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Effects of global change on savanna grassland ecosystems

Sally Koerner

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**EFFECTS OF GLOBAL CHANGE ON SAVANNA
GRASSLAND ECOSYSTEMS**

by

SALLY ELIZABETH KOERNER

B.S., Biology, Clemson University, 2005

DISSERTATION

Submitted in Partial Fulfillment of the
Requirements for the Degree of

**Doctor of Philosophy
Biology**

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Abstract

Humans are altering the environment locally and globally through climate and land use change. Global temperature is increasing, precipitation patterns are becoming more variable, disturbance regimes are being altered, and ecosystems are being simplified as multi-species communities are replaced by monocultures of crops or livestock. Grasslands, which cover approximately a third of the terrestrial lands, are ecologically and economically significant, thus their responses to environmental change will have dramatic consequences for global patterns of productivity, biodiversity, and food production. This dissertation research investigates how the three main drivers of mesic grassland ecosystems – precipitation, grazing, and fire - interact to affect community composition, structure, and dynamics. I utilized an existing cross-continental study to determine the degree to which mechanisms controlling diversity and dynamics in North American (NA) savanna grasslands apply to Southern African (SA) systems, and vice versa. I conducted my research in two savanna grassland ecosystems: Kruger National Park (Kruger), in northeastern South Africa, and Konza Prairie Biological Station (Konza), in northeastern Kansas, USA. Overall, this dissertation

shows that on small scales different grasslands exhibit similar responses to grazing and fire, and to grazing, fire, and drought. However, the generality seen in small-scale responses may not transfer to larger landscape scale processes because patch dynamics within these landscapes are strongly affected by grazing and fire in NA but not in SA. This research also showed that grazing more frequently affected community properties like diversity, cover, and ANPP, while both drought and changes in rainfall variability rarely affected those properties. Instead grasslands responded to changes in rainfall by altering stem densities, and only then in the presence of grazing. As the majority of grasslands globally are grazed, current climate change experiments in grasslands may be underestimating the effects of altered precipitation patterns on the population dynamics of species within these ecosystems.

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Chapter 1

Introduction

Anthropogenic climate and land use change are altering the environment on local and global scales. Understanding how ecosystems will respond to global change is an important societal concern and a focus of intense scientific research (Mooney 1991, Sala et al. 2000, Weltzin et al. 2003). Climate models predict that global temperatures will increase and that precipitation patterns will become more variable (Easterling et al. 2000b, Karl et al. 2009). These and other global change drivers (e.g., nitrogen deposition, increased CO₂ concentrations, land-use change) will likely transform community compositions as well as alter natural disturbance regimes. Savanna grasslands, a continuous layer of grasses with widely scattered shrubs and trees (Scholes and Archer 1997), cover approximately 36% of the terrestrial land surface (Sala 2001), sequester significant amounts of soil C, house the majority of the world's remaining megafauna, and are economically important as grazing lands (Owen-Smith 1988, Schimel et al. 1994, Allen-Diaz 1996, Fuhlendorf and Engle 2001). Grassland responses to global change may have significant consequences for rangeland management and global patterns of productivity and diversity. For my dissertation, I investigated how three factors - climate change, loss of megaherbivore diversity, and altered disturbance regimes - interact to affect plant community composition in savanna grasslands in North America (NA) and South Africa (SA).

Climate models predict that precipitation regimes are likely to become more variable in the future, including more extreme and prolonged droughts across seasons and fewer but more intense rainfall events within seasons (Gordon et al. 1992, Easterling et al. 2000a, IPCC 2007). Such changes have already been documented (Groisman et al. 2005, Groisman and Knight 2008, Knapp et al. 2008, Min et al. 2011, Smith 2011), but overall, potential ecological consequences of increased precipitation variability have received much less attention than have the effects of elevated CO₂ and temperature (Heisler and Weltzin 2006, Knapp et al. 2008). Mid-continental areas, where many mesic savanna grasslands occur, are expected to become drier during the growing season with an increased chance of prolonged drought (Kothavala 1999, Wetherald and Manabe 1999), particularly in central and southeastern North America and tropical Africa (Zwiers and Kharin 1998). Grasslands should be especially susceptible to changes in both rainfall amount and variability as production is largely precipitation limited under existing climatic conditions (Sala et al. 1988, Esser 1992, Knapp et al. 2001).

Large herbivores are also important drivers of grassland ecosystem dynamics. They increase diversity and patchiness in mesic grasslands by increasing resource heterogeneity and altering plant community structure through selective grazing, soil disturbances, and nutrient deposition. Herbivores also have significant effects on primary production, particularly in grasslands that support large herds of grazers (Frank and Groffman 1998). In several grassland ecosystems, grazing has been shown to have a stimulating effect on plant production (McNaughton 1976, Pandey and Singh 1992, Loeser et al. 2004). This facilitation occurs because grazing

increases the availability of light, water, and/or nitrogen to plants (McNaughton 1985, Frank and Groffman 1998, Knapp et al. 1998b). Light to moderate grazing also increases plant species richness (Collins 1987, Hartnett et al. 1996). The loss of dominant herbivores from mesic grassland ecosystems in NA has been shown to decrease plant species richness and diversity, and the effects of losing the remaining megafauna species are well understood. However, in SA, where the large herbivore community is still extant, the impacts of herbivore species loss are still emerging (Milchunas and Lauenroth 1993, Anderson et al. 2007b, Burns et al. 2009).

Fire, unlike herbivory, is a large-scale generalist “herbivore” (Bond and Keeley 2005b) that homogenizes resources (Blair 1997) and plant community composition (Collins 1992, Collins and Smith 2006). Fire increases biomass production by stimulating growth, removing moribund material, and increasing light availability at the soil surface. It changes community structure by uniformly removing aboveground biomass, promoting fire-tolerant species, and preventing growth of woody vegetation (Briggs et al. 2005). Savanna grasslands burn on average every two to three years making them the most frequently burned ecosystem in the world (Beerling and Osborne 2006); however, changes in climate coupled with changes in land use, harvest, and demography have already and will continue to alter fire regimes (Kloster et al. 2012).

Independently, fire and grazing have opposite effects on community composition, but together grazing and fire can increase plant species diversity and community heterogeneity (Collins 1987, Collins and Smith 2006). Grazing and fire frequency also interact on a landscape scale through positive and negative

feedbacks (Fuhlendorf and Engle 2001). Herbivores alter fire frequency by removing aboveground biomass and, therefore, decreasing the fuel load, while fires modify herbivore density by altering plant chemistry in a way that attracts herbivores and by removing biomass that could otherwise be consumed by herbivores (Fuhlendorf and Engle 2004).

Much research has focused on the effects of climate change on grassland biodiversity, yet little is known about the interaction between climate variation and grazing or fire. Through my dissertation I have examined the interactive effects of climate change, large herbivore diversity loss, and altered fire regimes on plant community structure in savanna grasslands (Figure 1). I have investigated these interactive effects in three chapters.

For Chapter 1, I utilized a long-term climate manipulation study, the Rainfall Manipulation Plots (RaMPs) experiment (Figure 2), at Konza Prairie Biological Station in northeastern Kansas, USA. I addressed whether a decade of more variable rainfall events impacted the plant community response to grazing. Initiated in 1998, the RaMPs simulate a more variable rainfall regime, which is predicted to occur with climate change in the central Great Plains of the US (IPCC 2007). The altered precipitation patterns in the RaMPs have resulted in a significant reduction in soil moisture (14%) and increased soil moisture variability (18%; (Fay et al. 2011b). The RaMPs experiment is therefore an ideal infrastructure within which to study how long-term changes in rainfall variability will impact the plant community response to grazing.

For Chapters 2 and 3, I utilized an existing cross-continental study to determine the degree to which mechanisms controlling diversity and dynamics in NA savanna

grasslands apply to SA systems, and vice versa (Knapp et al. 2004). I conducted my research in two savanna grassland ecosystems: Kruger National Park (Kruger), in northeastern South Africa, and Konza Prairie Biological Station (Konza). Despite differences (Table 1), these grasslands share important features, which allow for cross-continental comparison. Herbaceous structure at both sites is dominated by C₄ grasses with an abundance of forb and shrub species scattered within that grassy matrix (Freeman 1998, Venter et al. 2003). Both sites have distinct dormant and growing seasons. The dormant season is cold winter in NA and a drought season in SA. During the active growing season, both sites share similar mean (500-600 mm) and variability in rainfall patterns. Native megaherbivores are present in both sites with NA having bison, and SA being home to over 30 megaherbivore species. Most importantly, precipitation (Briggs and Knapp 1995, Snyman 2000, Knapp et al. 2002, Scholes et al. 2003b), grazing (Frank et al. 1998, Snyman 2002, du Toit 2003) and fire (Collins and Wallace 1990, Roques et al. 2001, Briggs et al. 2002, Bond et al. 2003) are the key drivers that maintain both of these grassland ecosystems. Using this cross-continental comparison, I determined how fire and grazing interact to affect the patch structure of the dominant grasses in Chapter 2. In Chapter 3, I determined how short-term grazing and drought manipulations interact with long-term fire regimes to affect plant community structure and ecosystem function.

In total, my research is an in-depth study of how the three primary drivers of savanna grasslands worldwide – grazing, fire, and precipitation – interact to affect grassland community structure and function. With comparable experimental designs and identical sampling protocols in both NA and SA, this approach will greatly enhance the ecological generality of my findings. My research is a rigorous

assessment of the cumulative effects of long-term fire and grazing regimes, as well as responses to short-term manipulations of herbivores and climate on grassland structure and function. Ultimately, the insight gained from my studies will improve savanna grassland models that include fire, grazing, and climate effects on community processes and aid in understanding how future climate scenarios may impact mesic savanna grassland ecosystems.

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Tables and Figures

Table 1. Differences between the grasslands in NA and SA study sites.

Attribute	NA	SA
Age of extant community	8-10,000 years	4-6 million years
Climate	temperate	tropical
Soil nutrient levels	high	low
Megaherbivore species richness	low	high



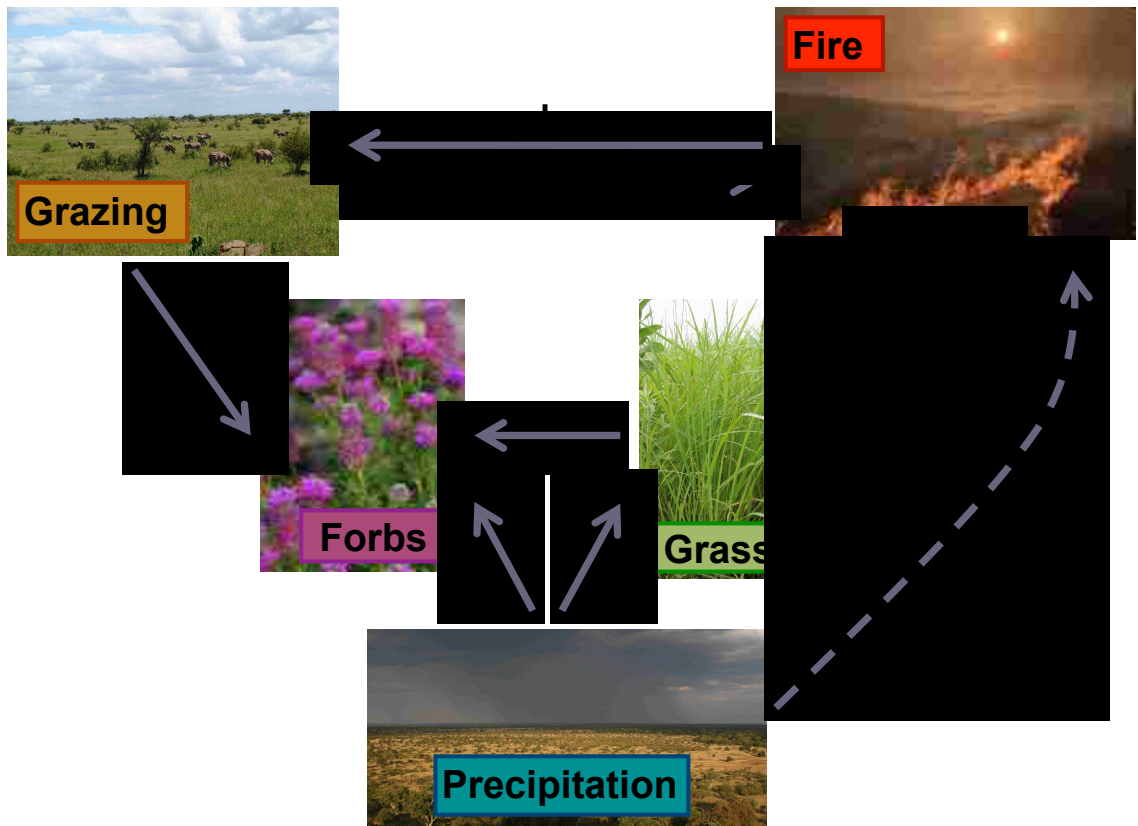


Figure 1. Conceptual diagram of the key drivers and interactions in grassland ecosystems.



Figure 2. a) Aerial overview of Rainfall Manipulation Plots (RaMPs) layout and b) a side view of a RaMP showing watering tanks.

CHAPTER 2

Increased rainfall variability intensifies grazing effects in tallgrass prairie

Abstract

Mesic grasslands experience a complex disturbance regime including frequent fire, grazing by large ungulates, and strong interannual climate variability. As a result of climate change, growing season precipitation regimes are predicted to become more variable, with larger event sizes and longer dry periods resulting in more temporally dynamic soil moisture regimes, a pattern already occurring in many regions. In ungrazed tallgrass prairie increased soil moisture variability decreases annual net primary production of C₄ grasses while forb production is unaffected. However, climate variability is likely to interact with other disturbances common in tallgrass prairie; thus we investigated the individual and combined effects of increased rainfall variability and grazing on plant community composition, structure, and function in an annually burned grassland to assess how grazing impacts may be modified under an altered climate regime. To do so, we simulated a growing season of intense grazing and then monitored recovery over two years in plots established within an ongoing rainfall manipulation experiment in which larger, but less frequent, rainfall events were imposed without altering the total rainfall amount. We found that neither grazing nor rainfall treatments affected species richness; however, grazing decreased total and grass annual net primary production (ANPP) and increased forb ANPP relative to ungrazed plots. Grass stem

density recovered from intense grazing under ambient rainfall but did not fully recover even after two years in the altered rainfall treatment. Thus, altered precipitation and more temporally variable soil moisture patterns may exacerbate the effects of grazing on grasses and inhibit post-grazing recovery in North American tallgrass prairie.

Introduction

Over the past decades precipitation regimes have become more variable with an increase in rain event sizes, longer dry periods, and an increase in the number of rainfall events classified as statistically extreme (Groisman et al. 2005, Groisman and Knight 2008, Knapp et al. 2008, Min et al. 2011, Smith 2011). These trends are projected to intensify as atmospheric carbon dioxide concentrations continue to rise (Easterling et al. 2000b, Karl et al. 2009). Worldwide, grasslands are experiencing more prolonged droughts and fewer but more intense rainfall events within seasons (IPCC 2007). With grasslands and savannas estimated to cover up to 40% of the terrestrial surface (Chapin et al. 2001), their responses to changes in rainfall will have significant consequences for global patterns of productivity and diversity under future climate scenarios (Fay et al. 2003).

Experimentally imposed increases in rainfall variability in mesic grasslands lead to more temporally variable soil moisture patterns (Fay et al. 2011a), which reduces annual net primary production (ANPP) independent of changes in total annual precipitation (Knapp et al. 2002, Fay et al. 2003, Knapp et al. 2008, Heisler-White et al. 2009). Studies in North American tallgrass prairie have shown that altered rainfall patterns can reduce average ANPP by approximately 10% with a maximum of 22% in any given year depending on total annual rainfall (Knapp et al. 2002, Fay et al. 2011a). The decrease in ANPP was mainly driven by changes in the sub-dominant C₄ grasses while the dominant grass *A. gerardii* and forbs were unaffected (Fay et al. 2003). However, changes in rainfall amount and increased rainfall variability minimally impact plant community composition and diversity, which are

primarily controlled by long-term regional climate (Knapp et al. 2002, Collins et al. 2012), as well as other local factors including fire frequency and grazing in mesic grasslands (Collins 1987, Glenn et al. 1992, Knapp et al. 1999, Collins and Smith 2006, Veen et al. 2008, Spasojevic et al. 2010, Collins and Calabrese 2012).

Most natural grasslands are grazed by livestock or large herds of wild herbivores (Coupland 1992, Gibson 2009), which influence both ecosystem and community dynamics (McNaughton 1985, Gibson 2009). Grazers alter plant communities, often increasing diversity through selective grazing of the dominant grasses, creating soil disturbances, and altering temporal and spatial patterns of nutrient deposition (McNaughton 1985, Collins 1987, Hartnett et al. 1996, Collins et al. 1998, Olf and Ritchie 1998, Fuhlendorf and Engle 2001, Collins and Smith 2006, Gibson 2009). The impact of grazing on ANPP varies with both under- and overcompensation (a net decrease or increase in total production) documented in mesic grasslands (McNaughton 1979, Frank et al. 1998). Despite the ubiquity of grazers, current climate change research in grasslands largely ignores the interaction between climate variation and grazing (Zhou et al. 2002, Swemmer and Knapp 2008, Cheng et al. 2011) in part due to logistical constraints that limit the incorporation of grazing into climate change manipulations. Therefore, current knowledge on grazing-climate interactions relies on observational studies utilizing naturally occurring climate events (Savage and Jacobson 1935b, Weaver and Albertson 1936, Clarke et al. 1943b, Coupland 1958) or gradients across space (Swemmer and Knapp 2008) or time (Fuhlendorf et al. 2001, Cheng et al. 2011). These studies demonstrate that grazing and climate interact to alter diversity, shift dominance,

and influence productivity and forage quality; thus, the effects of predicted changes in climate on grassland vegetation need to be defined within the context of grazing.

To address this deficiency we experimentally manipulated rainfall variability and grazing in a native tallgrass prairie. The Rainfall Manipulation Plots (RaMPs) were established in 1997 to manipulate rainfall variability in large intact plots of native tallgrass prairie in north-eastern Kansas by increasing rain event size while decreasing event frequency, relative to ambient rainfall patterns, without altering the total growing season rainfall. The result is a more temporally dynamic soil moisture regime, with greater fluctuations between high and low soil water availability (Knapp et al. 2002, Fay et al. 2011a). Within this ongoing, long-term experiment, we simulated a year of intense, selective grazing to directly examine grassland responses. We then monitored recovery from grazing for two years under both ambient and more variable rainfall.

