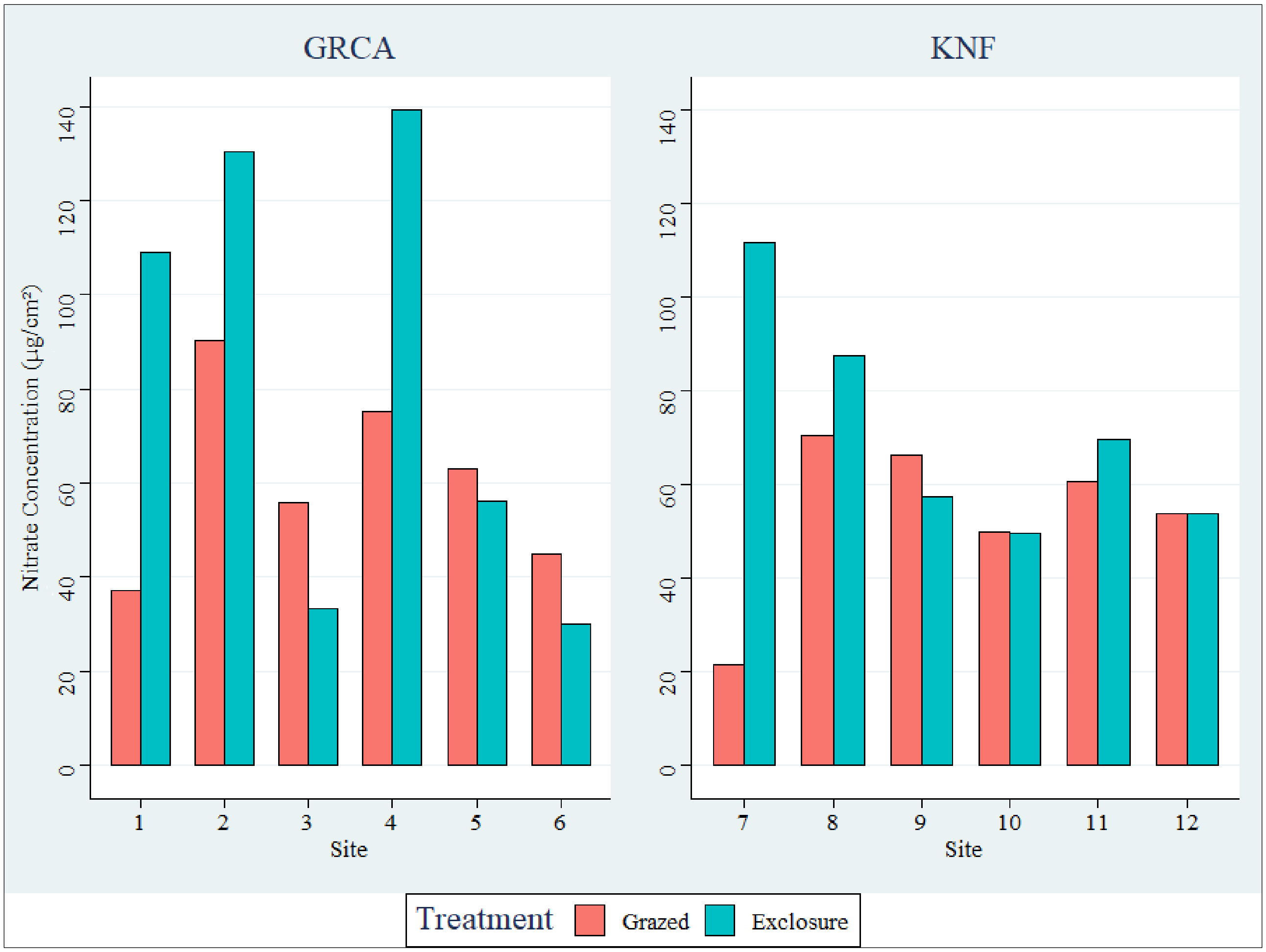


Figure 10. Average Nitrate concentration based on measurements collected from four to six pairs of PRS Soil Probes for each site during 2021, separated by treatment: grazed vs. exclosure, and stratum: Grand Canyon National Park, GRCA (left) vs. Kaibab National Forest, KNF (right).

