Interactive effects of grazing, drought, and fire on grassland plant communities in North America and South Africa

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Abstract:

Grazing, fire, and climate shape mesic grassland communities. With global change altering all three factors, understanding how grasslands respond to changes in these combined drivers may aid in projecting future changes in grassland ecosystems. We manipulated rainfall and simulated grazing (clipping) in two long-term fire experiments in mesic grasslands in North America (NA) and South Africa (SA). Despite their common drivers, grasslands in NA and SA differ in evolutionary history. Therefore, we expected community structure and production in NA and SA to respond differently to fire, grazing, and drought. Specifically, we hypothesized that NA plant community composition and production would be more responsive than the SA plant communities to changes in the drivers and their interactions, and that despite this expected stability of SA grasslands, drought would be the dominant factor controlling production, but grazing would play the primary role in determining community composition at both sites. Contrary to our hypothesis, NA and SA grasslands generally responded similarly to grazing, drought, and fire. Grazing increased diversity, decreased grass cover and production, and decreased belowground biomass at both sites. Drought alone minimally impacted plant community structure, and we saw similar treatment interactions at the two sites. Drought was not the primary driver of grassland productivity, but instead drought effects were similar to or less than grazing and fire. Even though these grasslands differed in evolutionary history, they responded similarly to our fire, grazing, and climate manipulations. Overall, we found community and ecosystem convergence in NA and SA grasslands. Grazing and fire are as important as climate in controlling mesic grassland ecosystems on both continents.

Article:

Introduction

Climate, fire, and grazing are the primary factors influencing vegetation dynamics in mesic grasslands. Climate, in particular soil moisture availability, is the primary determinant of productivity in grasslands, with other factors such as grazing and fire operating within the constraints imposed by different moisture conditions (Milchunas and Lauenroth 1993, Biondini et al. 1998, Collins et al. 2012). These three drivers along with inherent differences in soil shape grasslands worldwide. Currently global environmental change is simultaneously altering precipitation patterns, grazing by herbivores, and fire regimes; thus, understanding the generality of grassland responses to changing drivers will aid in predicting future global patterns of grassland productivity and diversity (Fay et al. 2003).

Precipitation, and thus soil moisture availability, limits net primary production in grasslands, with growing-season precipitation, more so than annual precipitation, predicting total aboveground net primary production (ANPP) within sites over time (Nippert et al. 2006, La Pierre et al. 2011, Robinson et al. 2013). Like ANPP, grassland species richness also increases with precipitation; however, this relationship only holds in arid and semiarid grasslands (Cleland et al. 2013). Climate models predict that precipitation regimes are likely to become more variable in the near future, including more extreme and prolonged droughts across seasons (IPCC 2012). For mesic grasslands, increased drought occurrence will therefore negatively impact ANPP while having variable impact on plant community composition.

In addition to climate change, fire and grazing regimes have also been altered through land-use change, landscape fragmentation, shifts in sociopolitical attitudes and policy, and large herbivore extinctions (Reid and Ellis 1995, Leach and Givnish 1996, Fuhlendorf and Engle 2001). Although rainfall is regarded as the primary influence on grassland productivity (Bredenkamp et al. 2002), fire and grazing also impact ANPP and strongly affect plant community composition (Scholes and Walker 1993). Moderate grazing can stimulate ANPP, leading to grazing compensation (McNaughton 1976, Pandey and Singh 1992), and increase richness and diversity (Collins 1987, Hartnett et al. 1996). Fire also generally increases short-term ANPP (Knapp and Seastedt 1986, Johnson and Matchett 2001) but reduces plant community diversity and heterogeneity (Collins 1992, Briggs et al. 2002). 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). Thus, changes in these regimes can have significant consequences for biodiversity and ANPP.

Grazing and fire effects have been extensively studied in grasslands, but most research has examined grazing and fire effects through observational studies utilizing year-to-year variation in ambient precipitation. These studies have shown that precipitation modifies the impacts of both grazing and fire (Knapp and Hulbert 1986, Milchunas et al. 1994, Anderson et al. 2007, Porensky et al. 2013). For example, soils are generally drier in burned sites, and differences in soil moisture are accentuated in low rainfall years (McMurphy and Anderson 1965, Knapp et al. 1998*a*). Likewise, grazed grasslands tend to be drier and more responsive to changes in precipitation than ungrazed grasslands (Skinner et al. 2002, Frank 2007). The effects of grazing intensity on plant responses to drought are often species-specific (Olson et al. 1985). Combined,

these studies suggest that the interactive effects of altered precipitation, grazing, and fire regimes could significantly affect plant community composition and grassland ANPP. Because these drivers may be synergistic, additive, or antagonistic (Zavaleta et al. 2003), they must be manipulated and studied in combination to draw realistic conclusions about grassland structure and function under future environmental change scenarios.

We experimentally manipulated rainfall and grazing in two long-term fire experiments in North America (NA) and South Africa (SA) to examine the interactive effects of grazing, drought, and fire on small-scale vegetation dynamics in grassland ecosystems. Frequent fire, grazing by large herbivores, and climatic variability are important drivers in both ecosystems (Scholes and Walker 1993, Knapp et al. 1998b, du Toit et al. 2003), and both sites are dominated by a continuous layer of C_4 grasses with less abundant C_3 forbs and woody plants (Knapp et al. 2004). Under ambient rainfall conditions total ANPP, species diversity, richness, and community heterogeneity responded similarly to fire frequency and grazing history (+30 year manipulations) in both NA and SA grasslands (Buis et al. 2009, Knapp et al. 2012, Koerner and Collins 2013). Despite the similarities found between these two sites, they differ in evolutionary history. The extant NA grassland plant community is 8000–10000 years old, while the SA community is 4–6 million years old (Axelrod 1985, Bond et al. 2003). A manifestation of the longer evolutionary history of grazing, fire, and variable climate in South African savanna grasslands may be stability in the face of altered disturbance regimes. In fact, plant community richness and diversity rapidly declined in NA but remained unchanged in SA in response to a seven-year grazing removal experiment (S. E. Koerner et al., *unpublished data*).