The main objectives were to investigate the individual and combined effects of increased rainfall variability and grazing on the plant community composition and ecosystem function and to determine if grasslands will be more or less sensitive to grazing events under an altered climate regime. We hypothesized that (1) grazing under ambient rainfall patterns would increase plant community diversity with minimal impacts on grass ANPP, while grazing under the altered rainfall and soil moisture treatment would decrease plant community diversity and grass ANPP due to greater water stress experienced by the dominant grasses (Knapp et al. 2002, Fay et al. 2011a), and (2) more variable rainfall patterns would slow the recovery of

grassland community structure in response to grazing, due to more frequent and intense periods of water stress relative to ambient rainfall regime.

Methods

Study Site

Konza Prairie Biological Station (Konza) is a 3,487-ha research site located in the Flint Hills of northeastern Kansas, an area that includes the largest remaining area of native tallgrass prairie in North America. Konza has been a Long-Term Ecological Research (LTER) site since 1981, and plant communities there are primarily unplowed, native tallgrass prairie. A small number of perennial C₄ grasses including *Andropogon gerardii* and *Sorghastrum nutans* dominate the plant community and account for the majority of herbaceous primary productivity (Knapp et al. 1998a), while plant species diversity is generally a function of the richness and relative abundance of subdominant forb species (Collins and Glenn 1991). The climate is temperate with mean monthly air temperature in July of 27°C. Annual precipitation averages 835 mm/year, with approximately 75% falling as rain during the May-Sept growing season. Variation from average precipitation patterns is common, both in yearly totals and seasonal distribution (Hayden 1998). This area and tallgrass prairie in general evolved under grazing pressure from bison (*Bison bison*), which likely played a keystone role in the development of this ecosystem (Knapp and Seastedt 1998, Knapp et al. 1999). In the mid to late 1800s during European settlement, free-ranging herds of bison were eliminated, and for more than 150 years cattle (*Bos taurus*) have been the dominant herbivore (Towne et al. 2005).

We utilized the existing Konza RaMPs infrastructure and ongoing rainfall manipulations for this study. A set of twelve fixed-location rainout shelters, arranged in three blocks, was established in 1997. Shelters exclude and collect natural rainfall inputs from the plots, and collected rainfall is reapplied at different frequencies and different event sizes. Fay et al. (2000) provide details on shelter design and efficacy. The RaMPs are located in ungrazed lowland prairie that is burned annually in late March. The dominant plant species in the plots include *A. gerardii*, *S. nutans*, *Panicum virgatum*, and *Sporobolus asper*, all rhizomatous, warm-season, C₄ tall grasses. Dominant perennial forbs include *Solidago canadensis*, *Aster ericoides*, and *S. missouriensis*. Productivity in the RaMPs has averaged 725g m⁻² to date with approximately 25% of the productivity being derived from forbs (unpublished data).

In six RaMPs (the “ambient” treatment) intercepted rainfall was reapplied to the plots via overhead sprinklers each time a natural rainfall event occurred in the naturally occurring quantity. Rainfall inputs in the other six RaMPs were experimentally altered to create a more variable rainfall pattern. The altered rainfall treatment was based on increasing the dry interval between ambient rainfall events by 50%, thereby decreasing the rainfall event frequency and increasing event size without altering the total growing season rainfall amount. From 2007 to 2011, average growing season rainfall was 571 mm. In the ambient plots, rain fell on approximately 32 days each growing season creating an average rain event size of 18 mm and 5 days between each event. In the altered rain treatment, rain fell on approximately 14 days each growing season creating an average rain event size of

42 mm and increasing the length of the dry period to 11 days. The altered rainfall treatment decreased average soil moisture (14%) across the growing season and increased soil moisture variability (18%) throughout the growing season (Knapp et al. 2002, Fay et al. 2011a).

Experimental Manipulation

Within the long-term RaMPs experiment, we examined how altered precipitation patterns interacted with grazing to affect plant community composition and productivity. Under each RaMP a 2 x 2 m plot subdivided into four 1 x 1 m subplots was established in 2007, and pre-grazing treatment data were collected. In 2008 two subplots were grazed and two were left unmanipulated as controls. To simulate repeated grazing by large herbivores (cattle and bison), all graminoids were clipped to 5 cm (leaving all forbs unclipped) once each month during the growing season (June-August). Bison diets are typically composed of 90% graminoids (Krueger 1986, Plumb and Dodd 1993). Our clipping methods simulated this selective grazing. Plots were clipped in 2008 only, simulating a dynamic landscape scale-grazing regime (Fuhlendorf and Engle 2001), with 2009-2011 serving as recovery years.

In all subplots, cover of all species was visually estimated to the nearest 1% twice during each growing season (June and August). Cover data for each species on the 1-m² scale were used to compute standard metrics of community structure, including grass, forb, and total species richness, Shannon–Weiner diversity, evenness, and grass, forb, and total cover. All metrics were calculated using the maximum average cover values of each species for the entire growing season and

then averaged for two adjacent 1-m² subplots. At the end of each of the five growing seasons all aboveground biomass was collected from one 0.1 m² plot nested within each subplot, sorted by growth form, and weighed to determine aboveground net primary production (ANPP). During the grazing treatment year, clipped biomass from the grazing simulations was dried, weighed, and added to the end-of-season biomass to calculate total ANPP and to determine if grazing compensation occurred. To provide an additional mechanistic response variable, stem density counts for all species were performed in one 0.1 m² plot nested within one of each of the grazed and ungrazed subplots within each RaMP in 2009 and 2010 only. In 2011 less intensive monitoring occurred, and only aboveground biomass was collected.

Data Analysis

Each RaMP was treated as an experimental unit; therefore, all measured responses reported here were based on the average value of the two subplots in each RaMP. We tested for differences among treatments in diversity (Shannon-Weiner), evenness, richness, grass cover, forb cover, grass, forb, and total ANPP, and grass, forb, and total stem numbers. All responses and all years were analyzed separately using split-plot design mixed-model ANOVAs in SAS (SAS Institute V.9.3; Cary, N.C.). Early season and late season stem density counts were analyzed independently. Because early season stem density for total, grass, and forb stems showed similar or weaker trends as the fall (Table 2), only the fall stem density data are presented. When main effects or interactions were significant, mean separations were performed using Least Square Means. Significance was set at $\alpha = 0.05$.

Results

Despite the previous nine years of altered rainfall treatments, plant community diversity and richness and ANPP were not significantly different between the rainfall and grazing treatments in 2007 (pre-treatment year). In addition, during the next 2 years of this study (treatment and one recovery year), rainfall and grazing treatments had no significant effects on plant species richness (Table 1) with approximately 14 species per m² in all plots. In 2011, ambient plot richness was significantly higher when grazed. Diversity was significantly affected by the interaction of rainfall and grazing only during the grazing year with ambient grazed plots having significantly higher diversity than any of the other treatments (Table 1, Figure 1).

The repeated grazing treatment significantly reduced total ANPP in each year, and we found a significant rainfall-grazing interaction in 2009 (Table 1). In 2008 (grazing year) grazing decreased total ANPP by 15%. In the recovery years, the grazing treatment resulted in decreased total ANPP by 39%, 37%, and 42% in 2009-2011, respectively (Figure 2a). In 2009, the altered rainfall treatment significantly reduced total ANPP by 19% but only in the ungrazed plots.

Grass ANPP was significantly reduced by grazing in 2008-2011 (Table 1). In 2008 (grazing year) grazing decreased grass ANPP by 43%. In the recovery years, the grazing treatment resulted in decreased grass ANPP of 93%, 78%, and 74% in 2009-2011, respectively (Figure 2b). Altered rainfall also decreased grass ANPP by 31% in 2011, but no significant interaction with grazing occurred.

Grazing significantly affected forb ANPP during the grazing year (2008) and for the first year of recovery (Table 1). In the grazing year (2008), grazed plots had 57% higher forb ANPP than ungrazed plots. In 2009 (recovery year one) grazed plots had 78% higher forb ANPP than ungrazed plots, but in 2010 and 2011 forb ANPP was not significantly affected by the grazing treatment (Figure 2c).

Late season total stem density showed similar patterns in 2009 and 2010 (Table 2). Only the 2010 data are presented here. Late season total stem density was significantly affected by grazing and by a grazing-rainfall interaction (Table 2). Grazing decreased total stem density by 42%, but this effect was moderated by rainfall. There was no significant difference between grazing treatments in ambient rainfall (grazed: mean=72±12 S.E. stems; ungrazed: mean= 81±13 S.E stems), while in the altered rainfall plots, grazing reduced stem density by 67% (grazed: mean=34±8 S.E. stems vs. ungrazed: mean=103±17 S.E. stems per m²). The decrease in total stem density was driven primarily by a decrease in grass stem densities. As with total stem density, there was no significant difference between grazing treatments with ambient rainfall, while in the altered rainfall treatment, grazing reduced grass stem density by 81% (Figure 3). This decline in stem densities due to grazing was offset somewhat by a 32% increase in late season forb stem density (Table 2), with mean forb stem density of 16 (S.E.=±1) and 11 (S.E.=±2) for grazed and ungrazed plots, respectively.

Discussion

In this study altered rainfall alone had no impact on the plant community, yet increased variability in precipitation regimes interacted with a simulated, repeated

grazing event in 2008 to alter plant community structure and aboveground productivity for up to three years after grazing occurred (Figs. 1 & 2). As predicted, grazing under ambient rainfall patterns increased plant community diversity. This was expected as numerous studies in tallgrass prairie have shown that grazing increases diversity by reducing grass dominance and increasing forb richness (Damhoureyeh and Hartnett 1997, Collins et al. 1998, Knapp et al. 1999, Damhoureyeh and Hartnett 2002, Towne et al. 2005, Collins and Smith 2006). However, grazing under ambient conditions did not have the predicted minimal impact on grass ANPP. Instead grass ANPP was negatively impacted by grazing during the grazing year producing a >40% under-compensation response by grasses and an increase in forb ANPP regardless of the rainfall treatment.

Negative growth response is common under repeated heavy defoliation in tall and mid-height grasses (Holland and Detling 1990), and a recent study indicates that such under-compensation can occur even under moderate grazing (Knapp et al. 2012). One study found that clipping *A. gerardii* monthly throughout the growing season caused approximately a 70% decrease in production (Woodis and Jackson 2008). Preferred forage species like *P. virgatum* and *A. gerardii* decrease under heavy grazing or if plants are not allowed adequate recovery time after each defoliation event (Vinton and Hartnett 1992, Vinton et al. 1993). Mousel et al. (2003) recommended a grazing system with a minimum 40 day rest period during summer in order to maintain a viable population of *A. gerardii*. In addition, Mousel et al. (2003) found that grazing in August after a June grazing event decreased basal cover. Our simulated grazing treatment included a 30-day rest period with an

August grazing event following grazing in June and July, all of which resulted in high intensity grazing from which *A. gerardii* and other grasses were unable to recover.

The grazing effects carried over in the following years, even though grazing was no longer simulated. The legacy effect of grazing in the previous year caused a further decrease in grass ANPP of almost 95% and a further increase in forb ANPP of almost 78%. Consistent with our findings, Vinton and Hartnett (1992) found that *A. gerardii* tillers that had been grazed repeatedly the previous year had lower relative growth rates, final tiller mass, and tiller survival. The immediate increase in relative growth rate caused by grazing likely results in reductions in allocation to stored reserves in the perennating organs and gradual reductions in new rhizome production and belowground biomass, in general (Biswell and Weaver 1933, Weaver and Hougen 1939, Hartnett 1989).

There are two carbon limitation mechanisms to explain the long-term (3 years) decrease in grass ANPP due to a single year of grazing. Grazing depletes belowground biomass in the grasses, and individuals are unable to accumulate enough carbon to replenish their below ground stores. The presence of grazers has been shown to decrease bud banks due to the increased risks of grass tiller mortality (Archer and Detling 1984, Vinton and Hartnett 1992) resulting in fewer tillers the following year (Dalglish and Hartnett 2006). Even if the grazed tillers survive the growing season through to the next spring, a reduction in biomass accumulation may reduce bud production, again resulting in fewer tillers the following season. In addition, repeated grazing or clipping in one season has been shown to negatively impact root to shoot ratio in *A. gerardii* and eventually mycorrhizal root colonization is lost (Hetrick et al. 1990) because there is less C in

the plant roots. This loss of mycorrhizal fungi may explain the almost complete elimination of grass stems in the year following grazing. Hetrick et al. (1990) found that regrowth of *A. gerardii* in the spring from mature rhizomes is dependent upon mycorrhizae, because the stored nutrients in the rhizomes are not sufficient to support plant growth on their own, leading to significant reductions in plant fitness and survival in subsequent seasons.

Belowground carbon limitation may also explain the grazing-rainfall interactions observed in this study. Grass stems were less dense in the altered rainfall plots that were grazed but not in the grazed ambient rainfall plots. When coupled with water stress in the altered rainfall patterns, the grasses were unable to recover enough carbon to replenish belowground stores. Reduced overall carbon gain from grazing would be exacerbated by low soil moisture, and might result in grasses producing fewer buds, less tillers, and ultimately fewer stems (Dalglish and Hartnett 2009). An alternative explanation is the loss of mycorrhizal associations due to decreased root carbon. Mycorrhizal fungi associations are likely to be particularly beneficial to plants when plants are under stress like drought (Stahl and Smith 1984). In ambient plots with more consistent soil moisture (Fay et al. 2011a), grasses were able to recover from the intense grazing season after several years; however, in the water stressed environment, perhaps grasses were unable to overcome the loss of the mycorrhizal associations and therefore, regrowth was hindered.

Forbs potentially benefit from the decreased fitness of the dominant grasses. Forb abundance and richness are generally negatively correlated to ANPP and grass cover in tallgrass prairie (Hartnett and Fay 1998, Collins and Calabrese 2012). As grasses were

negatively impacted by grazing in the present study, most strongly in altered rainfall treatment, forb ANPP increased. In addition, altered rainfall may not have impacted the forbs as strongly as the grasses. The forbs in this grassland are primarily cool season C₃ species, which have been shown to exhibit niche differentiation in timing and in space of water use strategies (Weaver 1954, Nippert and Knapp 2007). Many of the forbs renew growth early in the spring with maximum growth occurring from mid-March to early June (Weaver 1954). In this experiment, the two treatments have similar soil moistures in early spring, as the manipulation does not begin until approximately mid-April and treatments diverge gradually as stored soil water is depleted and the rainfall treatments are imposed. The dominant grasses, on the other hand, are warm season C₄ species which begin active growth much later in the spring and continue growing through early fall, with maximum biomass being produced midsummer (Weaver 1954) when soil moisture differences between the treatments are maximized. Forbs may also avoid competition with C₄ grasses for water by utilizing deeper water sources when this resource is limiting and leaf water stress is high (Nippert and Knapp 2007).

Altered precipitation patterns exacerbated the effects of a chronic defoliation event on grass biomass and stem densities and inhibited their recovery. Grazing decreased grass biomass by over 40% and increased forb biomass by almost 60%, and these effects persisted for two years following the grazing treatment. When exposed to altered precipitation patterns and intense grazing, grass stem densities were significantly lower than when exposed to grazing alone. In ambient rainfall, grass stem density was not significantly affected by grazing. Altered rainfall patterns have been shown to produce moderate reductions in ANPP, though the magnitude

of the reduction varies across years with different ambient rainfall patterns. In the present study, we found no effect of more extreme rainfall patterns on total ANPP and no effect on stem densities. However, when combined with repeated grazing these predicted rainfall patterns prevent recovery of grasses and have a detrimental effect on grassland function. As the majority of grasslands are grazed, current climate change experiments may be underestimating the effects of altered precipitation patterns on community structure in mesic grasslands.

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Tables and Figures

Table 1. Split-plot ANOVA F-statistic (p-value) for vegetation responses to rainfall treatment and grazing treatment. Each vegetation response was evaluated with a separate model for each year. Specific vegetation responses were total species richness and Shannon–Wiener diversity per 1-m², and grass, forb, and total biomass for g 1-m⁻².

Year	Parameter	Total Richness	Diversity	Grass Biomass	Forb Biomss	Total Biomass
2007	Rainfall	0.25 (0.628)	1.59 (0.236)	1.01 (0.339)	0.20 (0.663)	0.41 (0.538)
2007	Grazing	0.08 (0.787)	0.43 (0.527)	0.08 (0.789)	1.28 (0.271)	1.00 (0.340)
2007	Rainfall*Grazing	2.78 (0.126)	0.04 (0.839)	0.25 (0.625)	1.82 (0.192)	0.29 (0.601)
2008	Rainfall	0.28 (0.605)	0.67 (0.431)	1.50 (0.248)	0.71 (0.420)	0.27 (0.618)
2008	Grazing	1.81 (0.208)	2.06 (0.182)	34.17 (<0.001)	12.35 (0.006)	10.61 (0.008)
2008	Rainfall*Grazing	3.55 (0.089)	6.16 (0.034)	2.25 (0.165)	1.83 (0.206)	0.15 (0.704)
2009	Rainfall	0.01 (0.912)	0.00 (0.990)	1.93 (0.180)	0.05 (0.833)	0.50 (0.495)
2009	Grazing	0.92 (0.360)	1.46 (0.255)	151.17 (<0.001)	11.29 (0.003)	68.56 (<0.001)
2009	Rainfall*Grazing	1.17 (0.306)	0.76 (0.402)	2.09 (0.164)	1.30 (0.268)	11.20 (0.007)
2010	Rainfall	0.26 (0.621)	0.07 (0.798)	4.07 (0.057)	0.28 (0.601)	0.28 (0.604)
2010	Grazing	0.58 (0.464)	0.65 (0.438)	151.51 (<0.001)	0.50 (0.489)	32.21 (<0.001)
2010	Rainfall*Grazing	13.26 (0.005)	1.17 (0.304)	0.47 (0.500)	1.61 (0.219)	2.52 (0.128)
2011	Rainfall	NA	NA	5.62 (0.039)	4.30 (0.065)	0.04 (0.847)
2011	Grazing	NA	NA	57.69 (<0.001)	0.89 (0.367)	37.09 (<0.001)
2011	Rainfall*Grazing	NA	NA	0.40 (0.540)	0.58 (0.465)	1.42 (0.261)

Table 2. Split-plot ANOVA F-statistics (p-value) for grass, forb, and total stem densities responses to rainfall treatment and grazing treatment. Each stem type response was evaluated with a separate model for each year and season. Specific vegetation responses were grass, forb, and total number of stems per 0.1-m².