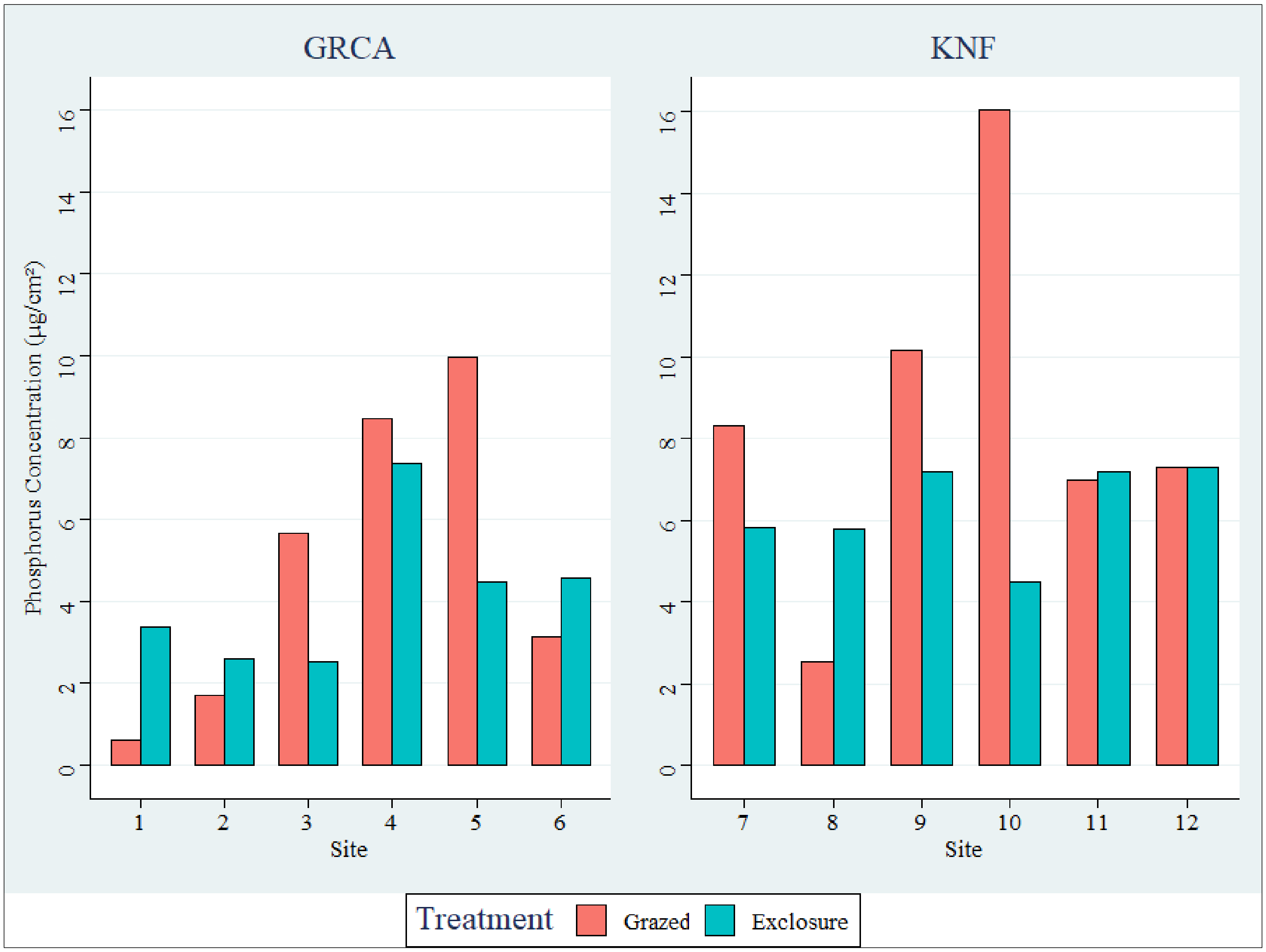


Figure 11. Average Phosphorus concentration based on measurements collected from four to six pairs of PRS Soil Probes for each site during 2021, separated by treatment: grazed vs. exclosure, and stratum: Grand Canyon National Park, GRCA (left) vs. Kaibab National Forest, KNF (right).

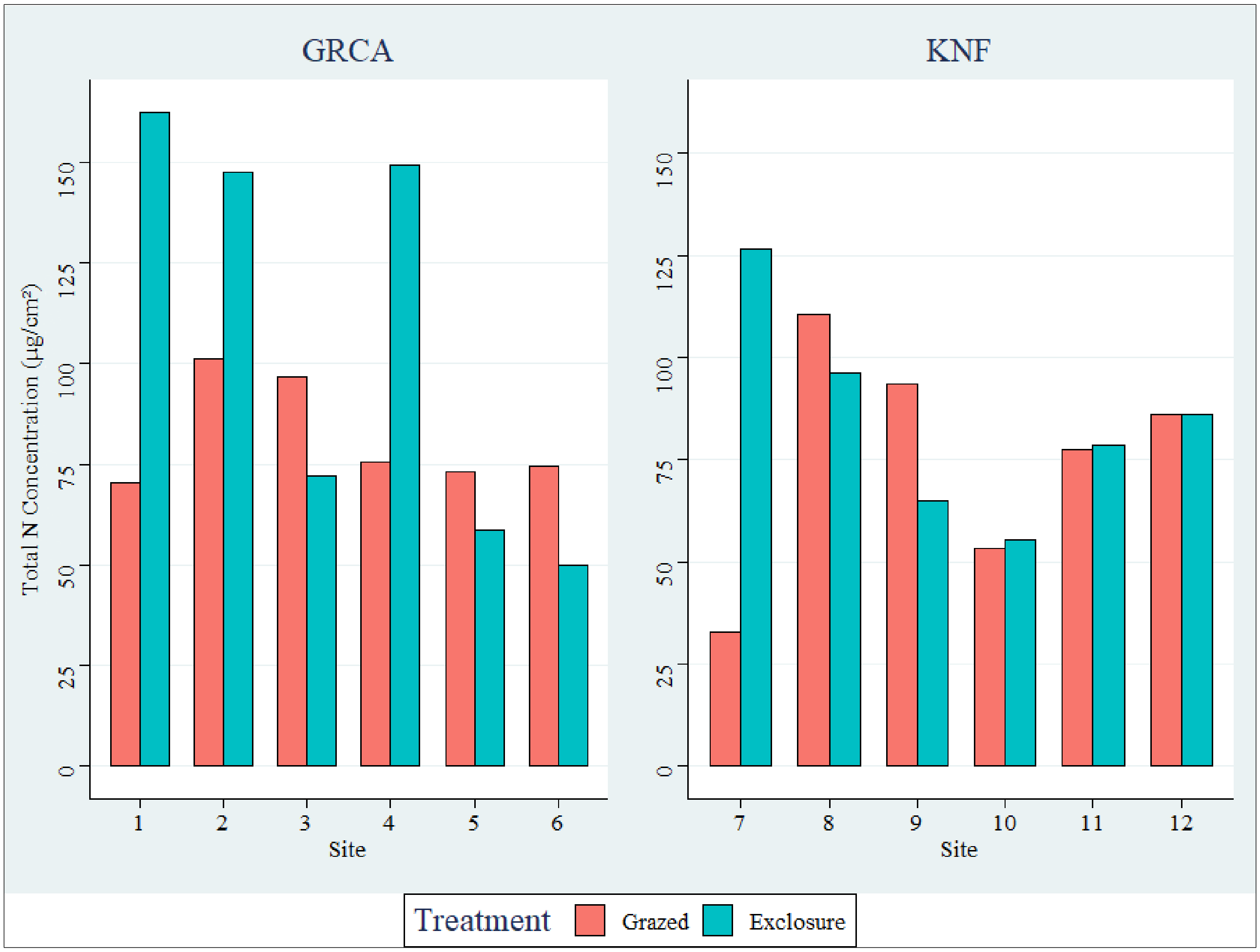


Figure 12. Average Total belowground Nitrogen concentration ($NH_4^+ + NO_3^-$) based on measurements collected from four to six pairs of PRS Soil Probes for each site during 2021, separated by treatment: grazed vs. exclosure, and stratum: Grand Canyon National Park, GRCA (left) vs. Kaibab National Forrest, KNF (right).

Aboveground Nitrogen in Plant Tissue

There was a significant difference in the aboveground plant tissue nitrogen yield of both graminoids (p=0.0263) and forbs (p=0.015) when comparing between stratum, in which plant samples collected from GRCA sites exhibited significantly higher N-yield values for both graminoids and forbs compared to plant samples collected within KNF. On average, samples in GRCA yielded 2.04g/m^2 (±0.308) of nitrogen in graminoids and 2.43g/m^2 (±0.301) in forbs, whereas KNF samples yielded 1.24g/m^2 (±0.0893) of nitrogen in graminoids and 1.55g/m^2 (±0.0898) in forbs.