Here we evaluated the independent and interactive effects of fire, grazing (simulated by clipping), and precipitation on plant species richness, diversity, composition, stem density, aboveground net primary production (ANPP), and belowground biomass in NA and SA grasslands with similar fire, grazing, and precipitation regimes (Knapp et al. 2004, 2012). We expected that community structure and production would respond differently to grazing and drought manipulations under multiple long-term fire regimes in both NA and SA. We tested three main hypotheses. (1) NA plant community composition and production would be more responsive to changes in the three drivers and their interactions than the SA plant communities. Specifically we predicted that simulated grazing would increase diversity while drought would decrease diversity, and that both grazing and drought would decrease grass cover and above- and below-ground production in NA more than SA grasslands. (2) Despite the expected stability of SA grasslands in response to changes in these three factors, drought would be the dominant factor controlling production, but simulated grazing would play the primary role in determining community composition at both sites. Finally, (3) we predicted that the impacts of grazing on composition and production would decrease due to burning but increase due to drought, and that the impacts of drought on composition and production would be compounded by simulated grazing and burning in both sites.

Methods

Study sites

In NA, community composition, structure, and function were measured at the Konza Prairie Biological Station (KPBS) in Kansas, USA. KPBS is a 3487-ha site located in the Flint Hills of northeastern Kansas, an area that includes the largest remaining areas of native tallgrass prairie in NA. The climate is temperate (July mean temperature, 27°C), and mean growing-season (April–September) precipitation is 609 ± 183 mm/yr (Knapp et al. 2006). Soils are fine-textured silty clay loams (udic argiustolls) underlain by cherty limestone and shales (Melzer et al. 2010). KPBS is dominated by a small number of rhizomatous C_4 grasses, mainly *Andropogon gerardii* and *Sorghastrum nutans*, which form a continuous herbaceous layer (Appendix A: Fig. A1A). These dominant C_4 grasses account for the majority (>90%) of herbaceous primary productivity (Knapp et al. 1998*a*) while community diversity is generally a function of forbs (Collins and Glenn 1991), the majority of which are perennial. A watershed-level fire experiment was established in 1977 with a range of burn frequencies that encompass the hypothesized range of natural fire frequencies (Knapp et al. 1998*b*). For this experiment, we utilized two ungrazed (30+ years) watersheds (from here on referred to as blocks), one burned annually (frequently burned) and one burned every four years (infrequently burned).

In SA, community composition, structure, and function were measured in the south-central Satara region of Kruger National Park, SA. Kruger is a 2-million-ha area of savanna grassland located in northeast SA. The Satara region of the park has an annual precipitation, soil type, and mix of herbaceous and woody plants that are similar to KPBS. Our research site was in the south-central region where rainfall is approximately 518 ± 176 mm/yr (Buis et al. 2009). 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 clay and loam (rhodic nitisols, haplic luvisols, and leptic phaeozems) underlain by basalt (Melzer et al. 2010). The vegetation is characterized by the coexistence of dominant primarily caespitose perennial C_4 grasses, such as *Bothriochloa radicans*, *Digitaria eriantha*, *Panicum coloratum*, and *Themeda triandra*, along with scattered individuals of *Acacia nigrescens* and *Sclerocarya birrea* trees. Grasses form a fairly continuous canopy layer (Appendix A: Fig. A1B), and again perennial forbs account for most plant species diversity. In 2002, a 900-ha permanent enclosure was erected and stocked with 50–80 Cape buffalo (*Syncerus caffer*), a relatively nonselective grazer of grass (Hofmann 1973) similar to bison in North America. Inside the enclosure, we utilized one block, which has been burned annually since 2002 with relatively frequent burning prior to construction of the enclosure. Also inside the enclosure, we utilized a 9-ha infrequently burned area that was fenced to prevent grazing in 2002. Two recorded fires occurred in 1998 and 2002 but no fires occurred during our study.

Experimental design

In both NA and SA, we set up seven replicate rainout shelters (2.44×3.05 m) in one block that was burned annually and one block that was burned every four to six years (Fig. 1). A total of 28 shelters was built, each with a permanent 1-m^2 vegetation plot underneath the shelter and a paired 1-m^2 ambient rainfall plot within 3–8 m adjacent to the shelter (see Plate 1). All pairs of 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. Because cape buffalo were present in the annually burned block in SA, fences were built around each rainout shelter and paired plot to protect the infrastructure and prevent grazing during the experiment. Rainout shelters were

