DISSERTATION

DYNAMICS OF STRESS AND MORTALITY FOR GRASS DOMINATED ECOSYSTEMS: AN INTERPLAY OF WATER LIMITATION, HEAT, AND EROSION

Submitted by

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ABSTRACT

DYNAMICS OF MORTALITY FOR GRASSES OF THE SHORTGRASS STEPPE: AN INTERPLAY OF WATER LIMITATION, HEAT, AND EROSION

Grass dominated systems account for ~40% of the earth's terrestrial surface and typically occur in semi-arid and arid regions. The plant species that grow in these systems are known for their ability to withstand disturbance, including drought, grazing, and fire. While it is understood that the plants in these systems often experience multiple forms of stress in a growing season, interactions among these stress variables are not well represented in the literature.

In this research, I sought to determine how combinations of stress variables influence the shortgrass steppe, this includes: long-term grazing, drought, erosion, and temperature. Specifically, I examined (1) how the interaction of long-term grazing and drought influences the recovery of the vegetation on the SGS following single-year and multi-year droughts, (2) how the interaction of grazing and erosion influence mortality following exposure to extreme surface temperatures, and (3) performed a comparative analysis of the microclimate of grass dominated systems in the United States to determine the intensity and frequency of stressful abiotic conditions that the vegetation experiences.

First, I quantified the interactive effects of single and multi-year droughts with grazing pressure, because the *Bouteloua* species that dominate the region have been shown to be tolerant of grazing and drought independently, but the interactive effects of the two have not been well studied. Past research has focused on heavy cattle grazing but I included a mixture of moderate cattle grazing with prairie dogs, which is more intensive grazing than heavy cattle grazing. I

found that the combined stress of multiple years of drought along with high grazing pressure has the potential to increase mortality in these *Bouteloua* species.

Next, I quantified the erosion severity by ranking the amount crown exposure of the *Bouteloua* species during a drought on the SGS and then determined how erosion influenced bud outgrowth (production of a tiller) during the recovery year. I combined these data with environmental data collected by the National Ecological Organization Network (NEON) to determine the environmental conditions that the meristems of the plants experienced during the drought. My results showed that the temperatures at the surface of the soil, and exposed meristems, frequently reached levels thought to be lethal to plant cells. I acknowledge that it was likely a combination of water deficit and temperature that led to mortality of *Bouteloua* species that experienced erosion, but the high temperatures alone had the capacity to cause mortality of the meristems.

Finally, I compared several near surface micrometeorological variables of grass dominated systems across the United States. Ultimately, I wanted to determine the frequency that these systems experienced temperatures near the surface that would be damaging to plants, if conventional methods for determining heatwaves represents damaging conditions to grassland plants, and what environmental factors lead to potentially damaging surface temperatures. I found that damaging temperatures occur often at arid sites, conventional heatwaves overestimate heat stress in sites that are wet or at higher latitudes, and underestimates heat stress for arid sites.

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DEDICATION

I would like to dedicate this research to my son, Oliver, as a testament that we can accomplish anything we put our minds to. You are an incredibly smart and talented kid, who will likely go on to do great things with your life!

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CHAPTER 1: INTRODUCTION

1.1 Grasslands

Grass dominated ecosystems generally occur in regions that are prone to low precipitation, climatic seasonality, and complex disturbance regimes (Mayer & Khalyani, 2011). Grasses have many adaptations that allow for them to survive in these environments, such as: small leaf area, high water use efficiency, and basal meristems (Lauenroth, Sala, Coffin, & Kirchner, 1994). The production of grasslands is tightly correlated to the amount of precipitation that the system receives (Irisarri et al., 2016; Lauenroth & Sala, 1992; Sala et al., 1988). These herbaceous plants are able to grow quickly in response to precipitation allowing them to utilize water when it is present.

Along with the ability of perennial grasses to grow quickly, they also possess basal meristems, which allow them to withstand disturbances that remove aboveground vegetation (i.e., fire or grazing) because the buds are protected and can regrow quickly after the disturbance. These disturbances maintain grass dominance in these systems (Mayer & Khalyani, 2011; Milchunas et al., 1988) by removing otherwise competitive plant species that lack these adaptations. In heavily grazed grassland systems, the dominance of the dominant species increases with increased grazing pressure (Milchunas et al., 1988).

1.2 Bud Banks

Perennial grasses have basal meristems, or buds, which contain preformed leaves and are kept at or below the soil surface, and the accumulation of these are referred to as ‘bud banks’ (Harper, 1977; Ott et al., 2019). The position of these buds is generally considered to provide protection from aboveground disturbances and harsh environmental conditions and protect the buds from getting consumed or trampled by herbivores. In large part, the recruitment of new aboveground tillers following disturbances comes from the outgrowth of these buds (i.e. the activation of a bud and formation of a tiller), so their survival is paramount to the persistence of grasslands. Protecting these tissues is especially important because many perennial grasses have poor seedling establishment and rely heavily on the asexual reproduction for the next year's production (Lauenroth et al., 1994).

In the years following drought years, grasslands production is impacted by the previous year's precipitation (Reichmann & Sala, 2014; Sala, Gherardi, Reichmann, Peters, & Jobba, 2012; Yahdjian & Sala, 2006); this phenomenon is referred to as the 'legacy effects' of the drought. These 'legacy effects' have been attributed to the number of viable buds in the bud bank (Geber, 1990; Ott et al., 2019a; Reichmann & Sala, 2014). Droughts have a negative legacy effect because it can impact the number of buds through two mechanisms, low production of new buds or bud mortality. Because new buds are produced as tillers develop and mature, the lack of viable buds could result from the lack of tiller production during drought events, which would limit the number available for recruitment the following year. Mortality of buds caused by harsh environmental conditions experienced during the drought would also reduce the size of the bud bank but, unfortunately, the environmental conditions that buds experience during droughts have not been well-quantified and so it is unknown how likely bud mortality might be during droughts.

1.3 Soil Erosion in Grasslands

Soil erosion in grasslands occurs from both wind and water; the soil is either lifted away by the wind moving across the soil surface or by the impact and runoff of rain drops (Toy et al., 2002). Both forms of erosion are increased during drought years because there is less vegetative cover to reduce wind speed at the soil surface and protect the soil/crown from the impact of rain drops (Munson et al., 2011; Toy et al., 2002). The amount of soil being removed by the wind is also increased because there is no moisture in the upper layers of the soil to allow the particles to bind together. Although most of the erosion is thought to have small scale impacts (Martinez-Turanzas, Coffin, & Burke, 1997), the lack of vegetation during droughts reduces the plant's capacity to act as a wind break, thus decreasing the capability to promote soil accretion and increasing the potential for erosion (Munson et al., 2011; Toy et al., 2002).

Erosion around the crown of perennial grasses not only removes the soil, but also the protection that it was providing for the bud bank. Since bud banks are so vital to the persistence of perennial grasses and because of their location near the soil surface, erosion could lead to bud exposure and threaten their survival. Thus, a better understanding of the interactive effects of drought and soil erosion on plant productivity and survival is important for predicting the future structure and function of arid and semi-arid grasslands.

1.4 Heat Stress in Grasslands

Many heat stress models assume that the lethal temperature for plants is 60°C (Choczynska & Johnson, 2009), based on research that showed that cellular death occurred at this threshold (Dickinson & Johnson, 2004). It is thought that protein denaturing is the primary cause for death at this temperature (Dickinson & Johnson, 2004) and that damage to lipids occurs around 45°C (Schönbeck et al., 2023). Grasses seem well adapted to withstand heat stress given that many of them grow in arid and semi-arid environments. Furthermore, grasses thrive in areas that are regularly disturbed by fire. The insulation of soil around the buds of grasses prevents them from experiencing temperatures that would result in 100% bud death when fires burn through grasslands (Choczynska & Johnson, 2009) .

The survival rates assumed by Choczynska and Johnson (2009) are based on the assumption that 60°C is the lethal temperature for grass buds. There are few studies that have tested the thermal limits of perennial grass buds (Jameson, 1961; Wright, 1970). Both studies on the subject suggest that grass buds may be able to withstand temperatures greater than 60°C and that their heat tolerance has some plasticity across the year.

1.5 SGS Site Description

1.5.1 The Shortgrass Steppe Ecoregion

The Western shortgrass steppe of North America (Figure 1.1) covers approximately 435,000 km^2, occurring just east of the Rocky Mountains (WWF, 2006). It is one of the richest ecoregions in North America for butterflies, birds, and mammals (WWF, 2006), indicating that it promotes biodiversity. Until 2013, this region contained a long-term ecological research (LTER) site which is where the majority of the research on this ecosystem occurred. The LTER site for the shortgrass steppe was situated within the Central Plains Experimental Range, controlled by USDA-ARS. The dominant land use for this region is for livestock grazing.

1.5.2 Climate

The shortgrass steppe receives between 250-500mm of precipitation, 75% of which falls during the growing season (April – September) (Kaplan et al. 2014; Mowll et al. 2015). The average temperature ranges from ~7-14°C (Mowll et al. 2015) with the coolest temperatures in December – February (mean < 0°C) and the warmest in July/August (mean ~ 20°C) (Parton and Greenland, 1987). The semi-arid climate is largely due to the rain shadow of the Rocky Mountains and elevation (Pielke and Doesken, 2008).

The shortgrass steppe has low humidity, high intensity solar radiation, and large diurnal temperature variations due to its high elevation and interior continental location (Pielke and

Doesken, 2008). Furthermore, the rain shadow that is generated by the upward motion of on the western side of the Rocky Mountains and followed by the downward motion on the eastern side. This causes cloud formation and precipitation on the eastern side of the mountains leading to limited clouds and precipitation on the shortgrass steppe (Pielke and Doesken, 2008). However, there is a period from March to May when moisture from the Gulf of Mexico brings cloud formation and precipitation to the SGS (Pielke and Doesken, 2008). The high temperatures along with low humidity led to generally high VPD in this region.

For the shortgrass steppe, spring precipitation usually occurs as snowfall (with March and April being the snowiest months of the year) and thunderstorms; these spring storms tend to move slower and so the precipitation events can last up to 3 days and cover large areas (Pielke and Doesken, 2008). Thunderstorms continue during the summer, but these storms are generally pulse rain events that are patchy with high intensity rainfall over small areas (Pielke and Doesken, 2008).

1.5.3 Soils

The semiarid climate of the shortgrass steppe has led to the formation of Mollisols and Aridisols in the surface layers with subsurface soil horizons consisting of cambic and calcic soils characterized by minimal alteration of parent material and zones of secondary carbonate, respectively, both of which are attributed to limited precipitation (Kelly et al., 2008). The texture of the soils for the shortgrass steppe consists of sandy loam throughout the soil profile (Kelly et al., 2008).

Most of the carbon and nitrogen in the shortgrass steppe are found in the belowground soil organic matter, due to the high allocation of resources into root biomass accompanied by slow decomposition rates (Burke et al., 2008b). Nitrogen deposition is the primary source for new nitrogen in the system. The addition of nitrogen (both wet and dry) caused an increase in NPP and a shift in community composition that favored forbs, which have a lower NUE, allowing the potential for a positive feedback from their higher nutrient litter (Burke et al., 2008b).

The texture of soil influences the infiltration rate of water during and following precipitation events, which is especially important in the SGS due to the periods of high evaporative demand between precipitation events. The phenomenon of soils with a greater sand content promoting deeper infiltration and subsequently less evaporative loss is known as the inverse texture hypothesis. This can be observed in semiarid regions where soil evaporation is significant and annual precipitation is less than 370 mm (Augustine et al., 2017; Noy-Meir, 1973). In these regions, sandier soil leads to increased NPP and favors species with higher requirements for soil moisture. This can be seen to some extent by the experiment by Heisler et al. (2009) which found that having larger precipitation events with longer dry periods in between events significantly increase production on the SGS by 30%, due to increased infiltration of water in the soil leading to a greater residence time for soil moisture; this caused a 19% increase in soil moisture for the SGS across the growing season. The relationship between production and soil texture/infiltration suggests that cattle may prefer to graze on areas with sandier soil that experience greater rain use efficiency. Cattle grazing is also influenced by the topography of the SGS.

1.5.4 Dominant Plant Species and Primary Production

The primary production of the shortgrass steppe varies between approximately 50-150g m^{-2} yr^{-1} depending on precipitation (Munson and Lauenroth 2014). This region is dominated by C_4 grasses, primarily *Bouteloua gracilis* and *Bouteloua dactyloides* (Munson and Lauenroth

2014). The height of plant cover is approximately 7-12 cm and is very patchy (Reigel 1941, Webb 1941).

B. gracilis and *B. dactyloides* account for 70% of the vegetation of the shortgrass steppe. Both are perennial grasses and occur within the same guild (Aguiar, 1995); however, *B. gracilis* has a cespitose growth form (Riegel, 1941) and *B. dactyloides* has a stoloniferous (Webb, 1941). Both species are resilient to grazing, but *B. gracilis* is more drought tolerant and *B. dactyloides* is more resilient to local disturbances (i.e., being covered with cattle feces) (Aguiar, 1995).

1.5.5 Disturbance

Both *B. gracilis* and *B. dactyloides* are tolerant of grazing (Winter et al., 2002) and drought (Aguiar, 1995), which are the major forms of disturbance for this system. However, *B. gracilis* has been shown to be extremely drought tolerant which allows it to outcompete other species that occur in this semi-arid ecosystem (Aguiar, 1995).

Herbivory is a major disturbance in the shortgrass steppe. Some herbivores include cattle, jackrabbits, cottontails, rodents (including the kangaroo rat and grasshopper mouse), macroarthopods, microarthropods, and nematodes. While the percentage of grass consumption varies between consumers, the total amount of herbivory is divided fairly equally between cattle, arthropods, and nematodes (Milchunas et al., 1998). While Milchunas et al. (1998) accounted for the majority of herbivores of the shortgrass steppe, they excluded prairie dogs.

Prairie dogs (*Cynomys*) on the shortgrass steppe occur in small, disconnected colonies (Stapp et al. 2008) that are fragmented by topography, soils, and abundance of vegetation (Koford, 1958). The colonies used to comprise 10-20% of the landscape but have been reduced to just 1.5% (Stapp et al. 2008). Prairie dogs play a major ecological role for both flora and fauna. They have been shown to alter plant species composition by providing germination sites for exotic species at their burrowing sites, however this does not cause an alteration in species richness (Stapp et al. 2008). Prairie dogs have little effect on the abundance of arthropods, except for grasshoppers, which tend to decline in populations on prairie dog communities (Stapp et al. 2008). They have varying effects on the abundance of individual bird species, but their colonies promote overall avian richness, likely due to increased raptors that prey on prairie dogs (Stapp et al. 2008).

There is not an abundant amount of research for fire disturbance in the shortgrass steppe. However, the research that has been done has shown fire disturbance has neutral to positive effects on *B. gracilis* and *B. dactyloides* (Stapp et al., 2008,Scheintaub et al., 2009; Augustine et al., 2014).

1.5.6 Land-Use

The conversion of grasslands to agricultural lands reduces the soil organic matter and fertility largely due to tillage increasing erosion and decomposition (Mosier et al. 2008). Most land-use changes on the shortgrass are to a wheat-fallow cropping system (Mosier et al. 2008). The tillage, irrigation, and fertilization associated with agriculture increase the invasibility of the shortgrass steppe (Burke et al., 2008a). However, the spread of exotics into natural conditions of the shortgrass are limited due to restrictions of water and nutrients, and livestock grazing, which allow native plants to out compete the exotic plants (Burke et al., 2008a).

1.5.7 Climate Change

The North American Plains are anticipated to experience decreased precipitation and increased temperatures as a result of global climate change ((Lukas et al., 2014)). The aridification of the western United States will likely lead to shifts in community composition (Burke et al., 2008a) and possibly ecoregion boundaries. These shifts will occur not only because of the direct effects of altered precipitation, but also because of the effects precipitation changes will have on nutrient cycling and decomposition rates (Burke et al., 2008a).

It is also anticipated that elevated CO_2 will result in alteration in water use efficiency; plants will be able to decrease water loss by decreasing stomatal aperture (Burke et al., 2008). This will allow the plants to maintain a high NPP with minimal water loss because the higher concentration of atmospheric CO_2 will allow for a higher diffusion rate of CO_2 through the stomatal opening. These changes in precipitation, nutrient cycling, and photosynthetic efficiency make the impacts of climate change on grassland systems very difficult to predict.

1.6 Conclusions

Grazing disturbances from both domesticated and natural herbivores on the shortgrass steppe maintain the dominance of *B. gracilis* and *B. dactyloides* (Porensky et al., 2016). In accompaniment with grazing, precipitation gradient is the major driver for the development and maintenance of the ecoregion, where the ability of the shortgrass species to take advantage of pulse rain events allow them to utilize small inputs of water that rarely infiltrates into lower soil horizons. Most of the competition on the SGS takes place belowground. The root systems of the dominant species on the SGS are shallow rooted to take advantage of pulse rain events however many of the species do have a lower proportion of roots that penetrate into deeper soil layers beyond 1m depth (LeCain et al., 2006).

Since the limited precipitation in the shortgrass system is a strong enough disturbance to maintain its species composition, alterations in precipitation patterns could have a major impact on the region, especially considering how tightly precipitation and production are linked (Hoover et al., 2021). Alterations in climate may lead to variations to annual precipitation or the annual distribution of precipitation, with climate models predicting droughts increasing in both frequency and intensity in the southwest of the United States (Groisman & Knight, 2008). It is also thought that this will likely involve longer dry periods followed by short intense storms. These changes will likely lead to shifts in community structure and will make management of this system even more difficult. However, understanding what drives the mortality of these species will provide valuable insight into how to manage the system in the face of a changing climate.

In this research, I sought to determine how combinations of stress variables influence the shortgrass steppe, this includes: long-term grazing, drought, erosion, and temperature. Specifically, I examined (1) how the interaction of long-term grazing and influences the recovery of the vegetation on the SGS following single-year and multi-year droughts, (2) how the interaction of grazing and erosion influence mortality following exposure to extreme surface temperatures, and (3) performed a comparative analysis of the microclimate of grass dominated systems in the United States to determine the intensity and frequency of stressful abiotic conditions that the vegetation experiences.

1.7 Figures and Figure Legends

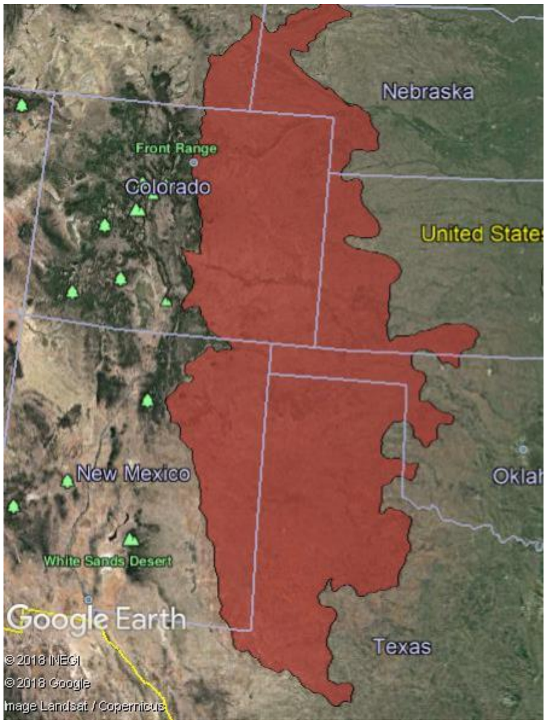

Figure 1.1: The red region on the map represents the Western short grasslands of North America as defined by the World Wildlife Fund (2006).