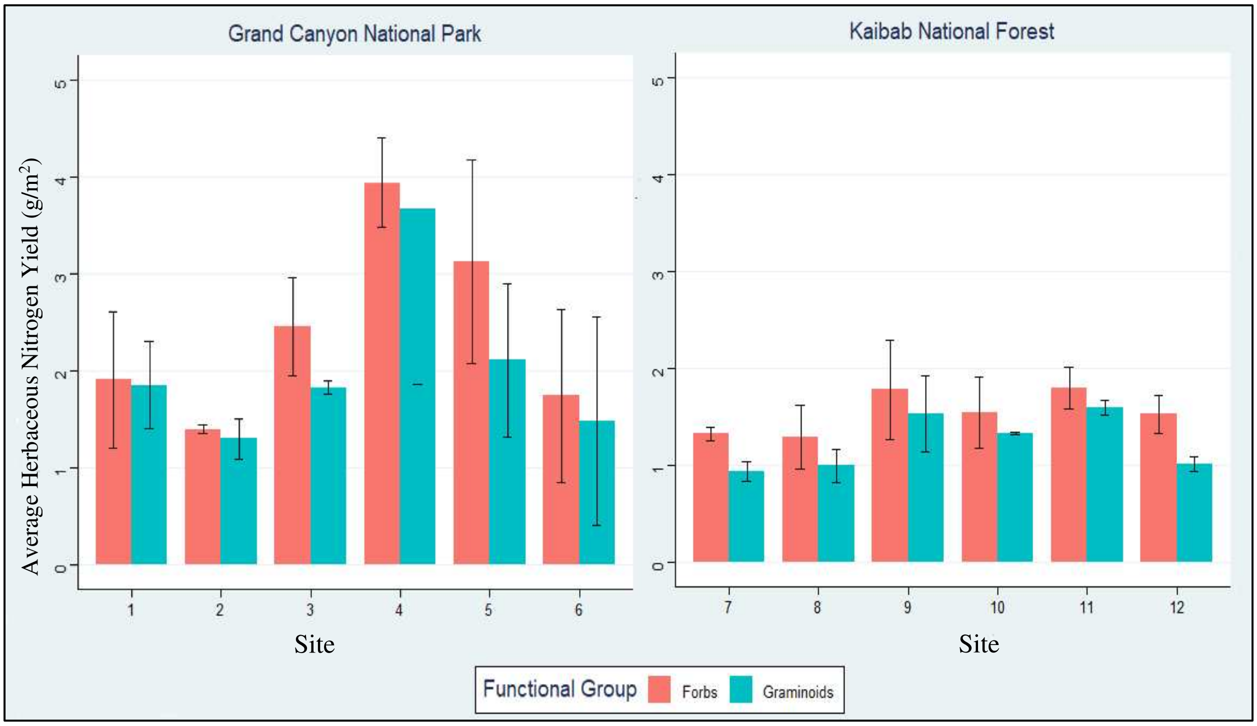


Figure 13. Results from grazed herbaceous plant Nitrogen Yield (g/m^2). Each value represents nitrogen yield from each site, where biomass clippings of graminoids and forbs in subplots outside each grazing cage were averaged (n=5 graminoids in 2021, n=5 forbs in 2021 and n=5 graminoids in 2022, n=5 forbs in 2022) for all twelve sites, for a total of n=48. Each sample was pooled, subsampled and separated by stratum: Grand Canyon National Park (left) and Kaibab National Forest (right). Using an elemental analyzer, a 1.0g aliquot from of each subsample was used to estimate nitrogen concentration, which was then converted to % Nitrogen Yield in g/m^2.

Discussion

This portion of the study was intended to contribute to the body of scientific literature which demonstrates the relationship between ungulate herbivores and grassland structure and function, in part, as described by above- and below- ground nutrient dynamics and aboveground primary production. The evaluation of soil properties, particularly aboveground soil nitrogen content found from this research indicate that bison impact the quality and the quantity of aboveground plant biomass of the North Rim, Grand Canyon grassland ecosystem. The enhanced aboveground primary productivity, as described in Chapter 2, and increased nitrogen yield in plants within grazed treatments in GRCA (Figure 13), suggests that the spatiotemporal grazing pattern of bison in GRCA promotes the sustainability of this grazing ecosystem despite the high grazing intensity that occurs within this habitat. Additionally, the homogeneity of stable soil aggregates across the study area, regardless of bison presence, indicates that during this study (2021-2022), bison grazing did not appear to have a negative effect on the soil's erosion potential (Figure 8).

The ecological consequences of bison grazing on grassland soil properties are difficult to predict and can vary depending on a range of abiotic and biotic factors. I expected that due to the sheer size of bison and the intensity in which they grazed would impact the physical structure of the topsoil layers by decreasing the proportion of stable aggregates in areas with bison compared to areas without, potentially impacting soil surface erosion. An increase in bare ground in a grazed area may lead to a loss in the soil A-horizon by run-off and wind erosion in grasslands (Kelly and Walker 1976, van de Koppel et al. 1997) and sites within GRCA exhibited higher proportions of bare ground compared to KNF (Chapter 2: Table 8); however, my assessment of soil aggregate stability indicated that there was no apparent difference in the proportion of stable aggregates among sites, regardless of bison grazing (Figure 8) and all sites produced values indicating good physical soil quality (Table 12). Although no consistent patterns in the proportions of stable aggregates were observed between stratum or treatment, there was higher variation within GRCA, which suggests that bison may have exerted some influence on stable aggregate proportions compared to areas void of bison.

When comparing the availability of nutrients between strata and treatments, on average, KNF sites had 38.8% higher phosphorus concentration than GRCA, and exclosure treatments had 25.6% higher nitrate than grazed treatment plots. No spatial differences were found in ammonium or total soil nitrogen availability across the landscape in 2021 (Table 11). Since soil probes were deployed after exclosure construction and prior to the arrival of most bison in my study area and no grazing treatment had taken effect. Additionally, I only collected relative availability of ammonium in 2021, and was consequently unable to ascertain potential changes in ammonium across years and how those changes may have attributed to overall changes in annual ANPP. It is unknown whether multiple years of measurements would provide insight into the relationship with ammonium and bison presence, especially since some nitrogen pool turnover rates may occur over a long time scale, either annually, every few years, of even over the span of decades or centuries (Parton et al. 1987). Regardless, the information obtained from soil probe measurements was subsequently used to account for pre-existing soil nutrient availability and to provide information to assist in the evaluation of spatiotemporal variability.

When adding soil nutrients to my mixed model (as described in Chapter 2), soil nitrogen concentration (specifically ammonium) was included in the highest-ranking models for explaining variability in aboveground primary productivity (Chapter 2: Tables 10 and 11). Although differences in nutrient concentrations could be detected between stratum for phosphorus, and between treatments for nitrate (Table 13), neither phosphorus nor nitrate was detected as a significantly influential factor in the linear mixed candidate models (Chapter 2: Table 10); however, soil ammonium was included. To better understand the relationship with soil ammonium concentration and aboveground primary productivity, stratum was parsed out between areas with bison (GRCA) and areas without (KNF) in the linear mixed model. There was a significant, negative relationship with belowground NH_4^+ concentration in GRCA (β_{NH4}=-0.004431; Table 11), but no relationship in KNF.

