Rainfall variability has minimal effects on grassland recovery from repeated grazing

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Abstract:

Question: Mesic grasslands experience a complex disturbance regime including frequent fire, grazing by large ungulates and strong inter-annual 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. Increased climate variability is likely to interact with other disturbances, such as grazing, in grassland ecosystems. We investigated the individual and combined effects of increased rainfall variability and grazing on plant community composition, structure and function in an annually burned, native tallgrass prairie. Our overarching question was: are grazing impacts modified under a more variable precipitation regime? **Location:** Konza Prairie, Kansas, USA. **Methods:** Plots were established within a long-term rainfall manipulation experiment in which larger, but less frequent, rain events were imposed during the growing season without altering the total rain amount. We then simulated intense grazing pressure during one growing season by repeatedly clipping all graminoids to 5 cm and monitored recovery over 3 yr. **Results:** Neither grazing nor rainfall treatments affected species richness; however, grazing decreased total and grass above-ground 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 2 yr in the altered rainfall treatment. **Conclusions:** We found that increased rainfall variability had little effect on tallgrass prairie structure and function, while grazing had large effects. Grazing and increased rainfall variability interacted to suppress grass stem density and delayed recovery relative to controls. Although stem density was reduced, individual stem size increased, resulting in no net change in ANPP. This suggests that ANPP in grazed and ungrazed North American tallgrass prairie may be relatively resilient under more temporally variable precipitation regimes.

Keywords: Climate change | Precipitation | Disturbance | Clipping | Stem density | Annual net primary production | Grass–forb interaction | Diversity | Konza

> **Abbreviations**
> RaMPs = Rainfall Manipulation Plots
> ANPP = Above-ground Net Primary Production
> **Nomenclature**
> Great Plains Flora Association = 1986

Introduction

Over the past decades precipitation regimes have become more variable, with longer dry periods and an increase in the number of extreme rainfall events (Min et al. 2011; Smith 2011). These trends are projected to intensify as atmospheric carbon dioxide concentrations continue to rise (Karl et al. 2009). Worldwide, grasslands are experiencing more prolonged droughts and fewer but more intense rainfall events within seasons (IPCC 2012). Because grasslands and savannas cover ca. 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 variable soil moisture patterns (Fay et al. 2011), which reduces above-ground net primary production (ANPP) independent of changes in total annual precipitation (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 ANPP by 10–22% depending on total annual rainfall (Fay et al. 2011). However, changes in rainfall amount and increased rainfall variability minimally impact mesic grassland composition and diversity (Knapp et al. 2002), which are primarily controlled by long-term regional climate (Collins et al. 2012), as well as fire frequency and grazing (Collins 1987; Knapp et al. 1999; Spasojevic et al. 2010; Collins & Calabrese 2012).

Most natural grasslands are grazed either by livestock or native herbivores, both of which influence ecosystem and community dynamics (Gibson 2009). In mesic grasslands, grazers may increase species diversity through selective grazing of the grasses, creating soil disturbances and altering temporal and spatial patterns of nutrient deposition (McNaughton 1985; Collins et al. 1998; Fuhlendorf & Engle 2001). In addition, grazing can lead to both under- and over-compensation (a net decrease or increase in ANPP) in mesic grasslands (McNaughton 1979; Frank et al. 1998) as a function of factors such as soil nutrient availability (Laliberte & Tylianakis 2012).

Despite the ubiquity of grazers, current climate change research in grasslands largely ignores the interaction between climate variation and grazing (Swemmer & 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 (Weaver & Albertson 1936; Coupland 1958), gradients across space (Swemmer & Knapp 2008) or time (Fuhlendorf et al. 2001; Cheng et al. 2011), or non-selective mowing as a proxy for grazing (Bernhardt-Römermann et al. 2011; Walter et al. 2012). These studies demonstrate that grazing and climate

interact to alter diversity, shift dominance and influence productivity; thus, the effects of grazing need to be defined within the context of predicted increases in precipitation variability.