CHAPTER 2: INTERACTIVE EFFECTS OF DROUGHT AND GRAZING ON THE PLANT SPECIES COMPOSITION ON THE SHORTGRASS STEPPE

2.1 Introduction

Grass dominated ecosystems account for approximately 40% of the earth's terrestrial surface and are known for being incredibly resistant to disturbances such as fire, grazing, and drought. Many of these grass dominated ecosystems occur in semi-arid climates, meaning that small changes in climate could push this system to a different precipitation regime with unknown consequences of vegetation structure and/or function. In addition to growing in water limited areas, vegetative production is consumed by a wide range of herbivores (Milchunas et al., 2008). The water limitation and grazing pressure promotes the dominance of perennial grasses due to their capacity to withstand high levels of disturbance.

2.2.1 Droughts in Grasslands

Even though perennial grasses are well adapted to varying environmental conditions, extended periods of drought can challenge the resilience of these vital ecosystems. Depending on the length, intensity, and frequency of droughts, perennial grasslands can experience reduced aboveground biomass (Carroll et al., 2021), shifts in species composition (Evans et al., 2011), altered allocation of resources (Oram et al., 2023), and delayed recovery (Reichmann et al., 2013; Reichmann & Sala, 2014). The delayed recovery, which is a negative legacy effect of the drought, is associated with meristem limitation in the bud bank in the year(s) following droughts (Ott et al., 2019b; Reichmann et al., 2013). Although production on grasslands is tightly related to current year precipitation (Sala et al., 1988), the production from the previous year also influences the capacity of production in the current year (Oesterheld et al., 2001), due to the relationship between tiller density and density of buds in the bud bank (Luo et al., 2023).

The shortgrass steppe (SGS) is particularly tolerant of droughts and is dominated by grasses that were observed growing from existing crowns (not from seed) following the Dust Bowl (Mueller & Weaver, 1942). Furthermore, precipitation exclusion experiments have shown that it can take up to a decade of severe drought to induce shifts in species composition that result in the loss of dominance by the C_4 perennial grasses, *Bouteloua* species (Evans et al., 2011). The *Bouteloua* species maintain their dominance on the SGS due to their tolerance of disturbance experienced by the SGS, because grazing and water availability are the driving factors for plant diversity on the SGS (Milchunas et al., 1988). While these studies have shown the stability of the SGS, they fail to account for the interaction of grazing and drought.

2.1.2 Grazing in Grasslands

Grazing tolerant species share a suite of traits that make them well adapted to survive this disturbance, mainly: fast regrowth, high allocation of resources to belowground, and basal meristems. Being able to quickly replenish the area of photosynthetically active vegetation that was consumed by herbivores allows the plants to only experience a small lag in lowered assimilation due to defoliation. This fast growth is supported by a robust root system that allows for rapid uptake of resources. Grazing tolerant species often invest heavily in their root systems accounting for up to 80 percent of the biomass of perennial grasses. Finally, in order to produce aboveground vegetation, the plant needs viable meristems. Perennial grasses have adapted basal meristems, which prevent the meristems from being damaged or consumed by herbivores. This is especially important for perennial grasses because they rely mainly on asexual reproduction. The combination of these traits allows for perennial grasses to dominate in ecosystems that experience removal of aboveground vegetation.

The plant species of the SGS evolved in the presence of grazing which led to the ecosystem being dominated by short grasses (Milchunas & Lauenroth, 1993). The *Bouteloua* species account for 70-90% of the vegetation cover in the SGS (Lauenroth & Burke, 2008). The dominance of C_4 perennial grasses increases with increased grazing intensity (Porensky et al., 2017). The SGS has proven to be incredibly resilient in the presence of grazing and takes decades of a continuous grazing intensity in order for changes in plant species composition to occur (Augustine et al., 2017; Porensky et al., 2016, 2017).

2.1.3 Drought and Grazing on the Shortgrass Steppe

Like all semi-arid regions, the low mean annual precipitation (MAP) makes the SGS susceptible to drought. It is anticipated that the frequency and severity of droughts will increase in the face of global climate change (Groisman & Knight, 2008). While there has been a fair amount of research on how the SGS responds to grazing and drought independently, there are only a few studies on how long-term grazing intensity impacts the resilience of the dominant perennial grasses to droughts (Irisarri et al., 2016; Milchunas et al., 2008; Varnamkhasti et al., 1995).

The interaction between grazing and drought in previous research was limited to heavy cattle grazing as the most intensive grazing metric. However, the combination of prairie dogs and moderate cattle grazing removes more biomass than heavy cattle grazing, as prairie dogs are able to crop vegetation at a lower height than cattle and are the most intensive form of herbivory that is experienced by the SGS. Furthermore, these studies only observe a drought in a single year, not multiple years. While there have not been back-to-back years of extreme drought in the 30-year climate record, it is a possibility that could occur and knowing if the system responds differently to the interactive effects of multiple years of drought and grazing in the system, is crucial for making informed decisions about land management as the effects of climate change begin to affect these regions. While I don't know how increasing the length of droughts will affect the system under varying grazing intensities, I anticipate the combination of stresses on plants limits their capacity to cope with either stress individually. This will inform land managers whether or not they need to limit the grazing during times of intense or prolonged drought in order to set the plants up for the best possible recovery following the drought.

To gain insight on the interaction between grazing and drought, I set up a precipitation removal experiment. During the experiment, the SGS experienced a natural drought during the summer of 2020, which was one of the driest years in the 30-year data record (Sup. Fig. 1). The drought of 2020 received 239 mm of precipitation, about 25% less than the MAP. This provided us with an opportunity to examine the difference between a one- and two-year drought with a grazing interaction based on three long-term grazing intensities, non-grazed, heavy grazed, and moderate cattle grazed with prairie dogs. Which led us to the following questions:

1. Is the SGS able to recover from a multi-year drought the same that it does a one-year drought?
2. What impact does grazing intensity have on vegetation cover during the two drought scenarios?
3. Does grazing intensity influence capacity for the recovery of vegetation from droughts?

2.2 Materials and Methods

This research was conducted at the Central Plains Experimental Range (CPER) located approx. 15 km north of Nunn, CO (40°49'N 107°47'W). The site receives, on average, 338 mm of precipitation annually with 70% occurring in the growing season, April-August (CPER HQ 1939-2021). I conducted this research on 3 sites that have experienced substantially different long-term grazing intensities since CPER was established long-term non-grazed (0% utilization), long-term heavy cattle stocking rate, and long-term moderate cattle stocking rate combined with intensive grazing by prairie dogs. The non-grazed treatment consists of a 1.6 km x 12 m strip of land that has neither been grazed by cattle nor prairie dogs over the past 70 years. The long-term heavy cattle grazing treatment occurs in an adjacent 130-ha pasture that has been stocked at 50% higher stocking rate than the long-term moderate stocking rate each year annually since 1939 (Porensky et al. 2017). The long-term moderate stocking rate was initially set by experiments conducted by Bement (1969) at CPER during 1939 – 1960 and has subsequently been increased slightly in recent decades in response to increasing ecosystem productivity (Augustine et al. 2020; Raynor et al. 2021). Moderate and heavy stocking have been estimated to result in removal of approximately 40% and 60% of ANPP in average years (Milchunas et al. 1995, 2008). My third study site has historically been grazed by cattle at a moderate stocking rate, and then was initially colonized by prairie dogs in the mid-1990s. Over the past 25 years, prairie dog colonies have expanded and contracted on the site in response to disease outbreaks (Hartley et al. 2009; Augustine et al. 2014). My third grazing intensity treatment consisted of a site that was both actively grazed by prairie dogs throughout 2018 – 2021 and was grazed by cattle at a moderate stocking rate during the growing season. There is no estimate for the utilization by the prairie dogs, but cattle are typically unable to crop vegetation below 1 cm height whereas prairie dogs can defoliate individual tillers nearly to the ground surface. As a result, the combination of moderate cattle stocking combined with prairie dogs removes more biomass than the heavy cattle grazing treatment (Whicker & Detling, 1988). Pastures at CPER were grazed by yearling steers that were present from mid-May until early October each year.

It should be noted that the grazing treatments were not replicated, because there is only one strip of land at CPER that has been in the absence of grazing since the grazing treatments were established at the site in 1939. However, the plots in each pasture were spatially separated by > 10 m, which allows for the sampling of genetically independent individuals of *B. gracilis* (Butterfield & Wood, 2015). The non-grazed plots were established on 4 different upland sections of a strip of land approximately 6 meters wide that lies just East of pasture 23E, respectively. The upland locations were selected to prevent water run-off and pooling from occurring in the plots. This had an effect on my species composition because C_3 grasses occur more in the lowland areas (Milchunas & Lauenroth, 1989) due to increased water availability. The moderately grazed with prairie dog plots were established in a nearly flat sections of the colony with similar soils as the other two grazing treatments, but plots were not located at the highest topographic positions because there were no prairie dog colonies at the highest elevation in this pasture.

Rainout shelters were constructed and implemented in June of 2018 and removed in March of 2020. The shelters were 3 x 3 m, with the side facing the prevailing wind direction (western side) approximately 0.25 m above the ground and the eastern side of the shelters were approximately 1 m above the ground. Corrugated polycarbonate panels were used to block 80% of the precipitation. The plots were 1m^2 located in the center of the rainout shelters.

In the two sites with cattle grazing, I constructed a 9.75 x 9.75 m exclosure around each shelter (4 per site) at the time the rainout shelters were established. Each exclosure included both the control plot and rainout shelter plot. Each growing season during 2019 – 2021, I simulated cattle grazing in my treatment plots to investigate the interactive effects of drought and grazing. Cattle grazing intensity was estimated by establishing four 1-m^2 plots outside of the grazing exclosures in the heavy grazed and moderated grazed + prairie dog pastures. I visited the plots outside the cattle exclosures every 30 days during the growing season and counted the number and type of bites associated with cattle grazing on each of the plots. I then manually simulated the same number and type of bites on the plots located inside the exclosure, in both the rainout shelter and in the adjacent control plot. Grazing in the plots was simulated by grasping vegetation between the thumb and side of the hand, then pulling the vegetation until it was removed from the plant. This mimics the way cattle grasp and tear the vegetation using their lower incisors and upper lip. Biomass removed via simulated grazing inside the exclosures was collected, dried at 60°C for at least one week, and then weighed (Sartorius CPA6202P, ± 0.005g, Göttingen, Germany). This amount of biomass removed by simulated grazing was added to the annual net primary production (ANPP, see below). No grazing was simulated in the long-term no-grazing plots. The biomass removed by the prairie dogs could not be accounted for because the animals consumed the vegetation directly from my plots as they were not excluded by my fencing, but scat, clipped vegetation, and the development of new burrows within the exclosures confirmed regular presence of prairie dogs throughout the study. I assume that the grazing pressure by prairie dogs inside the cattle exclosures at this site was similar to 'natural' conditions outside the exclosures.

Species composition, cover, and Green Vegetation Index (GVI, Lecain et al., 2002) were estimated using the point frame method. Point frame measurements were collected for nearly the entire growing season from 2019-2021. July data was used for analysis because it captured peak production for both C_4 and C_3 perennial grasses (data not shown), which together account for the majority of the vegetative cover. The point frame was 1 m^2 with perpendicular transects centered on the sides of the frame; the points were spaced 5 cm apart along the transects. If any green vegetation touched the pin, the species and number of times its green plant material touched the pin 'hits' were recorded. The parameters I derived from the point frame are represented by the following equations:

$$cover = \frac{number\ of\ pins\ with\ hits}{number\ of\ pins} \qquad \text{Eq. 1}$$

$$GVI = \frac{total\ \#\ of\ hits}{total\ number\ of\ pins} \qquad \text{Eq. 2}$$

To quantify production, I clipped all aboveground biomass to 1 cm above the soil surface at the end of the growing season (August or September) from 0.0625 m^2 sections of each plot, dried at 60°C for at least one week, and then was weighed (Sartorius CPA6202P, ± 0.005g), and scaled the data to 1 m^2. The biomass removed from simulating cattle grazing was then added to the scaled data. I only accounted for the biomass removed by cattle grazing; I was not able to account for biomass removed by prairie dogs.

Recovery was calculated by comparing the parameters in the recovery year to what they were prior to the droughts. This was done by subtracting the values for the recovery year (2021) by the values of a plot from the plot pairs that didn't experience drought (the 2019 single-year drought plots). The data was then fit to a linear regression model, main effects being 'grazing treatment' and 'drought treatment'.

Precipitation data was from a manual precipitation gauge located at CPER headquarters, which is checked every weekday morning.

Statistical analysis was conducted in R (v4.3.1, R Core Team, 2023) and consisted of a generalized block model using the lme4 package (Bates et al., 2015) with the major factors consisting of 'Grazing', 'Drought', and 'Year'. With the error accounting for the repeated measures of the individual plots.

2.3 Results

2.3.1 Weather Patterns

The SGS experienced a drought in 2020 that was the second driest year in the 30-year data record according to the CPER headquarters precipitation data (Sup. Fig. 2.1). The annual precipitation for the drought year was 33% lower than the 30-year average, with the years before and after the drought receiving 14.55% and 21.04% less than the 30-year average, respectively. Precipitation was lacking at CPER during the months of March, April, May, and July (Fig. 2.1), during the drought year.

2.3.2 Vegetation Response to Drought

There was a marginally significant interaction term for the 3-way interaction for four response variables: cover, GVI, C_3 GVI, and ANPP (Table 2.1). Given the low power of the 3-way interaction test, I interpreted this as support to test for effects of drought treatment in each of the 'year x pasture' combinations.

The plant vegetation cover of the multi-year drought was significantly lower than the single-year drought for the HG and PD pastures across all years (Fig. 2.2). While the NG pasture experienced a decrease in cover, the difference between the single-year and multi-year drought was only significant in 2019, before the natural drought.

The GVI had a similar trend as vegetation cover (Fig. 2.3), with all grazing treatments having a significant difference between the simulated drought and control in 2019. The difference was maintained in the drought year (2020) for the HG and NG pastures, with the control having a higher GVI than the simulated drought. There were no significant differences in any of the grazing treatments in the recovery year (2021).

The C_4 GVI had a significant 2-way interaction for the year x grazing combination which showed that 2019 was significantly different than 2020 and 2021 (Fig. 2.4). There was not a significant difference between the drought year (2020) and the recovery year (2021), indicating that the C_4 grasses were unable to recover to their pre-drought level of GVI.

While there were differences between the two drought conditions throughout the experiment, there were no significant differences in the ANPP (Fig. 2.5). There were some fluctuations in ANPP, but the drought treatments followed a similar trend throughout the experiment. However, it should be noted that the multi-year drought in the PD pasture failed to recover to the same extent as the single year drought.

2.3.3 Vegetation Recovery from Drought

I found recovery of the cover was the only parameter that show a significant difference between the two drought treatments (Fig. 2.6, $p<0.001$). Multi-year droughted plots experienced a 41-54% decline in cover, with cover decreasing with increasing grazing pressure. Single-year droughted plots experienced an 18-28% decline in cover, with cover increasing as the grazing pressure increased. While none of the grazing treatments had a complete recovery, my research showed grazing doesn't have negative impacts on recovery for single year droughts, but does have negative impacts in multi-year droughts.

There is a marginally significant difference in drought treatment in terms of GVI recovery (Fig 2.6, $p=0.076$). GVI was only able to recover 20-40% of what it was prior to the drought with the multi-year droughted plots having a poorer recovery than the single-year plots across all grazing treatments. While the impacts of grazing were not significant, both drought treatments are negatively correlated with grazing.

ANPP differed among the grazing treatments ($p=0.021$), but not for the drought treatments. Like GVI, there was a negative correlation with ANPP recovery and grazing intensity (Fig. 2.6). The NG and HG pastures recovered to at least 97% of what they had prior to the droughts. However, the PD treatment only recovered to 57% of what it was producing prior to the drought.

2.5 Discussion

The dominant plant species of the SGS are characterized as being tolerant of drought (Evans et al., 2011; Mueller & Weaver, 1942) and grazing (Milchunas et al., 1998, 2008; Milchunas & Lauenroth, 1989; Porensky et al., 2017), yet the combination of these disturbances is rarely studied. With changing precipitation patterns occurring in the regions where these ecosystems occur (Groisman & Knight, 2008), it remains unclear how vegetation will respond to the combined impact of drought and grazing. Here, I examined whether SGS vegetation response to single year versus multi-year drought conditions differs, and whether this difference is contingent on the grazing regime. Broadly speaking, I found that ANPP recovered equally well from single and multi-year drought both in communities that lack any form of mammalian grazing (and hence include mixture of C_3 and C_4 perennial grasses) and in communities that develop under and continue to experience heavy cattle grazing (dominated by C_4 perennial shortgrasses). In contrast, communities experiencing intensive grazing by a combination of prairie dogs and cattle differed in their response to single versus multi-year drought. Specifically, I found that with the most intense grazing treatment, ANPP recovered from a single-year drought (as it also did with heavy cattle grazing) but did not recover from a multi-year drought, in contrast to the recovery observed with heavy cattle grazing (Fig. 2.5). My results reinforce the idea that the SGS is an ecosystem resistant to disturbance, but also identifies a potential ‘tipping point’ when disturbance is too great for this system to resist. My results also highlight the need to investigate the interaction between different grazing treatments and drought because differences in grazing pressure, such as the added effect of prairie-dogs, can change the outcome on plant performance during drought.

I also found that the multi-year drought resulted in a greater decrease in vegetation cover than during a single-year drought, regardless of the intensity of the grazing pressure. Further, the vegetative cover failed to recover to the same extent following a multi-year drought compared to the single-year drought for all grazing intensities (Fig. 2.2). However, higher grazing intensities led to greater differences in the means of vegetative cover in response to drought. With the exception of the prairie dog treatment, all of the plots came close to recovering to the same pre-drought vegetation cover that they had prior to the natural drought (cover in 2019), during the first post-drought year (2021).

Interestingly, for the single-year drought, there was a positive relationship between grazing and recovery for vegetation cover, but in the multi-year drought the relationship was negative (Fig. 2.6). This suggests that grazing doesn’t have a negative impact on vegetation cover. It should also be noted that the NG treatment was less impacted by the multi-year drought having a mean reduction in cover of 20% compared to 38% and 32% reductions in cover for HG and PD pastures, respectively.

While some of the cover indices came close to a full recovery in 2021 (about 80% of what they were in 2019), the GVI failed to reach the same levels as in 2019 for all the grazing and drought treatments (Fig. 2.3). GVI accounts for both cover and density of the vegetation canopy, so this indicates that the density of the vegetation had failed to recover; this means that approximately same number of pins had hits but the number of hits per pin had decreased. The primary reason for this decrease in GVI is the reduction of the dominant perennial grasses (Fig.

2.4). It is common for perennial grasslands to experience negative legacy effects following droughts due to meristem limitation (Geber, 1990; Ott et al., 2019; Reichmann & Sala, 2014).