placed randomly within a block and designed to reduce ambient precipitation by 50% following the methods of Yahdjian and Sala (2002). Our rainout shelter treatment mimics a moderate growing-season drought. Rainout shelters were maintained for three growing seasons with the exception of the frequently burned SA site, which lasted two seasons. Volumetric water content was estimated weekly during each growing season with ECH2O soil moisture sensors (Decagon, Pullman, Washington, USA) that integrate the top 20 cm of soil moisture. Sensors were placed on the edge of the species-composition plots in three replicates for both sheltered and ambient plots at the beginning of the growing season in 2010 and 2011 and remained in place for the duration of each growing season. From 2009 to 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. Rainout shelters significantly reduced growing-season soil moisture by 30% at each site (Appendix A: Fig. A2).
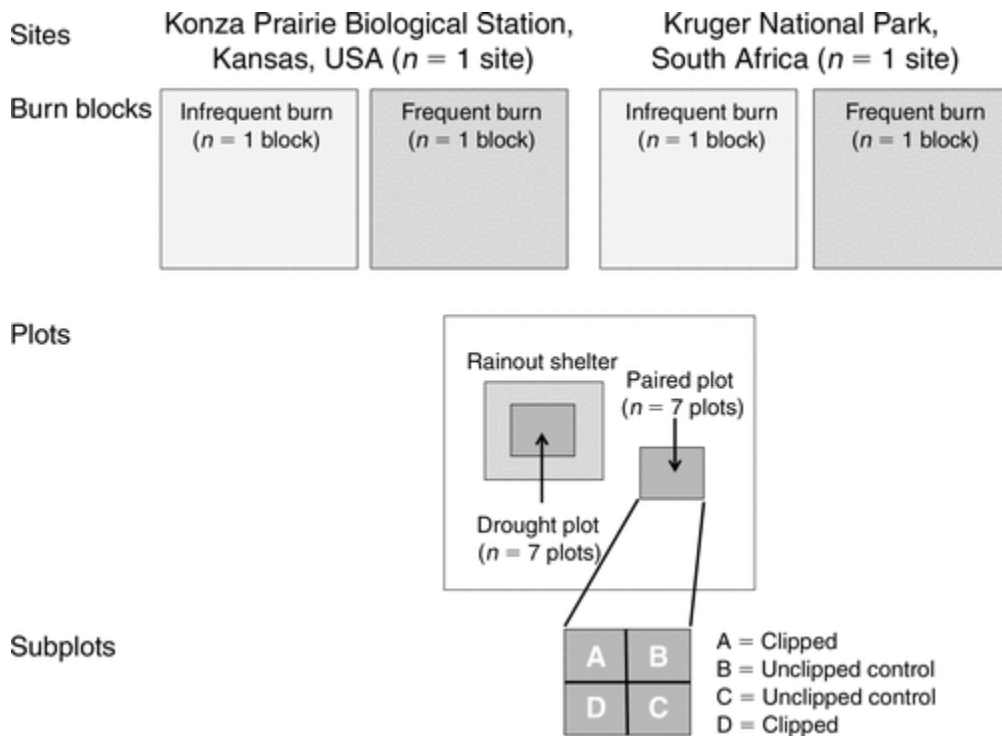

Figure 1. This study occurred at two sites: one in North America (NA) and one in Southern Africa (SA). Within each site, there were two blocks, one burned frequently (annually) and one burned infrequently (4 years in NA and 4–6 years in SA). Each of these four burn blocks (two in NA and two in SA) was analyzed using separate models because no replication occurs within these levels. Within each burn block, there are seven rainout shelters, each with a 1-m^2 permanent drought species-composition plot located under the shelter and a 1-m^2 permanent ambient rainfall species-composition plot located adjacent to the shelter. Finally, each of the 1-m^2 subplots was divided into four 0.25-m^2 subplots, two of which were clipped to simulate grazing and two of which were left unclipped as controls.

Pretreatment species-composition data were collected in December–March 2008 (SA) and June–August 2008 (NA) to confirm the lack of pretreatment differences in community structure between paired plots and drought plots, as well as lack of pretreatment differences among subplots half of which were to be clipped and the other half unclipped. We simulated grazing by clipping all grasses to 5 cm height, leaving the broad-leafed herbaceous species unclipped. Our clipping methods simulated ungulate grazing by selectively clipping the community in a way that mimics the selective consumption of grasses by many grazers (Plumb and Dodd 1993), which is

the most consistent direct effect of large ungulates on the plant community. Each 1-m^2 plot was divided into four 0.25-m^2 subplots, and two subplots were clipped and two remained unclipped. Clipping occurred twice a year at the beginning and middle of the growing season for three years (except the annually burned SA site where the experiment only lasted two years). This grazing simulation represented a moderate grazing intensity for both of these grasslands.

Figure Plate 1. Rainout shelter at Konza Prairie, Kansas, USA, in an annually burned watershed in early spring. Photo credit: S. E. Koerner.

Cover of each plant species rooted in each 0.25-m^2 subplot was visually estimated near the beginning and end of each growing season and 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 the two 0.25-m^2 subplots per plot.

More intensive sampling was performed at the end of the 2011 growing season. A wildfire occurred in the Konza infrequently burned block, eliminating the seventh rainout shelter and creating $n = 6$ replicates for the last year of the study for the infrequently burned Konza block only. Stem density counts for all species were performed in one 20 × 50 cm area in each subplot. Biomass was collected from a separate 0.1-m^2 quadrat nested within each subplot, sorted by growth form as well as live vs. dead tissue, and weighed to determine ANPP. For the clipped plots, biomass from grazing simulations was added to the end-of-season biomass to calculate total ANPP and to determine if grazing compensation occurred. In the frequently burned blocks at both sites, no biomass from the previous year was present due to burning. In the infrequently burned blocks at both sites, all aboveground biomass was clipped, and previous years dead was sorted from current year biomass to obtain ANPP for that growing season. At the end of the growing season, 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 (13 ± 3.7 cm) depending on soil depth. However, sample depths were the same for all paired clipped vs. unclipped plots within a rainout and corresponding ambient plot. Total roots from each core were washed, dried at 60°C, and weighed to determine

belowground biomass. Root biomass was then converted to grams per square meter 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). Each fire frequency and site combination was evaluated with a separate statistical model because we cannot replicate sites. We tested for differences among treatments for diversity (Shannon-Weiner), evenness, richness, grass cover, and forb cover using a split-plot design repeated-measures mixed-model analysis of variance (ANOVA) with clipping within rainfall treatment and both as fixed effects, plot as a random effect, 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 clipping nested within rainfall treatments and both as fixed effects, and rainout and rainout × rainfall treatments as random effects. Early-season and late-season stem density counts were analyzed independently. When main effects or interactions were significant, mean separations were performed using least square means. Satterthwaite degrees of freedom were calculated to correct for unequal variances. Significance was set at $\alpha = 0.05$, and all statistics were generated using SAS (version 9.3; SAS Institute 2011).