Year	Season	Parameter	Grass Stem Density	Forb Stem Denisty	Total Stem Density
2009	Early	Rainfall	0.68 (0.420)	0.88 (0.360)	0.16 (0.689)
2009	Early	Grazing	11.93 (0.003)	3.64 (0.071)	6.20 (0.022)
2009	Early	Rainfall*Grazing	0.01 (0.943)	0.31 (0.585)	0.020 (0.883)
2009	Late	Rainfall	0.15 (0.701)	0.97 (0.338)	0.00 (1.000)
2009	Late	Grazing	33.03 (<0.001)	5.00 (0.037)	23.1 (<0.001)
2009	Late	Rainfall*Grazing	6.15 (0.022)	0.66 (0.425)	4.56 (0.058)
2010	Early	Rainfall	1.00 (0.328)	0.03 (0.855)	0.82 (0.377)
2010	Early	Grazing	23.00 (<0.001)	3.14 (0.091)	16.75 (<0.001)
2010	Early	Rainfall*Grazing	7.24 (0.014)	0.03 (0.855)	6.28 (0.021)
2010	Late	Rainfall	0.48 (0.502)	0.30 (0.596)	0.36 (0.560)
2010	Late	Grazing	12.35 (0.006)	41.44 (<0.001)	10.04 (0.010)
2010	Late	Rainfall*Grazing	5.65 (0.039)	0.28 (0.609)	5.69 (0.038)

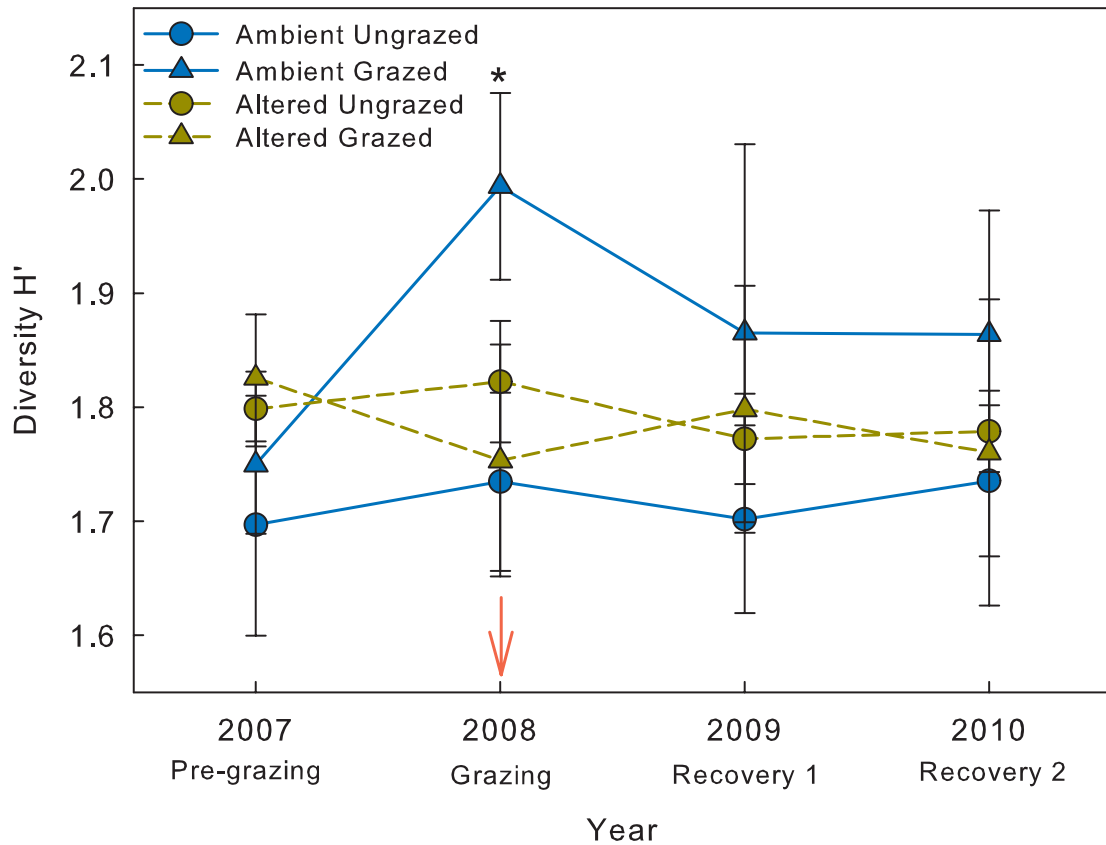


Figure 1. Plant community diversity (Shannon–Weiner) at 1-m² scale for ambient (blue with solid lines) and altered rainfall treatments (brown with dashed lines) separated by the ungrazed (circles) and grazed (triangles) treatments. The four years of data correspond to pre-grazing treatment in 2007, grazing treatment in 2008 (red arrow), recovery year one in 2009, and recovery year two in 2010. Significant differences within each year are denoted by “*”. Error bars represent ± 1 S.E. See Table 1 for split-plot ANOVA results for each year.

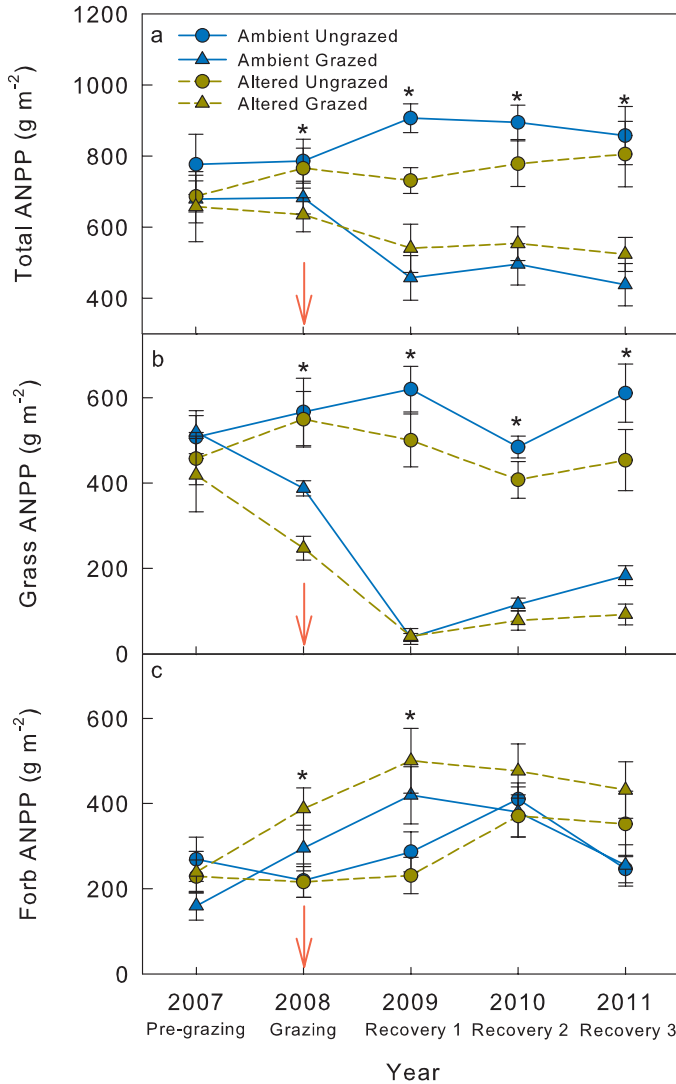


Figure 2. a) Total, b) grass, and c) forb annual net primary production (ANPP per 1-m²) for ambient (blue with solid lines) and altered rainfall treatments (brown with dashed lines) separated by the ungrazed (circles) and grazed (triangles) treatments. The five years of data correspond to pre-grazing treatment in 2007, grazing treatment in 2008 (red arrow), recovery year one in 2009, recovery year two in 2010, and recovery year three in 2011. Significant differences within each year are denoted by “*”. Error bars represent ± 1 S.E. See Table 1 for split-plot ANOVA results for each year.

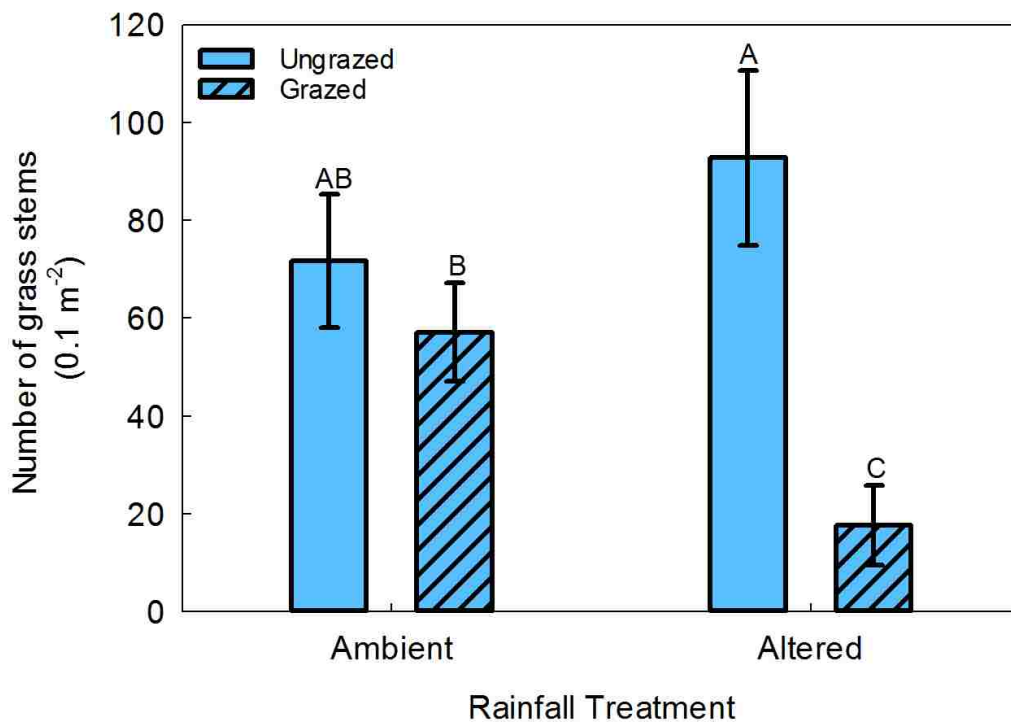


Figure 3. Number of grass stems per 0.1 m² for late season 2010 ambient and altered rainfall treatments for ungrazed (solid) and grazed (hashed) at the end of the second year of recovery from the 2008 grazing treatment. Letters denote significant differences between the treatments ($P \leq 0.05$). Error bars represent ± 1 S.E.

CHAPTER 3

Patch structure in North American and South African grasslands responds differently to fire and grazing

Abstract

Fire and grazing significantly impact small-scale patch structure and dynamics in savanna grasslands. We assessed small-scale grass-forb interaction in two long-term fire and grazing experiments in North America (NA: Konza Prairie Biological Station, Kansas, USA) and Southern Africa (SA: Kruger National Park, South Africa). We predicted that (1) the patch structure of each of the dominant grasses in NA and SA would respond similarly to fire and grazing, and (2) that forb richness would be correlated to grass patch structure. Semi-variance analysis was used to determine patch structure of dominant grasses and forb cover. Community composition responded similarly in NA and SA to fire, grazing, and fire-grazing interactions. Species richness, diversity, and community heterogeneity were highest in unburned-grazed grasslands in both sites. Grazing increased forb cover and decreased the cover of the dominant grasses, and the effects of fire on community structure depended on the grazing regime. Contrary to our overarching hypothesis, we found that grassland patch structure in NA and SA responded differently to grazing and fire. We found strong patch structure of the dominant grasses in both NA and SA grasslands; however, grazing and fire affected patch structure in NA but not SA, and in no instance did grass patch structure control forb community structure. Fire and

grazing have larger impacts on plant communities in NA than they do in SA. As a consequence findings from one site cannot be generalized across multiple sites with different evolutionary histories and different life-form characteristics of dominant plants.

Introduction

Savanna grasslands cover approximately one third of the terrestrial surface (Sala 2001) and provide economically important services such as grazing lands, tourism, and carbon sequestration (Owen-Smith 1988, Schimel et al. 1994, Allen-Diaz 1996, Fuhlendorf and Engle 2001, Gibson 2009). Grazing and fire control the structure and function of savanna ecosystems (Scholes and Walker 1993, Knapp et al. 1998b, du Toit et al. 2003), yet the direction and magnitude of response varies with site and location. The majority of fire and grazing studies are site specific, small scale, or short-term (Knapp et al. 2004, Lehmann et al. 2009), which limits the potential to generalize grassland responses across systems. Studying the effect of long-term fire and grazing regimes across sites is an important step towards understanding how these drivers control function in different grassland ecosystems.

Globally, grasslands exhibit hierarchical patch structure due to the combined effects of grazing and fire (Collins and Barber 1985, Wu and Loucks 1995), and this patch structure occurs over a range of spatial scales (Forman and Gordon 1986, Wu and Loucks 1995). A patch is defined as a region in an environment where the abundance of something (organism or resource) is high (Roughgarden 1977). On larger scales, a patch can be a watershed burned by fire or a grazing lawn created by bison (Wu and Loucks 1995). On smaller scales in plant communities, patches are expressed as distinct groupings of species (Forman and Gordon 1986). Three main characteristics - strength of patch formation, patch size, and patch repeatability across a landscape - are commonly used to describe patch structure of vegetation.

Grazing and fire maintain and control patch structure by differentially influencing community dominance, diversity, and resource heterogeneity. Large herbivores increase diversity by altering plant community structure (Collins 1987, Hartnett et al. 1996) through selective grazing and increased resource heterogeneity through soil disturbances and nutrient deposition (Steinauer and Collins 1995). Conversely, fire is a large-scale generalist “herbivore” (Bond and Keeley 2005b) that homogenizes resources (Blair 1997) by uniformly removing aboveground biomass and moribund material and homogenizes community composition by promoting the growth of fire-tolerant C₄ grasses (Collins 1992, Collins and Smith 2006). When considered independently, fire and grazing have opposite effects on community composition and resource heterogeneity, but together grazing and fire interact to further increase heterogeneity (Collins and Smith 2006). On a landscape scale grazing and fire frequency also interact through positive and negative feedbacks (Senft et al. 1987, Fuhlendorf and Engle 2001). Herbivore removal of aboveground biomass alters fire frequency and fire spread in a landscape by decreasing the fuel load, and fires modify herbivore distribution by altering plant chemistry creating a ‘magnet effect’ that attracts herbivores and by removing biomass that could otherwise be consumed by herbivores (Fuhlendorf and Engle 2004, Archibald et al. 2005).

In North American tallgrass prairie, a small number of dominant grasses make up the majority of plant biomass while richness is a function of the number of forb species. At the scale of small watersheds, richness is negatively correlated with grass cover across a range of grazing and fire treatments implying that abundance of

the dominant grasses impacts local species diversity (Collins and Calabrese 2012). Although it is widely acknowledged that grazing and fire contribute to the maintenance of grassland patch structure globally, the interactive effects of grazing and fire on the strength, size, and repeatability of small-scale patch structure are poorly understood.

Here, we examined the effects of grazing and fire on small-scale patch structure and dynamics of herbaceous vegetation in grassland ecosystems in North America and South Africa to address four main questions. (1) How do grazing and fire independently and interactively affect community structure including richness, diversity, and grass and forb abundance? (2) How do fire and grazing affect patch structure of dominant grasses? (3) Are grass and forb patches spatially separated forming a mosaic of grass and forb patch types? And (4) is patch structure of dominant grasses a driver of forb distribution and abundance and therefore species diversity in grasslands?

To address these questions we sampled patch structure in mesic grassland sites at Konza Prairie Biological Station, Kansas, USA (NA) and Kruger National Park, South Africa (SA). Both sites are dominated by long-lived, clonal C₄ grasses and have a diverse forb flora, and both contain long-term experiments (+30 year) that manipulate the individual and combined effects of grazing and fire. These sites were selected because of their different evolutionary histories coupled with common drivers of plant community structure: grazing by megaherbivores, frequent fire, and similar growing season climatic regimes (Knapp et al. 2004, Knapp et al. 2006). These similarities provide an excellent opportunity to examine the ecological

generality of community responses to fire and grazing in mesic grasslands. When measured comparably at the two sites, we predicted that community properties and patch structure and dynamics would respond similarly to grazing and fire in both NA and SA.

Methods

Study Site

Patch composition and structure were measured in long-term fire and grazing experiments at the Konza Prairie Biological Station (Konza) in Kansas, USA, and in the south-central Satara region of Kruger National Park (Kruger), South Africa. Konza Prairie is one of the last remaining large remnants (3,487 ha) of native unplowed tallgrass prairie in NA. The system is dominated by a small number of C₄ grasses, such as *Andropogon gerardii* and *Sorghastrum nutans*, which account for the majority of herbaceous primary productivity (Knapp et al. 1998a), while community diversity is generally a function of forb species (Collins and Glenn 1991). The climate is temperate (July mean temperature = 27°C), and annual precipitation averages 835 mm/year with approximately 75% falling as rain during the April to October growing season. Soils are fine textured udic argiustolls underlain by cherty limestone and shales (Melzer et al. 2010).

Konza includes fully replicated watershed-level fire and fire/grazing experiments, established in 1977 and 1987, respectively. Replicate watersheds (mean size ~60ha) are burned at 1-, 2-, 4-, and 20-yr intervals, mainly in the spring, to encompass a range of natural fire frequencies and management practices (Knapp et al. 1998b). To address the role of native grazers and fire/grazing interactions

(Hobbs et al. 1991, Johnson and Matchett 2001), bison (*Bos bison*) were reintroduced in a 1000 ha fenced area that includes replicate watersheds burned at the same frequencies as the ungrazed areas. The overall grazing intensity is considered moderate with a bison density of approximately 0.2 animals/ha (Knapp et al. 1998b, Knapp et al. 1999).

Kruger is a 2 million ha protected area of savanna grassland located in northeast South Africa. The vegetation is characterized by the coexistence of dominant perennial C₄ grasses, such as *Bothriochloa radicans*, *Digitaria eriantha*, *Panicum coloratum*, and *Themeda triandra*, and woody species, including *Acacia nigrescens* and *Sclerocarya birrea* trees. Due to the large size of the park, climatic gradients are substantial, but this research focused on the south-central region where rainfall is approximately 544 mm/year (Venter et al. 2003), nearly all of which falls during the growing season between November and March. The climate is tropical with a mild, dry, and frost free dormant season and a warm summer with mean monthly maximum air temperature in January of 29°C. Soils are fine-textured, rhodic nitisols, haplic luvisols, and leptic phaeozems underlain by basalt (Melzer et al. 2010).

The Experimental Burn Plots (EBP) were established in Kruger in 1954 to determine the importance of fire seasonality and frequency in this savanna grassland ecosystem (Trollope 1982, Biggs and Potgieter 1999). Similar to Konza, experimental burns occur at 1-, 2- and 3-year intervals, along with unburned control plots (Biggs et al. 2003). The EBPs are one of the longest running fire ecology experiments in Africa. This research focused on the Satara EBP where precipitation, soil type, and the mix of herbaceous and woody plants are similar to Konza. Kruger

includes many of the large herbivores that occur in the savanna grasslands of southern Africa (du Toit et al. 2003), which have unrestricted access to the EBPs (Enslin et al. 2000, Biggs et al. 2003, Govender et al. 2006). The extant abundance and grazing intensity of herbivores in Kruger is considered moderate for regional savanna grasslands (WSW Trollope, pers. comm.), and 12-14 megaherbivores (e.g. elephant, rhinoceros, wildebeest, zebra) are commonly seen on the Satara EBPs. Adjacent to the Satara EBPs is the Cape buffalo enclosure, erected in 2002 for veterinary purposes. The 900 ha permanent enclosure contains 50-80 Cape buffalo (*Syncerus caffer*), a relatively non-selective grazer of grass (Hofmann 1973). The enclosure is divided into five blocks, two of which were burned annually for the duration of the project. Also, a 9 ha area within the enclosure remains unburned and was fenced to prevent grazing. The grazing intensity in the Cape buffalo enclosure is comparable to the moderate levels imposed throughout Kruger. Thus, Kruger offers sites with a gradient of known long-term fire history and gradients of megaherbivore diversity (0, 1, and 12-14 species) all located on the same soil type within a 1-km² area.