To address this deficiency, we experimentally manipulated rainfall variability and grazing in the Rainfall Manipulation Plots (RaMPs), which were established in 1997 to manipulate rainfall variability in native tallgrass prairie. RaMPs treatments increase rain event size while decreasing event frequency, relative to ambient patterns, without altering the total growing season rainfall (Fay et al. 2000). The result is a more temporally dynamic soil moisture regime, with larger fluctuations between high and low soil water availability (Knapp et al. 2002; Fay et al. 2011). Within this ongoing, long-term experiment, we simulated a year of intense selective grazing and then monitored plant community structure for 2 yr and ANPP for 3 yr under both ambient and more variable rainfall regimes.

Our main objectives were to investigate the individual and combined effects of increased rainfall variability and grazing on plant community structure and ANPP, and to determine if grasslands will be more or less sensitive to severe grazing under an altered climate regime. We hypothesized that: (1) grazing under ambient rainfall patterns would increase plant community diversity with minimal impacts on ANPP, while grazing under altered rainfall would decrease plant community diversity and ANPP due to increased water stress experienced by the dominant grasses (Knapp et al. 2002; Fay et al. 2011); and (2) more variable rainfall patterns would slow the recovery of grassland community structure and ANPP in response to grazing, due to more frequent and intense periods of water stress relative to the ambient rainfall regime.

Methods

Study site

Konza Prairie Biological Station (Konza) is a 3487 ha native tallgrass prairie located in the Flint Hills of northeast Kansas, USA. Perennial C_4 grasses, including *Andropogon gerardii* and *Sorghastrum nutans*, dominate the plant community and account for most herbaceous ANPP (Knapp et al. 1998). Plant species diversity is a function of sub-dominant forb species (Collins & Glenn 1991). The climate is temperate, with mean monthly air temperature in July of 27 °C. Annual precipitation averages 835 mm·yr^{-1}, with ca. 75% falling as rain during the May– September growing season. Variation from average precipitation patterns is common, both in yearly totals and seasonal distribution (Hayden 1998). North American tallgrass prairie evolved under grazing by native herbivores, especially bison (*Bison bison*), which likely played a keystone role in the development of this ecosystem (Knapp et al. 1999).

We utilized the existing RaMPs infrastructure for this study. A set of 12 14 × 9 m fixed-location rainout shelters was established in 1997. Each shelter covers a hydrologically isolated 6 × 6 m sampling plot. Shelters exclude and collect natural rainfall inputs, and collected rainfall is reapplied at either ambient or altered event sizes and frequencies. Fay et al. (2000) provide details on shelter design and efficacy. The RaMPs are located in ungrazed (+30 yr) lowland prairie that has been burned annually (+20 yr) in late March. The dominant plant species in the plots include *A. gerardii*, *S. nutans* and *Panicum virgatum*, all rhizomatous, warm-season, C_4 tall grasses. Dominant perennial forbs include *Solidago canadensis*, *Aster ericoides* and

S. missouriensis. Productivity in the RaMPs has averaged 725 g·m^{-2} with ca. 25% of the productivity being derived from forbs (unpubl. data).

In six RaMPs (the 'ambient' treatment), intercepted rainfall was reapplied to the plots via overhead sprinklers each time a natural rain event occurred in the naturally occurring quantity. To offset the slight increases in soil moisture caused by the rainout shelters, all rainfall application amounts were reduced by 10% from ambient (Fay et al. 2003). Rainfall inputs in the other six RaMPs were experimentally altered to create a more variable rainfall pattern. In the 'altered' rainfall treatment, the dry interval between ambient rainfall events was increased by 50%, thereby decreasing the rainfall event frequency and increasing event size without altering the total growing season rainfall amount.

Experimental manipulation, field methods and data analysis

Using the RaMPs infrastructure, we examined how altered precipitation patterns interacted with grazing to affect the plant community. Under each RaMP, a 2 × 2 m plot was subdivided into four 1 × 1 m subplots in 2007, and pre-grazing treatment data were collected. In 2008, two subplots were subjected to simulated grazing, and two were left as unmanipulated 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 2008 growing season (June–August). Our clipping method mimics the selective consumption of grasses by bison and cattle (Krueger 1986; Plumb & Dodd 1993). The clipped plots will be referred to as the grazing treatment hereafter. Plots were clipped in 2008 only, simulating a temporally dynamic landscape-scale grazing regime (Fuhlendorf & Engle 2001), with 2009–2011 serving as recovery years.