The slightly negative relationship between relative availability of soil nitrogen concentration and ANPP, coupled with the significantly higher nitrogen yield in grazed plants, may suggest an increase in mineralization and plant uptake of nitrogen. Herbivory-induced nutrient cycling has been observed from increased mineralization rates in frequently grazed plots in Serengeti National Park, Tanzania (McNaughton 1997), Konza Prairie, Kansas (Knapp et al. 1999), and Yellowstone National Park, Wyoming (Tracy and Frank 1998). These show herbivores accelerating effect on nutrient cycling, an important ecosystem process that directly influences rates of production, species abundance, and species composition (Ruess and McNaughton 1988, Maschinski and Whitham 1989). However, since treatment had yet to take effect during the burial period of soil probes in my study, these data are best utilized to account for pre-existing, site-specific soil nutrient conditions. Future measurements of soil nutrients over time (i.e., long-term measurements) and across the landscape (i.e., comparison of treatment conditions, or assessment while bison fully occupy their summer range vs. winter range) would enhance the ability to make inference regarding the relationship with bison herbivory and soil nutrient availability and nutrient cycling.

The results of aboveground herbaceous nitrogen yield during my study provided notable patterns. The site that supported the highest overall primary production rate throughout the study area occurred within the grazed treatment plot of site 4 in GRCA (184.1g/m^2±37.8; Table 2), which also recorded the highest grazing intensity (63.4%±7.0; Table 2), and the highest aboveground plant nitrogen yield (4.954g/m^2; Figure 13). Additionally, the enhanced quantity and quality of herbaceous biomass in grazed areas suggest that bison may have an accelerating effect on grassland ecosystem functions.

Forage quantity and quality are two important factors that lead to spatiotemporal herbivore grazing dynamics. Nitrogen is very often a limiting resource for plant growth, but it is more limiting for animals who require larger amounts of nitrogen for metabolic processes (Bakker et al. 2006). Therefore, herbaceous leaves with higher nitrogen content are typically preferred by large herbivores. Ungulate herbivores in the Serengeti National Park have been shown to 'actively' graze the landscape, using a hierarchical forage decision process regarding which grassland patch and what migratory behaviors support the highest forage efficiency (Frank et al. 1998). In that study, seasonal movements of ungulate grazers across the landscape were associated with the nutrient content in the forage they consumed (Frank et al. 1998). In my study, bison appeared to adopt strategic spatiotemporal grazing patterns by utilizing their own curated, nutrient-rich and highly productive patches of grassland in summer, then allowing sufficient recovery time for defoliated plants to regrow by migrating to other areas in winter. Similarly, Augustine et al. (2003) measured ungulate grazing intensity across spatially variable aboveground herbaceous production and found that ungulate grazers preferentially selected for the most productive patches. On the contrary, plants growing in nutrient-low environments may have higher carbon concentration in their leaves relative to nitrogen, rendering them a lower quality forage for herbivore consumption. The relationship that bison may have with the quality of forage on the landscape, and the potential alterations of the C:N ratio in plant tissue has global implications. As global carbon dioxide increases with the increasing human population, carbon emissions continue to grow, and this may directly affect C:N ratios in plants, which can alter nutritional value to herbivores and potentially limit herbivore populations (Gurevitch et al. 2006).

My research provides evidence that the soil properties within grasslands of the Grand Canyon ecosystem appear unimpacted by the current levels of grazing intensity, as demonstrated by higher quality of forage in grazed areas, and no differences in other soil parameters between areas with and without bison grazing. The results from this research suggest that the dynamics in which bison herbivory occurs through time and across the landscape not only maintains but enhances grassland production and forage quality. The seasonal migration of bison from their summer range to their winter range likely provides recovery time for grassland plants of the North Rim, enabling an increased capacity to not only tolerate, but adapt over-compensatory response mechanisms to enhance production and overall plant biomass. However, the mechanisms that drive both plant response and bison movements and the underlying ecosystem processes responsible for these patterns requires future research in this ecosystem to confirm other parameters with my findings. This need for additional, and long-term grassland monitoring is particularly urgent if the keystone Plains bison are to persist on the landscape.

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Appendix A: Linear Regression Results for Precipitation Data