While there were fluctuations in cover and decreases in GVI, the ANPP was fairly stable during both the drought years and recovery years. This was attributed to the replacement of the short statured grasses with taller species, such as *Elymus elymoides* and *Salsola iberica*. This shift in species composition has been observed at the SGS after multiple years of drought (Evans et al., 2011). While the overall increase in vegetation cover of the other species was small, the biomass per individual is much higher in the forbs. This maintained the ANPP because the presence of one new forb individual could make up for large losses of perennial grass biomass. The increase in forbs was observed in the in the NG and HG pastures but not in the PD pasture, which explains why the prairie dog plots experienced a greater decline in ANPP, than the other grazing treatments. Prairie dogs often clip large stature vegetation that would otherwise obstruct their view for potential predators (Whicker & Detling, 1988).

2.6 Conclusion

My research highlighted the stability of ANPP on the SGS while also showing that there is a tipping point to this ecosystem if there is a two-year drought combined with high grazing pressure. In contrast to the stability of ANPP, I found that cover and GVI experienced large reductions, most of which was attributed to declines in the dominant C_4 perennial grasses. The ANPP was able to remain stable because larger statured grasses and forbs increased in cover when the short statured C_4 perennial grasses decreased in cover.

This research supports the need to investigate the interactions between grazing and drought in other grassland systems. Given that the shortgrass steppe is known for being drought and grazing tolerant, and the combination of these stresses was capable of pushing the *Bouteloua* species past their tipping point of survival in such a short time suggests that grasslands that are not as well adapted to these conditions would likely start to fail under a combination of these conditions.

2.7 Figures and Figure Legends

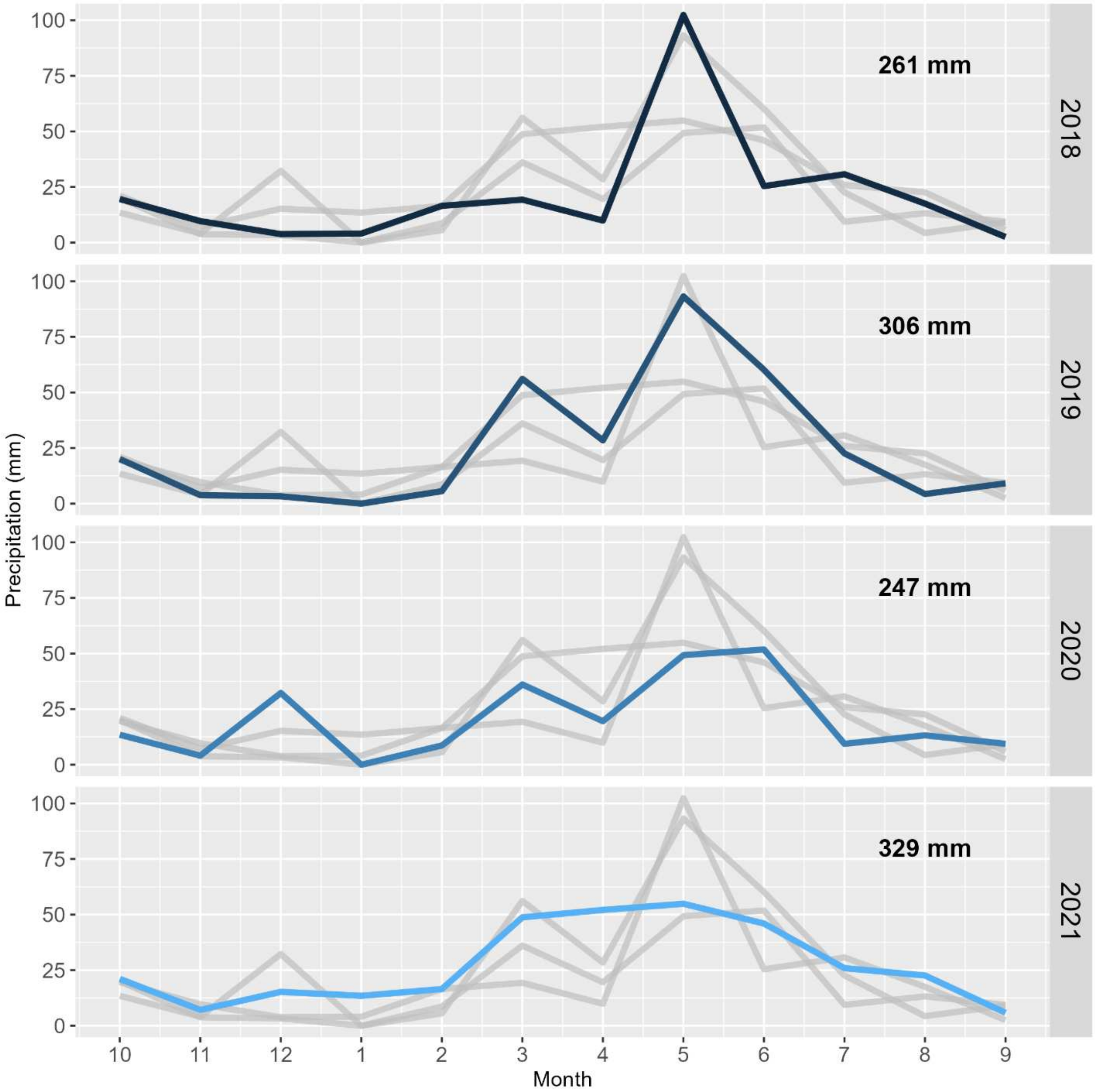

Figure 2.1: Monthly totals of water year precipitation for 2018-202 at the Central Plains Experimental Range located on the SGS in northeastern Colorado. The colored lines indicate the monthly precipitation totals of the year associated with the facet (indicated on the right) and grey lines represent the monthly precipitation totals of the other years in the study. The values in the upper-right corner of each facet are the total precipitation for the water year.

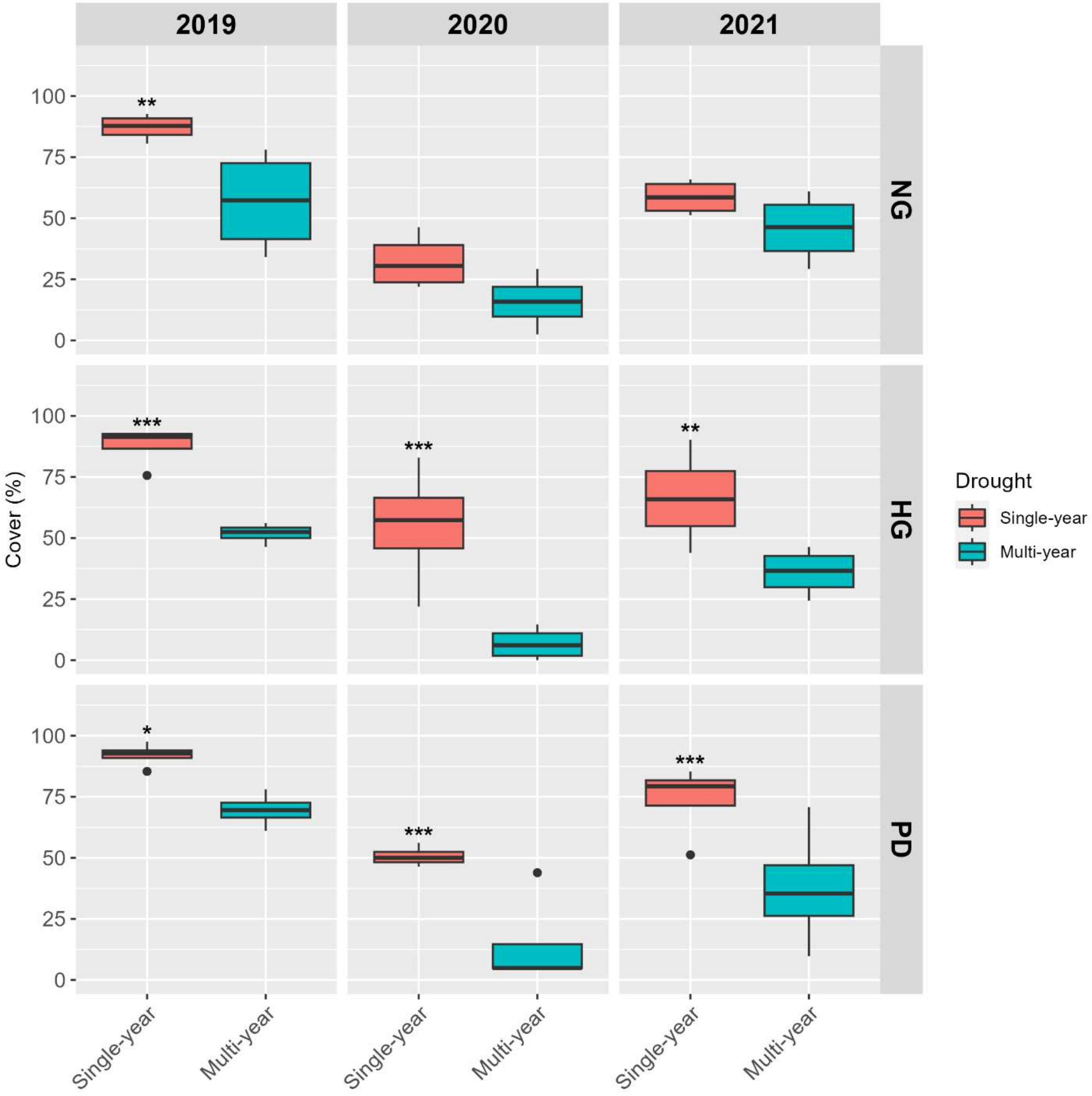

Figure 2.2: Percent green vegetation cover for the different grazing treatments, years, and drought treatment of the SGS from 2019-2021. Each column represents a different year (indicated at the top), and the rows are the grazing treatments (indicated on the right), with non-grazed (NG) across the top, heavy cattle grazed (HG) in the middle and moderately cattle grazed with prairie dogs (PD) across the bottom.

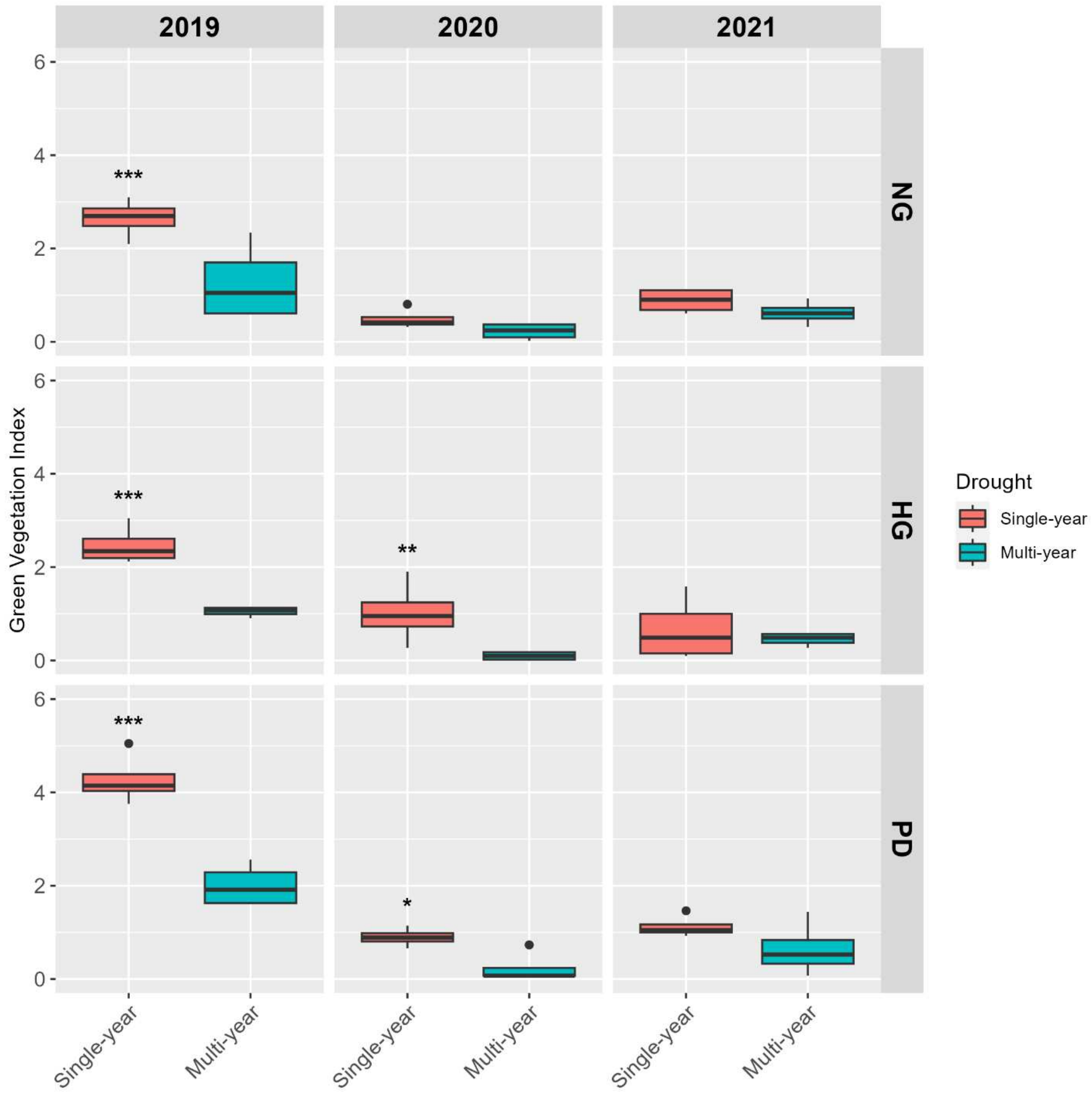

Figure 2.3: Green vegetation index for the different grazing treatments, years, and drought treatment of the SGS from 2019-2021. Each column represents a different year, and the rows are the grazing treatments, with non-grazed (NG) across the top, heavy cattle grazed (HG) in the middle and moderately cattle grazed with prairie dogs (PD) across the bottom.

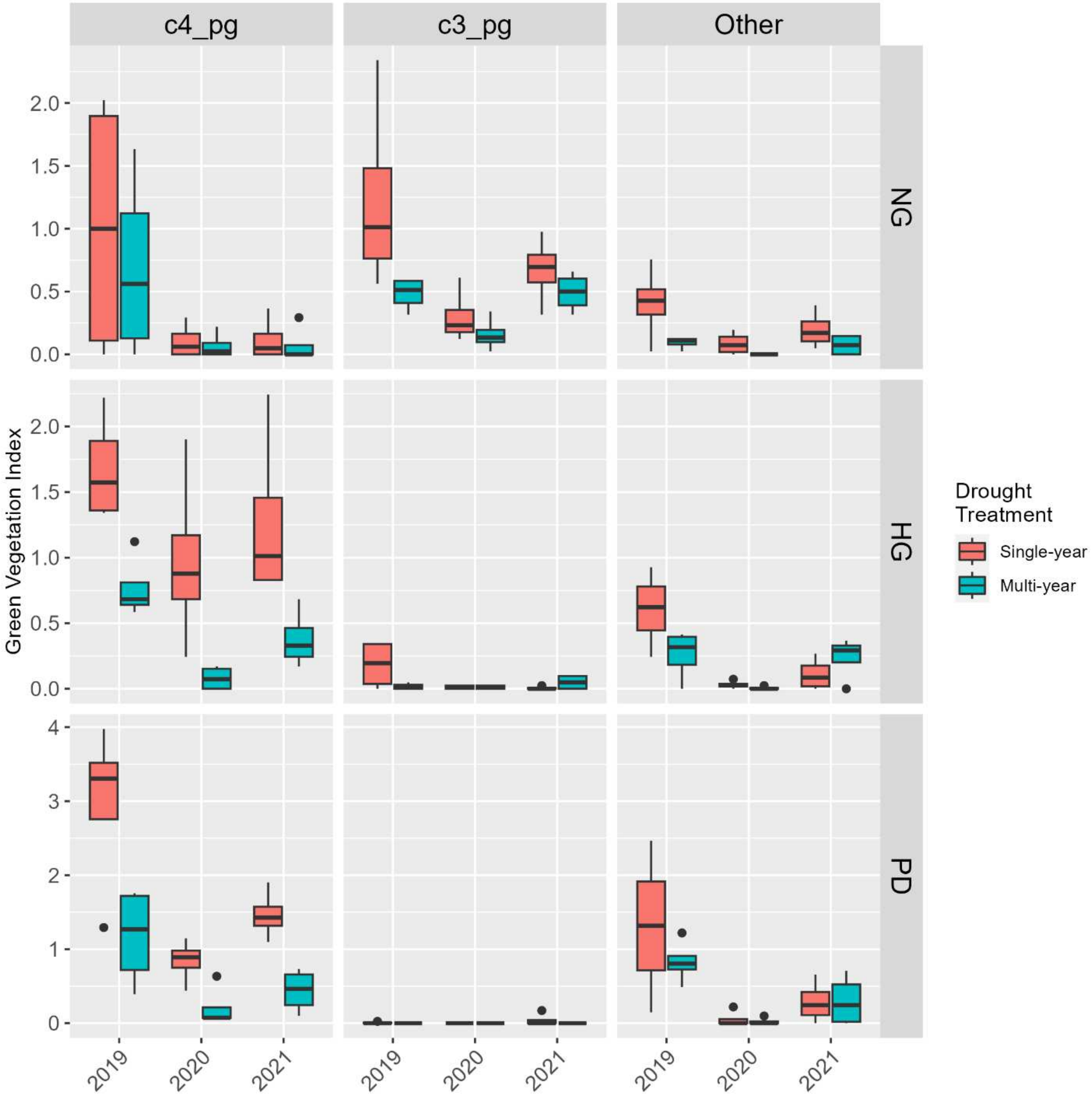

Figure 2.4: Green vegetation index of C4 perennial grasses, C3 perennial grasses, and ‘Other’ functional groups (all non-perennial grasses) at the SGS during the month of July from 2019-2021 for plots that had simulated drought for 1.5 years (turquoise bars) and plots that experienced ambient conditions (red bars). Note that the y-axis is scaled differently for each grazing treatment to help highlight significant differences between treatments. Each column represents a different functional group, and the rows are the grazing treatments, with non-grazed (NG) across the top, heavy cattle grazed (HG) in the middle and moderately cattle grazed with prairie dogs (PD) across the bottom.