Vegetation Sampling

Transects were established to measure grassland patch structure at multiple sites in NA and SA. In NA transects were established in a subset of the long-term experimental grazing and fire watersheds: (1) ungrazed, unburned; (2) ungrazed, annually burned; (3) single grazer (bison), unburned; (4) single grazer (bison), annually burned. In SA transects were established in three grazing treatments and two burn treatments: (1) ungrazed, unburned; (2) single grazer (Cape buffalo),

unburned; (3) single grazer (Cape buffalo), annually burned; (4) grazed by multiple herbivores, unburned; (5) grazed by multiple herbivores, annually burned. The ungrazed, annually burned comparison in SA is not possible because this treatment does not occur within the long-term experimental framework. We established 64-m transects of 0.25-m² contiguous quadrats at each site for a total of 128 quadrats per transect. Transects were oriented from north to south, on nearly level ground avoiding areas with high woody cover. Cover of each plant species rooted in each quadrat was visually estimated near the beginning and end of the growing season of 2008 in NA and 2009 in SA. Each study site was effectively uniform in topography, moisture, and vegetation structure. Cover data for each species on the 1-m² scale were used to compute standard metrics of community structure, including grass, forb, and total species richness, Shannon–Weiner diversity, evenness, and the relative cover of each species. Community heterogeneity (dissimilarity) at the 1-m² scale was calculated using Jaccard dissimilarity coefficient (SAS Institute V.9.3; Cary, N.C.). All metrics were calculated using the maximum average cover values of each species for the entire growing season and then averaged for four adjacent 0.25-m² plots.

Statistical analyses

We tested for differences among treatments for each community structure metric using mixed model analysis of variance (ANOVA) with grazing and fire treatments as fixed effects (SAS Institute V.9.3; Cary, N.C.). Spatial variation and patch structure at the 0.25-m² scale of the dominant grasses in each treatment were quantified with semi-variance analysis using GS+ version 7 software (Gamma

Design 2007). Semi-variograms show the average variance found in comparisons of samples taken at increasing distances. Four common semi-variogram models can be used in the analysis of spatial structure – linear, exponential, spherical, and gaussian. We ran all four models on each of the structural variables examined and reported results from the best-fit model in each instance. When not normally distributed, data were log-transformed. The active lag was 31.75 m, and the lag class distance interval was 0.5 m in each model.

If spatial dependence exists among sample units, then semi-variance increases with distance until leveling off at a more or less constant value (sill) where spatial dependence no longer exists (Figure 1; (Legendre and Fortin 1989, Steinauer and Collins 2001)). Parameters derived from the best-fit model quantified three main aspects of spatial structure. First, the strength of the patch or the proportion of sample variance explained by patchiness at the scales examined (i.e. the degree to which patches were differentiated from the surrounding area by their distinct, within-patch homogeneity) is reflected in the ratio between the sill (asymptote) and the nugget (y-intercept) of the variogram. The strength of the patch has three levels, strong (>0.666), moderate (between 0.333 and 0.666), and weak (<0.333) (Cambardella et al. 1994). Second, size or mean diameter of those patches is estimated by the range, or separation distance at which the variogram reaches an asymptote. And third, patch repeatability or the arrangement of patches across the area is reflected by the presence of significant fluctuations in semi-variance at spatial scales beyond the first peak. Such fluctuations indicated that patches were

aggregated whereas a lack of fluctuation would mean that the patches were arranged at random.

Results

North America

In NA, total richness per transect ranged from 30-80 species, and mean species richness per 1-m² ranged from 16-32 (Table 1). Grazing significantly increased total species richness ($F = 424.3$; $P < 0.0001$) while fire had the opposite effect, decreasing total species richness ($F = 2116.0$; $P < 0.0001$). The magnitude of the fire effect (a decrease of 1.5 species) was significantly less than the effect of grazing (increase of 15 species), and there was no interactive effect of grazing and fire (Table 1). Similar patterns were seen in species diversity. Grazing significantly increased forb cover ($F = 436.8$; $P < 0.0001$), and fire significantly reduced forb cover ($F = 13.4$; $P = 0.0004$). The interaction of grazing and fire ($F = 53.1$; $P < 0.0001$) increased forb cover significantly more than grazing alone, while fire in the absence of grazing decreased forb cover and richness (Table 1). Forb abundance and richness were not related to grass cover in any treatment. Community heterogeneity was significantly different between each treatment ($F = 479.1$; $P < 0.0001$) with unburned-grazed plots being the most dissimilar or having the highest heterogeneity while the annually burn ungrazed plots had the lowest heterogeneity (highest mean similarity) (Table 1). Based on species accumulation curves (Figure 2a), small-scale differences in richness were largely driven by grazing. As scale increased, grazing was still the primary determinant of richness, but in ungrazed plots richness also decreased with fire.

Cover of the dominant C₄ grass in each treatment in NA exhibited a strong spatial pattern (mean proportion = 0.757) (Table 2; Figure 3A). Grazing decreased and fire increased patch structure of grasses. The combined effects of grazing and fire decreased patch structure further than grazing alone (Figure 3A). The patch size of the dominant grass depended on the fire-grazing treatment (mean size = 25-m) (Table 2; Figure 3C). Grazing increased patch size while fire decreased patch size. Grazing and fire combined increased patch size more than grazing alone (Figure 3C). The unburned-ungrazed grasslands in NA exhibited significant fluctuations in semi-variance at spatial scales beyond the first peak while the other three treatments did not (Figure 4A).

Forb richness in each treatment exhibited moderate patch structure (mean proportion = 0.582) (Table 3). Both grazing and fire decreased patch structure of forbs. The combined effects of grazing and fire decreased patch structure though not as strongly as either grazing or fire individually (Table 3). Patch size of forb richness was random in response to either fire or grazing, but the largest patch size of forb richness occurred in unburned-ungrazed sites (Table 3). Forb richness did not show significant fluctuations in semi-variance at spatial scales beyond the first peak in any of the treatments (Figure 5A).

Total cover of forbs in each treatment exhibited moderate patch structure (mean proportion = 0.674) (Table 3). Individually, grazing increased and fire decreased patch structure of forb cover, whereas the combined effects of grazing and fire increased patch structure of forb cover (Table 3). Patch size of the forb cover was highly variable, but in general patch size increased with grazing and decreased with

fire. Patch size also decreased under a combination of fire and grazing (Table 3). No significant fluctuations in semi-variance at spatial scales beyond the first peak occurred (Figure 6).

South Africa

In SA, total richness per transect ranged from 37-55 species, and mean species richness per 1-m² ranged from 8-18 (Table 1). Total species richness per 1-m² increased as number of grazers increased ($F = 94.8$; $P < 0.0001$) while fire had the opposite effect, decreasing total species richness ($F = 76.9$; $P < 0.0001$). The magnitude of the fire effect (a decrease of 0.5 species) was significantly less than the effect of grazing (increase of 4.5 and 6.0 species with a single grazer and multiple grazers, respectively). Grazing and fire significantly interacted ($F = 142.3$; $P < 0.0001$). In the absence of fire, grazing increased total richness, while in annually burned sites multiple grazers decreased richness (Table 1). Similar patterns were seen in the diversity response. Forb cover increased as number of grazers increased ($F = 21.4$; $P < 0.0001$). Fire had no main effect on forb cover; however, fire and grazing significantly interacted ($F = 4.1$; $P = 0.0451$) with forb cover being highest in unburned-multiple grazer sites and lowest in unburned-ungrazed sites (Table 1). Forb cover and richness were not related to grass cover in any treatment. Grazing and fire significantly interacted to affect community heterogeneity ($F = 56.2$; $P < 0.0001$); however, no clear trend was apparent. The highest level of homogeneity was seen in the annual burn-multiple grazer treatment while the highest heterogeneity was seen in the unburned-ungrazed, the unburned-multiple grazers, and the annual burn-single grazer treatments (Table 1). Species accumulation

curves (Figure 2b) indicated that on larger scales, annual burning decreased richness with grazing levels having no effect. In unburned grasslands as grazing intensity increased species richness increased. On smaller scales, no clear patterns emerged with fire or grazing.

Unburned-ungrazed grasslands exhibited the strongest patch structure while the four other treatments showed moderate patch structure. Grazing decreased patch structure, and fire had no effect on patch structure (Table 2; Figure 3B). The patch size of the dominant grass changed little among treatments with a mean of 6-m (Table 2; Figure 3D). Ungrazed-unburned grasslands had the smallest patch size of 3.7-m. Grazing increased patch size, and fire decreased patch size in the presence of a single grazer but increased patch size in the presence of multiple grazers (Figure 3D). All five treatments exhibited significant fluctuations in semi-variance at spatial scales beyond the first peak (Figure 4B).

Forb richness in each treatment in SA exhibited moderate patch structure (mean proportion = 0.433) (Table 3). Grazing decreased and fire increased patch structure (Table 3). Patch size of forb richness varied with no clear trend in response to grazing or fire but the largest patch size occurred in unburned-ungrazed sites (Table 3). No significant fluctuations in semi-variance at spatial scales beyond the first peak were seen in any treatment for forb richness (Figure 5).

Forb cover in each treatment in SA exhibited moderate patch structure (mean proportion = 0.522) (Table 3). Grazing and fire both increased patch structure (Table 3). Patch size of forb cover varied, but in general, grazing and fire both

decreased patch size (Table 3). No significant fluctuations in semi-variance at spatial scales beyond the first peak were found in any treatment (Figure S1).

Discussion

As predicted, aspects of grassland community structure responded similarly in North America (NA) and South Africa (SA) to fire, grazing, and fire-grazing interactions. Species richness, diversity, and community heterogeneity were highest in unburned-grazed grasslands in both sites. Grazing increased the cover of forbs and decreased the cover of the dominant grasses, and the effects of fire on community structure were dependent upon the grazing regime. Contrary to our overarching hypothesis, we found that grassland patch structure in NA and SA responded differently to grazing and fire. We found strong patch structure of the dominant grasses in both NA and SA grasslands; however, grazing and fire affected patch structure in NA but not SA, and in no instance did grass patch structure control forb community structure and, therefore, diversity.

In NA grazing increased species richness, diversity, and forb cover, and fire decreased richness and diversity. These results are consistent with previous studies in a variety of grasslands ecosystems (Collins 1987, Collins et al. 1995, Bakker et al. 2003, Frank 2005). In SA, grazing also increased richness, diversity, and forb cover; however, fire effects on richness, diversity, and forb cover varied depending on the number of grazers. The inconsistent effects of fire on community measures could indicate that SA grasses are directly affected by fire but forbs are not, as is found in other grasslands with grazers (Lunt and Morgan 2002, Uys et al. 2004). SA forbs are highly resilient to fire and many forb species tolerate a wide range of seasonality

and frequency of fires (Uys et al. 2004). Local site conditions can have more influence than fire (Uys et al. 2004), and large herbivore grazing patterns strongly affect local site conditions in our study, as recently burned grassland often attract grazers. The single grazer site was limited in the number of individual herbivores that had access to the plots, maintaining an intermediate level of grazing. Meanwhile, the multiple grazers site had unlimited numbers of individuals with access to the plots, allowing for the possibility of diverse grazing strategies, leading to lower diversity and perhaps higher abundances of ruderal species.

NA and SA small-scale grass patch structure responded differently to grazing and fire. Overall, the dominant grass at each site showed strong spatial autocorrelation. Many grassland studies have found that disturbances impart spatial patterns on plant communities at varying scales through effects on soil moisture, nutrient availability, and removal of dominant species (Schimel et al. 1985, Collins 1992, Glenn et al. 1992, Frank et al. 1994, Schimel et al. 1994, Knapp et al. 1999, Steinauer and Collins 2001). In NA, patch structure of the dominant grasses fluctuated widely depending on the grazing and fire treatment, while in SA patch structure of the dominant grasses remained constant regardless of the grazing or fire treatment. In SA, patchiness was moderate to strong, patch size was approximately 6-m, and patches were repeatable across space. The only treatment in NA that exhibited similar grass structure to SA grasses was unburned-ungrazed. Therefore, when undisturbed, NA grass structure was similar to SA grass structure but disturbances altered NA grass patch structure, while SA grass structure remained stable regardless of the treatment.

The different response of patch structure to grazing and fire in NA and SA grasslands may result from differences in evolutionary histories. NA grasslands are young with the extant community only arising 8-10,000 years ago while SA grasslands are 4-6 million years old (Axelrod 1985, Bond et al. 2003). Stability in the face of different disturbance regimes could be a manifestation of the longer evolutionary history of SA grasslands with grazing and fire allowing species to adapt to a wide range of disturbance regimes. For example, functional redundancy is greater in SA grasslands, with multiple grass species exhibiting similar patch structure and each dominating a different disturbance regime (Burns et al. 2009). In SA as grazing decreases palatable grasses, an unpalatable grass species increases, altering dominance but maintaining patch structure. In the younger grasslands of NA one species dominates most disturbance regimes, and when grazed, patch structure is altered. Another factor impacting the responses to grazing and fire is the architectural difference in the dominant grasses between sites. Although both sites are dominated by tall C₄ grasses, NA is dominated by *A. gerardii*, a rhizomatous grass, whereas SA is dominated by bunch grasses including *B. radicans*, *T. triandra*, and *D. eriantha*. Grass form influences plant cover, and cover tends to be patchy in SA with large spaces of bare soil between individual bunches of grass, while the canopy is continuous in NA. Patchiness in cover can influence soil nutrient patterns in drier grasslands (Vinton and Burke 1995). Additionally, the plant interspaces in SA are likely to have lower root biomass (Hook et al. 1994) as compared to the more continuous root layer in NA soils (Reed et al. 2005). These architectural differences impose different patterns of heterogeneity at small scales. The homogeneous cover

and root layer associated with *A. gerardii* in NA creates little small-scale variation (Vinton and Burke 1997, Derner and Briske 2001), whereas the heterogeneous cover and root layer associated with bunch grasses in SA creates small-scale variation. In addition under similar environmental conditions, bunch grasses tend to concentrate nutrients in their rhizosphere (Hook et al. 1991, Vinton and Burke 1995, Burke et al. 1998, Burke et al. 1999), whereas rhizomatous grasses do not (Vinton and Burke 1995). Bunch grasses may create a positive feedback, and once a patch pattern is formed, grazing and fire are unable to overcome the small-scale patch structure imposed by soil nutrient heterogeneity created by the grasses themselves.

In both sites, the forb community was not related to grass patch structure. If forb patch structure were related to grass structure, we would predict similar semi-variogram, yet the semi-variograms show that the spatial structure of grasses is not the same as that of the forbs (Figure 4, 5; Table 2, 3). Therefore, grass patch structure did not control patterns of community structure. Forbs expressed a moderate degree of spatial autocorrelation; however, patch size and repeatability across space were not similar to the dominant grasses. This suggests different drivers for grass and forb patch structure. Spatial structure is just one of many factors that contribute to the maintenance of species diversity.

Fire and grazing are considered to be major factors influencing plant community structure and dynamics in mesic grasslands worldwide. These drivers generally alter the availability and spatial heterogeneity of limiting resources affecting community heterogeneity. The inherent patchiness in grasslands due to the

dominant long-lived clonal grasses can be altered by fire and grazing. In this study, both grasslands showed moderate to strong patch structure yet responded differently to disturbance. In both sites the strongest grass patch structure occurred in sites without grazing and fire. SA grassland patch structure was unaffected by disturbance, while NA grasslands were strongly affected. In SA, the ability to maintain consistent patch structure in different fire and grazing regimes is a reflection of the architecture of the dominant grasses and the longer evolutionary history with grazing and fire. Fire and grazing have larger impacts on plant communities in NA than they do in SA. As a consequence, findings from one site cannot be generalized across multiple sites with different evolutionary histories and different architectures of dominant plants.

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Tables and Figures

Table 1. Herbaceous vegetation characteristics for study sites. Means and standard error (SE) were calculated for richness, Shannon–Weiner diversity, community heterogeneity (Jaccard dissimilarity coefficient), grass species richness and the cover of the dominant grass species in each treatment, and forb species richness and forb cover for both NA and SA. Means were calculated at the 1-m² scale along transects in each treatment. The main effects of fire and grazing were significant ($P < 0.05$) for all variables at both sites. Letters denote significant ($P < 0.05$) grazing fire interactions within a site.

Site	Treatment	Total Species Richness (SE)	Diversity (SE)	Heterogeneity (SE)	Grass Species Richness (SE)	Cover of Dominant Grass (SE)	Forb Species Richness (SE)	Forb Cover (SE)
NA	Unburned-Ungrazed	17 (0.5)	2.05 (0.05)	0.40 (0.01) ^a	7 (0.3) ^a	58 (4.4)	10 (0.4) ^a	39 (2.9) ^a
	Unburned-Grazed	32 (0.9)	2.71 (0.04)	0.63 (0.01) ^b	14 (0.3) ^b	24 (4.3)	18 (0.7) ^b	73 (2.7) ^b
	Annual Burn-Ungrazed	16 (0.5)	1.85 (0.03)	0.17 (<0.01) ^c	10 (0.3) ^c	56 (2.0)	6 (0.4) ^c	12 (1.3) ^c
	Annual Burn-Grazed	31 (1.0)	2.61 (0.04)	0.49 (0.01) ^d	14 (0.4) ^b	28 (3.8)	17 (0.6) ^b	82 (2.7) ^d
SA	Unburned-Ungrazed	8 (0.3) ^a	1.09 (0.06) ^d	0.65 (0.01) ^a	4 (0.2) ^a	32 (4.2)	5 (0.3) ^a	11 (1.2) ^a
	Unburned-Single Grazer	12 (0.4) ^b	1.56 (0.04) ^{bc}	0.56 (0.01) ^b	5 (0.1) ^b	29 (2.4)	7 (0.4) ^b	15 (1.5) ^b
	Unburned-Multiple Grazers	18 (0.4) ^c	2.06 (0.04) ^d	0.62 (0.01) ^a	7 (0.2) ^c	28 (2.34)	10 (0.4) ^c	23 (1.2) ^c
	Annual Burn-Single Grazer	13 (0.4) ^d	1.68 (0.05) ^b	0.64 (0.01) ^a	6 (0.2) ^b	25 (2.83)	8 (0.4) ^b	14 (1.2) ^{ab}
	Annual Burn-Multiple Grazers	10 (0.3) ^e	1.47 (0.03) ^c	0.50 (0.01) ^c	5 (0.2) ^b	35 (2.99)	4 (0.2) ^a	18 (1.7) ^b

Table 2. Semi-variance model parameters for the dominant grass species in each treatment in NA and SA. Parameters reported are derived from the best-fit model.