Results

North America

In the infrequently burned block, clipping significantly increased diversity (Fig. 2A), richness (Table A1), and evenness on the 0.25-m^2 scale (Table 1). In the frequently burned block, clipping significantly increased diversity (Fig. 2C) and evenness, while drought decreased diversity only in unclipped subplots (Table 1). In both burn frequencies, clipping and drought both decreased grass cover (Fig. 3A and C). In the infrequently burned block, the strength of the clipping effect increased each year of the study with a 26% reduction in grass cover by 2011. Drought decreased grass cover by 10% but only in 2011 (Table 1). Clipping increased forb cover by 32% (Table 1). In the frequently burned block, the strength of the clipping effect also increased each year of the study, resulting in a 36% reduction in grass cover in 2011 (Table 1). Drought significantly decreased grass cover by 7%. Clipping and drought had no effect on forb cover (Table 1).

Early-season stem density for total, grass, and forb stems showed weaker responses to clipping and rainfall compared to late season; therefore, only the late-season stem density data are presented for both NA and SA. In the infrequently burned block, total stem density was affected by drought, clipping, and a drought-by-clipping interaction (Table 2; Fig. 4A). Clipping increased stem density by approximately 57% but only under ambient precipitation. 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 (Appendix B: Table B1). In the frequently burned block, drought decreased total stem density by 24% (Fig. 4B) primarily due to changes in grass stem density. Forb stem density was significantly lower under ambient unclipped conditions compared to either unclipped drought or clipped drought treatments (Table B1).
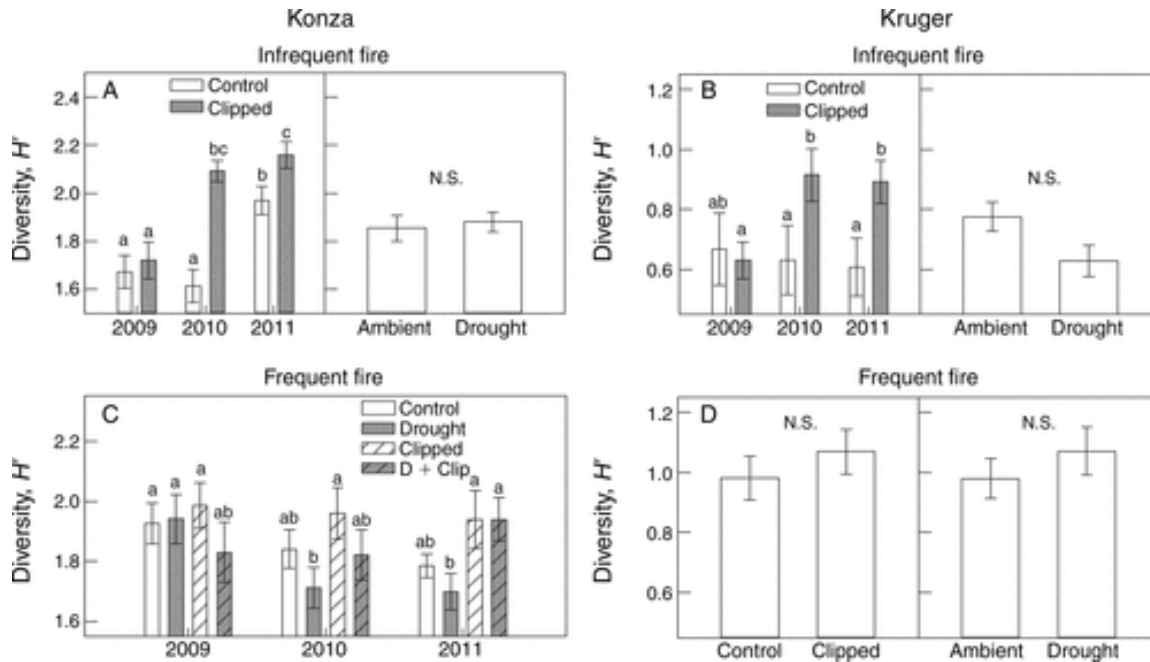
Figure 2. Effects of simulated grazing (control vs. clipped) and precipitation (ambient vs. drought) on plant community diversity (H') at the 0.25-m^2 scale in (A) North American (Konza) infrequently burned, (B) South African (Kruger) infrequently burned, (C) North American frequently burned, and (D) South African frequently burned grassland. Interactions between the simulated grazing treatment, the precipitation treatment, and year or between just the treatments are shown when significant ($P < 0.05$), and significant differences in all panels are denoted by lowercase letters ($P < 0.05$). Error bars represent ±SE. "N.S." stands for not significant.