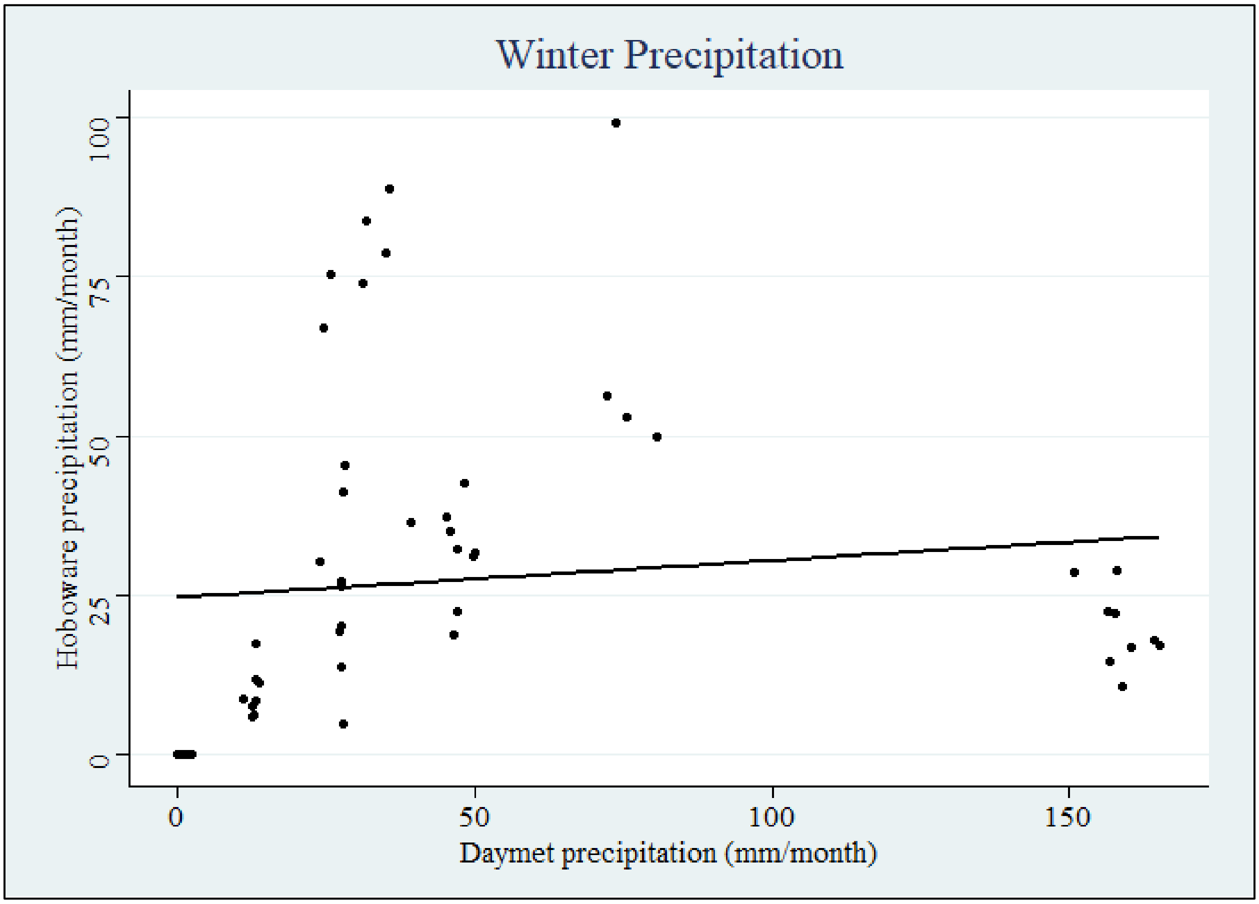

Figure A1. Relationship between Hoboware precipitation data and data collected during the same monthly totals from the Daymet precipitation data base on linear regression analysis results. Datapoints represent monthly average precipitation values from winter months for 2021 and 2022 (n=55 months). The regression model includes Daymet as the response variable against Hoboware as the predictor variable, with a slope of 0.0579 (±0.0658) and an R^2=0. 0144.

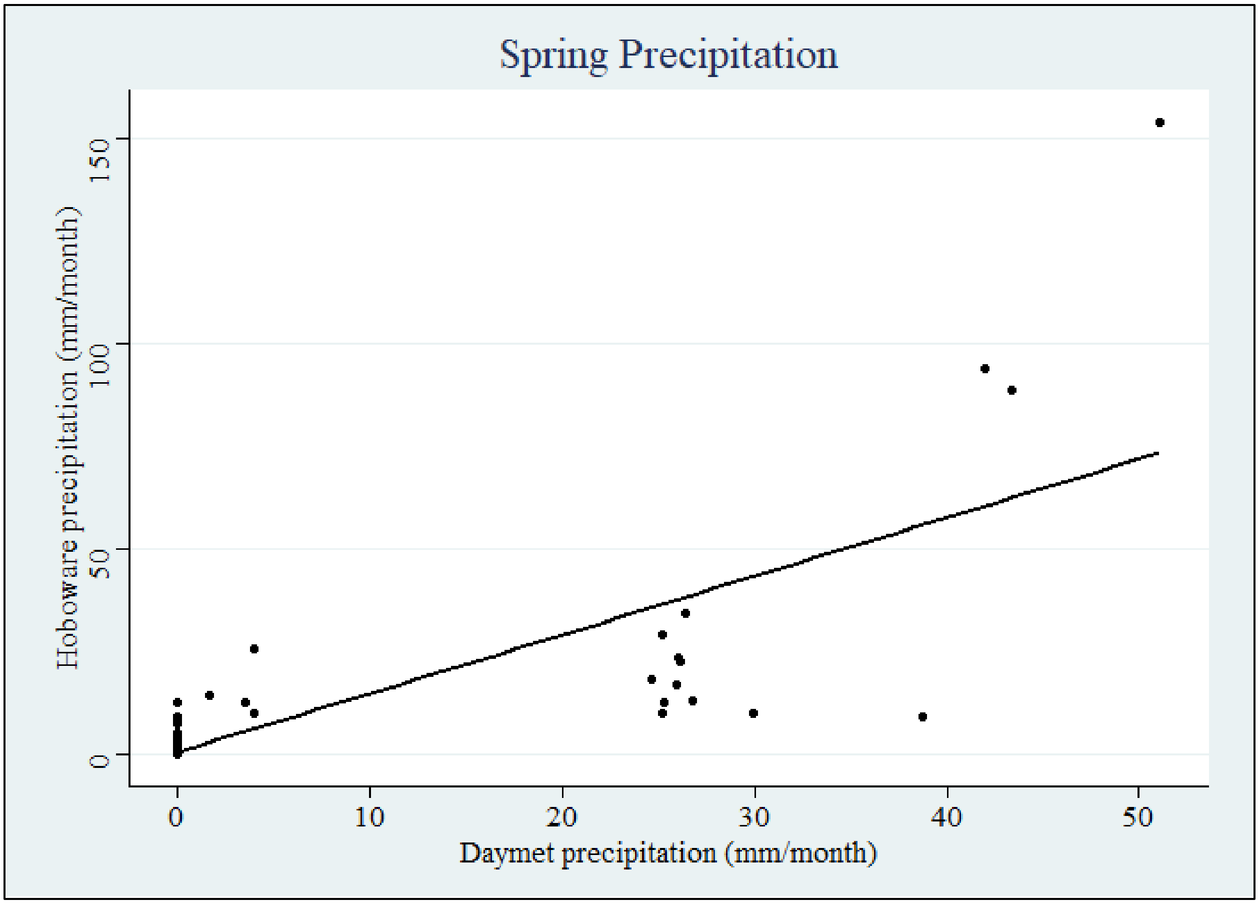

Figure A2. Relationship between Hoboware precipitation data and data collected during the same spring monthly totals from the Daymet precipitation data based on linear regression analysis results. Datapoints represent monthly average precipitation values from spring months for 2021 and 2022. The regression model includes Daymet as the response variable against Hoboware as the predictor variable, with a slope of 1.4265 (±0.2035) and an R^2=0.557.