Site	Treatment	Dominant Grass Species	Model Type	R ²	Nugget Variance (C ₀)	Structural Variance Sill (C ₀ +C)	Range (A ₀)	Proportion (C/C ₀ +C)	Class of Structural Dependence
NA	Unburned- Ungrazed	<i>Andropogon gerardii</i>	Spherical	0.44	208.0	11.6	5.0	0.82	Strong
	Unburned- Grazed	<i>Andropogon gerardii</i>	Exponential	0.95	286.0	1010.0	35.6	0.72	Strong
	Annual Burn- Ungrazed	<i>Schizachrium scoparius</i>	Exponential	0.06	51.0	407.0	1.1	0.88	Strong
	Annual Burn- Grazed	<i>Andropogon gerardii</i>	Gaussian	0.89	1.5	4.0	58.6	0.62	Moderate
SA	Unburned- Ungrazed	<i>Digitaria eriantha</i>	Spherical	0.58	0.4	3.2	3.7	0.89	Strong
	Unburned- Single Grazer	<i>Panicum coloratum</i>	Exponential	0.66	314.0	784.3	7.4	0.60	Moderate
	Unburned- Multiple Grazers	<i>Bothriocloa radicans</i>	Spherical	0.43	311.0	699.1	4.7	0.55	Moderate
	Annual Burn- Single Grazer	<i>Themeda triandra</i>	Spherical	0.43	336.0	847.0	5.1	0.60	Moderate
	Annual Burn- Multiple Grazers	<i>Bothriocloa radicans</i>	Exponential	0.52	1.1	2.5	8.9	0.56	Moderate

Table 3. Semi-variance model parameters for forb richness and forb cover in each treatment in NA and SA. Parameters reported are derived from the best-fit model.

	Treatment	Metric	Model Type	R ²	Nugget Variance (C ₀)	Structural Variance Sill (C _s +C)	Range (A _s)	Proportion (C/C _s +C)	Class of Structural Dependence
NA	Unburned Ungrazed	Forb Richness	Gaussian	0.87	2.6	9.1	70.7	0.72	Strong
		Forb Cover	Gaussian	0.96	167.0	744.9	59.6	0.78	Strong
	Unburned Single Grazer	Forb Richness	Exponential	0.42	0.0	0.1	10.7	0.50	Moderate
		Forb Cover	Exponential	0.69	383.0	766.1	74.4	0.50	Moderate
	Annual Burn Ungrazed	Forb Richness	Spherical	0.62	1.2	2.3	11.0	0.50	Moderate
		Forb Cover	Exponential	0.39	0.5	1.0	12.6	0.50	Moderate
	Annual Burn Single Grazer	Forb Richness	Exponential	0.54	0.0	0.1	11.6	0.61	Moderate
		Forb Cover	Exponential	0.09	0.0	0.1	1.0	0.92	Strong
SA	Unburned Ungrazed	Forb Richness	Exponential	0.85	1.6	3.1	93.1	0.50	Moderate
		Forb Cover	Exponential	0.87	1.1	2.3	89.1	0.51	Moderate
	Unburned Single Grazer	Forb Richness	Linear	0.85	0.2	0.4	31.5	0.40	Moderate
		Forb Cover	Exponential	0.81	0.8	1.7	96.7	0.52	Moderate
	Unburned Multiple Grazers	Forb Richness	Linear	0.61	4.4	5.8	31.5	0.24	Weak
		Forb Cover	Exponential	0.56	0.4	0.8	7.0	0.50	Moderate
	Annual Burn Single Grazer	Forb Richness	Spherical	0.72	2.0	4.2	17.3	0.53	Moderate
		Forb Cover	Spherical	0.72	0.6	1.3	18.0	0.50	Moderate
Annual Burn Multiple Grazers	Forb Richness	Exponential	0.61	0.9	1.9	23.0	0.50	Moderate	
	Forb Cover	Exponential	0.40	0.3	1.1	3.3	0.74	Strong	

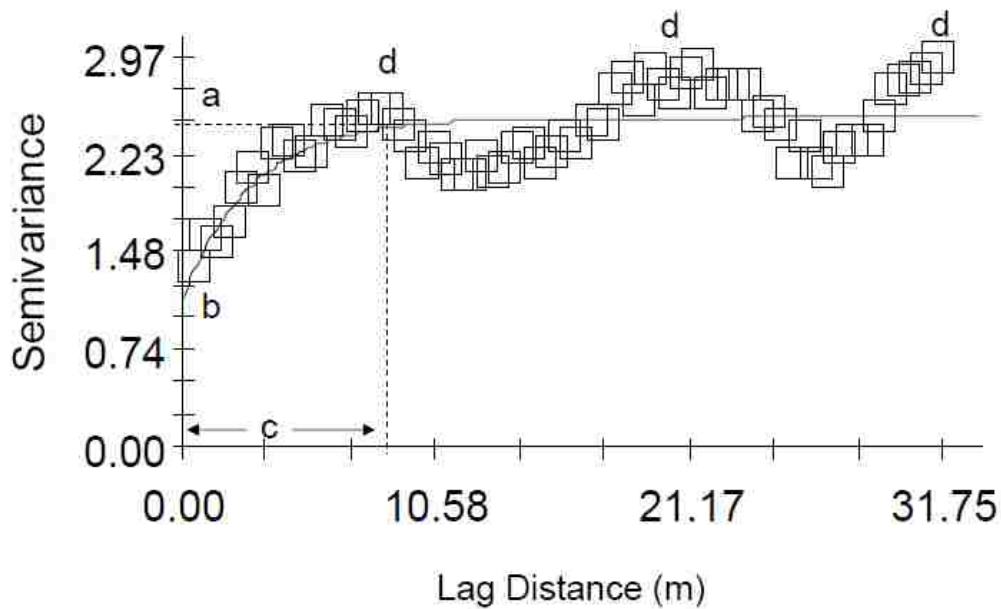


Figure 1. Example of a semi-variogram from annually burned South African (SA) grassland with multiple grazers. The y-intercept at (a) represents the sill, and the y-intercept at (b) represents the nugget. These two values are used to calculate $(a \div b)$ the proportion of variance that can be explained by patchiness. Point (c), the range or patch size, is the distance at which the variogram reaches an asymptote. The multiple peaks labeled as (d) show that for this grassland there exist significant fluctuations in semi-variance at spatial scales beyond the first peak. This indicates that patches are arranged regularly and are predictable across the landscape.

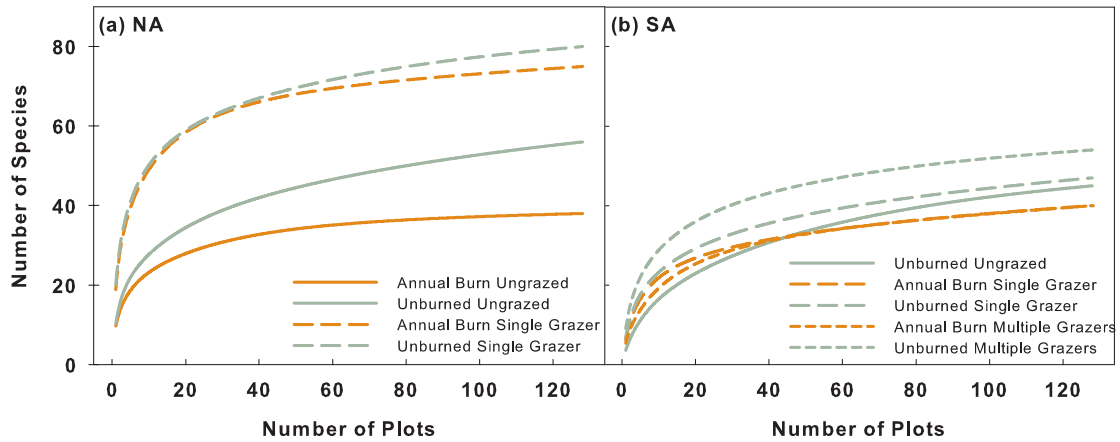


Figure 2. Species accumulation curves for grasslands in North America (a) and South Africa (b). In NA there were four treatments: (1) ungrazed, unburned; (2) ungrazed, annually burned; (3) single grazer (bison), unburned; (4) single grazer (bison), annually burned. In SA there were five treatments: (1) ungrazed, unburned; (2) single grazer (Cape buffalo), unburned; (3) single grazer (Cape buffalo), annually burned; (4) grazed by multiple herbivores, unburned; (5) grazed by multiple herbivores, annually burned.

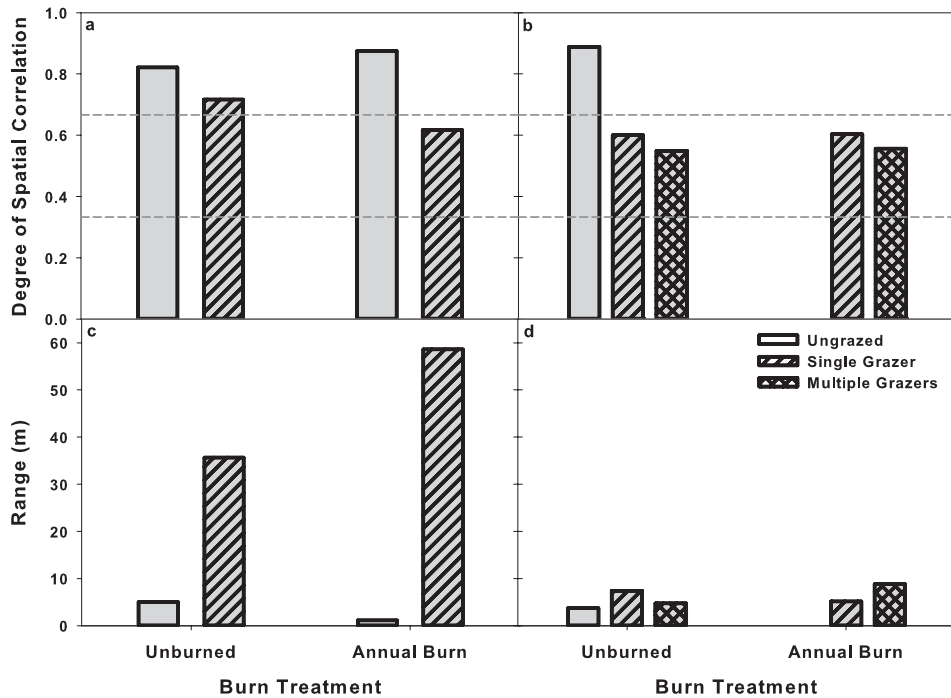


Figure 3. The strength of patch structure or the degree of spatial autocorrelation for North America (a) and South Africa (b) and the patch size of the dominant grasses in North America (c) and South Africa (d). Values were calculated based upon best-fit models for each treatment. Dotted lines in a and b represent the strong, moderate, and weak classes of spatial dependence. In NA there were four treatments: (1) ungrazed, unburned; (2) ungrazed, annually burned; (3) single grazer (bison), unburned; (4) single grazer (bison), annually burned. In SA there were five treatments: (1) ungrazed, unburned; (2) single grazer (Cape buffalo), unburned; (3) single grazer (Cape buffalo), annually burned; (4) grazed by multiple herbivores, unburned; (5) grazed by multiple herbivores, annually burned. Patch structure is moderate to strong in all treatments. Grazing increases patch size in NA, and fire effects depend upon the grazing regime. However, neither grazing nor fire affects patch size in SA.

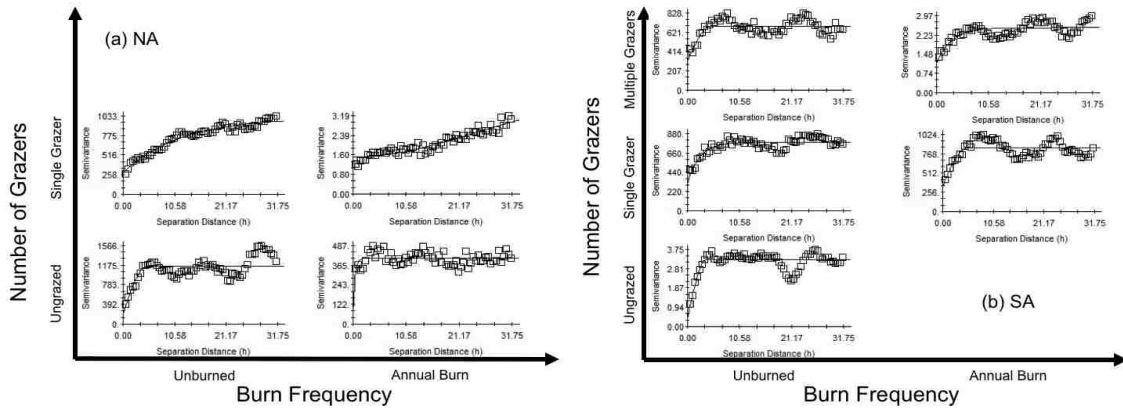


Figure 4. Semi-variograms of the dominant grasses in North America (a) and South Africa (b) for each of the treatments. In NA there were four treatments: (1) ungrazed, unburned; (2) ungrazed, annually burned; (3) single grazer (bison), unburned; (4) single grazer (bison), annually burned. In SA there were five treatments: (1) ungrazed, unburned; (2) single grazer (Cape buffalo), unburned; (3) single grazer (Cape buffalo), annually burned; (4) grazed by multiple herbivores, unburned; (5) grazed by multiple herbivores, annually burned. The multiple peaks seen in each of the SA treatments and in NA unburned-ungrazed signifies repeatability of patches across a landscape or a non-random distribution in those disturbance regimes.

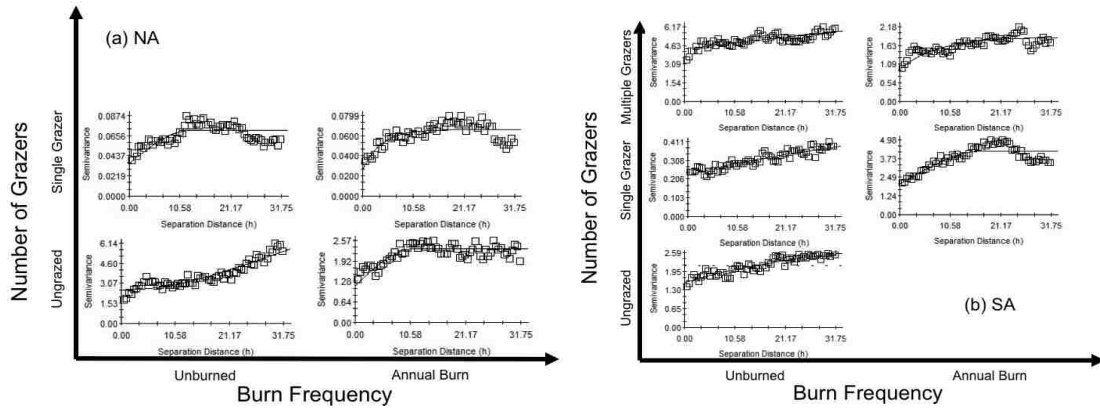


Figure 5. Semi-variograms of forb richness in North America (a) and South Africa (b) for each of the treatments. In NA there were four treatments: (1) ungrazed, unburned; (2) ungrazed, annually burned; (3) single grazer (bison), unburned; (4) single grazer (bison), annually burned. In SA there were five treatments: (1) ungrazed, unburned; (2) single grazer (Cape buffalo), unburned; (3) single grazer (Cape buffalo), annually burned; (4) grazed by multiple herbivores, unburned; (5) grazed by multiple herbivores, annually burned. The lack of repeated peaks in each of the semi-variograms signifies the lack of repeatability of patches across a landscape.

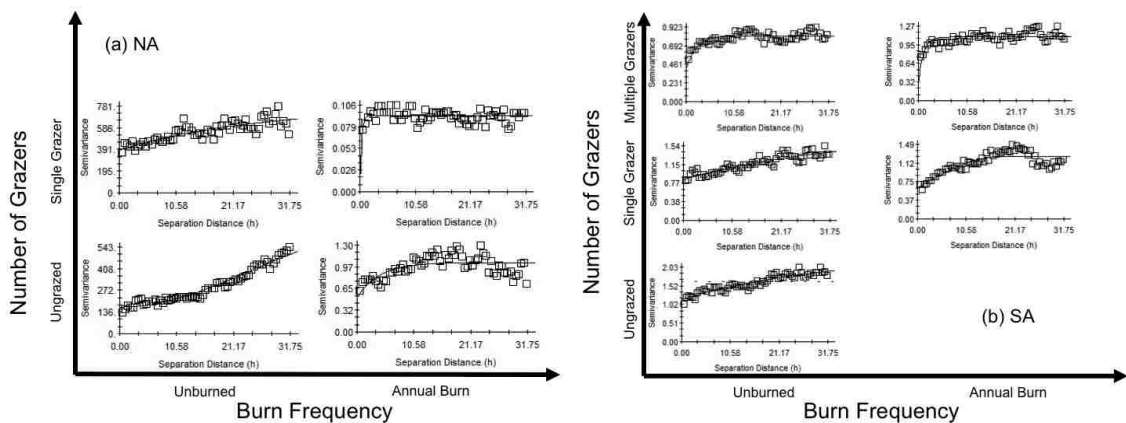


Figure 6. Semi-variograms of forb cover in North America (a) and South Africa (b) for each of the treatments. In NA there were four treatments: (1) ungrazed, unburned; (2) ungrazed, annually burned; (3) single grazer (bison), unburned; (4) single grazer (bison), annually burned. In SA there were five treatments: (1) ungrazed, unburned; (2) single grazer (Cape buffalo), unburned; (3) single grazer (Cape buffalo), annually burned; (4) grazed by multiple herbivores, unburned; (5) grazed by multiple herbivores, annually burned. The lack of repeated peaks in each of the semi-variograms signifies the lack of repeatability of patches across a landscape.

CHAPTER 4

Interactive effects of grazing, drought, and fire on grassland community composition and function: cross continental convergence

Abstract

Climate is considered to be the primary factor influencing vegetation dynamics in mesic grasslands with grazing and fire operating within the constraints imposed by different moisture conditions. With global change altering all three of these factors, understanding the generality of grassland responses may have significant consequences for future global patterns of productivity and diversity. We evaluated the independent and interactive effects of grazing, drought, and fire on (1) plant species richness, diversity, composition, and density; and (2) aboveground net primary production (ANPP) and belowground biomass. We experimentally manipulated rainfall and grazing in two long-term fire experiments, one in North America (NA) and one in South Africa (SA). We hypothesized that (1) community properties and ecosystem functions would respond similarly to grazing, drought, and fire in both NA and SA, and that (2) at both sites drought would be the dominant factor controlling grasslands, grazing would play a secondary role to drought, and the effects of grazing and drought would be exacerbated in frequently burned sites. Grazing impacted grasslands as expected in both sites increasing diversity and decreasing grass cover, grass ANPP, and belowground biomass. Drought alone minimally impacted the plant communities in both NA and SA; however, at

frequently burned sites in both NA and SA, drought increased grassland sensitivity to grazing. Our results show that the effects of drought are not the primary driver of grasslands but instead are of a similar magnitude to the effects of grazing and fire, and grasslands with different evolutionary histories respond similarly to these three drivers and their interactions.