Figure 3. Effects of simulated grazing (control vs. clipped) and precipitation (ambient vs. drought) on absolute grass cover at 0.25-m^2 scale in (A) North American (Konza) infrequently burned, (B) South African (Kruger) infrequently burned, (C) North American frequently burned, and (D) South African frequently burned grassland. Interactions between the simulated grazing treatment, the precipitation treatment, and year or between just the treatments are shown when significant ($P < 0.05$), and significant differences in all panels are denoted by lowercase letters ($P < 0.05$). Error bars represent ±SE. "N.S." stands for not significant.
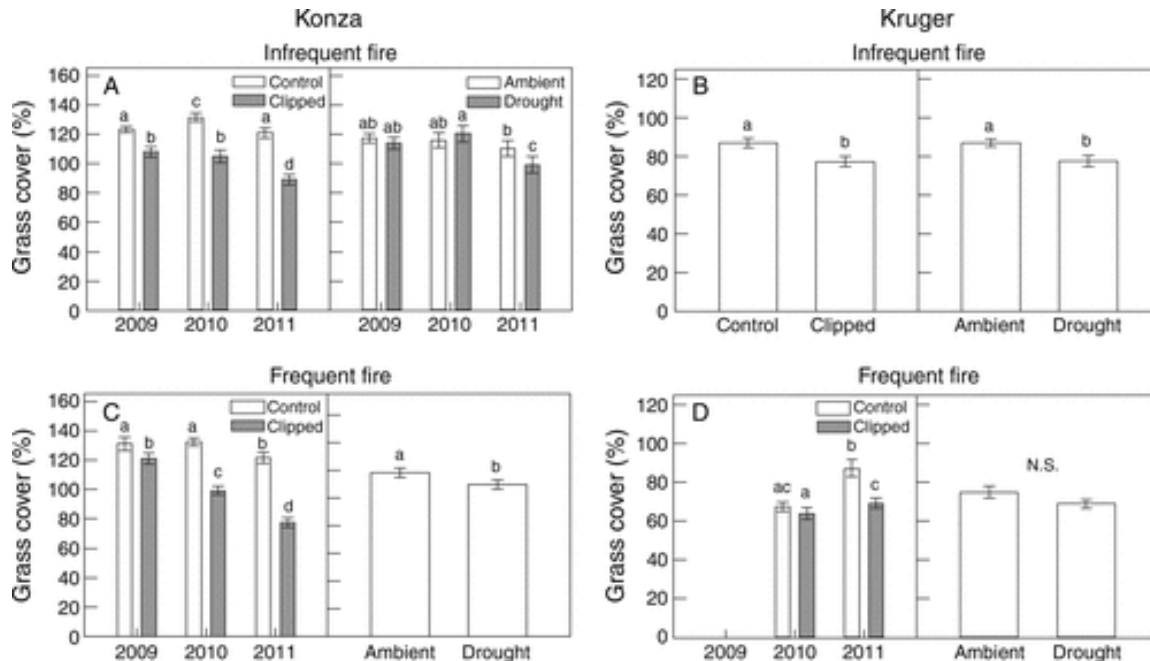
Table 1. Split-plot repeated measures analysis of variance F statistics, with P values in parentheses, for vegetation responses to year (Year, Yr), rainfall treatment (Drought, D), and simulated grazing treatment (Clipping, Clip).

Parameter	df	Diversity	Species richness	Evenness	Grass cover	Forb cover
Infrequent burn block						
Konza						
Year	2, 46	**56.04 (<0.001)**	**15.58 (<0.001)**	**48.08 (<0.001)**	**12.11 (<0.001)**	**21.60 (<0.001)**
Drought	1, 24	0.16 (0.70)	0.00 (0.98)	0.50 (0.49)	0.87 (0.36)	0.61 (0.44)
Yr × D	2, 46	1.98 (0.15)	0.10 (0.90)	2.37 (0.10)	**3.46 (0.040)**	0.92 (0.40)
Clipping	1, 24	**8.63 (0.007)**	**4.61 (0.042)**	**9.99 (0.004)**	**48.92 (<0.001)**	3.95 (0.06)
Yr × Clip	2, 46	**21.51 (<0.001)**	**11.88 (<0.001)**	**11.33 (<0.001)**	**4.31 (0.019)**	**5.47 (0.007)**
D × Clip	1, 24	0.50 (0.83)	0.04 (0.84)	0.06 (0.80)	0.20 (0.66)	0.68 (0.42)
Yr × D × Clip	2, 46	0.65 (0.53)	0.52 (0.60)	0.55 (0.58)	0.06 (0.94)	1.00 (0.38)
Kruger						
Year	2, 48	2.29 (0.11)	**12.24 (<0.001)**	**3.61 (0.035)**	**4.71 (0.014)**	0.01 (0.99)
Drought	1, 24	1.30 (0.27)	0.83 (0.37)	0.53 (0.47)	**6.11 (0.021)**	0.18 (0.68)
Yr × D	2, 48	0.27 (0.76)	1.05 (0.58)	0.48 (0.62)	0.69 (0.51)	0.90 (0.41)
Clipping	1, 24	2.36 (0.14)	3.30 (0.08)	0.70 (0.41)	**5.93 (0.023)**	0.00 (0.98)
Yr × Clip	2, 48	**4.49 (0.016)**	**7.57 (0.001)**	0.15 (0.86)	2.69 (0.08)	**4.51 (0.016)**
D × Clip	1, 24	0.07 (0.80)	0.01 (0.92)	0.00 (0.96)	0.37 (0.55)	0.03 (0.87)
Yr × D × Clip	2, 48	0.37 (0.70)	0.04 (0.96)	0.51 (0.61)	1.77 (0.18)	0.30 (0.74)
Frequent burn block						
Konza						
Year	2, 48	**8.85 (<0.001)**	**15.57 (<0.001)**	**4.76 (0.013)**	**47.95 (<0.001)**	3.03 (0.058)
Drought	1, 24	1.33 (0.26)	1.19 (0.29)	0.74 (0.40)	**6.28 (0.019)**	2.40 (0.13)
Yr × D	2, 48	2.05 (0.14)	0.09 (0.92)	**3.53 (0.037)**	0.46 (0.64)	0.07 (0.93)
Clipping	1, 24	1.76 (0.20)	0.14 (0.71)	3.88 (0.060)	**71.83 (<0.001)**	0.10 (0.76)
Yr × Clip	2, 48	**12.00 (<0.001)**	1.02 (0.37)	**9.20 (<0.001)**	**20.42 (<0.001)**	2.98 (0.060)
D × Clip	1, 24	0.05 (0.83)	0.00 (0.98)	0.17 (0.69)	0.26 (0.62)	0.94 (0.34)
Yr × D × Clip	2, 48	**4.09 (0.023)**	0.50 (0.61)	**4.14 (0.022)**	0.37 (0.69)	2.88 (0.066)
Kruger						
Year	1, 24	**28.86 (0.0001)**	**40.57 (<0.001)**	2.64 (0.12)	**43.26 (<0.001)**	**10.99 (0.0029)**
Drought	1, 24	0.81 (0.38)	0.56 (0.46)	0.05 (0.83)	2.04 (0.17)	2.09 (0.16)
Yr × D	1, 24	0.72 (0.41)	0.04 (0.83)	0.00 (0.97)	0.37 (0.55)	1.11 (0.30)
Clipping	1, 24	0.77 (0.39)	0.04 (0.85)	1.32 (0.26)	**6.61 (0.017)**	1.08 (0.31)
Yr × Clip	1, 24	0.00 (0.99)	0.38 (0.54)	0.15 (0.71)	**14.58 (<0.001)**	0.15 (0.70)
D × Clip	1, 24	0.79 (0.19)	1.26 (0.27)	0.40 (0.53)	0.01 (0.93)	**6.43 (0.018)**
Yr × D × Clip	1, 24	0.28 (0.60)	0.17 (0.68)	0.15 (0.70)	0.10 (0.76)	0.97 (0.33)