$$y = \beta_0 + \beta_1 x_1 + \varepsilon$$

$$Hoboware\ precip.(spring) = 0.7084 + (1.4265)(x_1) + 0.2035$$

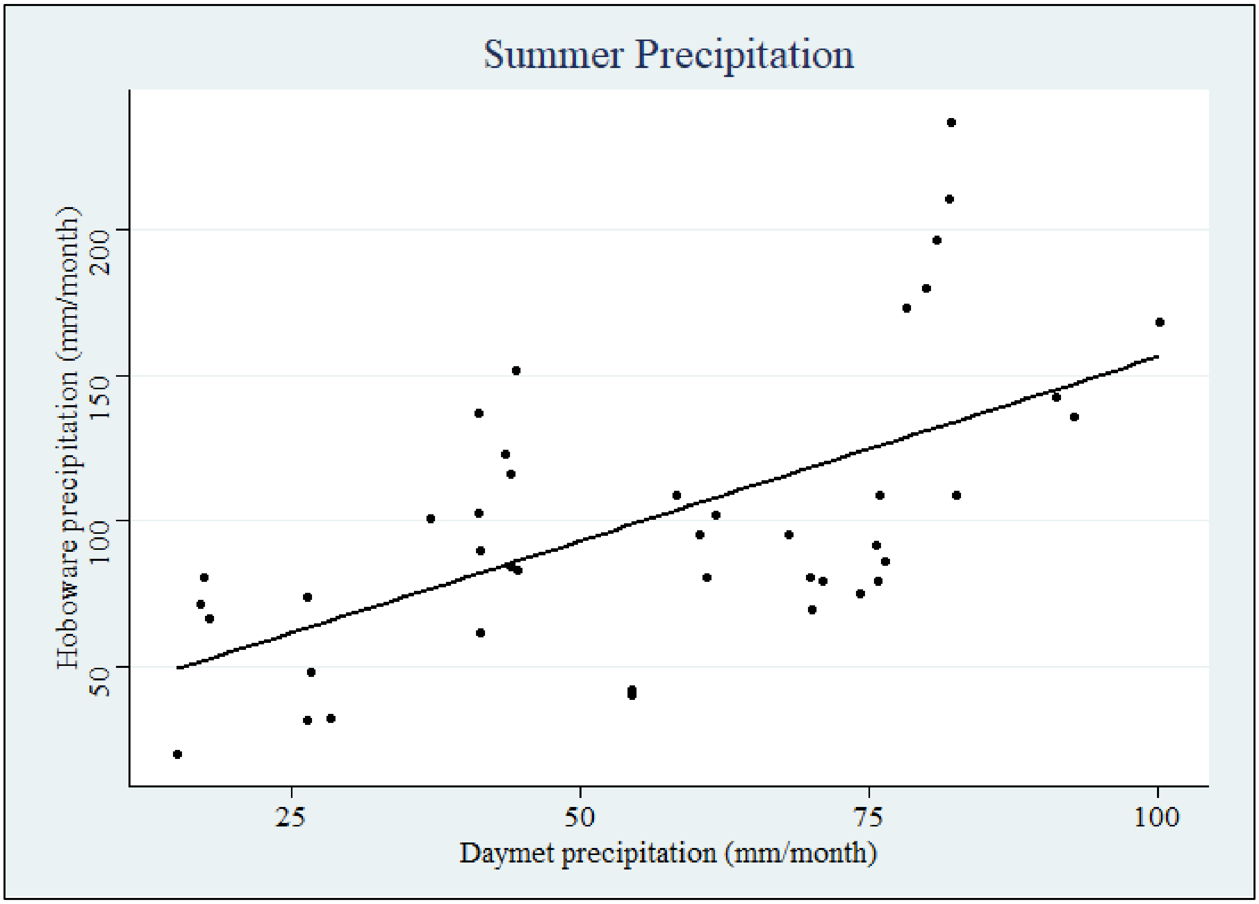

Figure A3. Relationship between Hoboware precipitation data and data collected during the same summer monthly totals from the Daymet precipitation data based on linear regression analysis results. Datapoints represent monthly average precipitation values from summer months for 2021 and 2022. The regression model includes Daymet as the response variable against Hoboware as the predictor variable, with a slope of 1.2653 (±0.2651) and an R^2=0.3629.

$$y = \beta_0 + \beta_1 x_1 + \varepsilon$$

$$Hoboware\ precip.(summer) = 29.7411 + (1.2653)(x_1) + 0.2651$$

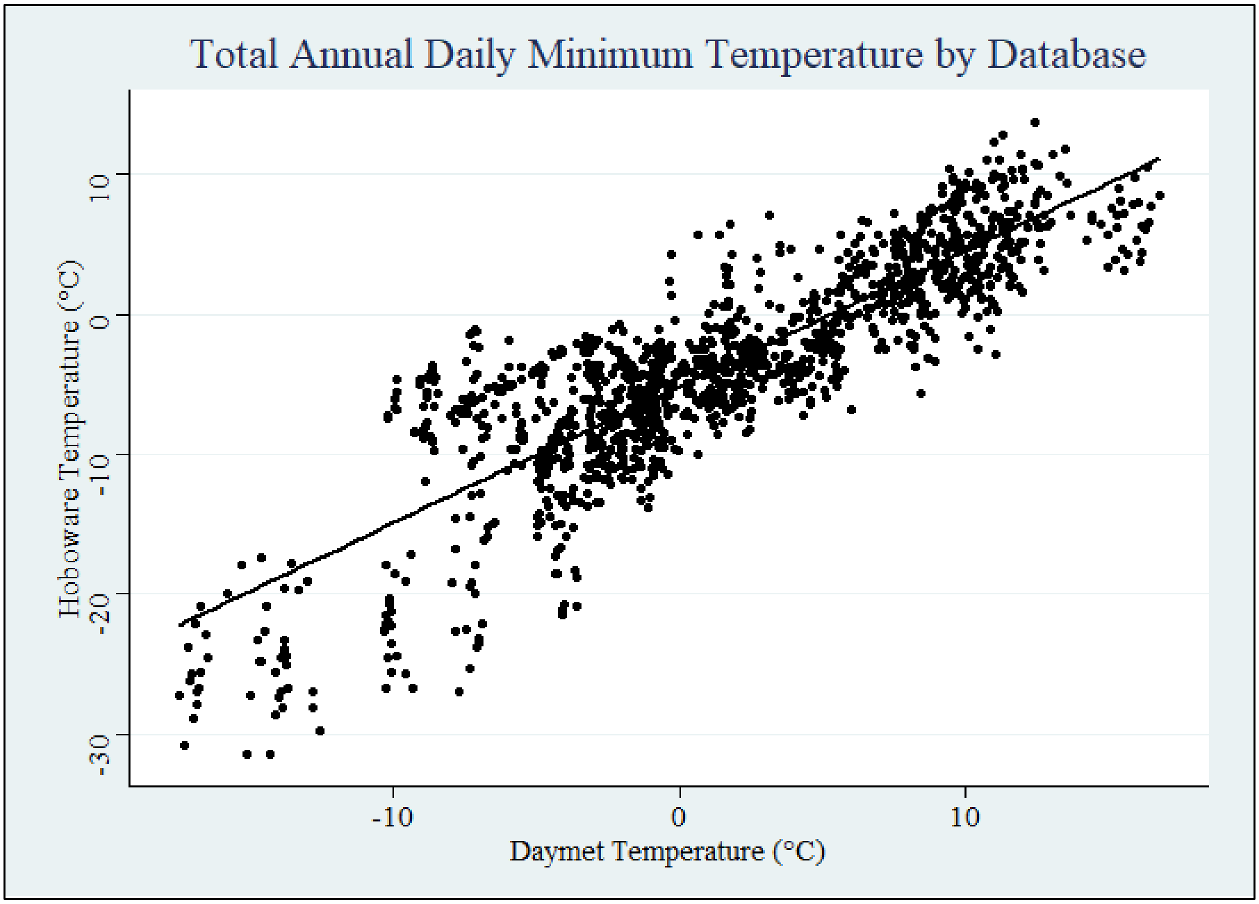

Figure A4. Daily minimum temperature for Hoboware and for Daymet based on measurements from 2020, 2021 and 2022. The slope is 0.97323 (±0.01546) and R^2= 0.7462.