Introduction

Climate, fire, and grazing are considered to be the primary factors influencing vegetation dynamics in mesic grasslands. Climate, in particular soil moisture availability, is the main determinant of productivity in grasslands, with other factors like grazing and fire operating within the constraints imposed by different moisture conditions (Milchunas and Lauenroth 1993, Dormaar et al. 1997, Biondini et al. 1998, Collins et al. 2012). Savanna grasslands cover approximately 40% of the terrestrial surface, and although they share the same drivers, they can vary in evolutionary history, soil fertility, and diversity of plants and large herbivores. These differences are often invoked to explain the divergent responses to disturbances seen in ecosystem structure and function in Northern Hemisphere vs. the Southern Hemisphere (particularly South Africa) grasslands (Bond et al. 2003, Scholes et al. 2003a, Scholes et al. 2003b, Lusk and Bellingham 2004, Uys et al. 2004). With global environmental change altering temperature and precipitation patterns, grazing by native herbivores and fire regimes, understanding the generality of grassland responses to changing drivers may have significant consequences for future global patterns of productivity and diversity (Fay et al. 2003).

Water limitation constrains net primary production in grasslands (Noy-Meir 1973, Sala et al. 1988, Esser 1992, Knapp et al. 2001), with aboveground net primary production (ANPP) increasing linearly along a 200-1,300 mm per year precipitation gradient across North American, South American, and African grasslands (Webb et al. 1978, Lauenroth 1979, Sala et al. 1988, McNaughton et al.

1993, Paruelo et al. 1998). Meanwhile, within site temporal dynamics of ANPP are not as tightly aligned with annual precipitation (Lauenroth and Sala 1992, Briggs and Knapp 1995, Jobbagy et al. 2002). Compared to grazing and fire, climate variability has the most consistent impact on grassland dynamics around the world (Knapp et al. 2002, Scholes et al. 2003b, Knapp et al. 2006), and droughts have been recognized to be important ecological events in these systems (Tilman and Haddi 1992, Hayden 1998, du Toit et al. 2003). While rainfall is regarded as the primary influence on grassland productivity (Bredenkamp et al. 2002), fire and grazing also impact vegetation composition and structure (Scholes and Walker 1993), yet the direction and magnitude of these influences remain uncertain.

Large herbivores increase richness and diversity in North American mesic grasslands (Collins 1987, Hartnett et al. 1996) by increasing resource heterogeneity and altering plant community structure through selective grazing, soil disturbances, and nutrient deposition. In contrast, grazing and mowing in Southern Africa have minimal impact on plant species composition and diversity (Morris et al. 1992, Morris and Tainton 1996). Herbivores, in particular, are thought to have significant effects on primary production in grasslands that support large herds of grazers (Frank and Groffman 1998). Although grazing effects are not consistent in all grasslands, grazing can stimulate plant production (McNaughton 1976, Pandey and Singh 1992, Loeser et al. 2004) due to increased availability of light, water, and or nitrogen (McNaughton 1985, Frank and Groffman 1998, Knapp et al. 1998a).

Fire, unlike herbivory, is a large-scale generalist “herbivore” (Bond and Keeley 2005a) that homogenizes resources (Blair 1997) and plant community composition

(Collins 1992, Collins and Smith 2006). Savanna grasslands burn on average every two to three years making savannas the most frequently burned ecosystem in the world (Beerling and Osborne 2006). Fire generally increases biomass production by stimulating growth, removing moribund material, and increasing light availability at the soil surface (Johnson and Matchett 2001). However, in southern Africa, annual, biennial, or triennial burning reduced biomass in the year following the fire with no long-term consequences (Tainton et al. 1978), and fire has been shown to have no effect on forb diversity (Uys et al. 2004). Frequent fires also alter community structure by promoting fire-tolerant species and preventing growth of woody vegetation (Briggs et al. 2005).

Independently, fire and grazing have opposite effects on community composition, but together grazing and fire can increase plant species diversity and community heterogeneity (Collins 1987, Collins and Smith 2006). Precipitation modifies the impacts of both grazing and fire (Knapp and Hulbert 1986, Milchunas et al. 1994, Anderson et al. 2007a). Soils are generally drier in burned sites than in unburned sites, and these differences in soil moisture are accentuated in low rainfall years (McMurphy and Anderson 1965, Knapp et al. 1998a). Likewise, grazed grasslands tend to be drier than ungrazed grasslands and are more responsive to changes in precipitation (Skinner et al. 2002, Frank 2007). The effects of grazing intensity on plant responses to drought are species specific (Olson et al. 1985), suggesting that the interactive effects of drought and grazing could significantly affect plant community composition. However, little information exists on how

climate variation may interact with grazing and fire regimes to shape community structure (but see Chapter 2).

Climate models predict that precipitation regimes are likely to become more variable in the near future, including more extreme and prolonged droughts across seasons (Gordon et al. 1992, Easterling et al. 2000a, IPCC 2007). At the same time, fire and grazing regimes have been altered (Archer 1989, Eckhardt et al. 2000, van Wilgen et al. 2000, Hoch et al. 2002, Bond et al. 2003) through changes in land-use, landscape fragmentation, shifts in socio-political attitudes and policy, and the extinction of megaherbivores (Reid and Ellis 1995, Leach and Givnish 1996, Fuhlendorf and Engle 2001, Hoch et al. 2002). To date, each ecosystem driver has been studied extensively in isolation, yet global change drivers may be synergistic, additive or antagonistic (Zavaleta et al. 2003).

To address this deficiency we experimentally manipulated rainfall and grazing in long-term fire experiments at Konza Prairie Biological Station, Kansas, USA (North America - NA) and Kruger National Park, South Africa (SA) to examine the interactive effects of grazing, drought, and fire on small-scale vegetation dynamics in grassland ecosystems. Both sites are dominated by long-lived clonal C₄ grasses, have a diverse forb flora, and contain long-term fire experiments (+30 years). These sites were selected because of their different evolutionary histories coupled with common drivers of plant community structure: grazing by megaherbivores, frequent fire, and similar growing season climatic regimes (Knapp et al. 2004, Knapp et al. 2006). These similarities allowed us to determine whether or not fire, grazing, and drought have similar effects in mesic grasslands with different

evolutionary histories. We evaluated the independent and interactive effects of these three drivers on (1) plant species richness, diversity, composition, and density; and (2) aboveground net primary production (ANPP) and belowground biomass. We tested two hypotheses: (1) community properties and ecosystem functions would respond similarly to grazing, drought, and fire in both NA and SA, and (2) at both sites drought would be the dominant factor controlling productivity and community composition, grazing would play a secondary role to drought, and the effects of grazing and drought would be exacerbated in frequently burned sites.

Methods

Study Sites

In NA, community composition, structure, and function were measured in long-term fire experiments at the Konza Prairie Biological Station (KPBS) in Kansas, USA. KPBS is a 3,487-ha research site located in the Flint Hills of northeastern Kansas, an area that includes the largest remaining areas of native tallgrass prairie in North America. The system is dominated by unplowed native tallgrass prairie in which a small number of C₄ grasses, such as *Andropogon gerardii* and *Sorghastrum nutans*, account for the majority of herbaceous primary productivity (Knapp et al. 1998a), and community diversity is generally a function of forb species (Collins and Glenn 1991). The climate is temperate (July mean temperature = 27°C), and annual precipitation averages 835 mm/year with approximately 75% falling as rain during the April to October growing season. Soils are fine textured udic argiustolls underlain by cherty limestone and shales (Melzer et al. 2010). A fully replicated watershed-level fire experiment was established in 1977 with burn frequencies of

1-, 2-, 4-, and 20-yr intervals, mainly in the spring, encompassing a range of natural fire frequencies (Knapp et al. 1998b).

In SA, community composition, structure, and function were measured in long-term fire experiments in the south-central Satara region of Kruger National Park, South Africa. Kruger is a 2 million ha protected area of savanna grassland located in northeast South Africa. The vegetation is characterized by the coexistence of dominant perennial C₄ grasses, such as *Bothriochloa radicans*, *Digitaria eriantha*, *Panicum coloratum*, and *Themeda triandra*, and woody species, including *Acacia nigrescens* and *Sclerocarya birrea* trees. Our research site was in the south-central region where rainfall is approximately 544 mm/year (Venter et al. 2003), nearly all of which falls during the growing season between November and March. The climate is tropical with a mild, dry, and frost-free dormant season and a warm summer (January mean temperature = 29°C). Soils are fine-textured, rhodic nitisols, haplic luvisols, and leptic phaeozems underlain by basalt (Melzer et al. 2010). The Satara region of the park has an annual precipitation, soil type, and mix of herbaceous and woody plants that are similar to KPBS. In 2002, a Cape buffalo enclosure was erected for veterinary purposes. The 900 ha permanent enclosure contains 50-80 Cape buffalo (*Syncerus caffer*), a relatively non-selective grazer of grass (Hofmann 1973). The enclosure is divided into five blocks two of which were burned annually for the duration of the project. Also, a 9 ha area within the enclosure remains unburned and was fenced to prevent grazing.

Experimental Design

To study the effect of fire frequency, we selected blocks within the long-term fire

experiments to represent infrequently burned (approximately 4-6 year return interval) and frequently burned (annual return interval) in NA and SA. To manipulate rainfall, rainout shelters that reduce ambient precipitation by 50% were constructed following the methods of Yahdjian and Sala (2002). The aim of the rainout shelters was to mimic a moderate drought inside the normal range of rainfall that both sites receive. Rainout shelter construction began in March 2008 (SA) and April 2009 (NA) and was maintained for 3 growing seasons at each site. One exception was the frequently burned site in SA, which was in place for the last 2 seasons only. During the years of the experiment (2009-2011), growing season rainfall was respectively 561 mm, 575 mm, and 432 mm in NA, and 481 mm, 662 mm, and 521 mm in SA. Soil moisture probes were installed at the beginning of the growing season in 2010 and 2011 and remained in place for the duration of each growing season (May-September in NA and November-March in SA). Volumetric water content was estimated via sensors that measured dielectric permittivity of the soil (ECH20 soil moisture sensors, Decagon, Pullman, WA, USA). Each sensor integrates soil moisture for the top 20 cm of soil, and sensors were placed in three replicates for both sheltered and ambient plots at all sites. Soil moisture was measured once a week. Rainout shelters significantly reduced soil moisture throughout the growing season on average by 30% (Figure 1) with a growing season average volumetric water content of the soils of 12.3% and 11% in the rainouts and 15.5% and 14.5% in the open plots in NA and SA respectively. Pretreatment vegetation data were collected in December – March 2008 (SA) and June – August 2008 (NA) to confirm the lack of pretreatment difference. Seven

rainout shelters were constructed in each of the burn treatments (n=7) in NA and in SA. A 1x1 m plot was established under each rainout shelter and in a corresponding open area. Plots were standardized by locating them in areas with typical dominant grasses, *D. eriantha*, *P. coloratum*, or *T. triandra* in SA and *A. gerardii* in NA. To manipulate grazing, each plot was divided into four subplots. Two 50x50 cm clipped and control subplots were assigned to each rainout shelter. We simulated grazing by clipping all grasses in two subplots to 5 cm leaving the broad-leaved herbaceous species unclipped. Clipping occurred twice a year at the beginning and middle of the growing season. This grazing simulation represents a moderate grazing intensity for both of these grasslands.

Cover of each plant species rooted in each subplot was visually estimated near the beginning and end of each growing season. Cover data for each species on the 0.25-m² scale were used to compute standard metrics of community structure, including grass, forb, and total species richness, Shannon–Weiner diversity, evenness, and grass, forb, and total cover. All metrics were calculated using the maximum average cover values of each species for the entire growing season and then averaged for two adjacent 0.25-m² plots.

More intensive sampling was performed at the end of the 2011 growing season. Stem density counts for all species were performed in one 0.1 m² plot nested within one of each of the grazed and ungrazed subplots per rainout and paired plot. All biomass was collected from 0.1 m² plots nested within each subplot, sorted by growth form, and weighed to determine ANPP. For the grazed plots, clipped biomass from the grazing simulations was added to the end-of-season biomass to calculate

total ANPP and to determine if grazing compensation occurred. Belowground biomass was collected via soil cores taken in each subplot. In SA cores were 10 cm in diameter and 0-20 cm and 20-40 cm in depth. In NA cores were 5 cm in diameter, and depth varied between 7 cm and 20 cm depending on the rockiness of soil. Total roots from each core were washed, dried at 60 °C, and weighed to determine belowground biomass. Root biomass was then converted to g/m² to standardize reported results.

Statistical analyses

Each rainout shelter was treated as an experimental unit; therefore, growing season responses were based on the average value in each rainout shelter (average of two subplots). We tested for differences among treatments for diversity (Shannon-Weiner), evenness, richness, grass cover, and forb cover using a split-plot design repeated mixed model analysis of variance (ANOVA) with grazing and rainfall treatments as fixed effects and year repeated. We tested for differences among treatments for ANPP, belowground biomass, and stem densities using a split-plot design mixed model ANOVA with grazing and rainfall treatments as fixed effects. Early season and late season stem density counts were analyzed independently. Early season stem density for total, grass, and forb stems showed weaker responses to grazing and rainfall when compared to late season; therefore, only the late season stem density data are presented for both NA and SA. A separate model was used for each site and each burn frequency within a site to generate all statistics (SAS Institute V.9.3; Cary, N.C.). When main effects or interactions were

significant, mean separations were performed using Least Square Means.

Significance was set at $\alpha = 0.05$.

Results

North America

At the infrequently burned sites grazing significantly increased diversity on the 0.25-m² scale (Figure 2a; Table 2) through increases in both richness (Table 1) and evenness (Table 2). This response was dependent upon year. At the frequently burned site, grazing increased diversity (Figure 2c; Table 2) and evenness, and drought significantly interacted with grazing. Ungrazed drought plots were the least diverse due to changes in evenness, and these effects were dependent upon year. At the infrequently burned site, grazing and drought decreased grass cover (Table 2; Figure 3a). The strength of the grazing effect increased each year of the study resulting in a 26% reduction in grass cover in 2011. Drought significantly decreased grass cover by 10% only in 2011. Grazing increased forb cover (Table 2; Figure 4a). At the frequently burned site, grazing and drought decreased grass cover (Table 2; Figure 3c). The strength of the grazing effect increased each year of the study resulting in a 36% reduction in grass cover in 2011. Drought significantly decreased grass cover irrespective of year by 7%. Grazing and drought had no effect on forb cover (Table 2; Figure 4c).

At the infrequently burned site, total stem density per 0.1-m² was affected by drought, grazing, and a drought by grazing interaction (Table 3; Figure 5a). Drought decreased stem density by 30%. Grazing increased stem density by 46%. Ambient grazed plots had approximately 57% more stems than the other three treatments.

The changes in total stem density were driven primarily by changes in grass stem density as forb stem density was not significantly affected by treatments (Table 3). At the frequently burned site, drought decreased total stem density by 24% primarily due to changes in grass stem density (Table 3). Forb stem density was significantly affected by an interaction between grazing and drought (Table 3). Ungrazed plots had a significantly lower forb stem density than grazed plots and ungrazed drought plots.

At the infrequently burned site, total ANPP was significantly impacted by drought, grazing, and a drought by grazing interaction. Belowground biomass was not significantly affected by any treatment (Table 4; Figure 6 a&c). Drought reduced ANPP by 20%, and grazing reduced ANPP by 15%. Ambient ungrazed plots had approximately 26% more ANPP than each of the other treatments. At the frequently burned site, grazing significantly reduced ANPP by 38% and belowground biomass by 35% (Table 4; Figure 6a&c). Forb ANPP was <15% of total ANPP in both burn frequencies and was unaffected by either grazing or drought. In general, changes in total biomass are driven by changes in grass biomass.

South Africa

At the infrequently burned site, grazing increased diversity (Figure 2b) on the 0.25-m² scale due to increases in richness (Table 1), while drought had no effect (Table 2). At the frequently burned site, neither grazing nor drought affected diversity, richness, or evenness (Figure 2d; Table 2; Table 1). At the infrequently burned site, grass cover decreased due to both grazing and drought (Table 2; Figure 3c). Grazing reduced grass cover by 26% in 2010 only, while drought reduced grass

cover by 11% regardless of year. At the frequently burned site, grass cover decreased due to grazing, but drought had no effect (Table 2; Figure 3d). At both burn frequencies, forb cover was not significantly affected by grazing or drought (Table 2; Figure 4b&d).

At the infrequently burned site, total stem density per 0.1-m² and grass stem density were not significantly affected by grazing or by drought (Table 3; Figure 5b). Forb stem density was affected by a drought by grazing interaction (Table 3) with the open grazed plots having more forb stems than the other three treatments. At the frequently burned site, drought reduced stem density by 32% (Table 3; Figure 5b). This change in stems was driven by grass stems as forb stems were unaffected by treatments (Table 3).

At the infrequently burned site, total ANPP was significantly affected by drought, grazing, and a drought by grazing interaction. In addition, grazing reduced belowground biomass by 24% (Table 4, Figure 6b&d). Drought decreased ANPP by 26%, and grazing decreased ANPP by 38%. Ambient ungrazed plots had approximately 90% more ANPP than each of the other treatments. At the frequently burned site, total ANPP was significantly reduced by grazing by 31%, and belowground biomass was unaffected by either grazing or drought (Table 4; Figure 6b&d). Changes in total ANPP in both burn frequencies were driven by changes in grass ANPP as forb ANPP was unaffected by grazing or drought.

Discussion

As hypothesized, NA and SA grasslands responded similarly to grazing, drought, and fire. Grazing impacted grasslands as expected at both sites increasing diversity

and decreasing grass cover, grass ANPP, and belowground biomass. Drought alone minimally impacted the plant communities in both NA and SA; however, in frequently burned sites in both NA and SA, drought increased grassland sensitivity to grazing. We also hypothesized that drought would primarily determine community composition and ecosystem function. This was not supported; instead drought impacts were minimal, only having significant effects in the context of grazing.

Grasses, the dominant functional group in both systems, exhibited stronger responses than forbs. Changes in the majority of community properties were driven by grass dynamics, as all measurements of forb performance, including cover, ANPP, and stem counts, were relatively unaffected by grazing and drought. One exception was the change in diversity, since richness in these systems is largely driven by forb dynamics (Collins and Glenn 1991, Freeman 1998, Uys et al. 2004). Therefore, the changes seen in diversity due to richness are largely driven by forb response to drought, grazing, and fire.