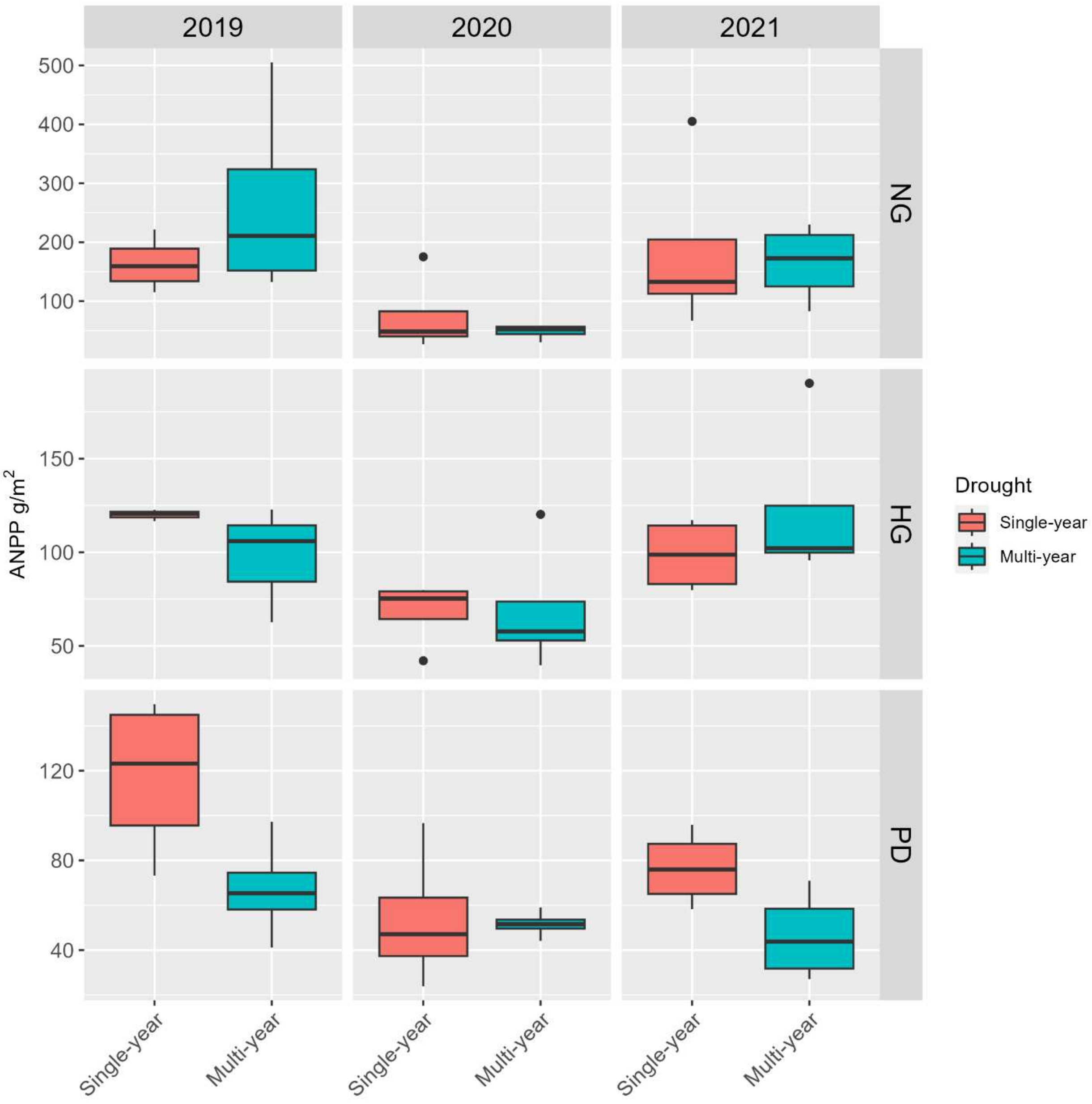

Figure 2.5: Annual aboveground net primary production (ANPP) for the different grazing treatments, years, and drought treatments on the SGS from 2019-2021. Note that the y-axis is scaled differently for each grazing treatment to help highlight significant differences between treatments. Each column represents a different year, and the rows are the grazing treatments, with non-grazed (NG) across the top, heavy cattle grazed (HG) in the middle and moderately cattle grazed with prairie dogs (PD) across the bottom.

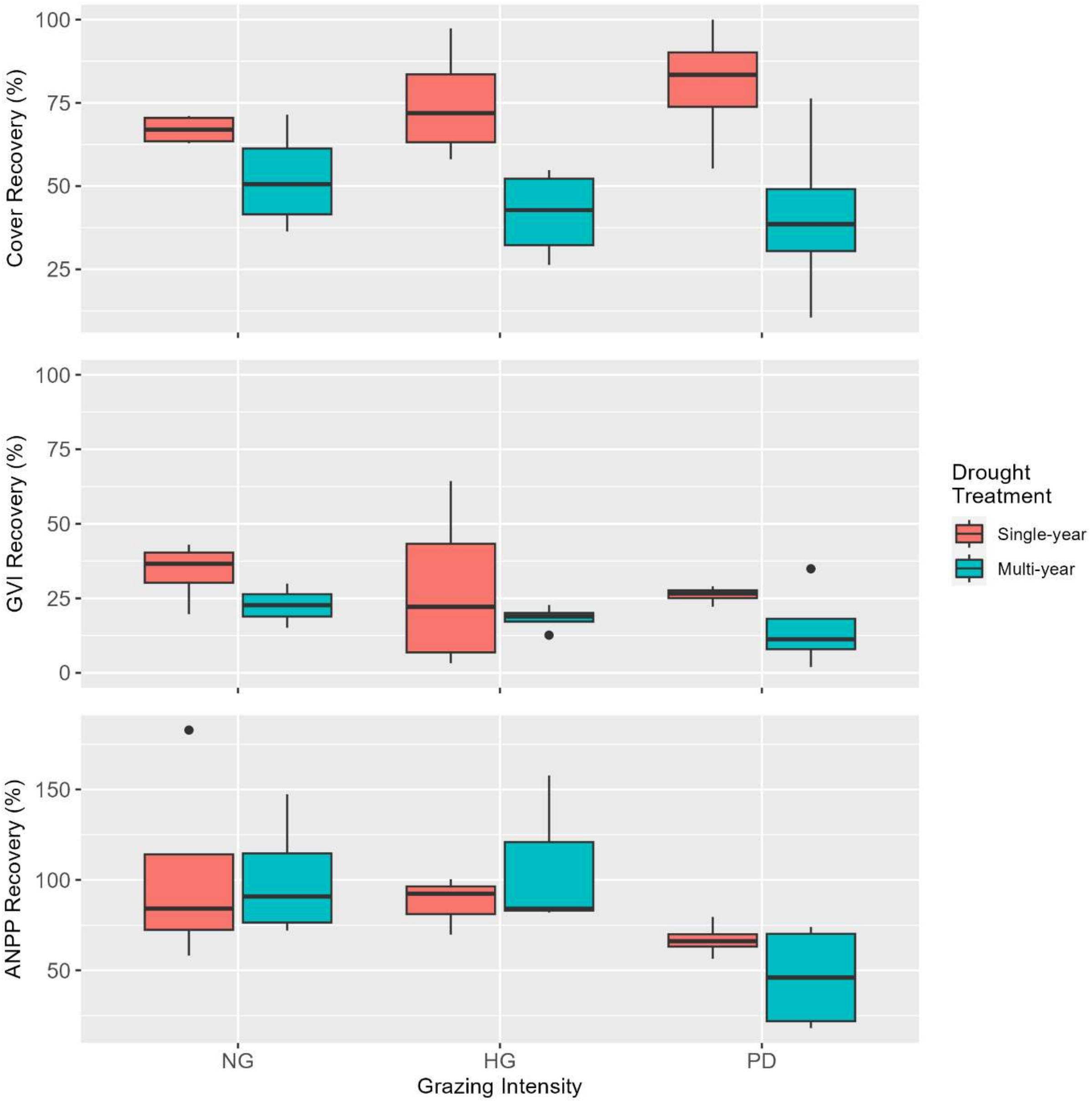

Figure 2.6: The y-axis represents the difference between the single-year drought (red) and multi-year drought (turquoise) in 2021 when compared to plots that haven't experienced a recent drought (the single-year plots in 2019). The x-axis represents grazing intensity in ascending order from left to right. The shading around the lines represents the 95% confidence intervals.

Table 2.1: Type three error p-values for a general complete block design of cover, GVI, and ANPP. The bold p-values indicate statistical significance.

	Cover	**GVI**	**C4_pg GVI**	**C3_pg GVI**	**Other GVI**	**ANPP**
Year	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**
Pasture	0.468	**0.006**	**0.003**	**< 0.001**	**< 0.001**	**0.016**
Drought	**< 0.001**	**< 0.001**	**< 0.001**	0.066	0.052	0.892
Year:Pasture	0.516	**< 0.001**	**0.029**	**< 0.001**	**0.003**	**0.004**
Year:Drought	0.422	**< 0.001**	0.126	**0.012**	0.061	0.758
Pasture:Drought	0.322	0.362	0.062	0.117	0.829	0.675
Year:Pasture:Drought	**0.086**	**0.112**	0.375	**0.056**	0.947	**0.048**

CHAPTER 3: EROSION AND SURFACE TEMPERATURES PUSH THE THERMAL LIMITS OF C4 GRASSES ON THE SHORTGRASS STEPPE

3.1 Introduction

Grasslands are often characterized by, among other things, their ability to tolerate disturbances to their aboveground vegetation such as drought, fire, and grazing. The majority of this biome is dominated by perennial grasses that have traits allowing them to persist on the landscape despite the limited water, including high water use efficiency, small leaf area, and belowground meristems (Lauenroth, Sala, Coffin, & Kirchner, 1994). The belowground meristem possessed by these species occur in the form of buds that contain preformed leaves and are kept at or below the soil surface, referred to as 'bud banks' (Harper, 1977; Ott & Hartnett, 2019). The position of these buds is generally considered to provide protection from aboveground disturbances and harsh environmental conditions (Coughenour, 1985). In large part, the recruitment of new aboveground tillers following disturbances comes from the outgrowth of these buds, so their survival is paramount to the persistence of grasslands. Protecting these tissues is especially important because many perennial grasses have poor seedling establishment and rely heavily on the asexual reproduction for the next year's production (Lauenroth et al., 1994). However, as air temperatures increase and precipitation amounts decrease (Groisman & Knight, 2008; Huntington, 2006), how well these buds are adapted to future climate conditions is uncertain.

Primary production from grassland ecosystems is tightly linked to current year precipitation (Hoover et al., 2021), but there are also impacts to primary production that occur in the previous year's precipitation (Reichmann & Sala, 2014; Sala, Gherardi, Reichmann, Peters,

& Jobba, 2012; Yahdjian & Sala, 2006). These ‘legacy effects’ have been attributed to the number of viable buds in the bud bank, increasing the size of the bud bank following wet years and decreasing the size of the bud bank following drought years (Geber, 1990; Ott et al., 2019; Reichmann & Sala, 2014). The legacy of drought could negatively impact the number of buds through two mechanisms, low production of new buds or bud mortality. Because new buds are produced as tillers develop and mature, the lack of viable buds could result from the lack of tiller production during drought events, which would limit the number available for recruitment the following year. Mortality of buds as a result of the harsh environmental conditions experienced during the drought would also reduce the size of the bud bank but, unfortunately, the environmental conditions that buds experience during droughts have not been well-quantified and so it is unknown how likely bud mortality might be during droughts. If the soil is dry enough and temperatures hot enough, it is feasible that the buds could experience either dehydration or heat related mortality, which would reduce the number of viable buds to resprout following these events.

Indirect effects of drought on plants are often overlooked but could have significant impacts on the long-term productivity of these systems. For example, increased erosion during drought events (Toy et al., 2002) can remove enough soil to expose the otherwise protected buds to more extreme environmental conditions. Erosion on grasslands occurs from both wind and water; the soil is either lifted away by the wind moving across the soil surface or by the impact and runoff of rain drops (Toy et al., 2002). Both forms of erosion are increased during drought years because there is less vegetative cover to reduce wind speed at the soil surface (Li et al., 2007; Munson et al., 2011) and protect the soil/crown from the impact of rain drops (Toy et al., 2002). The amount of soil being removed by the wind is also increased because there is no moisture in the upper layers of the soil to allow the particles to bind together. Although most of the erosion is thought to have small scale impacts (Martinez-Turanzas, Coffin, & Burke, 1997), the lack of vegetation during droughts reduces the plant's capacity to act as a wind break, thus decreasing the capability to promote soil accretion and increasing the potential for erosion (Toy et al., 2002). Since bud banks are so vital for the persistence of perennial grasses (Lauenroth et al., 1994; Ott & Hartnett, 2019) and because of their location near the soil surface, erosion could lead to bud exposure and threaten their survival, so a better understanding of the interactive effects of drought and erosion on plant productivity and survival is important for predicting the future structure and function of the SGS.

Along with increasing the potential for erosion, the limited vegetation associated with drought conditions decreases the shading on the soil and results in increased solar radiation at the soil surface. When the soil around the crown is eroded, the buds are exposed to the harsh environments that the grasses have evolved to avoid. This makes them more susceptible to mortality due to grazing, trampling, dehydration, and heat; with the latter two being the most likely to result in mortality during drought. Primarily focusing on dehydration and heat stress, the loss of the soil around the crown removes the insulation from the dry air and exposes the meristems to solar radiation and surface temperatures, both of which increase the risk of mortality. However, being exposed to surface temperatures alone has the capability to exceed the thermal limits of the meristems (Jameson, 1961) resulting in bud mortality and, potentially, reducing the number of viable buds in the bud bank. Although the thermal limits of perennial grass buds are largely unknown, it is assumed to be at 60°C (Choczynska & Johnson, 2009; Dickinson & Johnson, 2004; Van Wagner, 1973).

To better understand the interactive effects of drought and erosion on the ability of grasses to regrow following drought, I measured the intensity of erosion and regrowth of 2 important species on the Shortgrass Steppe (SGS). The SGS experiences highly variable precipitation, which results in chronically low soil water availability and extended periods of intense water stress (Heisler-White, Blair, Kelly, Harmoney, & Knapp, 2009). *Bouteloua gracilis* and *Bouteloua dactyloides* are the dominant grasses of the SGS, and these perennial C_4 grasses account for 70-90% of the vegetation cover (Lauenroth & Burke, 2008). These C_4 grasses keep their crown/bud bank close to the soil surface (Jacqueline Ott, USFS, Rocky Mountain Research Station, personal communication), making their meristems at a higher risk of being exposed due to erosion compared to other common species that occur at the location. During the summer of 2020 I noticed that the crown tissue of these species was exposed and sitting above the soil surface when it is normally just below the surface. I have compiled a data set of micrometeorological and environmental data along with observational data to investigate whether the combination of erosion and drought would negatively impact the ability of meristems to grow. I hypothesized that:

1) Erosion was severe enough to expose buds to and upper roots to air temperatures across the SGS.
2) The severity of the erosion was intensified with increased grazing intensity.
3) Meristems were exposed to temperatures that were beyond their assumed thermal limits for survival.
4) Greater erosion severity reduced the outgrowth of tillers from buds.

3.2 Methods

This research was conducted at the Central Plains Experimental Range (CPER) located ~15 km north of Nunn, CO (40°49’N 107°47’W). The site receives, on average, 338 mm of precipitation annually with 70% occurring in the growing season, April-August (CPER HQ 1939-2021). I utilized four of the long-term cattle grazing treatments established at this site: historically non-grazed (HNG, 0% utilization), recently non-grazed (RNG, grazing stopped in after the 2015 growing season), heavy grazed (HG, 60% utilization), and moderately grazed (30% utilization) with prairie dog grazed (MG-PD). There is no estimate for the utilization by the prairie dogs, but the combination of the moderate cattle grazing, and prairie dogs removes more biomass than the heavy cattle grazed treatment (unpublished data). In 2020, the grazing season began mid-May and ended in mid-October, which is typical for CPER.

Micrometeorological and environmental data were collected from the National Ecological Observatory Network (NEON: datasets 2023b, 2023d, 2023c, 2023a) and USDA Ag data commons (Hoover *et al*., 2020). The NEON tower, where micrometeorological and environmental data were collected, was located between the MG-PD and HG pastures that were used to monitor erosion. The NEON data were cleaned by removing any data that didn’t pass NEON’s final quality test, as suggested by NEON. The micrometeorological data from the Ag data commons was cleaned and gap filled prior to its release and was averaged for 30 meteorological stations across the CPER property.

The air temperature (NEON, 2023c) was from a set of aspirated air temperature sensors at 1-m height. The surface temperature (NEON, 2023a) was collected using 3 Apogee SI-111 infrared (IR) temperature sensors at 0.27, 0.32, and 1.77m height and an angle of -68°; one of the sensors was focused on bare soil while the other two were focused on the vegetation canopy. The mean soil temperature (NEON, 2023d) was taken with a platinum resistance thermometer from 5 different locations and 9 different depths: 0.02, 0.06, 0.16, 0.26, 0.46, 0.66, 1.06, 1.56, 1.96 (± 0.01m) meters beneath the soil surface and data were logged every 1 minute. Maximum temperature was determined for each day of the year.

Biological (IR) temperatures were also used to calculate the number of days that had temperatures above 60, 65, and 70°C. Days that exceeded the respective thresholds were isolated and the amount of time spent at or above the thresholds was calculated and then averaged.

The particulate mass data (NEON, 2023b) were collected using particulate collection filters with a porosity of 10 micrometers (Whatman 1851-8531 quartz microfiber filters). The filters were changed every two weeks and were placed in a HiVol 3000 collector at the top of the CPER NEON terrestrial tower. Filters are weighed pre- and post-deployment in an external facility and the difference in these weights is used to determine the mass of the particulate matter. The particulate matter data were cleaned by removing any data where the filter was damaged or had other anomalies (i.e., lab filter condition was not classified as “OK”); and filtered to remove any months where the ground may be frozen, or snow covered. The data were totaled for each month and subjected to a linear regression model (monthly precipitation vs. monthly particulate mass) using the scipy stats package.

In Fall 2021, data were collected to measure the presence and severity of erosion on pastures with differing grazing intensity (HNG, RNG, HG, MG-PD). In each pasture, an upland site and a lowland site were selected, and five 100-m transects were established. Along each transect 0.125m^2 plots were established every 10-m; in each plot erosion severity was quantified with a rank classification consisting of 5 severity classes (Table 1). The presence of all forms of severity were recorded for each plot meaning there could be more than one erosion type in each plot.

Field data were analyzed using Spyder 4.2 (Python 3.7) and the R Statistical Package (v4.3.1, R Core Team, 2023). I tested if the abundance of different erosion severities differed between pasture and topographic position. In order to account for differences in the frequency of *Bouteloua* species, which were my focal species, I calculated a relative abundance of erosion severities by dividing the number of plots with each erosion severity present by the number of plots in which a *Bouteloua* species occurred. Differences among treatments in both the relative and absolute occurrence of resprouting tillers were assessed using ANOVA analysis. For each response variable listed above I included 'erosion severity', 'pasture' and 'topographic position' as explanatory variables and 'transect' as the error term. When differences occurred, I used pairwise t-tests (pairwise.t.test function in R) to identify the specific treatments that differed using a Bonferonni correction for multiple comparisons.

3.3 Results

When comparing recent precipitation data (within the last decade) with historical data (30 years prior to the last decade), there is a notable decrease in summer precipitation (Fig. 3.1). This starts in June and continues through September. Most notably the mean precipitation for June, July, and August have been reduced by 31.08, 30.94, and 61.38 %, respectively. While the month of August is the only month where the 95% Confidence Intervals (CI) do not overlap for historic and current precipitation patterns. There is an overlap in June and July, but that goes away at about 70% and 80% CI respectively, indicating that the potential for having lower than average precipitation during these months is fairly high. The drought year of 2020, in particular, lacked any precipitation in April and August, meaning the growing season began with a water deficit and ended the year with 237mm, 28% lower-than-average precipitation.

I found that the amount of wind erosion was strongly correlated with precipitation for a given month (Fig. 3.2). There was a negative relationship between particulate mass captured on a filter and precipitation (r^2=0.81, p=0.004) during the growing season. I excluded any months where there was potential for snow and/or the ground was frozen, which would prevent any wind-driven particulate movement.