Notes: Three years of data were collected at each site except for the Kruger frequently burned block, which has two years of data. All measures and blocks have $n = 7$ replicates except for the Konza infrequently burned block, which has $n = 6$ replicates in the last year due to a wildfire. 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 m^2. Significant values ($P < 0.05$) are shown in boldface type
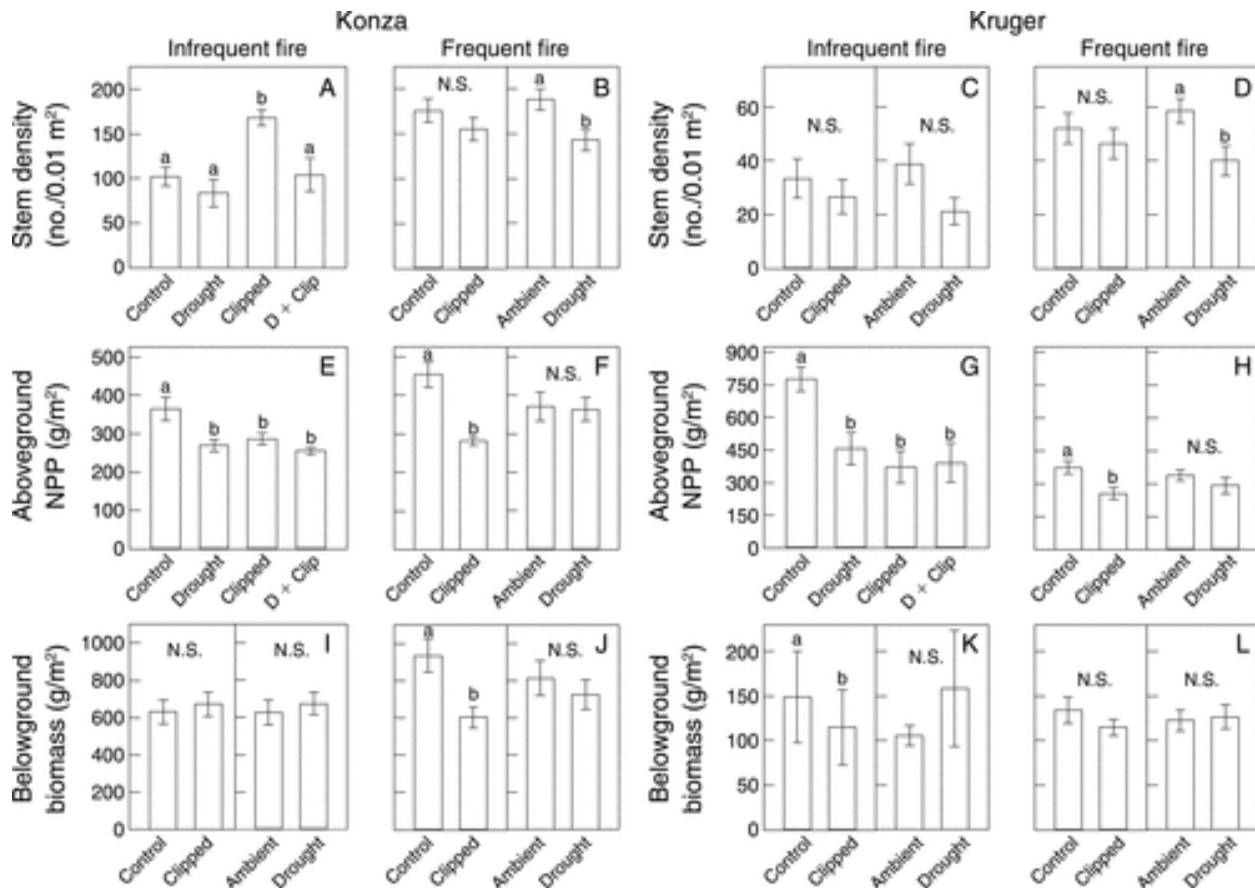
Figure 4. Effects of simulated grazing (control vs. clipped) and precipitation (ambient vs. drought [D]) at the end of the experiment on (A–D) the number of stems per 0.1 m², (E–H) total aboveground annual net primary production (ANPP, g/m²), and (I–L) belowground biomass (g/m²) in the top 10 cm of soil for Konza and the top 20 cm of soil for Kruger for (A, E, I) North American infrequently burned, (B, F, J) North American frequently burned, (C, G, K) South African infrequently burned, and (D, H, L) South African frequently burned grassland. Interactions between the simulated grazing and precipitation treatments are shown when significant ($P < 0.05$), and significant differences in all panels are denoted by lowercase letters ($P < 0.05$). Error bars represent ±SE. "N.S." stands for not significant.