Grazing impacted grasslands as expected at both sites increasing diversity and decreasing grass cover and grass ANPP. Diversity was enhanced by grazing due to increases in both richness and evenness of forb species. Grazing enhances diversity in grasslands around the world (Canals and Sebastia 2000, Augustine and Frank 2001, Nai-Bregaglio et al. 2002, Pykala 2004), as grazers preferentially consume grasses altering plant community structure (Collins 1987, Hartnett et al. 1996). Grazing effects were not dependent upon site fire history, as grass cover and ANPP decreased due to grazing in both infrequently and frequently burned grasslands.

Grazing history, however, was influential, as effects of grazing were compounded each year.

Grazing also decreased belowground biomass in nearly all sites. Response of belowground biomass to grazing and drought varies between grasslands worldwide, as grazing can increase (Frank et al. 2002, Skinner et al. 2002), decrease (Pandey and Singh 1992, Biondini et al. 1998) or have little or inconsistent effects (Milchunas and Lauenroth 1993, Turner et al. 1993, McNaughton et al. 1998) on belowground production. Our results support a decrease in belowground production likely due to reallocation of resources aboveground to compensate for aboveground shoot removal. Grazing also interacts with precipitation to affect belowground biomass, and grazed grasslands can be more (Frank 2007) or less (Skinner et al. 2002) sensitive to changes in precipitation than ungrazed grasslands. However, belowground biomass dynamics in our study were controlled by grazing with no impact by a three-year drought, similar to previous studies (Hild et al. 2001). Grazing had stronger effects on belowground biomass than drought in this study.

Drought minimally impacted the plant communities in both NA and SA. In frequently burned grasslands in NA, drought decreased diversity and grass cover; however, the positive effects of grazing on diversity were larger than the negative effects of drought. Grass cover in infrequently burned grasslands decreased in both sites due to drought, but again, the effects of grazing were stronger. Unlike grazing, drought effects were consistent across years rather than additive over time. The general lack of or limited response to drought has occurred in other grasslands.

Knapp and Smith (2001) found an asymmetric response to high and low water availability with unusually high precipitation leading to a large production response but the proportional decrease in production during drought years did not occur. Frank (2007) also showed that ANPP was unaffected by drought in both ungrazed and grazed grasslands in Yellowstone National Park, Wyoming. However, there is little doubt that a drought of longer duration than the one studied here, like the seven year Dustbowl drought of the 1930s which was also accompanied by extreme high temperatures, would have eventually led to changes in community composition and decreased ANPP (Weaver 1954, Frank 2007).

The general lack of interactions between drought and grazing on diversity and cover in both infrequently and frequently burned sites was surprising. Several studies have found grazing to produce more dynamic systems by increasing grassland sensitivity to changes in precipitation (Skinner et al. 2002, Koerner et al. Submitted). We did, however, see evidence of increased sensitivity due to grazing in stem density responses in frequently burned sites; drought decreased stems in grazed grasslands but not in ungrazed grasslands. Grasslands in the regrowth stage are more sensitive to drought and, therefore, lose more biomass than grasslands at later stages with a more fully developed canopy (Vogel et al. 2012). Frequently grazed grasslands have a higher probability of experiencing drought during a regrowth stage. We also saw differential responses between SA and NA grasslands in infrequently burned sites. In NA, grazing increased stem density in ambient conditions but drought eliminated the positive effects of grazing. In SA, drought without grazing decreased stem densities, but in the presence of grazing drought

had no effect on stem density. In NA, drought eliminated the effects of grazing on stem density, while in SA grazing eliminated the effects of drought. The response seen in NA also occurred in mixed grass prairie of Montana with intense short duration grazing during intense summer drought having minimal impact on vegetation growth dynamics (Heitchmidt and Haferkamp 2003).

Several response variables differed based upon fire history in both NA and SA. Diversity responded differentially to drought based on fire history with drought decreasing diversity only at frequently burned sites. This is not surprising as frequently burned sites are generally dryer than infrequently burned sites (McMurphy and Anderson 1965). However, drought had no effects on above or belowground productivity in frequently burned sites. Because frequently burned grasslands tend to be dryer than ungrazed grasslands, it was surprising that drought effects occurred in infrequently burned but not frequently burned sites. However, infrequently burned grasslands tend to have a more heterogeneous plant community and are more variable through time than frequently burned grasslands (Collins and Steinauer 1998). In SA the frequently burned grassland was not significantly affected by drought or grazing in terms of diversity, richness, evenness, forb cover, or forb ANPP. This lack of response could be driven by two factors. First, SA forbs are relatively unaffected by disturbance regimes like fire (Uys et al. 2004). Forbs perhaps show no direct responses to disturbances, and instead respond indirectly to disturbance due to changes in fitness of the dominant grasses. The second reason could be that the grazing history of this site was different from the others. This site was moderately grazed prior to the start of the rainfall treatments. Grazers

were excluded by fencing around each shelter. Recovery from grazing could be the primary driving influence in these plots and may also explain the decrease in diversity through time.

Previous research supports the hierarchical nature of factors that influence vegetation structure in grasslands, generally placing grazing and fire secondary to drought in affecting community and ecosystem processes (Clarke et al. 1943a, Olson et al. 1985, Hart et al. 1988, Biondini and Manske 1996, Biondini et al. 1998). Our results do not support this hierarchy. The imposed drought did not impact the variables we examined to the extent hypothesized. We attribute the weak impact of summer drought, particularly in terms of community composition, to the evolutionary history of these systems. Summer drought is a common event and does not serve as a notable ecological perturbation. The dominant vegetation can persist through drought periods in which water stress is comparable to that in desert biomes (Knapp 1984). Our results show that the effect of drought of the intensity and duration imposed by this experimental manipulation is not the primary driver of grasslands but instead is of a similar magnitude to the effects of grazing and fire. The small-scale responses of grassland community composition and ecosystem function to the interactive effects of grazing, drought, and fire were similar in grasslands with different evolutionary histories suggesting community and ecosystem convergence.

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Tables and Figures

Table 1. Species richness (\pm S.E.) per 0.25-m² for each rainfall and grazing treatment combination for each year of the study. See Table 1 for significance.

Burn Frequency	Site	Rain Trt	Grazing Trt	2009	2010	2011
Infrequent	NA	Ambient	Ungrazed	9.9 \pm 0.9	9.9 \pm 1.0	11.1 \pm 0.7
		Drought	Ungrazed	9.8 \pm 0.6	10.1 \pm 0.6	11.4 \pm 0.7
		Ambient	Grazed	10.3 \pm 0.8	13.4 \pm 1.0	12.1 \pm 0.9
		Drought	Grazed	10.6 \pm 0.9	13.1 \pm 0.4	11.8 \pm 0.8
	SA	Ambient	Ungrazed	3.7 \pm 0.8	3.6 \pm 0.8	2.9 \pm 0.4
		Drought	Ungrazed	2.8 \pm 0.4	3.4 \pm 0.6	2.8 \pm 0.4
		Ambient	Grazed	3.3 \pm 0.2	5.4 \pm 0.7	3.9 \pm 0.4
		Drought	Grazed	2.6 \pm 0.3	5.0 \pm 0.6	3.9 \pm 0.5
Frequent	NA	Ambient	Ungrazed	11.2 \pm 0.8	10.4 \pm 0.7	9.8 \pm 0.4
		Drought	Ungrazed	10.5 \pm 0.8	10.0 \pm 0.5	8.9 \pm 0.4
		Ambient	Grazed	11.1 \pm 0.8	10.9 \pm 0.8	10.1 \pm 0.7
		Drought	Grazed	10.4 \pm 0.6	10.1 \pm 0.6	9.6 \pm 0.6
	SA	Ambient	Ungrazed	-	5.5 \pm 0.4	3.1 \pm 0.3
		Drought	Ungrazed	-	6.3 \pm 0.6	3.8 \pm 0.6
		Ambient	Grazed	-	5.8 \pm 0.3	3.6 \pm 0.4
		Drought	Grazed	-	5.4 \pm 0.6	3.6 \pm 0.7

Table 2. Split-plot repeated measures analysis of variance F-statistics (p-values) for vegetation responses to year, rainfall treatment, and grazing treatment. Each vegetation response in each site and each burn frequency was evaluated with a separate model. Specific vegetation responses were Shannon–Wiener diversity, evenness, total species richness, grass cover, and forb cover per 0.25-m². Significant values are in bold (P <0.05).

Burn Frequency	Site	Parameter	Shannon's Diversity	Species Richness	Evenness	Grass Cover	Forb Cover
Infrequent	NA	Model	39.46 (<0.001)	36.05 (<0.001)	14.37 (<0.001)	5.82 (0.016)	26.84 (<0.001)
		Year	56.04 (<0.001)	15.58 (<0.001)	48.08 (<0.001)	12.11 (<0.001)	21.60 (<0.001)
		Rain	0.16 (0.696)	0.00 (0.983)	0.50 (0.488)	0.87 (0.361)	0.61 (0.442)
		Year*Rain	1.98 (0.149)	0.10 (0.903)	2.37 (0.104)	3.46 (0.040)	0.92 (0.404)
		Grazing	8.63 (0.007)	4.61 (0.042)	9.99 (0.004)	48.92 (<0.001)	3.95 (0.058)
		Year*Grazing	21.51 (<0.001)	11.88 (<0.001)	11.33 (<0.001)	4.31 (0.019)	5.47 (0.007)
		Rain*Grazing	0.50 (0.829)	0.04 (0.839)	0.06 (0.801)	0.20 (0.660)	0.68 (0.417)
	Year*Rain*Grazing	0.65 (0.527)	0.52 (0.597)	0.55 (0.580)	0.06 (0.940)	1.00 (0.376)	
	SA	Model	37.53 (<0.001)	28.16 (<0.001)	25.73 (<0.001)	9.65 (0.002)	32.95 (<0.001)
		Year	2.17 (0.099)	7.92 (<0.001)	2.14 (0.103)	8.04 (<0.001)	6.51 (<0.001)
		Rain	1.53 (0.228)	1.22 (0.280)	0.83 (0.371)	4.66 (0.041)	0.05 (0.831)
		Year*Rain	0.27 (0.849)	0.84 (0.478)	0.34 (0.793)	2.24 (0.091)	0.38 (0.769)
		Grazing	1.66 (0.210)	2.01 (0.169)	0.94 (0.341)	5.19 (0.032)	0.04 (0.853)
		Year*Grazing	2.88 (0.042)	4.76 (0.004)	0.11 (0.952)	3.05 (0.034)	1.51 (0.220)
Rain*Grazing		0.14 (0.710)	0.03 (0.863)	0.27 (0.610)	0.43 (0.520)	0.10 (0.749)	
Year*Rain*Grazing	0.32 (0.814)	0.05 (0.986)	1.30 (0.281)	1.30 (0.282)	0.28 (0.843)		
Frequent	NA	Model	58.63 (<0.001)	49.91 (<0.001)	23.63 (<0.001)	6.37 (0.0116)	39.10 (<0.001)
		Year	8.85 (<0.001)	15.57 (<0.001)	4.76 (0.013)	47.95 (<0.001)	3.03 (0.058)
		Rain	1.33 (0.260)	1.19 (0.285)	0.74 (0.397)	6.28 (0.019)	2.40 (0.134)
		Year*Rain	2.05 (0.139)	0.09 (0.917)	3.53 (0.037)	0.46 (0.636)	0.07 (0.934)
		Grazing	1.76 (0.197)	0.14 (0.709)	3.88 (0.060)	71.83 (<0.001)	0.10 (0.756)
		Year*Grazing	12.00 (<0.001)	1.02 (0.369)	9.20 (<0.001)	20.42 (<0.001)	2.98 (0.060)
		Rain*Grazing	0.05 (0.830)	0.00 (0.984)	0.17 (0.686)	0.26 (0.617)	0.94 (0.341)
	Year*Rain*Grazing	4.09 (0.023)	0.50 (0.611)	4.14 (0.022)	0.37 (0.694)	2.88 (0.066)	
	SA	Model	2.01 (0.156)	0.20 (0.652)	1.83 (0.176)	13.39 (<0.001)	1.17 (0.280)
		Year	-	-	-	43.26 (<0.001)	-
		Rain	-	-	-	2.04 (0.166)	-
		Year*Rain	-	-	-	0.37 (0.548)	-
		Grazing	-	-	-	6.61 (0.017)	-
		Year*Grazing	-	-	-	14.58 (<0.001)	-
Rain*Grazing		-	-	-	0.01 (0.929)	-	
Year*Rain*Grazing	-	-	-	0.10 (0.760)	-		

Table 3. Split-plot analysis of variance F-statistics (p-values) for total, grass, and forb stems per 0.1 m² for late season 2011 responses to rainfall treatment and grazing treatment. Each stem category in each site and each burn frequency was evaluated with a separate model. Significant values are in bold (P <0.05).

Burn Frequency	Site	Parameter	Total Stems	Grass Stems	Forb Stems
Infrequent	NA	Rain	5.30 (0.040)	4.91 (0.047)	1.01 (0.334)
		Grazing	27.59 (<0.001)	21.07 (<0.001)	1.14 (0.307)
		Rain*Grazing	7.60 (0.017)	6.11 (0.029)	0.08 (0.781)
	SA	Rain	3.65 (0.080)	3.38 (0.091)	2.39 (0.139)
		Grazing	0.54 (0.475)	0.61 (0.448)	2.39 (0.139)
		Rain*Grazing	1.10 (0.314)	1.25 (0.286)	4.69 (0.044)
Frequent	NA	Rain	7.68 (0.032)	8.08 (0.029)	0.75 (0.403)
		Grazing	2.97 (0.111)	4.07 (0.067)	2.54 (0.137)
		Rain*Grazing	4.00 (0.069)	2.35 (0.151)	6.70 (0.024)
	SA	Rain	7.39 (0.035)	7.80 (0.032)	0.00 (1.000)
		Grazing	0.75 (0.402)	0.70 (0.418)	1.14 (0.296)
		Rain*Grazing	1.71 (0.215)	1.71 (0.215)	0.29 (0.598)

Table 4. Split-plot analysis of variance F-statistics (p-values) for total ANPP, grass ANPP, forb ANPP, and belowground biomass responses to rainfall treatment and grazing treatment for end of season 2011. Each measure of productivity in each site and each burn frequency was evaluated with a separate model. Significant values are in bold ($P < 0.05$).

Burn Frequency	Site	Parameter	Total ANPP	Grass ANPP	Forb ANPP	Belowground Biomass
Infrequent	NA	Rain	7.24 (0.023)	12.13 (0.006)	0.53 (0.484)	0.23 (0.653)
		Grazing	12.90 (0.005)	11.91 (0.006)	0.10 (0.758)	0.23 (0.644)
		Rain*Grazing	6.27 (0.031)	1.39 (0.265)	2.75 (0.129)	0.16 (0.696)
	SA	Rain	4.81 (0.042)	4.39 (0.051)	0.02 (0.876)	0.42 (0.542)
		Grazing	11.63 (0.003)	11.44 (0.003)	0.16 (0.691)	9.69 (0.009)
		Rain*Grazing	6.07 (0.024)	5.56 (0.030)	0.06 (0.816)	0.71 (0.416)
Frequent	NA	Rain	0.05 (0.838)	0.73 (0.426)	2.28 (0.157)	0.66 (0.424)
		Grazing	31.81 (<0.001)	45.23 (<0.001)	0.57 (0.465)	9.33 (0.006)
		Rain*Grazing	0.57 (0.463)	0.79 (0.391)	0.01 (0.941)	0.00 (0.974)
	SA	Rain	1.02 (0.332)	1.03 (0.330)	0.08 (0.780)	1.69 (0.219)
		Grazing	14.68 (0.002)	12.27 (0.004)	2.27 (0.149)	2.61 (0.132)
		Rain*Grazing	0.89 (0.363)	0.65 (0.434)	1.15 (0.298)	0.48 (0.502)

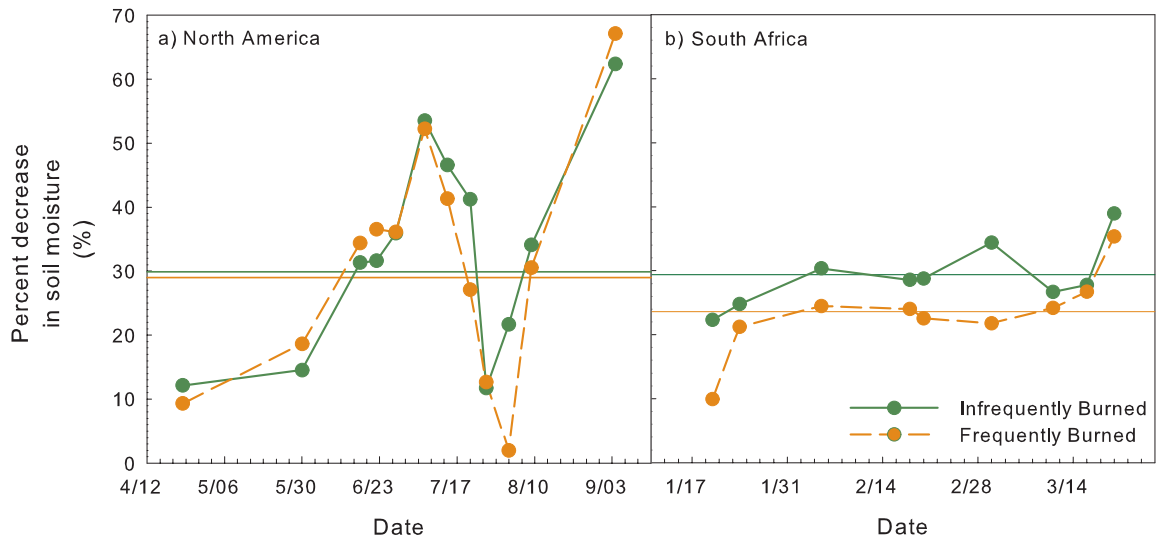


Figure 1. Percent decrease in soil moisture relative to ambient conditions under 50% rainfall exclusion shelters in a) North America and b) South Africa in infrequently burned (green with solid lines) and frequently burned (orange with dashed lines) sites throughout the 2011 growing season. Reference lines are the mean percent decrease in soil moisture over the growing season.