The relative frequency of erosion was determined by dividing the number of plots with a given erosion severity by the number of plots along the transect, plots that did not include *Bouteloua* species were excluded from the analysis. The relative frequency of erosion severity differed by Erosion Severity, Pasture, and their interaction (Table 3.3). The relative frequency of the most severe erosion (5) exhibited increasing frequency with increasing grazing pressure (HNG<RNG<HG<MG-PD). The relative frequency of erosion severities 3 & 4 was similar among all pastures, but the two lowest severity erosion classes had much lower relative abundance on the heavy grazed pastures. When the absolute presence of each erosion severity class was analyzed, Topographic Position was also a significant parameter in addition to Erosion Severity, Pasture, and their interaction (Table 3). This is likely because there were fewer *Bouteloua* individuals in the lowlands compared to the uplands. Although somewhat obvious, this is important to acknowledge when considering the spatial variability of heat vulnerability on the SGS. Erosion severity varied among pastures with the most intensely grazed pasture (MG-PD) showing the greatest amount of high severity erosion (Fig. 3.3). There were fewer occurrences of all levels of erosion in the non-grazed pastures.

Temperatures in 2020 were hottest at the soil surface, and quickly declined with depth in the soil. The temperatures at the surface were 20-30°C hotter than the upper layers of soil (1-3 cm depth) where the crown is adapted to live (Fig. 3.4). The hottest temperature recorded in

2020 was 71.2°C at the soil surface on July 17, but the temperature at 2 cm was only 46.9°C. The hottest temperatures at the soil surface occurred during June, July, and August, with the middle of July being the hottest. These months coincide with the times when precipitation is becoming limiting and wind erosion is increasing (Fig. 3.2).

At CPER, exceeding the assumed lethal temperature (60°C) for plant cells at the soil surface was quite common and occurred on consecutive days. Furthermore, the length of time that the surface temperature was above the lethal limit was sustained for 2-3 hours each day (Table 2).

The occurrence of bud outgrowth was highest in the two lowest erosion severity categories (1 and 2) and nearly 100% of the ramets in these two categories had bud outgrowth in the year following the drought of 2020 (Fig. 3.5). However, the occurrence of bud outgrowth was only ~20% in category 3 and then decreased to nearly zero in the two most severe erosion categories (4 and 5) that describe a condition when even the roots, positioned below the buds, were exposed to air (Fig. 3.5).

3.4 Discussion

The negative impact of drought on grassland productivity has been well documented, but the indirect effect of drought, through erosion, on grass regrowth is largely unexplored. In this study, I combined long-term climatic records with an observational study on erosion severity and regrowth to better understand the impact of high surface temperatures and erosion on grass regrowth following drought events. I found that erosion occurs in the driest months and can remove enough soil particulates to expose the belowground meristem and roots of the dominant species on the Shortgrass Steppe (SGS). This reduces the regrowth of individual grasses and occurs most frequently when pastures are heavily grazed. If precipitation continues to decrease and wind speeds remain the same, I expect the erosion will become a significant part of understanding the productivity of grassland ecosystems across years.

3.4.1 Precipitation and Erosion on the SGS

The precipitation on the SGS has experienced reductions in MAP over the past decade; perhaps more importantly is that this reduction occurs primarily during the summer months (Fig. 3.1). Precipitation for June, July, and August have been reduced by 31.08, 30.94, and 61.38 %, respectively, which is likely driving a cascade of events that could result in large mortality events for the dominant C_4 grasses. While it has been shown that early season precipitation is the most important for production on the SGS (Irisarri et al., 2016; Lauenroth & Sala, 1992), the loss of summer precipitation has other negative impacts on this plant community that have not been fully considered. I found a negative relationship between monthly precipitation and erosion ($r^2 = 0.81$, p=0.004, Fig. 3.2) and that most erosion occurred in the driest months, regardless of the annual precipitation. This suggests that as the upper soils dry out, particulates are made airborne and result in the movement of soil particles from the upper soil layers. It has been shown that erosion on the SGS is usually considered to occur on small scales, where the soil is eroded from a disturbed area and it accretes in areas with vegetation (Martinez-Turanzas, Coffin, & Burke, 1997;Augustine & Derner, 2015; Koler et al., 2008). However, with shifting climates and repeated droughts, the erosion dynamics in this system could shift to having larger scale impacts on the system.

3.4.2 Increased Surface Temperatures

During the growing season of 2020, the temperature at the soil surface were 20-30°C hotter than 2cm below the surface, *B. gracilis* and *B. dactyloides* typically keep their buds between 0-1 cm beneath the surface in the absence of erosion (Jacqueline Ott, USFS, Rocky

Mountain Research Station, personal communication). But even when erosion does occur, the buds could remain below their thermal threshold if there was enough soil moisture and a full plant canopy. Moisture that evaporates from the soil surface (latent heat loss) utilizes energy that would otherwise cause an increase in temperature, but when moisture is gone in the upper layers of the soil surface, that energy is converted to sensible heat flux and causes both air and soil heating resulting an extremely high temperatures at and near the soil surface. Further, during years with greater precipitation that leaf canopy of plants can provide shade for eroded crowns preventing the meristems from experiencing temperatures that would result in cellular mortality. However, in years of low production the crown has limited vegetative shading increasing the potential for surpassing thermal limits. Whether from general warming of air temperatures or reduced soil moisture, the occurrence of soil surface temperatures >60°C (the commonly assumed thermal tolerance of plants) are increasing at the SGS. If the SGS experiences increased frequency and intensity of droughts as is predicted with global climate change (Groisman & Knight, 2008; Huntington, 2006), then the buds of the perennial grass species dominating this site will continue to experience conditions they may not be adapted to survive.

3.4.3 Erosion Severity and Grass Regrowth

In my observational study, I found many instances of erosion causing both the belowground meristem and roots below this point to be exposed to the air. The frequency and severity of erosion differed between the grazing treatments I included in my study. The occurrence and severity of erosion was lowest in the historically non-grazed treatment, likely because of the dominant species and overall plant cover is dominated by, the relatively tall, *Pascopyrum smithii* and the plant cover is relatively dense in this pasture (Porensky *et al.* 2017), which has limited the presence of the *Bouteloua* species. Although the reduced frequency and severity of erosion was likely due, in part, to the lower density of *Bouteloua* species, the relatively tall *P. smithii* would also increase the boundary layer thickness, leading to reduced erosion.

I did not find any differences in the frequency or severity of erosion between the HG and MG-PD pastures, but both pastures experienced much more severe erosion than the HNG pasture. Erosion categories 4 & 5 describe a situation where the buds AND some root tissues are exposed to air, so I considered these the two most ‘severe’ scenarios. The HG and MG-PD pastures both had many plants that experienced this severity of erosion. When the soil around the buds and roots erodes, they lose the buffering capacity of the soil making them more susceptible to mortality from the elevated temperatures at the soil surface (see section above).

I speculate that the increased severity of erosion in the HG and MG-PD areas results from 2 factors as a result of the presence of grazers: reduced canopy cover and destruction of soil crust (Martinez-Turanzas et al., 1997). The removal of vegetation by the grazers reduces the canopy cover, which can decrease the thickness of the boundary layer exposing the soil to higher wind speeds and, therefore, increasing the potential for erosion. The movement of the grazers inevitably disturbs the physical soil crust that forms when the soil becomes dry (Fick et al., 2020; Warren & Eldridge, 2003). During average years, the effects of the grazers on erosion potential are minimal, however in drought conditions, these may be major drivers of soil erosion.

As described above, I found that temperatures often exceeded this threshold at the soil surface and for sustained periods of time, presenting the opportunity for mortality to occur. Coupled with this data, I found that plants that experienced the 2 most severe levels of erosion (levels 4&5) were rarely able to regrow after exposure to these elevated temperatures. Although more work needs to be done to characterize the point of mortality in grasses during drought, my results suggest that erosion that exposes belowground meristems to elevated temperatures will negatively impact the ability of these ecosystems to recover from drought and heat stress. While the erosion of soil around the crown tissue of the dominant C_4 grasses might not result in large mortality events in years of severe drought, like 2020, the limited vegetation cover exposes the eroded crown tissues to high levels of solar radiation which can result in the meristems in the crown to experience temperatures in excess of 60°C for long periods of time daily for several consecutive days, which is likely lethal to meristems that are exposed. For reference, the surface temperature during prescribed burns on the SGS had a maximum time above 60°C of 209 seconds (Augustine et al., 2014). While the maximum temperature of the fire is much hotter, the length of time of lethal temperature exposure is orders of magnitude greater on the surface during drought years. Furthermore, unlike the lethal temperatures from a fire which are infrequent, the lethal surface temperatures during droughts are experienced multiple times often in consecutive days. This likely results in high levels of bud mortality for these grasses during severe drought years, not because of water limitations but due to heat induced mortality.

Although I did not directly assess mortality, the lack of regrowth from plants that experience severe erosion suggests that the elevated temperatures they experienced might have been too extreme for these tissues to survive. Although there is limited data on the upper temperature limits of survival in grass buds, literature on other functional groups suggests that cells may be able to survive temperatures over to 60°C (Jameson, 1961), which is the value used in models of fire effects on plants (Choczynska & Johnson, 2009). Although there is evidence that this may change over the course of the season (Jameson, 1961), I used the 60°C threshold as a benchmark for when temperatures are likely to start inducing cell mortality. Considering the thermal threshold of buds was assessed by dunking plant tissue into a heated water bath for a short period of time (Jameson 1961), this suggests that exposure to lethal temperatures causes mortality rapidly. Wright (1970) showed the relationship between exposure time and temperature on the mortality of two C_3 grasses that occur on the SGS which ranged from minutes to hours depending on the temperature and time of year. It is important to note that in both of these studies, mortality occurred from a single exposure to lethal temperatures. However, the surface temperatures at CPER can get above 60°C for >3 hours (Table 2) and on consecutive days, so even if the mortality is not instant, I expect the damage to tissues exposed to these prolonged and elevated temperatures to have significant negative impacts to the plant. Further, the frequency of hot surface days is increasing (Fig. 3.6, $r^2=0.31$); it is likely that the interactions between seasonal shifts in precipitation, erosion, and increasing surface temperatures could result in declining populations of the C_4 grasses.

3.5 Conclusions

The strong correlation between erosion severity and bud outgrowth suggests that the more erosion the crown experiences the greater the likelihood of experiencing a reduction in bud outgrowth. I suggest that the reduced bud outgrowth is related to temperature thresholds of the meristems rather than dehydration because the, relatively, deep roots of these species (LeCain et al., 2006) likely still had access to soil moisture. I acknowledge that these stresses are likely being experienced with the heat stress and the compounding stresses reduce the plants capability to cope with any one of them. However, it is important to note that the majority of tiller production on eroded crowns either occurred on portions that were still beneath the soil surface or emerged from the underside of the crown where the meristem was protected from the solar radiation. Future research should examine the thermal limits of the meristems in a way that replicates the temperatures at the soil surface compared to the temperatures where the crown is usually found in the soil profile.

Continued summer droughts will promote the erosion of C_4 grasses and increase surface temperatures. Erosion of the *Bouteloua* species will not immediately lead to increased mortality if there is adequate vegetative shading. However, if there is an early season drought that reduces the vegetation shading, this could result in large mortality events for *B. gracilis* and *B. dactyloides* buds, which has the potential to start a positive feedback loop where: 1) Early-season drought leads to reduced plant cover, 2) bud mortality reduces vegetation cover resulting in 3) higher surface temperatures and additional mortality. Evans *et al*. 2011 showed that when the C_4 cover (mainly the *Bouteloua* species) is reduced the abundance of ruderal species increases, and these ruderal species do not provide the same ecosystems services as the C4 species. Considering that precipitation events on the SGS are predicted to become more intense with longer dry periods in between (Groisman & Knight, 2008; Huntington, 2006) the amount of erosion is likely to increase in the future and the potential for species composition shifts (based on the proposed positive-feedback loop above) should be carefully monitored.

The loss of vegetation and increased bare soil between ramets is generally considered to be early signs of desertification. The results of this study suggest the SGS may be seeing early signs of desertification. and will likely have a positive feedback loop as the reduction in tiller production will reduce the thickness of the boundary layer resulting in higher erosion rates that will result in lowered bud outgrowth. I show here that the primary driver of erosion on the SGS is lack of precipitation during the summer months. If the current precipitation patterns continue or the SGS experiences increased frequency and intensity of drought as it is predicted to, the rate of tiller loss might become too high for the C_4 grasses to recover, resulting in increased area of bare ground or major shifts in the species composition.

3.6 Tables

Table 3.1: The erosion severity classes based on visual estimations.

Erosion Severity	Amount of Visible Crown	Amount of Visible Root
1	0-50%	n/a
2	50-75%	n/a
3	75-100%	n/a
4	100%	< 1 cm
5	100%	> 1 cm

Table 3.2: The number of times the surface temperature exceeds the specified threshold (left column) and the average length time (minutes) that the temperature is equal to or greater than respective threshold. Data on number of days for multiple years and time above threshold show the mean and standard error.

	Number of Days At or Above Threshold		Minutes At or Above Threshold	
Temperature Threshold	2016-2019	2020	2016-2019	2020
>= 60	13.5 ± 5.17	24	151.9 ± 10.8	133.9 ± 14.6
>= 65	4.5 ± 1.66	7	46.7 ± 13.1	41.9 ± 13.1
>= 70	0.25 ± 0.25	2	0.0 ± 0.0	7.5 ± 1.5

Table 3.3: Results from ANOVA analyses comparing the presence of each erosion severity class between pastures and topographic location. Significant parameters in each model are shown with bold font.

	Model Parameter	**Relative Presence ANOVA model**	**Absolute Presence ANOVA model**
P-Values	Erosion Severity	**<0.001**	**<0.001**
	Pasture	**<0.001**	**<0.001**
	Topography	0.612	0.755
	Erosion Severity X Pasture	**<0.001**	**<0.001**
	Erosion Severity X Topography	0.382	0.223
	Pasture X Topography	0.743	**0.042**
	Erosion Severity X Pasture X Topography	0.75	0.537

3.7 Figures and Figure Legends

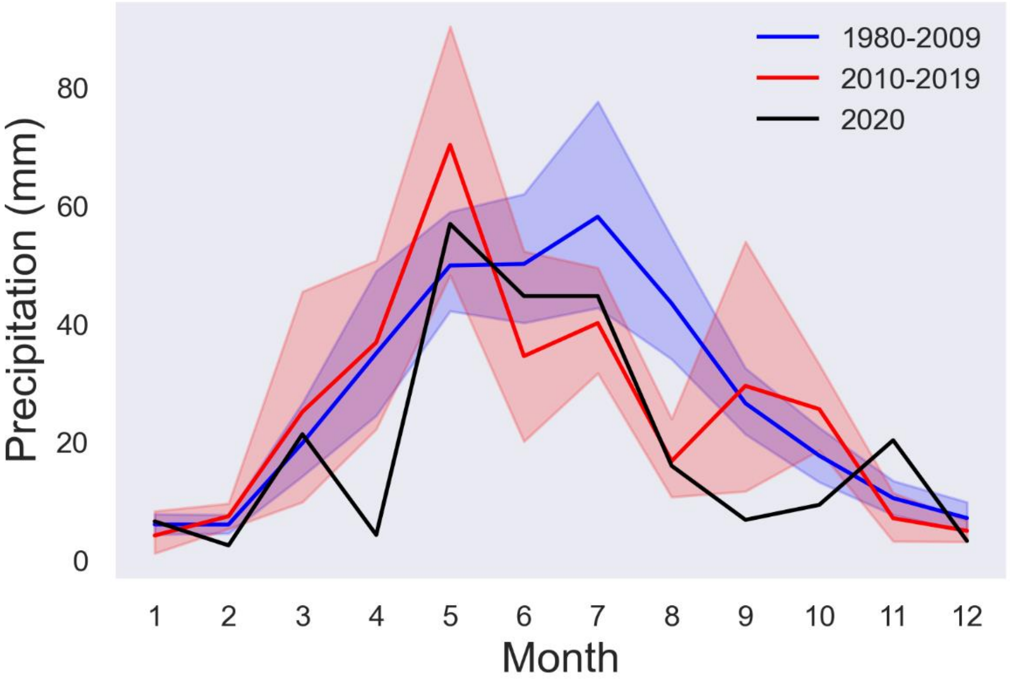

Figure 3.1: Monthly averages for precipitation representing historical (1980-2009), recent (2010-2019), and 2020. Monthly mean for precipitation historically (blue), 10 years prior to 2020 (red), and 2020 (black) with the shading around the lines representing 95% confidence intervals.

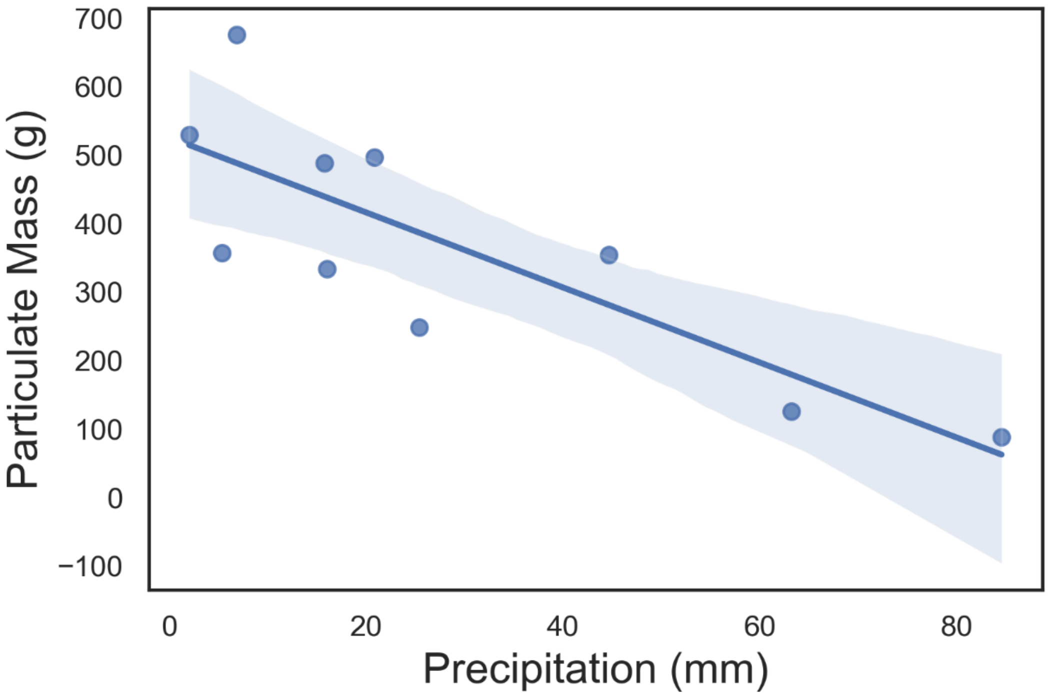

Figure 3.2: Linear regression of cumulative monthly precipitation and particulate mass collected by pulling air through a quartz microfiber filter with a porosity of 10 microns at the CPER NEON site. Shading around the trendline represents 95% confidence intervals.