In all subplots, cover of all species was visually estimated to the nearest 1% in June and August of each growing season. Cover data were used to compute grass, forb and total species richness, Shannon–Weiner diversity 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 adjacent 1-m^2 subplots per RaMP. At the end of each of the five growing seasons, all above-ground biomass was collected from one 0.1 m^2 plot nested within each subplot, sorted by growth form and weighed to determine above-ground 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-m^2 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 above-ground biomass was collected.

Each RaMP was treated as an experimental unit, with all measured responses reported here based on the average value of the two subplots in each RaMP. We tested for differences among treatments in species diversity and richness, grass, forb and total ANPP, and grass, forb and total stem densities. Species diversity was calculated using H' = $-\sum p_i \ln p_i$, where p_i is the relative cover of species *i*. All responses and all years were analysed separately using split-plot design mixed-model ANOVAs (v.9.3; SAS Institute, Cary, NC, US). Early season and late season stem density counts were analysed independently. Because early season stem density for total, grass

and forb stems showed similar or weaker trends as late season (Table 2), only late season 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

From 2007 to 2011, growing season rainfall averaged 406 ± 40 mm (Fig. S1a), well below the long-term average. In the ambient plots, rain fell on ca. 32 d each growing season, creating an average rain event size of 13 mm, with a mean of 5 d between events. In the altered rain treatment, rain was applied on ca. 14 d each growing season, creating an average rain event size of 30 mm, with a mean of 11 d between events. The number of days in which plants experienced a soil volume water content (VWC) below 13% (equal to -1.5 MPa) increased from 17 to 21 d in the altered rainfall treatment (Fig. S1b). The rainfall treatments resulted in significant differences among years in growing season mean soil moisture (Fig. S1c). Under ambient rainfall, mean annual growing season soil moisture ranged from 17% to 32% (Av. = $26 \pm 2\%$). The altered rainfall treatment decreased seasonal average soil moisture and increased soil moisture variability in 2008 (Fig. 1) and 2009 (Fig. S1c,d).

Plant responses

Despite 10 yr of altered rainfall treatments, species diversity, richness and ANPP were not significantly different prior to the grazing treatment (Table 1). In addition, during the treatment year and first year of recovery, the rainfall and grazing treatments had no significant effect on plant species richness (Table 1). In 2011, however, species richness was significantly higher in the grazed treatments under ambient rainfall. In 2008, the year in which clipping occurred, species diversity was highest in the grazed, ambient rainfall treatment (Fig. 2).

Table 1. Split-plot ANOVA F-statistic (P-value) for vegetation responses to ambient and altered rainfall regimes in grazed and ungrazed tallgrass prairie. Each vegetation response was evaluated with a separate model for each year. Specific vegetation responses were total species richness and Shannon diversity (m^{-2}), and grass, forb, and total ANPP ($g \cdot m^{-2}$)