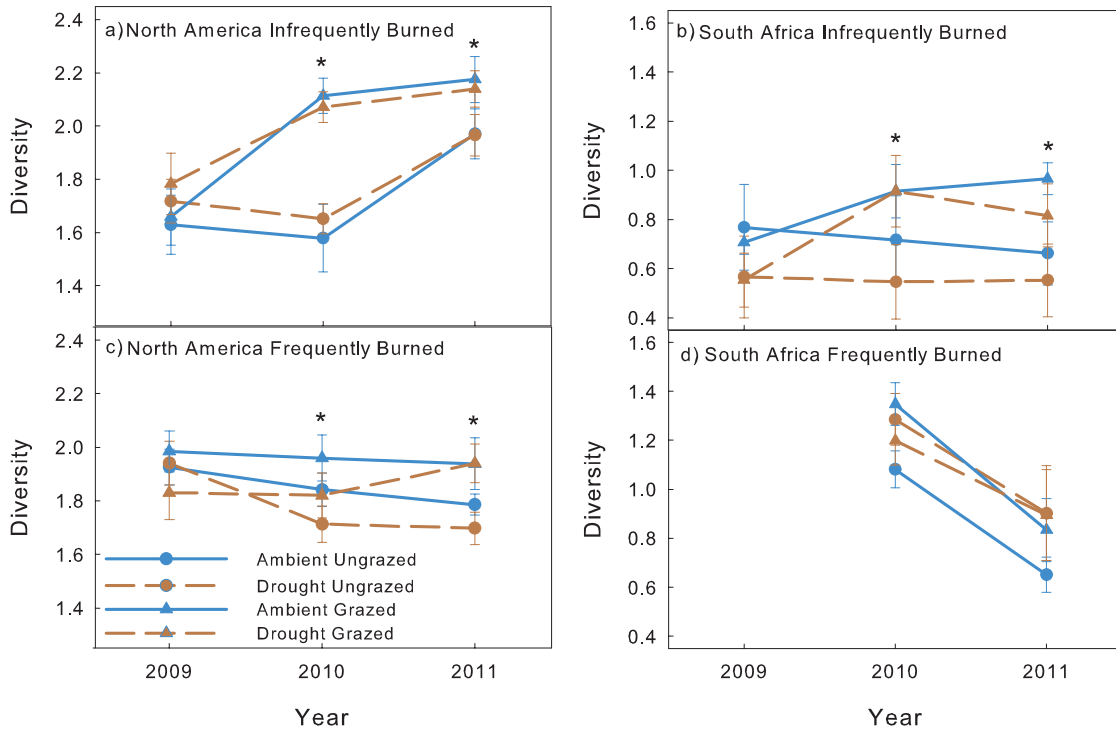


Figure 2. Plant community diversity (Shannon–Weiner) at 0.25-m² scale for ambient (blue solid lines) and drought rainfall treatments (brown dashed lines) in ungrazed (circles) and grazed (triangles) sites in a) North American infrequently burned, b) South African infrequently burned, c) North American frequently burned, and d) South African frequently burned grassland. Significant differences within each year are denoted by “*”. Error bars represent ± 1 S.E.

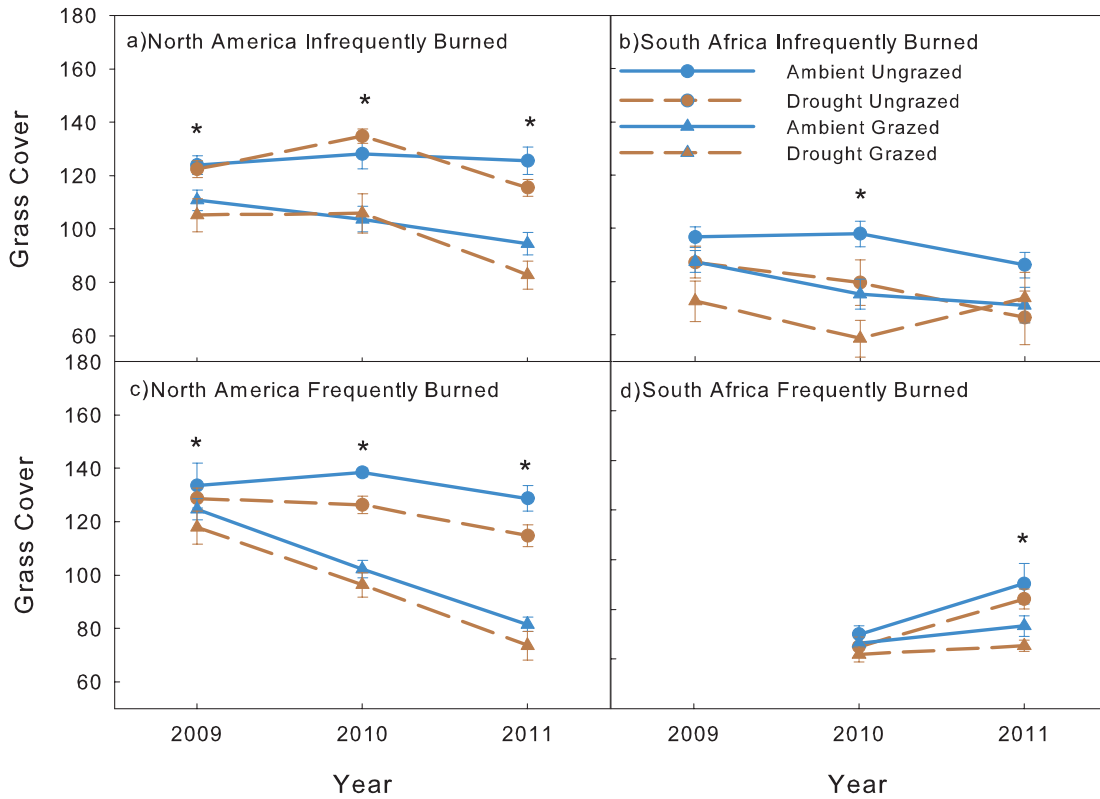


Figure 3. Absolute grass cover at 0.25-m² scale for ambient (blue) and drought rainfall treatments (brown) in ungrazed (circles with solid lines) and grazed (triangles with dashed lines) sites in a) North American infrequently burned, b) South African infrequently burned, c) North American frequently burned, and d) South African frequently burned grassland. Significant differences within each year are denoted by “*”. Error bars represent ± 1 S.E.

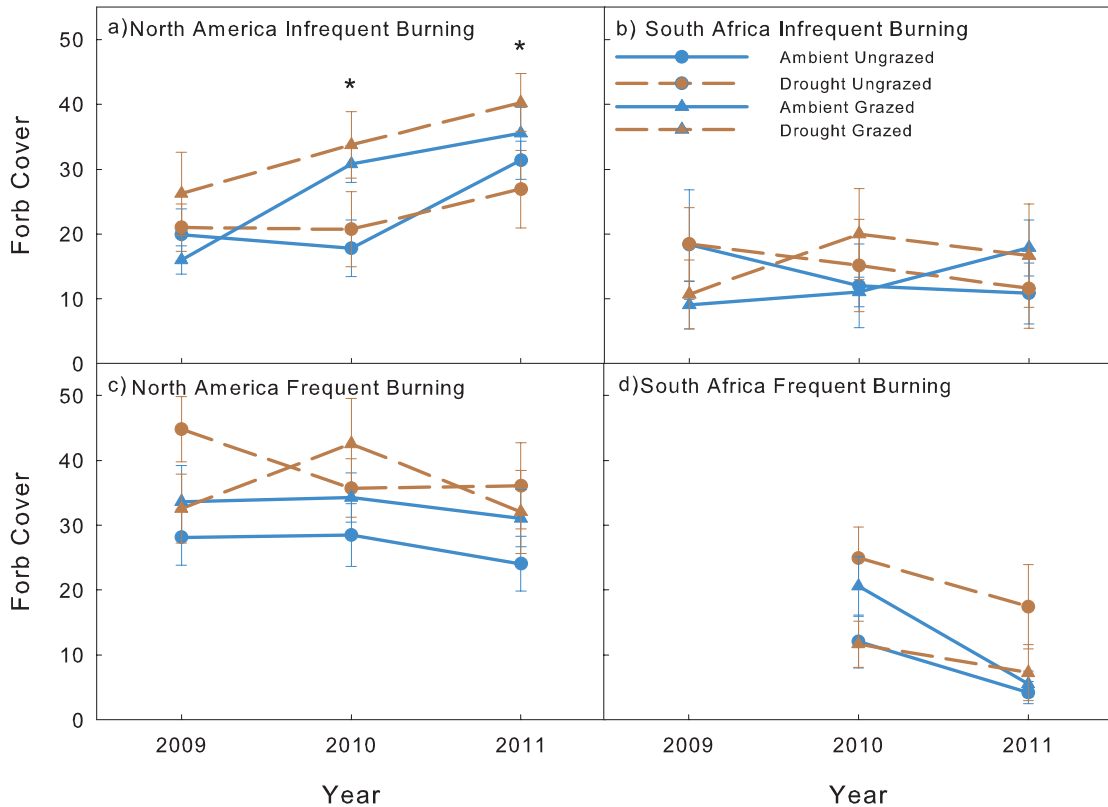


Figure 4. Absolute forb cover at 0.25-m² scale for ambient (blue) and drought rainfall treatments (brown) separated by ungrazed (circles with solid lines) and grazed (triangles with dashed lines) sites in a) North American infrequently burned, b) South African infrequently burned, c) North American frequently burned, and d) South African frequently burned grassland. Significant differences within each year are denoted by “*”. Error bars represent ± 1 S.E.

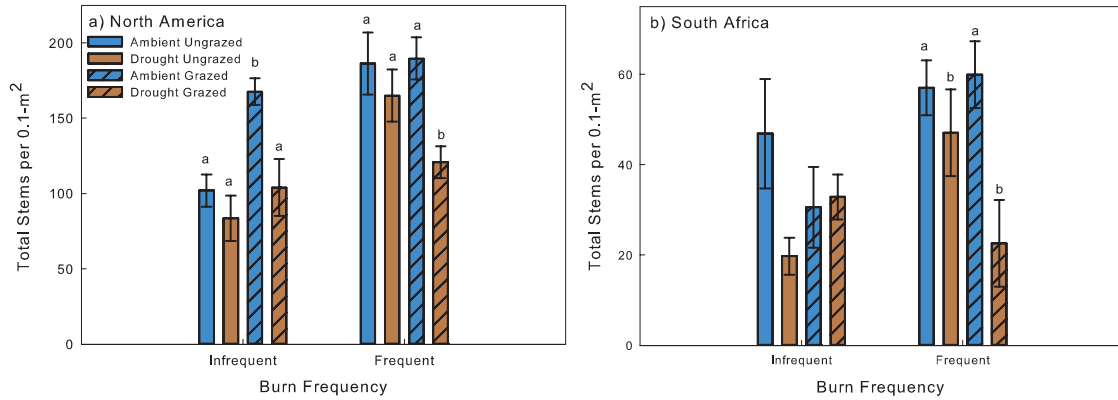


Figure 5. Number of stems per 0.1 m² for late season 2011 ambient (blue) and drought (brown) rainfall treatments for ungrazed (solid) and grazed (hashed) at the end of the experiment for a) North America and b) South Africa. Letters denote significant differences between the treatments within a site (P < 0.05). Error bars represent ±1 S.E.

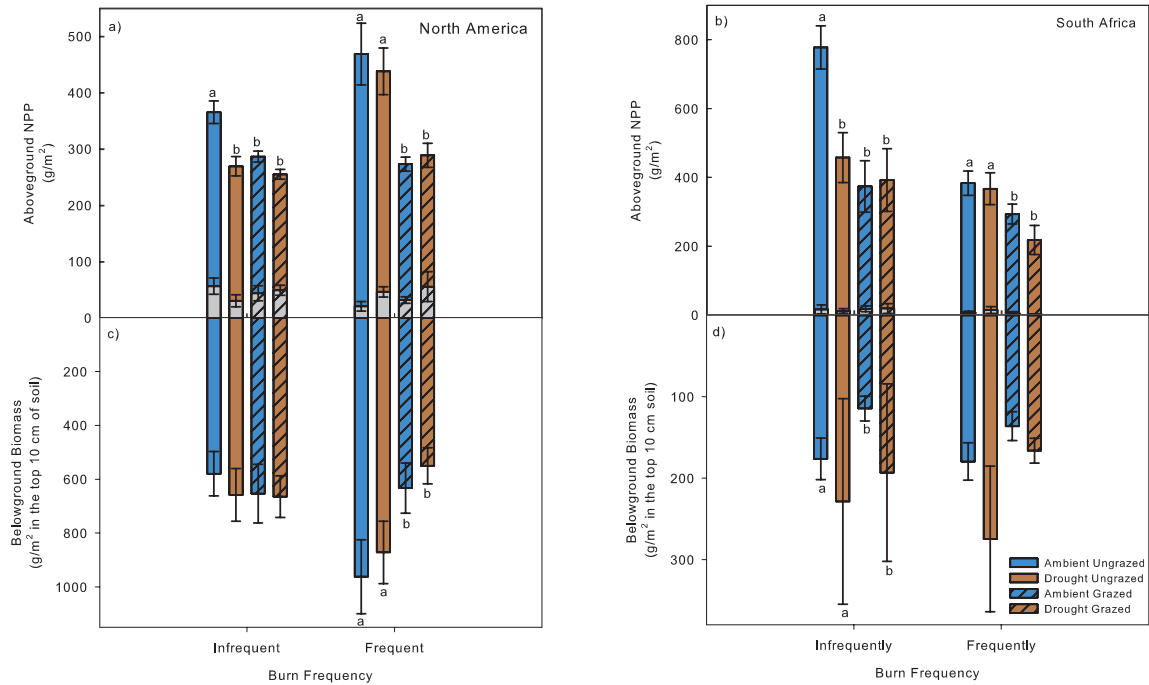


Figure 6. Annual net primary production (ANPP) for grasses (colored) and forbs (grey) per 1-m² (top) and belowground biomass per 1-m² in 10 cm of soil (bottom) for ambient (blue) and drought rainfall (brown) for ungrazed (solid) and grazed (hashed) treatments at the end of the experiment for a&c) North America and b&d) South Africa. Letters denote significant differences between the treatments within a site ($P < 0.05$). Error bars represent ± 1 S.E.

Chapter 5

Conclusions

Mesic grasslands worldwide experience a complex disturbance regime including frequent fire, grazing by large ungulates, and strong interannual climate variability. As a result of anthropogenic global change, all three of these ecosystem drivers are being altered. Land-use changes are disrupting natural disturbance regimes often altering fire regimes and eliminating native grazers from the system (Knapp and Seastedt 1998). Furthermore, climate change models predict that precipitation regimes are likely to become more variable, including more extreme and prolonged droughts across seasons (IPCC 2007). In my dissertation, I investigated how grassland plant community dynamics and ecosystem function respond to the interactive effects of these altered disturbance and climate regimes. To address these questions, I utilized a combination of cross-site comparisons, long-term experiments, and short-term manipulations.

In Chapter 2, I utilized a long-term climate manipulation experiment, the Rainfall Manipulation Plots (Knapp et al. 2002, Fay et al. 2011) at Konza Prairie, Kansas, USA, to address how predicted climate regimes will affect grassland sensitivity to short-term grazing events. Growing season precipitation regimes are predicted to become more variable, with larger event sizes and longer dry periods resulting in more temporally dynamic soil moisture regimes (Easterling et al. 2000, Karl et al. 2009), a pattern already occurring in many regions (Groisman and Knight 2008,

Knapp et al. 2008, Min et al. 2011, Smith 2011). This climate variability is likely to interact with other disturbances common in tallgrass prairie (Savage and Jacobson 1935, Weaver and Albertson 1936, Clarke et al. 1943, Coupland 1958, Fuhlendorf et al. 2001, Swemmer and Knapp 2008, Cheng et al. 2011). Thus, I investigated the individual and combined effects of increased rainfall variability and grazing on plant community composition, structure, and function in an annually burned grassland. We found that neither grazing nor rainfall treatments affected species richness; however, grazing decreased total ANPP and grass ANPP and increased forb ANPP relative to ungrazed plots. Grass stem density recovered from grazing under ambient rainfall but did not fully recover even after two years in the altered rainfall treatment. Thus, more variable soil moisture – a result of altered precipitation patterns – may exacerbate the effects of grazing on grasses and inhibit post-grazing recovery.

In Chapter 3, to observe how long-term changes in megaherbivore diversity loss and fire regime change interact to affect landscape scale patch dynamics, I utilized long-term (+30 years) grazing and fire experiments at two mesic grassland study sites, one in North America (NA, Konza Prairie) and one in South Africa (SA, Kruger National Park) (Knapp et al. 2004). I assessed small-scale grass-forb interaction using semi-variance analysis. Fire and grazing generally alter the availability and spatial heterogeneity of limiting resources affecting the inherent patchiness in grasslands caused by the dominant long-lived clonal grasses. In this study, grasslands in NA and SA showed moderate to strong patch structure yet responded differently to disturbance. In both sites the strongest grass patch structure occurred

in sites without grazing and fire. SA grassland patch structure was unaffected by disturbance, while NA grasslands were strongly affected by fire and grazing. In SA, the ability to maintain consistent patch structure in different fire and grazing regimes is a reflection of the architecture of the dominant grasses and the longer evolutionary history with grazing and fire. As fire and grazing have larger impacts on grass patch structure in NA than SA, findings from one site cannot be generalized across multiple sites with different evolutionary histories and different life-form characteristics of the dominant plants.

In my last chapter, I again used sites in NA and SA (Knapp et al. 2004) to address how short-term manipulations (3 years) in mean rainfall and grazing interact to affect plant community structure, dynamics, and function in areas with different long-term fire histories. This experimental set-up allowed for the direct comparison of NA and SA grasslands and their sensitivities to these three drivers of communities. Climate, in particular soil moisture availability, is thought to be the primary determinant of productivity in grasslands, with other factors like grazing and fire operating within the constraints imposed by different moisture conditions (Milchunas and Lauenroth 1993, Dormaar et al. 1997, Biondini et al. 1998). Our results do not support this hierarchy. The imposed drought did not impact the variables we examined to the extent hypothesized, and instead our results show that the effects of drought are not the primary factor but instead are of a similar or lesser magnitude to the effects of grazing and fire. Overall, NA and SA grasslands responded similarly to grazing, drought, and fire and their interactions.

The combination of cross-site work and long-term experiments greatly enhances the generality and depth of my findings. Overall, this research shows that on small scales different grasslands exhibit similar responses to grazing and fire (Chapter 3), and to grazing, fire, and drought (Chapter 4). However, the generality seen in small-scale responses may not transfer to larger landscape scale processes because patch dynamics within these landscapes are strongly affected by grazing and fire in NA but not in SA. This research also showed that grazing more frequently affected community properties like diversity, cover, and ANPP, while both drought (Chapter 4) and changes in rainfall variability (Chapter 2) rarely affected those properties. Instead grasslands responded to changes in rainfall by altering stem densities, and only in this metric were there significant interactions with grazing. As the majority of grasslands globally are grazed, current climate change experiments in grasslands may be underestimating the effects of altered precipitation patterns on the population dynamics of species within these ecosystems. However, the combined effects of altered rainfall regimes and grazing do not scale up to community and ecosystem level processes suggesting that mesic grasslands may ultimately be resilient to moderate changes in precipitation.

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