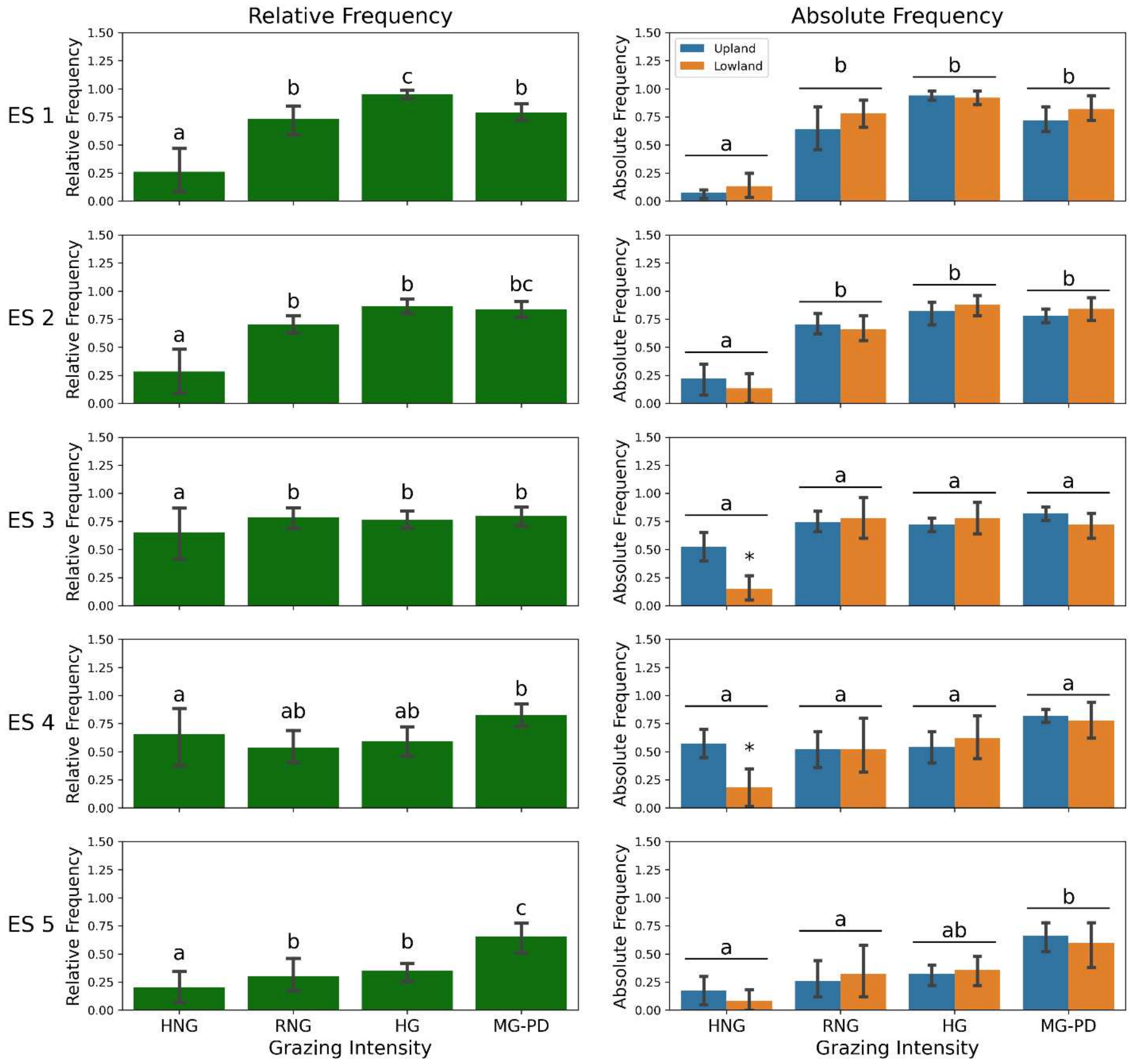

Figure 3.3: The relative and absolute frequency of erosion severity (ES) presence for *B. gracilis* and *B. dactyloides* at varying grazing intensities (Historically non-grazed (HNG), Recently non-grazed (RNG), Heavy grazed (HG), and Moderately grazed with prairie dogs (MG-PD)). Significant differences are shown with letters for between grazing treatments and * indicates significant differences between topography ($p<0.05$), Error bars represent 95% confidence intervals.

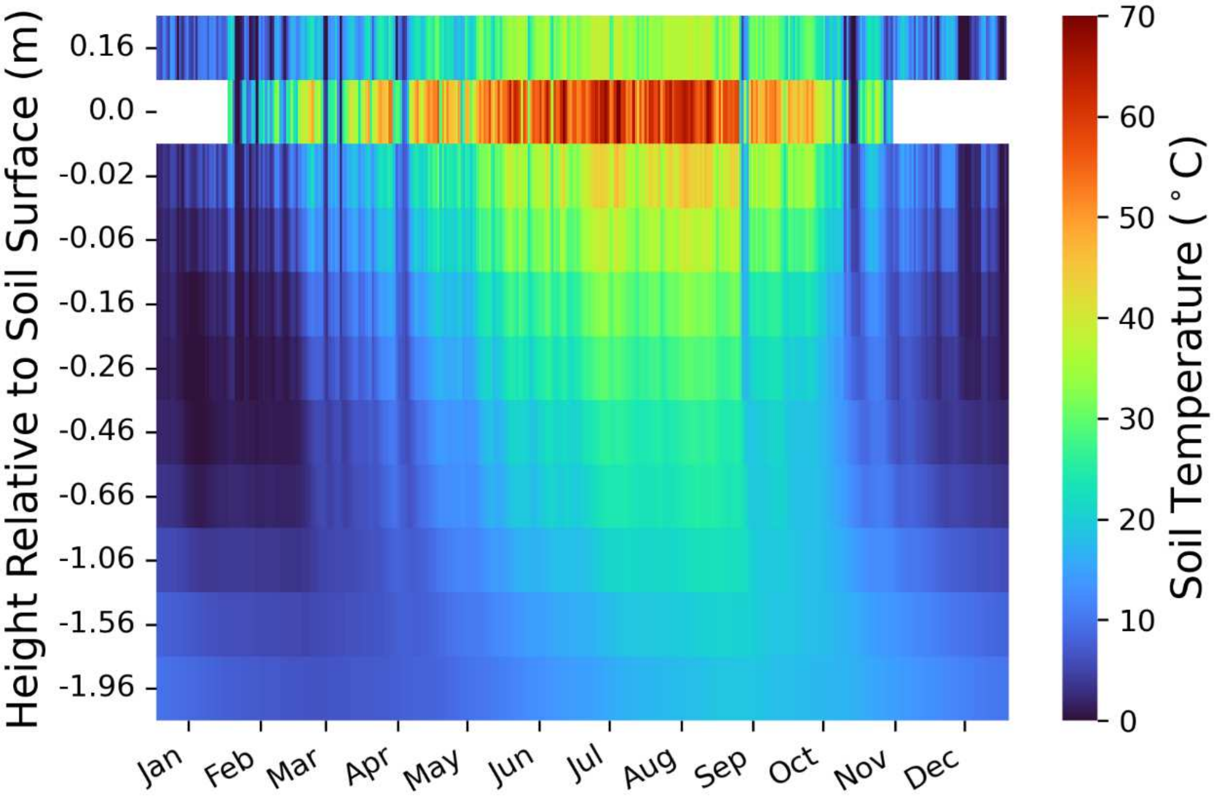

Figure 3.4: Heatmap representing daily maximum temperatures of the air, surface, and soil profile to nearly 2m at CPER for the year 2020. The color represents the temperature according to the scale on the right. The y-axis represents the position of the temperature sensor relative to the soil surface ± 0.01 m.

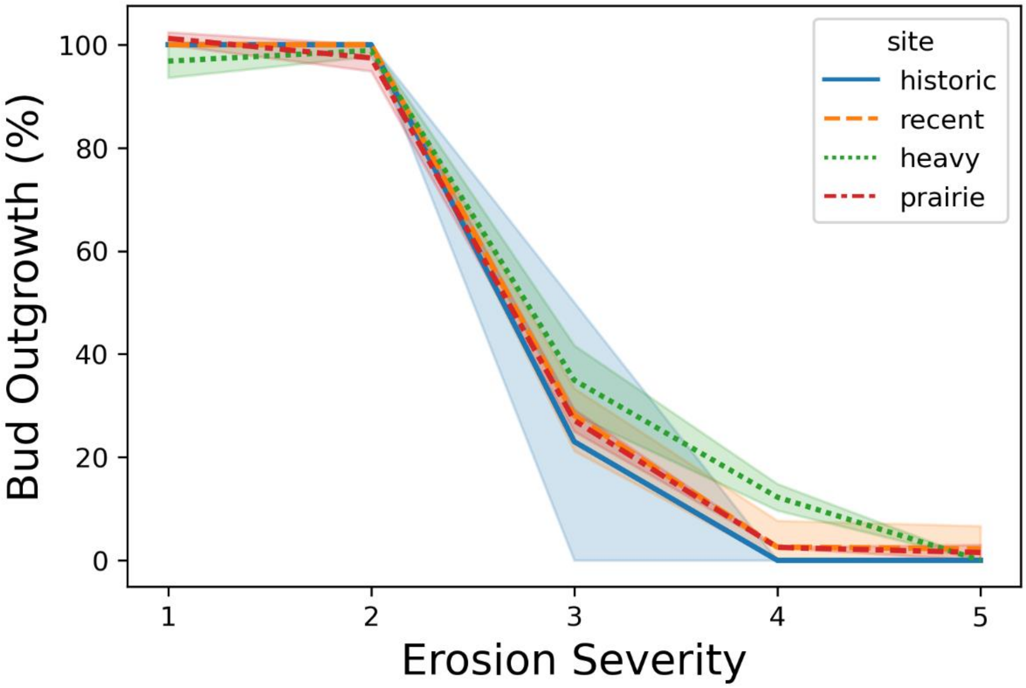

Figure 3.5: Bud outgrowth refers to whether there was any tiller production that occurred in the 2021 growing season associated with the respective erosion severity categories. The graph shows what percent of the crown experienced tiller production for each level of erosion severity. The 95% confidence intervals are based on topography differences in each pasture.

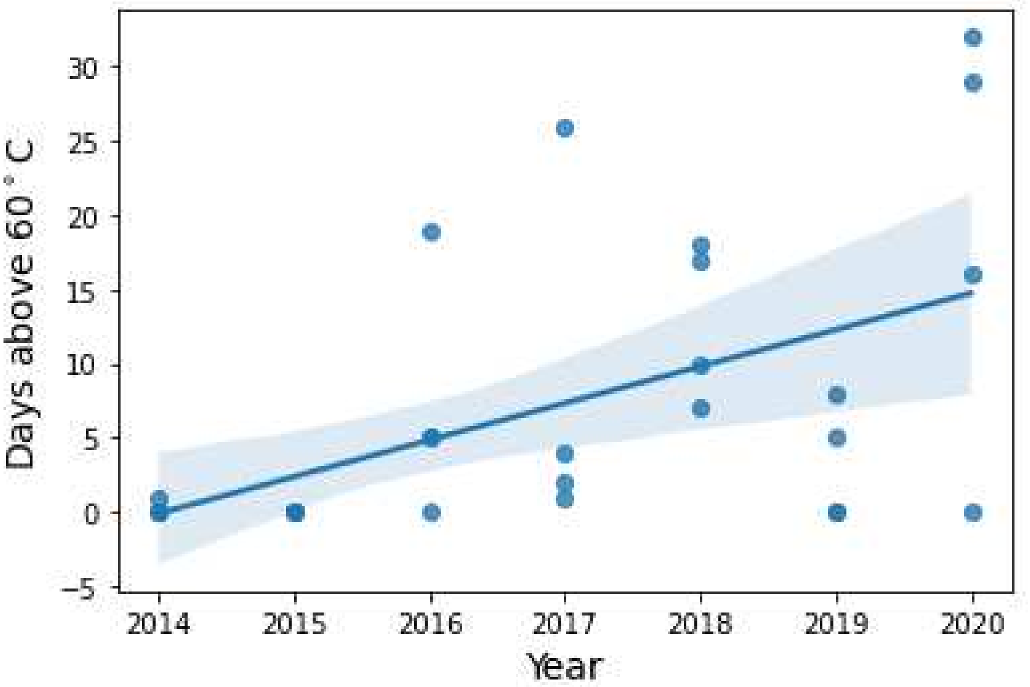

Figure 3.6: The total number of days the surface temperature was above 60°C for individual months in each year. Shading around the trendline represents 95% confidence intervals.

CHAPTER 4: COMPARATIVE ANALYSIS OF THE NEAR SOIL SURFACE MICROCLIMATE OF GRASS DOMINATED SYSTEMS ACROSS THE UNITED STATES

4.1 Introduction

Recent heat waves have brought to light the potential negative impacts these disturbance events can have on the function and survival of plants across the globe. For example, mass die-off of trees in the Pacific Northwest region of the US in response to heat waves in 2021 shocked many ecologists as this is a region with fairly moderate temperatures throughout the year, although it does experience a dry summer due to its Mediterranean climate. While it was thought that plants had a high capacity to regulate the temperature of their leaves, (Helliker & Richter, 2008), new evidence suggests that there is almost no thermoregulation at the canopy level (Still et al., 2022). During heatwaves it would be difficult for plants to maintain an optimal temperature. If the leaf temperature exceeds ~45°C, damage to the lipid membranes occurs (Schönbeck et al., 2023; Slot & Winter, 2017) and at 60°C, cellular death occurs due to protein denaturing (Dickinson & Johnson, 2004). Heat waves are generally characterized by elevated air temperatures of greater than the 90th percentile for the location for at least 3 days, and for forest ecosystems, this metric likely best characterizes the temperature stress these ecosystems experience.

However, from desert ecosystems to open-canopy woodlands and savannas, it might be both air and soil temperature that could cause adverse effects. For example, these systems generally have a large component of resprouting species (either shrubs, forbs, sedges, or grasses) that rely on belowground meristem to survive disturbance events. A primary characteristic of perennial grasslands is their ability to resist disturbances through the survival of their belowground bud banks(Ott et al., 2019). Because of this need for belowground survival, air temperatures (by themselves) might not characterize the most important stressor on these systems, but near-surface temperatures (both above and belowground) may better represent the stress these plants experience during heatwaves.

Extreme temperature events are pushing plants past their thermal limits and leading to mass plant mortality (Hammond et al., 2022). These observations have highlighted a simple but unanswered question, what are the thermal limits of plants? Models that include thermal limits of plants have been developed for fire-effects modelling and, as far as I can tell, always use the threshold of 60°C (Choczynska & Johnson, 2009). This threshold is based, initially, on studies of isolated plants cells and some verification on tree cambium temperatures during fires(Dickinson & Johnson, 2004). This threshold is based, initially, on studies of isolated plants cells and some verification on tree cambium temperatures during fires (Dickinson & Johnson, 2004). However, the conditions and limited species represented in these studies should be concerning, because rarely (if ever) do all plants respond to the same stimuli at the same threshold (Jameson, 1961; Wright, 1970). Further, we know that some plants, specifically those in hot and dry environments can experience extreme temperatures and dehydrated conditions by protecting their cell membranes and proteins from damage, while others may not possess these abilities. Physiological thresholds of belowground meristems, in particular, are rarely studied despite their importance in maintaining perennial plant populations (especially in herbaceous-dominated systems).

However, if we do assume a mortality threshold of 60°C, then this leads to a simple meristem-depth hypothesis, that plants adapted to ecosystems surface (or near-surface) soil temperatures should have deeper placement of their meristem. Unfortunately, the literature reporting meristem depths of plants is extremely sparse, currently leaving no way to test this hypothesis. Further, it’s unclear where and when near-surface temperatures would exceed the thermal limits of plants (even if it is 60°C). Most grasses keep their buds near the surface of the soil, but there is a high variability in where the buds are located in relation to the soil surface: stolons are aboveground, rhizomes are belowground(Ott et al., 2019). The depth of the buds is likely related to the heat tolerance of the species in arid systems.

Based on physical principles I would expect soils to heat up the most when there is high-radiation loading (high incident solar radiation and low plant cover) and when soil moisture is low, which otherwise would help dissipate the radiant energy through latent, rather than sensible, heat loss. The length of growing season should positively correlate with pyranometer and temperature data since more time for incoming solar radiation will impart more energy into the system overall. Darker and bare soils should heat up more due to lower albedo and little to no shading effect of plants. Snow in winter provides soil insulation effect and increases albedo of the system to have more energy reflected rather than absorbed leading to likely more air temp variability in winter with less variable soil temps. Less solar radiation to soil in snowy environments like to show lower average soil temperatures in winter months compared to summer months. Many models include these processes to estimate soil temperature and so the physical principles are fairly well understood (Holmes et al., 2008; Persaud & Chang, 1983; Zheng et al., 1993).

In order to understand the potential impact of heat waves on near-surface conditions I have analyzed air, surface, and belowground temperatures from NEON sites and combined these results with the Drought Severity Index to identify when and where heat waves are likely to have the biggest impact on ecosystem structure and function through the survival and/or mortality of different plant species.

4.2 Materials and Methods

In this data analysis, I used nine grass dominated sites from National Ecological Observatory Network (NEON), each site was within a different NEON Domain (Fig. 4.1, Table 4.1). Sites were filtered by sites where the phenocam is has a region of interest that is focused on herbaceous vegetation.

Data for daily surface temperatures, soil temperature, air temperature, relative humidity, soil moisture, and solar radiation were obtained from the NEON database. I used both released and provisional data from NEON and filtered the data based on the finalQF variable as recommended by NEON. Canopy greenness was obtained through the PhenoCam Network through the analysis of phenocam images from NEON's cameras. Drought indices were obtained via the Drought Monitoring Network. Precipitation and long-term (30-year) air temperature data were gathered from NOAA; the NOAA data was collected from a meteorological station at the NEON site or the nearest meteorological station that has similar vegetation as the NEON site.

Although NEON provides details on their instrumentation and sampling protocols (https://www.neonscience.org/data-collection), I briefly describe the data collection methods below. The air temperature (NEON, 2022d) was from a series of single aspirated platinum resistance temperature sensor (Thermometrics Corporation Climate RTD 100 Ω Probe; Northridge, CA), housed within a Met One Instruments (Grants Pass, OR) 076B fan aspirated radiation shield at heights varying from 0.1 to 5 m. The surface temperature (NEON, 2022b) was collected using 3 Apogee SI-111 infrared (IR) temperature sensors (Apogee Instruments; Logan, UT) at 0.27, 0.32, and 1.77m height and an angle of -68°; one of the sensors was focused on bare soil while the other two were focused on the vegetation canopy; the daily maximum from the three sensors was used. The maximum soil temperature (NEON, 2022e) was taken with a platinum resistance temperature sensor (Thermometrics Corporation - Climate RTD 100-ohm Probe; Northridge, CA) logged every minute from 5 different locations and 9 different depths: 0.02, 0.06, 0.16, 0.26, 0.46, 0.66, 1.06, 1.56, 1.96 (± 0.01m) meters beneath the soil surface. I used the daily maximum temperatures for the air, surface, and soil. Soil Moisture was collected with Sentek Technologies (Stepney, SA, Australia) – EnviroSCAN TriSCAN sensors at depths of approximately 6-200 cm depth beneath the soil surface. Sites that experience permafrost or shallow soils do not go the full 200 cm depth. Each site has 5 soil moisture sensors and the data from these five sensors was consolidated by taking the average of the 30 min data across the five sensors and then the minimum daily value was extracted to give a single daily datapoint for each depth of soil for each site. Relative humidity was collected with Vaisala (Vantaa, Finland) HUMICAP Humidity and Temperature Probe – HMP155, installed at the top of the tower and at the soil array. Vapor pressure deficit (VPD) was calculated at 30 min intervals and then the daily maximum VPD was calculated for each site. Solar radiation intensity was collected with Delta-T Devices (Cambridge, UK) SPN1 Sunshine Pyranometer, and daily means were calculated based on the global radiation for each site.