$$y = \beta_0 + \beta_1 x_1 + \varepsilon$$

$$Hoboware\ temp.(min) = -5.17453 + (0.97323)(x_1) + 0.01546$$

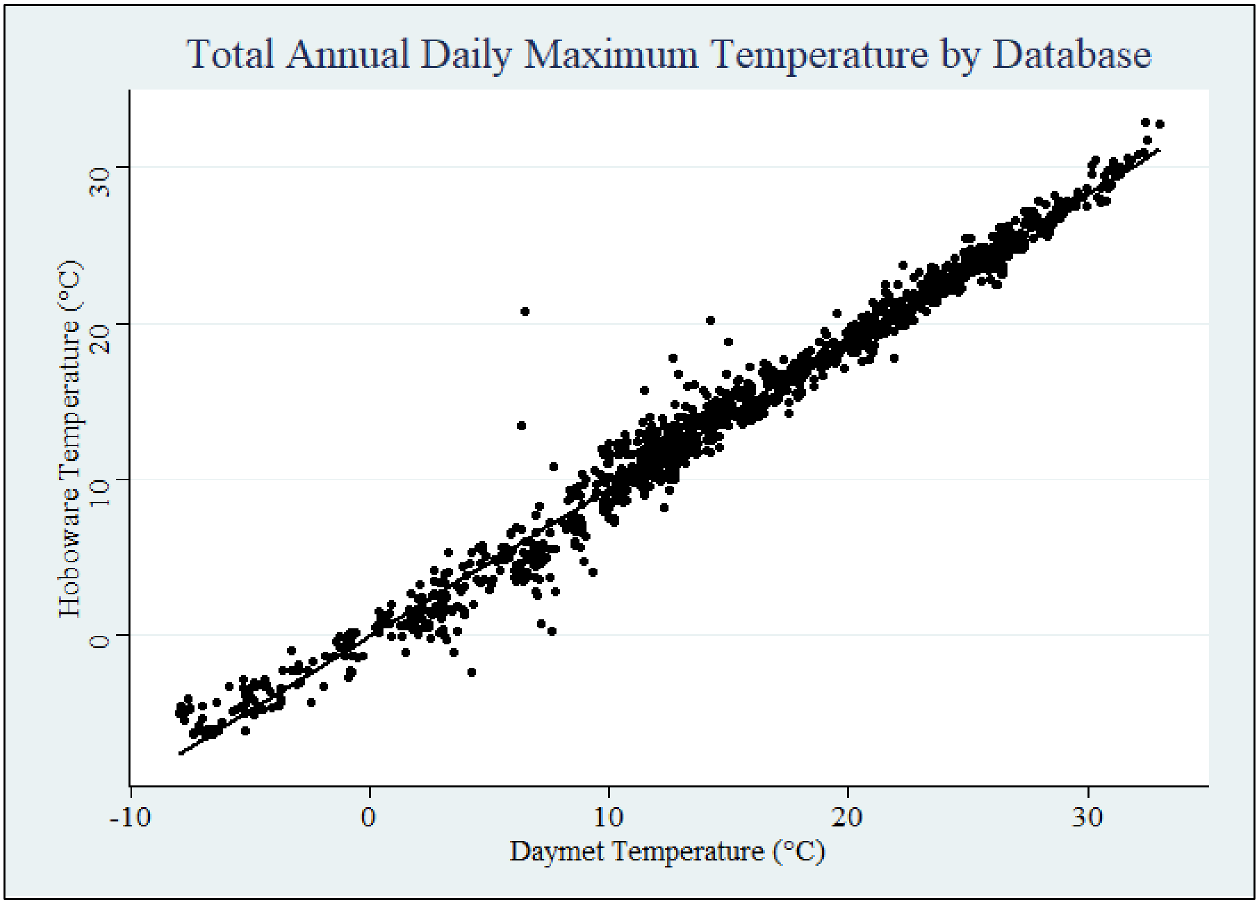

Figure A5. Linear Regression analysis results for daily maximum temperatures, for all sites, for each year. Slope = 0.94841 (±0.003652) and R^2=0.9804.

$$y = \beta_0 + \beta_1 x_1 + \varepsilon$$

$$Hoboware\ temp.(max) = -0.133882 + (0.94841)(x_1) + 0.003652$$

Appendix B: SSPI versus SPNI

Table B1. Summary of 2021 results from calculations of annual aboveground herbaceous productivity for both grazed ($ANPP_g$) and exclosed ($ANPP_{ug}$) treatments, and total growing season offtake by herbivory (O_t). Values in **bold** indicate sites that produced p-values <0.10, and therefore, require the addition of the incremental difference in biomass as described in the SSPI methods section.

	Sum of all positive and negative increments (SPNI)			*Sum of all significant positive increments (SSPI)*		
Site	$ANPP_g$ (g/m^2)	$ANPP_{ug}$ (g/m^2)	O_t (g/m^2)	$ANPP_g$ (g/m^2)	$ANPP_{ug}$ (g/m^2)	O_t (g/m^2)
1	58.60	47.04	25.4	**58.60**	38.86	**25.40**
2	59.05	54.53	35.58	**59.05**	44.04	**35.58**
3	74.47	64.50	37.74	**74.47**	64.50	**37.74**
4	221.85	144.54	156.19	**221.85**	144.54	**156.19**
5	89.32	120.59	34.7	**89.32**	116.97	**34.71**
6	110.86	57.94	93.57	**110.86**	57.94	**72.09**
7	68.81	42.94	21.74	68.64	42.94	20.96
8	53.66	55.34	-7.17	43.02	48.25	-3.87
9	54.29	103.55	4.09	98.95	103.55	4.59
10	70.21	80.54	14.74	66.53	70.57	8.50
11	39.44	82.63	-7.43	70.32	82.63	-16.81
12	79.83	78.16	19.73	69.06	78.16	16.98

SSPI Method 2021:
Results from linear regression analysis to determine whether statistically significant increases in biomass occurred between sampling occasions (ANPP) and between sublots (Ot). P-values indicating significant, positive increase are indicated in **bold**, with significant set at $p \leq 0.01$ (for small sample size):

P-values for 2021 SSPI method:
$ANPP_g$: **0.0001** (GRCA); 0.4076 (KNF)
$ANPP_{ug}$: 0.3014 (GRCA); 0.4494 (KNF)
O_t: **<0.0001** (GRCA); 0.4227 (KNF)

Table B2. Summary of 2022 results from calculations of annual aboveground herbaceous productivity for both grazed ($\mathrm{ANPP_g}$) and exclosed ($\mathrm{ANPP_{ug}}$) treatments, and total growing season offtake by herbivory ($\mathrm{O_t}$). Values in **bold** indicate sites that produced p-values <0.10, and therefore, require the addition of the incremental difference in biomass as described in the SSPI methods section.