In the infrequently burned block, total ANPP was significantly impacted by drought, clipping, and a drought-by-clipping interaction (Table 2, Fig. 4E). ANPP was ~26% higher under ambient unclipped conditions compared to the other treatments. Belowground biomass was not significantly affected by any treatment (Table 2, Fig. 4I). In the frequently burned block, clipping significantly reduced ANPP by 38% and belowground biomass by 35% (Table 2, Fig. 4F and J). Forb ANPP was <15% of total ANPP in both burn frequencies and was unaffected by either clipping or drought (Appendix B: Table B1). In general, changes in total biomass are driven by changes in grass biomass.

Table 2. Split-plot analysis of variance results testing the effects of the precipitation treatment (Drought, D) and simulated grazing treatment (Clipping, Clip) on total stems per 0.1 m^2, total aboveground annual net primary production (ANPP), and belowground biomass for end of season 2011.

Parameter	Total stems			Total ANPP (g/m^2)			Belowground biomass (g/m^2)		
	df	F	P	df	F	P	df	F	P
Infrequent burn block									
Konza									
Drought	**1, 12**	**5.30**	**0.040**	**1, 10**	**7.24**	**0.023**	1, 5	0.23	0.65
Clipping	**1, 12**	**27.59**	**<0.001**	**1, 10**	**12.90**	**0.005**	1, 10	0.23	0.64
D × Clip	**1, 12**	**7.60**	**0.017**	**1, 10**	**6.27**	**0.031**	1, 10	0.16	0.70
Kruger									
Drought	1, 12	3.65	0.080	**1, 18**	**4.81**	**0.042**	1, 6	0.38	0.56
Clipping	1, 12	0.54	0.48	**1, 18**	**11.63**	**0.003**	**1, 12**	**6.01**	**0.031**
D × Clip	1, 12	1.10	0.31	**1, 18**	**6.07**	**0.024**	1, 12	0.02	0.90
Frequent burn block									
Konza									
Drought	**1, 6**	**7.68**	**0.032**	1, 6	0.05	0.84	1, 24	0.66	0.42
Clipping	1, 12	2.97	0.11	**1, 12**	**31.81**	**<0.001**	**1, 24**	**9.33**	**0.006**
D × Clip	1, 12	4.00	0.069	1, 12	0.57	0.46	1, 24	0.00	0.97
Kruger									
Drought	**1, 6**	**7.39**	**0.035**	1, 12	1.02	0.33	1, 6	0.05	0.84
Clipping	1, 12	0.75	0.40	**1, 12**	**14.68**	**0.002**	1, 12	2.46	0.14
D × Clip	1, 12	1.71	0.22	1, 12	0.89	0.36	1, 12	0.24	0.63

Notes: All measures and blocks have $n = 7$ replicates except for the Konza infrequently burned block, which has $n = 6$ replicates due to a wildfire. Each metric in each site and each burn frequency was evaluated with a separate model. Significant values ($P < 0.05$) are shown in boldface type

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In the infrequently burned block, clipping increased diversity (Fig. 2B) on the 0.25-m^2 scale due to increases in richness (Appendix A: Table A1), while drought had no effect (Table 1; Fig. 2B). In the frequently burned block, neither clipping nor drought affected diversity, richness, or evenness (Table 1, Fig. 2D, Table A1). In the infrequently burned block, grass cover decreased due to both clipping and drought (Table 1; Fig. 3B). Clipping reduced grass cover by 26% in 2010 only, while drought reduced grass cover by 11% regardless of year. In the frequently burned block, grass cover decreased due to clipping, but drought had no effect (Table 1, Fig. 3D). In the infrequently burned block, clipping and drought did not affect forb cover; however, in the frequently burned block unclipped drought plots had higher forb cover than unclipped ambient plots and clipped drought plots (Table 1).

In the infrequently burned block, clipping and drought did not significantly affect total stem density or grass stem density (Table 2, Fig. 4C). Forb stem density was affected by a drought-by-clipping interaction (Appendix B: Table B1) with clipping increasing forb stems but only under ambient precipitation. In the frequently burned block, drought reduced stem density by 32% (Table 2, Fig. 4D). This change was driven by grass stems as forb stems were unaffected by treatments (Table B1).

In the infrequently burned block, total ANPP was significantly affected by drought, clipping, and a drought-by-clipping interaction (Table 2). ANPP was approximately 90% higher under ambient

unclipped conditions than each of the other treatments (Fig. 4G). In addition, clipping reduced belowground biomass by 24% (Table 2, Fig. 4K). In the frequently burned block, clipping reduced total ANPP by 31%, whereas belowground biomass was unaffected by either clipping or drought (Table 2, Fig. 4H and L). Changes in total ANPP in both burn frequencies were driven by changes in grass ANPP as forb ANPP was unaffected by clipping or drought (Appendix B: Table B1).

Discussion

Contrary to our hypothesis, NA and SA grasslands generally responded similarly to simulated grazing, drought, and fire (Table 3). Clipping increased diversity and decreased grass cover, grass ANPP, and belowground biomass at both sites. Drought alone, although occasionally statistically significant, minimally impacted the plant communities in both NA and SA, and we saw similar treatment interactions at the two sites. We also hypothesized that drought would primarily determine production while grazing primarily controlled community composition and structure. This was not supported; instead clipping primarily controlled both productivity and community composition and structure. Drought impacts, when they occurred, were minimal with either lesser or equal impacts compared to grazing and, for ecosystem function (ANPP), drought only had significant effects in the absence of clipping.

Table 3. Summary of results testing the effects of the precipitation treatment (Drought, D) and simulated grazing treatment (Clipping, Clip) on Shannon–Wiener diversity, grass cover per 0.25 m^2, total stems per 0.1 m^2, total ANPP, and belowground biomass for 2011 only.