Daily greenness was estimated by using images taken from each NEON tower and standard calculations utilized by the PhenoCam Network. The PhenoCam Network utilizes StarDot Technologies (Buena Park, CA) NetCam SC cameras to capture daily images and calculates NDVI and green chromatic coordinate to estimate the greenness of the vegetation in the image. For this project, greenness was based on the 90th percentile of daily greenness which was calculated by the PhenoCam Network prior to downloading the data. The region of interest for each image was focused on the herbaceous vegetation. The data was cleaned by removing any data that didn't pass the outlier flag for the 90th percentile.

Drought index was estimated by compiling weekly spatial datasets from the US Drought Monitor (NDMC; USDA; NOAA) with the coordinate locations to match the nine NEON tower locations. Six years of weekly drought monitoring data was spatially joined in ESRI's ArcPro software with the NEON tower coordinate locations to generate tables of drought index values for each NEON tower for each week from January of 2018 to December of 2022. These tables were then summarized and simplified into a singular dataset containing the NEON tower site code, the Drought Index Value, and the Date associated with that value for all 260 weeks of data.

Due to lack of precipitation data for some of the NEON sites (CPER, KONZ, SJER), precipitation data was gathered from the nearest location with similar vegetation structure from NOAA. If the nearest location had insufficient data, the next closest weather station was used to gap-fill the missing data. The data were cleaned by removing any values that didn't pass the NOAA precipitation quality check. This data was also used for long-term air temperature data.

Heatwaves were classified as a temperature that exceeded the 90th percentile of temperature for a location for three or more days. The 90th percentile of temperature was calculated from the NOAA data and then that value was applied to the NEON air temperature data to quantify heatwaves.

A principal component analysis (PCA) was performed to determine the relationships between the several of the microsite variables, with specific interest in surface temperatures. The PCA inputs were surface temperature, air temperature, soil temperature, soil moisture, VPD, cumulative precipitation, drought severity, greenness, solar radiation, and temperature difference between air and surface.

4.3 Results

The number of days when air temperatures exceeded the threshold for lipid (45°C) and protein (60°C) denaturation were few and only occurred at the most southernly sites. Across all sites, the threshold for denaturing proteins never occurred when air temperatures were measured as low as 0.1 m height. San Joaquin was the most northernly site that experienced air temperatures where lipid deformation would be expected to occur. Jornada experienced the most consistent temperatures above the thresholds across the years and experienced at least 78 days above this threshold in 4 of the 5 years I investigated.

Surface temperatures routinely exceeded air temperatures at these sites and experienced temperatures that exceeded both lipid and protein denaturing at 8 of the 9 sites. Disney, Jornada, Colorado, Moab, Oklahoma, and San Joaquin all experienced >100 days of surface temperatures that would cause lipid damage in plant tissue. There were also >10 days of temperatures exceeding the protein denaturization threshold at 5 of the 9 sites, including: Disney, Jornada, San Joaquin, Moab, Oklahoma, Colorado, and North Dakota; with Jornada experiencing two years that had >100 days above this threshold. The only site without any days above either threshold was Toolik Lake in Alaska.

As is expected from my understanding of the physical principles of soil heating, soil surface temperatures were hottest during the time of year when solar radiation was most intense (summer months) and when the canopy was the least green (Fig. 4.2). There was a strong negative correlation between greenness and surface temperature across all sites within each month (the regression for each month was analyzed separately). The hottest surface temperatures occurred in May, June, July, and August during years or in places where the green canopy cover was low. There was very little variability around each regression despite the large range of latitudes I analyzed, highlighting the strong control of surface temperatures by solar radiation and greenness.

The PCA analysis was utilized to determine if dryness and plant cover impacted the difference between soil and air temperature across my sites (Fig. 4.6). The first 2 axes of the PCA explained 68% of the variation in my data. Since so much variability was explained by the first 2 axes, I will focus my attention on only those axes. The first axis (PC1) was most associated with temperature and the second (PC2) was related to precipitation and soil moisture. On PC1, all the temperature variables were highly correlated with each other and inversely correlated with VPD. Since VPD is a function of both air humidity and temperature, it makes sense that this variable was strongly correlated with both axes. As I hypothesized, the temperature difference between soil and air was correlated with both axes and appears as a vector directly between the two axes. Also important is that this vector is inversely related to greenness, suggesting that the temperature difference between air and soil is greatest when greenness (or plant cover) is at its lowest.

4.4 Discussion

Heat waves are becoming more common and have negative consequences for all organisms, from human health and mortality to plant survival. However, the term ‘heat wave’ is not well defined and, when it is, only includes a description of the conditions of the bulk air in a region. However, for many plants and other small organisms, the conditions near the soil surface are more important than the bulk air. Here, I show that the conditions near the soil surface experience ‘heat wave’ conditions more frequently than the bulk air, highlighting the need to understand and focus on the threshold of survival in this near-surface region.

It is currently accepted that temperatures above 45°C are damaging to plants due to decreases in photosynthesis from the loss of membrane integrity (Schönbeck et al., 2023; Slot & Winter, 2017), and that 60°C is lethal to plants due to the denaturing of proteins (Dickinson & Johnson, 2004). I found that temperature at the soil surface/vegetation canopy often times exceed those temperatures quite frequently in arid or grass dominated systems (Fig. 4.2 & 4.3). Although the temperatures at and near the soil surface experience such elevated temperatures, we know that plants survive and maintain green canopy at some of these sites during these periods (Fig 4.2). This suggests that the thermal limits of plants may not be uniform across the plant kingdom, and some plants may have adaptations that allow them to tolerate these extreme temperatures. Unfortunately, models of plant mortality in response to elevated temperatures (these come from the fields of fire ecology and/or behavior) all plants have the same threshold of 60°C. An important question facing the field of plant ecology is whether the thresholds of 45°C and 60°C are important for plants? Or rather, the temperature elevation relative to historic conditions is more important. For example, if plants in Alaska have the same thermal threshold as plants in New Mexico, then we need not worry about plant survival during heat waves in this system. However, rarely do all plants have the same thresholds, and investigating the differences in thermal thresholds (if they exist) is an important frontier to understand and quantify.

There is a negative relationship between surface temperature and greenness for almost every month of the year (Fig. 4.4). This is likely caused a result of the cooling effect of latent heat flux from plant transpiration, along with the shading effect of leaves. The negative correlation is strongest during the summer months of June, July, and August, which is also when the northern hemisphere has its highest solar inputs. This highlights the interaction between drought and heat waves (citations). Drought inhibits the production of a full plant canopy, allowing greater amounts of solar radiation to reach the soil surface. Further, the lack of soil moisture during drought causes greater soil heating due to less solar energy being used for evaporation (i.e., latent heat). As both of these extreme events are projected to increase in the future, the combined impact of these on perennial herbaceous plants could cause larger mortality events than have been observed in the past. When drought is combined with elevated temperatures, plants are less likely to regrow the following year (Bradfield et al. In Review), leading to legacy effects on the plant production of these systems. The question now is what the relative contributions to plant mortality are from dehydration (drought) and elevated temperatures. This is important because surface temperatures rarely reach lethal temperatures when soil moisture is still available. So, understanding the interaction between these two factors on plant survival in the future is vital to predicting the impact of drought and heat waves on plant growth and survival.

4.5 Figures and Figure Legends

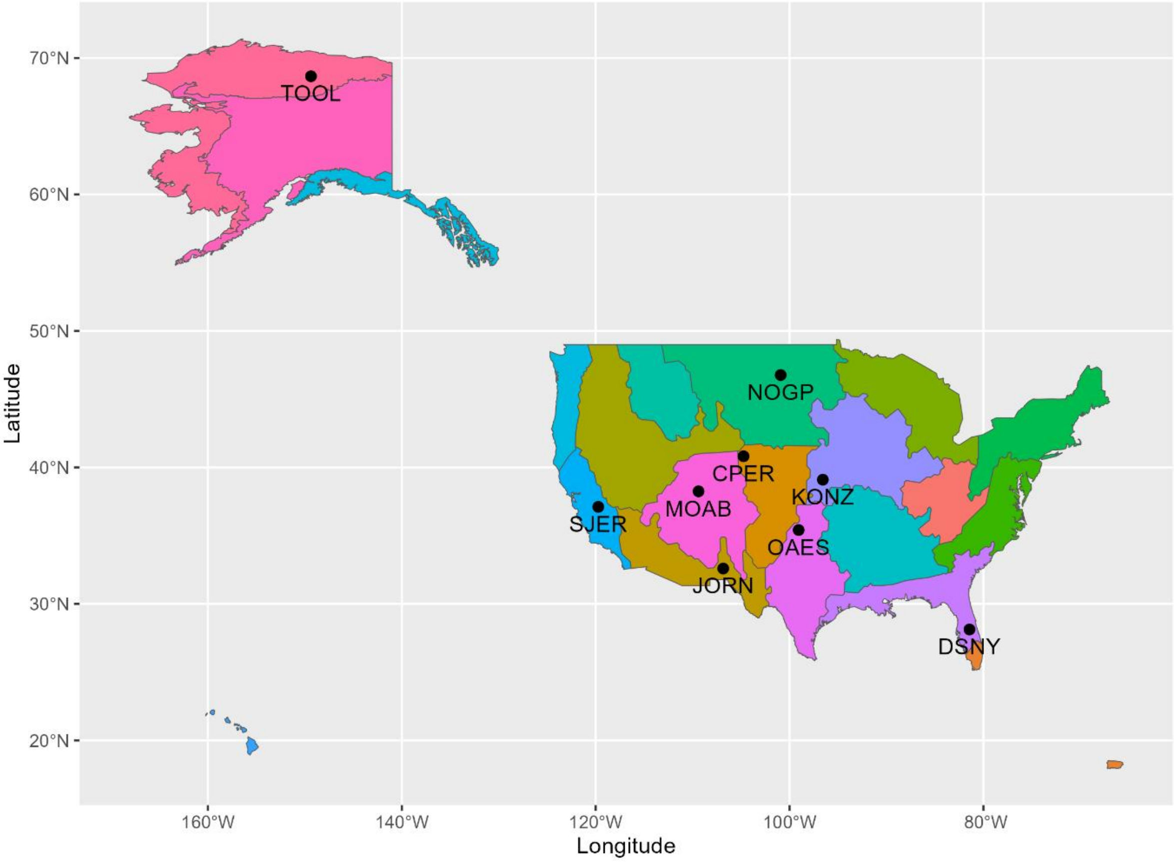

Figure 4.1: Map showing the location of the NEON sites used in this study and the boundaries of the NEON Domians. Colors indicate the different domains. More information about the NEON sites and domains can be found in Table 4.1.

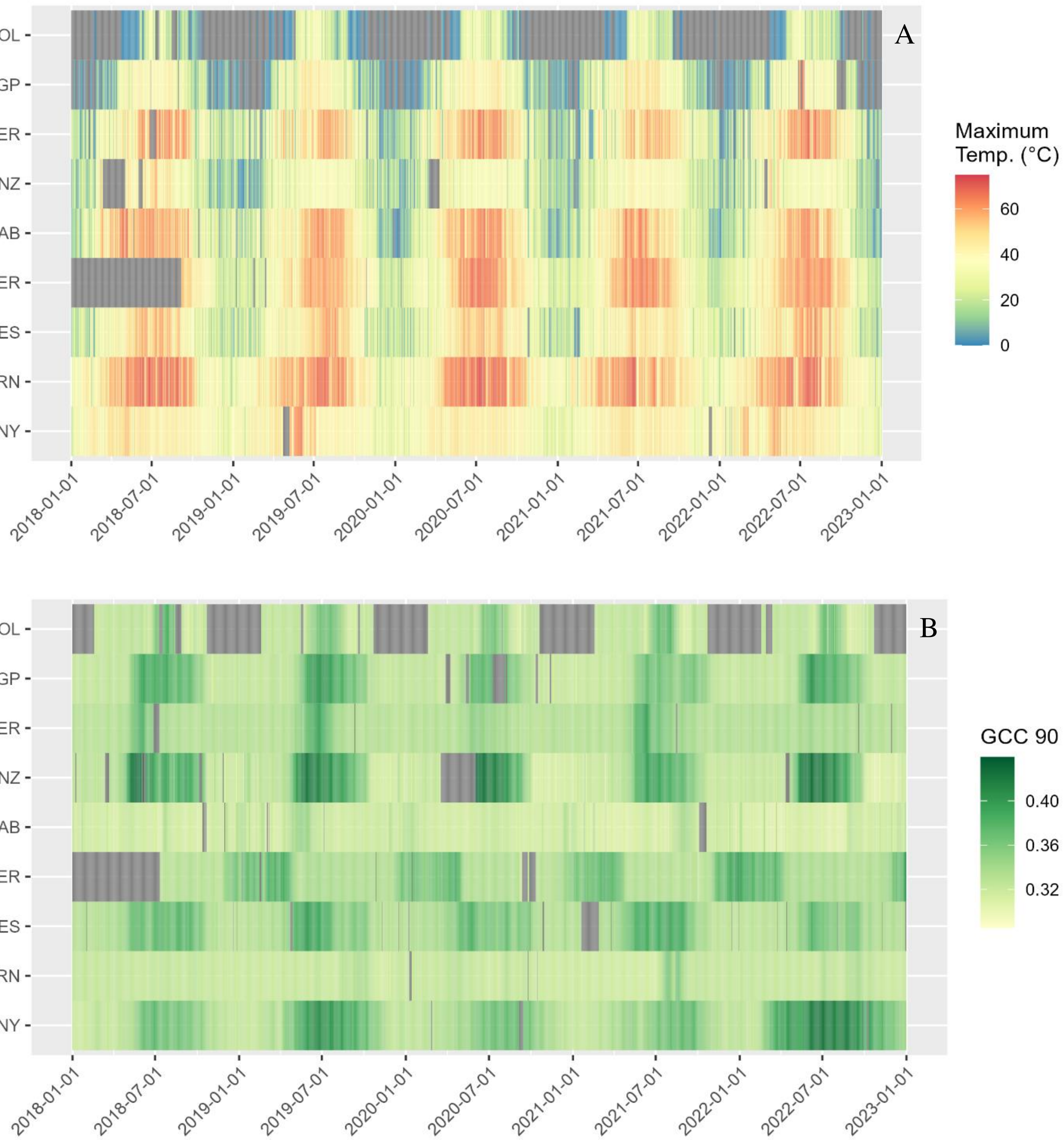

Figure 4.2: Maximum daily surface temperature (A) and daily 90th percentile for green chromatic coordinate (B) across arid or grass dominated NEON sites. The sites on the y-axis are in ascending order based on their latitude.

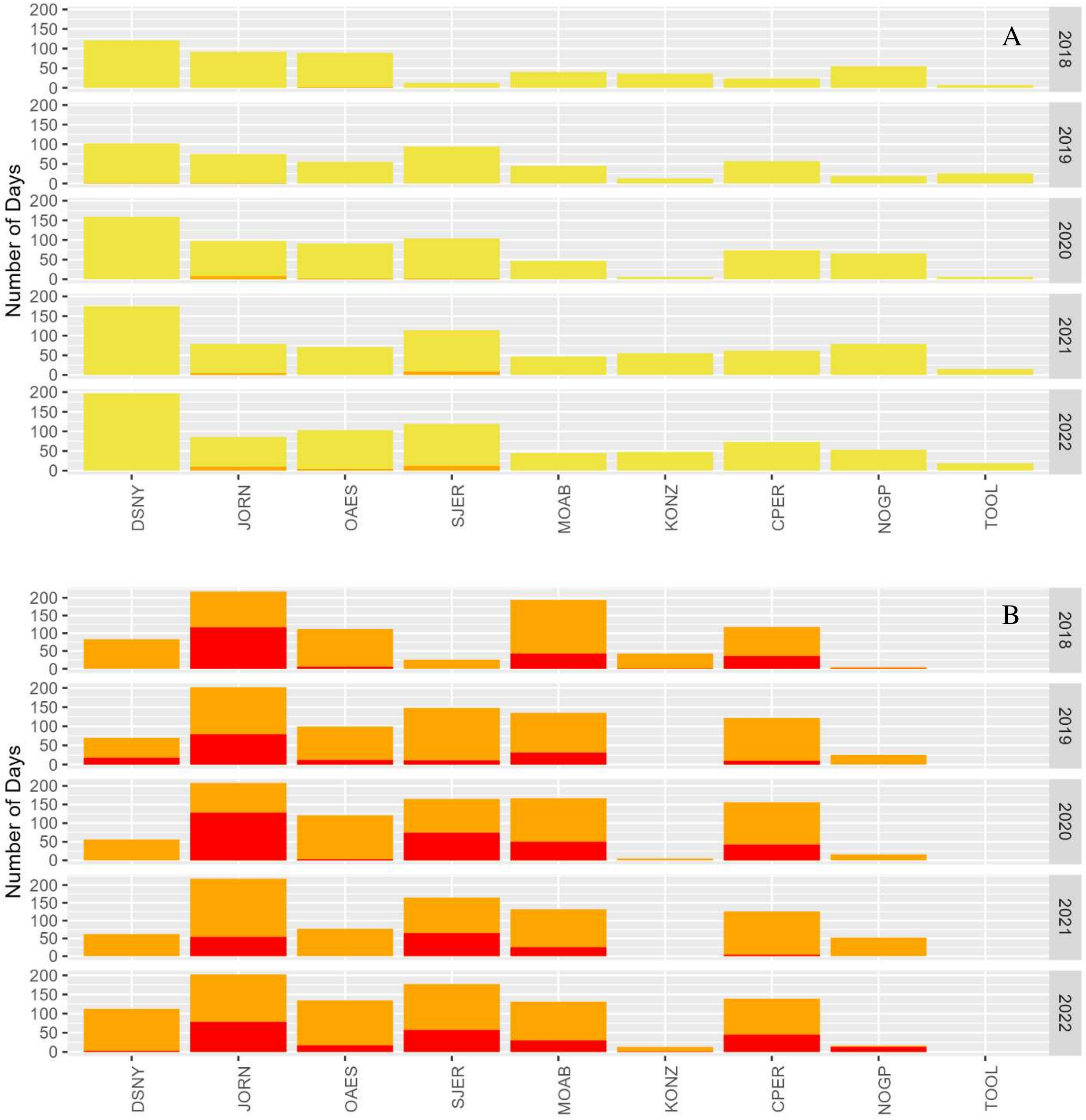

Figure 4.3: The number of days the temperature of the air (A) or surface (B) temperature exceeds the critical temperature threshold for heatwaves (air temperature above the 90th percentile for three days, yellow), lipids (45°C, orange) or proteins (60°C, red) across grass dominated NEON sites. The sites are arranged in ascending order based on their latitude.