	Sum of all positive and negative increments (SPNI)			*Sum of all significant positive increments (SSPI)*		
Site	$\mathrm{ANPP_g}$ (g/m^2)	$\mathrm{ANPP_{ug}}$ (g/m^2)	$\mathrm{O_t}$ (g/m^2)	$\mathrm{ANPP_g}$ (g/m^2)	$\mathrm{ANPP_{ug}}$ (g/m^2)	$\mathrm{O_t}$ (g/m^2)
1	101.57	71.43	47.94	**101.57**	**71.43**	**47.93**
2	69.88	72.66	23.06	**69.88**	**72.66**	**23.06**
3	123.45	77.50	45.18	**123.45**	**77.50**	**45.18**
4	146.21	99.03	82.32	**146.21**	**99.03**	**82.33**
5	141.58	92.66	84.59	**141.58**	**92.66**	**84.60**
6	58.14	67.08	0.35	**58.14**	**67.08**	**-4.15**
7	76.54	71.78	-14.1	76.54	71.78	-3.07
8	79.99	47.14	44.6	79.99	47.14	13.29
9	91.55	141.96	3.70	91.55	141.96	-10.26
10	91.94	95.58	17.15	91.94	95.58	4.00
11	113.72	109.38	62.24	113.72	109.38	2.68
12	82.58	66.90	13.28	82.58	66.90	9.62

SSPI Method 2022:
Results from linear regression analysis to determine whether statistically significant increases in biomass occurred between sampling occasions (ANPP) and between sublots (Ot). P-values indicating significant, positive increase are indicated in **bold**, with significant set at $p \leq 0.01$ (for small sample size):

P-values for 2022 SSPI method:
$\mathrm{ANPP_g}$: **<0.0001** (GRCA); 0.0179 (KNF)
$\mathrm{ANPP_{ug}}$: **0.0022** (GRCA); 0.0438 (KNF)
$\mathrm{O_t}$: **<0.0001** (GRCA); 0.1417 (KNF)

Supplemental Information

Supplementary Table 1. Result estimates in the presence (ANPP_g) and absence (ANPP_{ug}) of bison grazing, total growing season herbaceous offtake (O_t), and the proportion of annual biomass growth to consumption (Grazing Intensity) using the SSPI method, showing site-specific measurements during both years (2021 and 2022) using the SSPI method. Sites 1-6 are located within Grand Canyon National Park and sites 7-12 in Kaibab National Forest. ANPP_g, ANPP_{ug}, and O_t are measured in g/m^2, and grazing intensity is given as a percent.

	2021 *Sum of all significant positive increments (SSPI)*				2022 *Sum of all significant positive increments (SSPI)*			
Site	ANPP_g (g/m^2)	ANPP_{ug} (g/m^2)	O_t (g/m^2)	Grazing Intensity (%)	ANPP_g (g/m^2)	ANPP_{ug} (g/m^2)	O_t (g/m^2)	Grazing Intensity (%)
1	58.60	38.86	25.40	43.3%	101.57	71.43	47.93	47.2%
2	59.05	44.04	35.58	60.3%	69.88	72.66	23.06	33.0%
3	74.47	64.50	37.74	50.7%	123.45	77.50	45.18	36.6%
4	221.85	144.54	156.19	70.4%	146.21	99.03	82.33	56.3%
5	89.32	116.97	34.71	38.9%	141.58	92.66	84.60	59.7%
6	110.86	57.94	72.09	65.0%	58.14	67.08	-4.15	-7.1%
7	68.64	42.94	20.96	30.5%	76.54	71.78	-3.07	-4.0%
8	43.02	48.25	-3.87	-9.0%	79.99	47.14	13.29	16.6%
9	98.95	103.55	4.59	4.6%	91.55	141.96	-10.26	-11.2%
10	66.53	70.57	8.50	12.8%	91.94	95.58	4.00	4.4%
11	70.32	82.63	-16.81	-23.9%	113.72	109.38	2.68	2.4%
12	69.06	78.16	16.98	24.6%	82.58	66.90	9.62	11.6%

Appendix C: Candidate Model Selection

Table C1. Summary of candidate models, including the total number of estimable parameters (K), AIC$_c$ values, the change in AIC$_c$ values (Δ_i AIC$_c$), Akaike weights (w_i), and the log-likelihoods. Models are ordered in terms of delta AIC$_c$.

Candidate Models - with environmental covariates						
Model Number	**Model**	**K**	**log-Likelihood**	**AIC$_c$**	**Δ_i AIC$_c$**	**w_i**
1	Trt+spring_GDD+NH4	6	-2.69	19.42	0.00	0.36
2	Trt+spring_GDD+Total_N	6	-3.31	20.67	1.25	0.19
3	Trt+Stratum+spring_GDD+NH4	7	-2.21	21.22	1.81	0.14
4	Trt*Stratum+spring_GDD+Total_N	8	-1.42	22.53	3.11	0.08
5	Trt*Stratum+spring_GDD+NH4	8	-1.47	22.63	3.21	0.07
6	Trt+Stratum+spring_GDD+Total_N	7	-2.97	22.73	3.31	0.07
7	Trt*Stratum+spring_GDD	7	-2.99	22.78	3.37	0.07
8	Trt+winter_mm+NH4	6	-6.89	27.83	8.41	0.01
9	Trt*Stratum+Year+NH4	8	-4.30	28.28	8.86	0.00
10 (Base)	*Trt*Stratum+Year*	7	-5.81	28.41	8.99	0.00
11	Trt*Stratum+Year+Total_N	8	-4.45	28.60	9.18	0.00
12	Trt+winter_mm+Total_N	6	-7.61	29.28	9.86	0.00
13	Trt+Stratum+winter_mm+NH4	7	-6.32	29.45	10.03	0.00
14	Trt+Stratum+winter_mm+Total_N	7	-7.19	31.19	11.77	0.00
15	Trt*Stratum+winter_mm+NH4	8	-5.78	31.26	11.84	0.00
16	Trt*Stratum+winter_mm	7	-7.31	31.43	12.01	0.00
17	Trt*Stratum+winter_mm+Total_N	8	-6.05	31.79	12.37	0.00

List of Abbreviations

GRCA	Grand Canyon National Park
KNF	Kaibab National Forest
KP	Kaibab Plateau
ANPP	Aboveground Net Primary Productivity
$ANPP_g$	Aboveground Net Primary Productivity (grazed)
$ANPP_{ug}$	Aboveground Net Primary Productivity (exclosed)
O_t	Total Growing Season Herbivory Offtake
GI	Grazing Intensity
SSPI	Sum of Statistically Positive Increments
SPNI	Sum of Positive and Negative Increments
WSA	Wet Stable Aggregates
AIC	Akaike Information Criterion
NPS	National Parks Service
USGS	U.S. Geological Survey
USFS	U.S. Forest Service
CSU	Colorado State University
ITBC	InterTribal Buffalo Council
YNP	Yellowstone National Park
GRSA	Great Sand Dunes National Park