Metric and treatment	Konza		Kruger	
	Infrequently burned	Frequently burned	Infrequently burned	Frequently burned
Plant community diversity				
Drought	—	↓	—	—
Clipping	↑	↑	↑	—
D × Clip	—	—	—	—
Grass cover				
Drought	↓	↓	↓	—
Clipping	↓	↓	↓	↓
D × Clip	—	—	—	—
Stem density				
Drought	—	↓	—	↓
Clipping	↓	—	—	—
D × Clip	—	—	—	—
ANPP				
Drought	↓	—	↓	—
Clipping	↓	↓	↓	↓
D × Clip	↓	—	↓	—
Belowground biomass				
Drought	—	—	—	—
Clipping	—	↓	↓	—
D × Clip	—	—	—	—

Notes: Up arrows (↑) symbolize that the treatment increased the community or ecosystem metric above the control plot. Down arrows (↓) symbolize that the treatment decreased the community or ecosystem metric above the control plot. A dash symbolizes that the metric was not significantly affected by the treatment.

Grasses, the dominant functional group in both systems, exhibited stronger responses than forbs in both sites. Only grasses were clipped in this experiment, whereas forbs were indirectly manipulated through reduced competition with grasses. Nevertheless, forb cover, ANPP, and stem counts were relatively unaffected by clipping as well as drought. One exception was the change in community diversity, as 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, clipping, and fire.

Clipping impacted grasslands as expected at both sites, increasing diversity while decreasing grass cover and ANPP. Diversity was increased by clipping due to increases in both richness and evenness of forb species. Grazing enhances diversity in grasslands around the world (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). Clipping effects were not noticeably dependent upon site fire history; clipping history, however, was influential, as effects of clipping increased each year.

Clipping also decreased belowground biomass. 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 clipping with no impact from our three-year drought treatment.

Experimentally imposed drought minimally impacted the plant communities in both NA and SA. At frequently burned grasslands in NA, drought decreased diversity and grass cover; however, the positive effects of clipping on diversity were larger than the negative effects of drought. Grass cover and ANPP in infrequently burned grasslands decreased in both sites due to drought, but again, the effects of clipping were of equal or greater magnitude. Unlike clipping, drought effects were consistent across years rather than additive over time. Drought decreased stem density in frequently burned grasslands more than clipping in both NA and SA; however total ANPP was equal in the two rainfall treatments. Grasses compensated by increasing tiller size, creating no net effect on ecosystem function (ANPP) in response to rainfall reductions. The generally limited response to drought has occurred in other studies. Koerner et al. (2013) found lower stem density under increased precipitation variability in annually burned, clipped NA tallgrass prairie. In that study, decreased tiller density was compensated by increased tiller size resulting in no net impact on total ANPP or community diversity. Frank (2007) also showed that ANPP was unaffected by drought in grasslands in Wyoming, USA, regardless of grazing treatment. Together these studies suggest that short-term drought per se has limited impacts on community structure and ecosystem function in mesic grasslands.

Another possible reason the drought imposed by this experiment did not impact the plant community to the extent hypothesized is that the drought was of low severity. At Konza, the

rainout shelters reduced growing-season rainfall approximately one standard deviation (30%) below the long term mean in two of three years. A strong drought only occurred in the third year of the manipulation. At Kruger, growing-season rainfall was never reduced below one standard deviation of the long-term mean. Our treatment created light to moderate drought conditions over multiple years. Although these plant communities likely have been exposed to moderate drought in the past, multiyear droughts are historically uncommon (Weaver 1954, du Toit et al. 2003). Climate change models predict that multiyear droughts may increase in frequency, and our results imply that these grasslands may be relatively resistant to extended moderate drought.

The general lack of interactions between drought and clipping on richness, evenness, diversity, and cover in both infrequently and frequently burned sites was surprising as grazing has been found to increase grassland sensitivity to changes in precipitation (Skinner et al. 2002). In our case the opposite occurred. We saw evidence of decreased sensitivity of ANPP to drought under simulated grazing. With infrequent burning drought decreased ANPP in ungrazed grasslands but not in grazed grasslands in both NA and SA. Grazing buffered these systems to a moderate three-year drought.

Several response variables differed based upon fire history in both NA and SA. Drought decreased diversity only at frequently burned sites. This is not surprising as frequently burned sites are generally functionally dryer than infrequently burned sites (McMurphy and Anderson 1965). However, surprisingly, drought affected ANPP at infrequently burned sites but not at frequently burned sites, likely because 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, neither drought nor clipping affected diversity, richness, evenness, or forb ANPP at frequently burned grassland. This lack of response occurs because forbs are relatively unaffected by disturbance regimes (Uys et al. 2004) and thus they are not directly responding to disturbances themselves, but instead are responding indirectly due to changes in the abundance of dominant grasses.

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 (Olson et al. 1985, Hart et al. 1988, 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. Previous studies typically focused on single-season events, whereas our drought occurred over multiple years. Nevertheless, our results show that the intensity and duration of drought imposed by this experimental manipulation were not the primary drivers of grassland community structure. Instead drought responses were of a similar or lesser magnitude to the effects of grazing and fire. The small-scale responses of grassland structure and function to the interactive effects of clipping, drought, and fire were largely similar in North American and South African grasslands, despite their different evolutionary histories. This suggests that these grasslands exhibit general convergence in many of their responses to common drivers of mesic grassland dynamics.

Acknowledgments

Supplemental Material

Appendix A

Study site information including pictures, a figure of soil moisture decreases due to rainfall exclusion shelters, and a table of species richness values for each site (Ecological Archives E095-009-A1).

Appendix B

Statistical results of split-plot ANOVA for grass and forb ecosystem measurements in response to simulated grazing and precipitation treatments (Ecological Archives E095-009-A2).

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