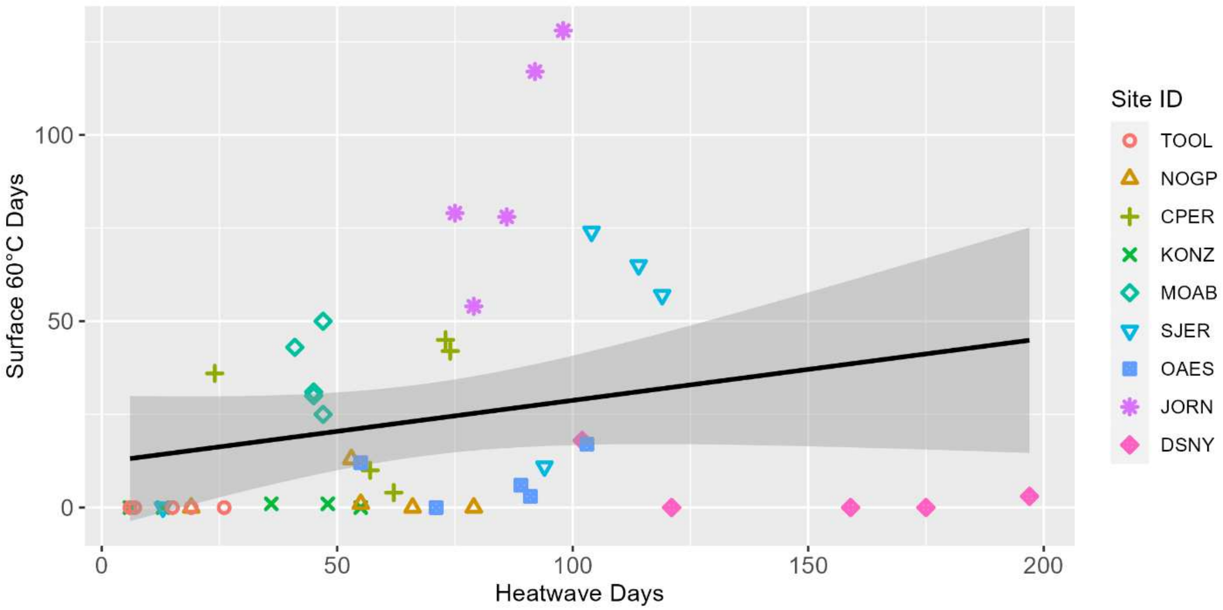

Figure 4.4: Linear regression of the annual number of heatwave days from the air and the annual number of days that the surface temperature reaches or exceeds 60°C. The shading around the line represents the 95% confidence interval.

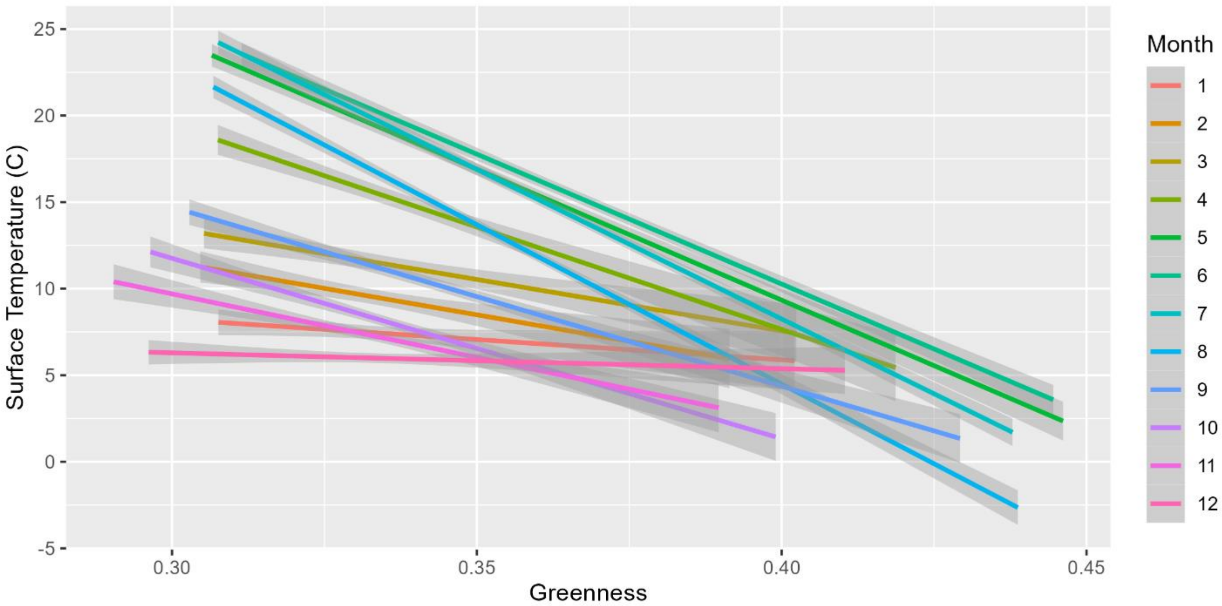

Figure 4.4: Multiple linear regression model based on the relationship between surface temperature and greenness for each month across arid or grass dominated NEON sites. Shading represents 95% confidence intervals.

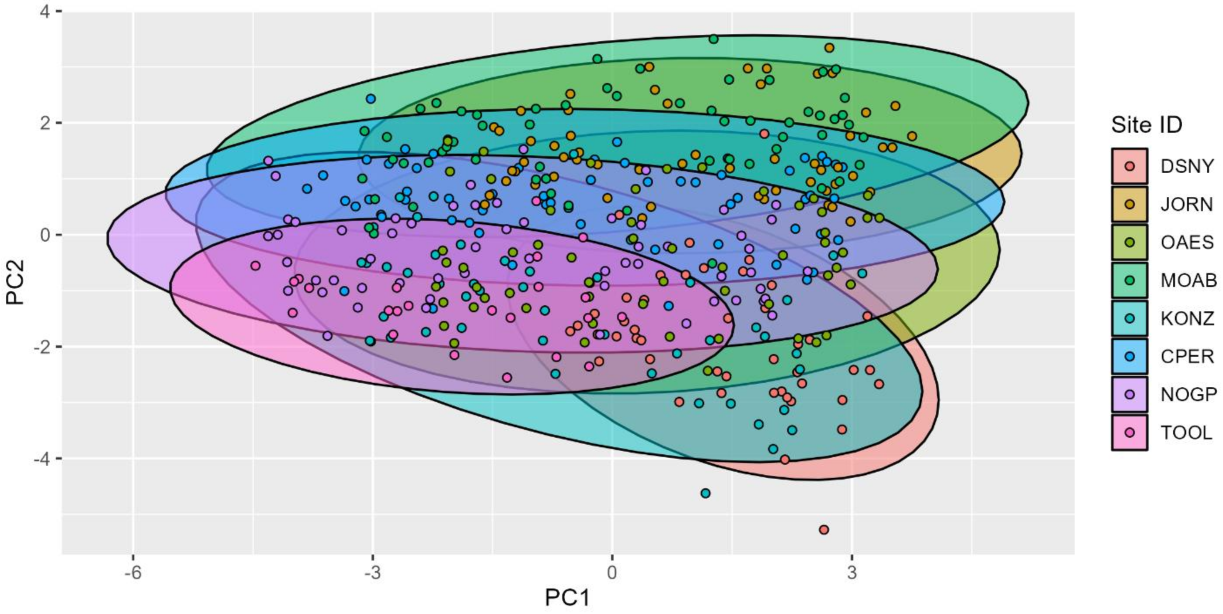

Figure 4.5: Principal component analysis of Grass dominated NEON site groupings based on Euclidean distance of monthly data of microsite parameters. The ellipses represent the 95th confidence interval of arid and grass dominated NEON sites.

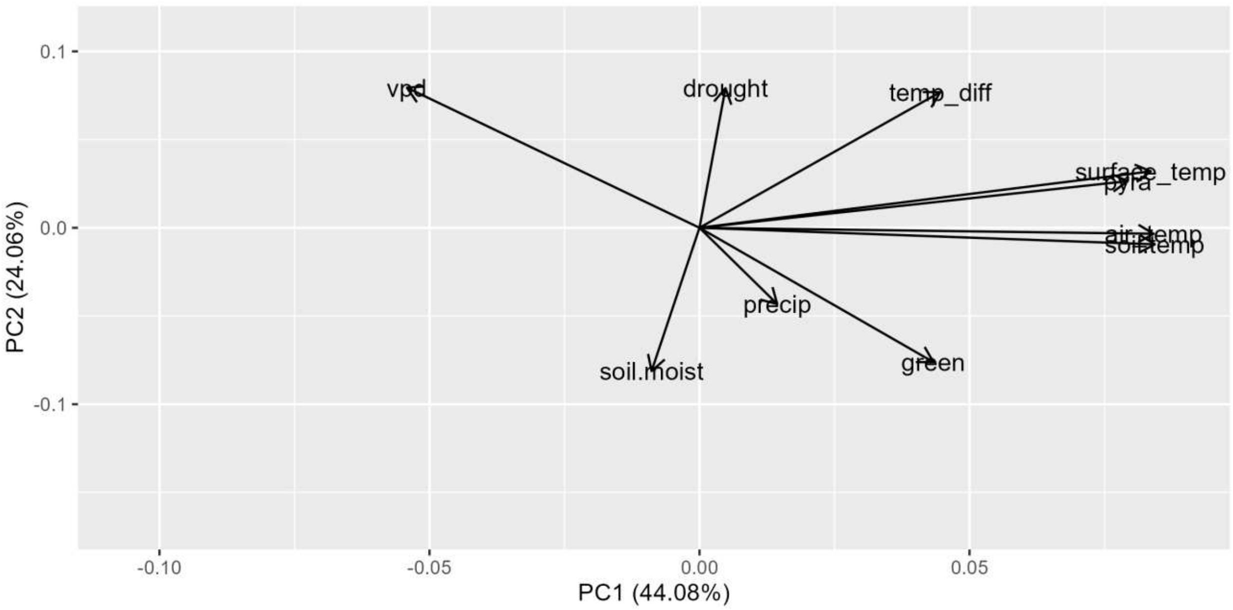

Figure 4.6: Principal component analysis based on Euclidean distance matrix showing the relationship between variables that correlates with surface temperatures. The direction and length of the lines indicate the strength and degree of the relationship among the parameters.

4.6 Tables

Table 4.1: Description of the NEON sites used in this research. The descriptions on the table are from the site descriptions provided by NEON.

Site	Domain	MAT (°C)	MAP (mm)	Dominant Grasses
DSNY	Southeast	22.5	1216	*Aristida stricta, Aristida spiciformis, Andropogon spiciformis*
JORN	Desert Southwest	15.7	271	*Bouteloua eriopoda, Sporabolus flexuosus*
OAES	Southern Plains	15.5	788	*Bouteloua dactyloides, Aristida purpurea*
SJER	Pacific Southwest	16.4	539	*Predomoinatly Bromus sp., bunch grasses on northern slopes*
MOAB	Southern Rockies & Colorado Plateau	10.1	320	*Bouteloua gracilis*
KONZ	Prairie Peninsula	12.4	870	*Andropogon gerardii, Schizachyrium scoparium, Sorghastrum nutans, Panicum virgatum*
CPER	Central Plains	8.6	344	*Bouteloua gracilis, Bouteloua dactyloides*
NOGP	Northern Plains	5.9	455	*Bromus inermis, Poa pretensis, Nassella viridula*
TOOL	Tundra	-9	316	*Carex bigelowii, Eriophorum vaginatum*

Table 4.2: Euclidean distances for Principal Components 1 and 2. Any variable that was equal to or greater than 0.4 is highlighted green and any variable that was equal to or less than -0.4 are highlighted red.

Variable	**PC1**	**PC2**
Surface Temperature	0.449502	0.172039
Air Temperature	0.452346	-0.0182
Surface-Air Difference	0.239823	0.413467
Vapor Pressure Deficit	-0.29139	0.427071
Pyranometer	0.426544	0.142196
Drought Index	0.02588	0.425725
Greenness	0.233031	-0.40956
Soil Temperature	0.453567	-0.0505
Soil Moisture	-0.04774	-0.43696
Precipitation	0.077415	-0.23247

CHAPTER 5: CONCLUSIONS

Many grasslands occur in regions that are located in arid or semi-arid regions, meaning that they are prone to limited precipitation and high seasonality (Mayer & Khalyani, 2011). While there has been a substantial amount of research done on grasslands and water deficit, literature about thermal stress and limitations of the plants in these ecosystems is scarce (Jameson, 1961; Wright, 1970). These systems also evolved in the presence of grazing making them resilient to vegetation removal (Milchunas et al., 1988). Today these systems support a variety of domesticated and natural herbivores (Milchunas et al., 2008), and the intensity of their grazing likely has major implications for the capacity of grasslands to survive droughts.

Given the projections for increased frequency and severity of drought for the grasslands of the United States (Groisman & Knight, 2008) and the shifts in precipitation patterns observed on the SGS over the last few decades (Fig. 3.1), it is imperative that we understand how the dominant plants in these systems will respond to these shifts at both the individual and community level. This research has demonstrated the impacts that grazing has on the on the dominant C_4 and C_3 perennial grasses on the SGS in the presence of droughts; both in terms of a multi-year drought and heat stress.

I observed a greater reduction in the dominant grasses when there was a multi-year drought in comparison to a single year drought. The vegetation cover didn’t recover as well for the multi-year drought and the green vegetation index (GVI) remained low for both droughts scenarios, indicating that the vegetation that did grow back was less dense than it was prior to the droughts. The leading cause for the decrease in cover and GVI during and following the droughts was the loss of the density dominant perennial grasses.

Previous research showed that in the absence of grazing, it takes at least 10 years of continuous drought to extirpate the *Bouteloua* species from the SGS and the amount of ruderal species increased as the cover of the *Bouteloua* species decreased (Evans et al., 2011). I saw a major decline in perennial C_4 species in the multi-year drought treatment (Fig. 2.4). While there were signs of recovery of these functional groups, the most extreme grazing pressure (moderate cattle grazing with prairie dogs) showed the combined stresses might be a tipping point, as the recovery from this treatment was minimal (Fig. 2.5). Although grazing and water limitation are thought to promote the dominance of the *Bouteloua* species, it appears that the combination of high intensity grazing and drought might be detrimental to the species.

The scarcity of vegetation during droughts at CPER makes the crown tissue of the dominant species susceptible to erosion because it is located so closely to the soil surface (Ott, personal communication). Grazing during droughts increases the potential for erosion by removing the already scarce vegetation and breaking up soil crusts. The temperatures at the surface of the soil and crown tissue, when eroded crowns fail to produce vegetation, exceeds the currently accepted lethal temperature of plants, 60°C (Choczynska & Johnson, 2009; Dickinson & Johnson, 2004) much more frequently than I had anticipated when I began this research (Fig. 4.2). Leading us to question the variability in lethal temperatures of plants and what adaptations perennial grasses have that allow them to survive in areas that frequently reach these theoretically lethal temperatures.

The analysis of microclimate data across grass dominated systems in the US revealed that sites that are arid or at lower latitudes experienced a greater occurrence of 'lethal temperature' days compared to sites that are wet or in higher latitudes. There were some anomalies of lethal days at the wet sites, but it was very infrequent and often isolated, whereas the lethal temp days at the arid sites tended to have consecutive days where temperatures were at damaging thresholds. I acknowledge that there is some plasticity in the thermal tolerance throughout the year (Jameson, 1961) and that there is a relationship between exposure time and temperature (Wright, 1970), but both of these studies suggest that multiple hours of exposure at temperatures above 60°C should result in mortality of the meristems for a single exposure, but the fact that these conditions are present for 40-100 days at the arid sites suggests that the plants are clearly capable of surviving beyond the current assumed thresholds.

Ultimately my research highlighted the capabilities of grass dominated systems to withstand pressures from grazing, drought, and heat. However, it also pointed out that the combinations of stresses have the potential to push these systems beyond their limits (i.e., grazing with drought, erosion with heat stress). It is imperative that I understand the negative impacts and limitations of the plants to withstand these interactions because climate change will likely increase the frequency and severity of these stresses, which could have the potential to cause major shifts in the species that are capable of surviving in these systems.

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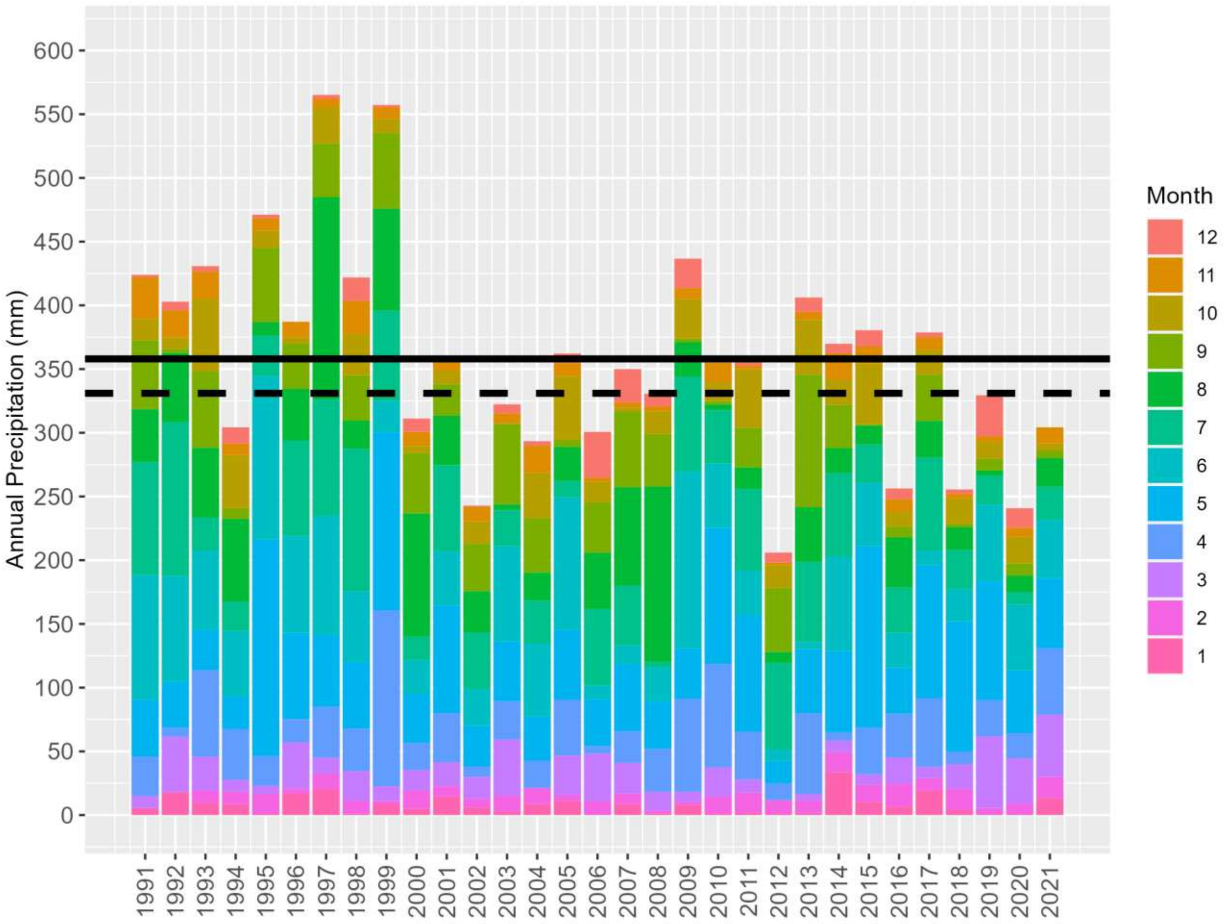
APPENDICES

Supplementary Figures



Sup. Fig. 1: The total precipitation for each year in the 30-year data record from the CPER headquarters. The different colors indicate the monthly totals. The solid reference line represents the MAP for the 30-year precipitation data, and the dashed reference line represents the MAP calculated from the entire historical record dating back to 1939.