| Year	Parameter	Total Richness	Diversity	Grass ANPP	Forb ANPP	Total ANPP
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	–	–	5.62 (0.039)	4.30 (0.065)	0.04 (0.847)
2011	Grazing	–	–	57.69 (<0.001)	0.89 (0.367)	37.09 (<0.001)
2011	Rainfall*Grazing	–	–	0.40 (0.540)	0.58 (0.465)	1.42 (0.261)
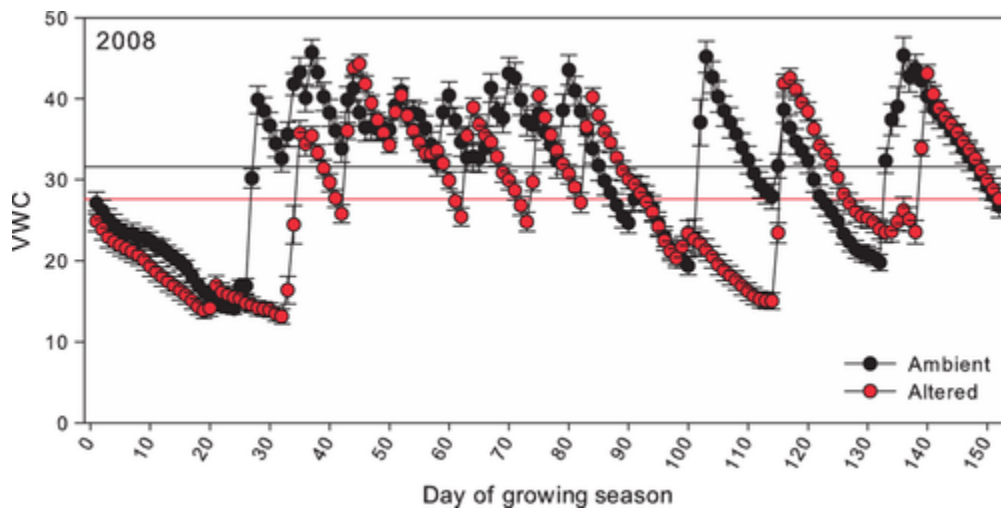
Figure 1. Daily soil volumetric water content (VWC) for 0–15 cm for the 2008 growing season (1 May–30 Sept) for the ambient (black dots) and altered (red dots) rainfall treatment with the mean growing season VWC for the ambient (black line) and altered (red line) rainfall treatments as reference lines. This was the year in which grazing occurred.
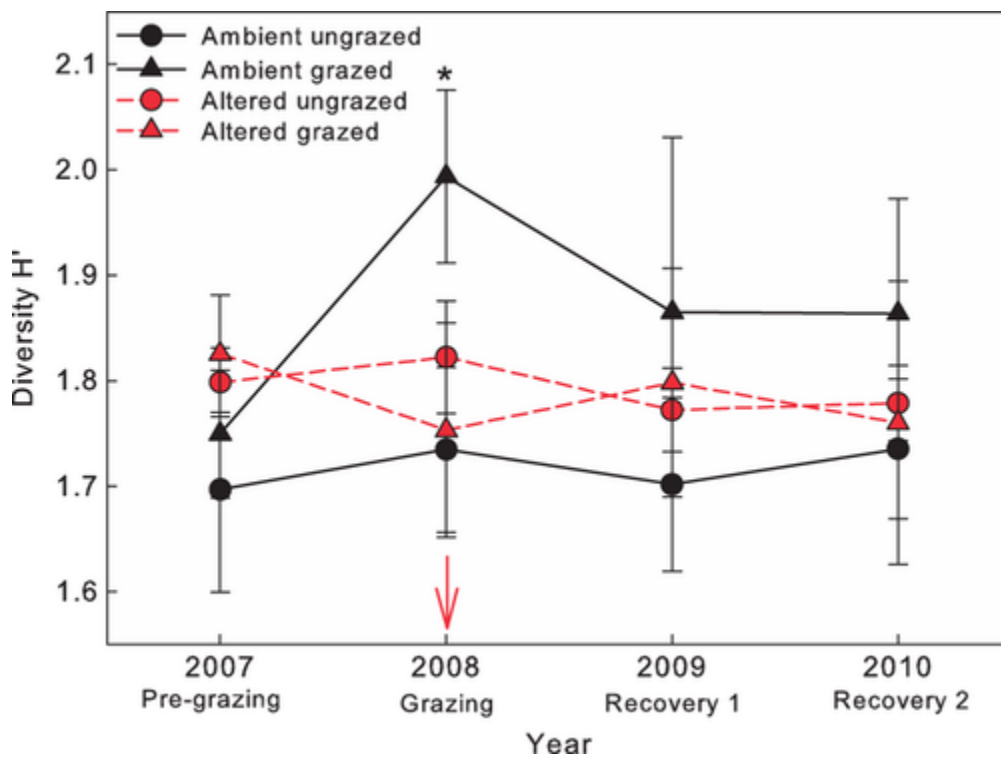

Figure 2. Plant species diversity (Shannon–Weiner) (1 m^{-2}) for ambient (black with solid lines) and altered rainfall treatments (red with dashed lines) in ungrazed (circles) and grazed (triangles) tallgrass prairie. The 4 yr of data correspond to pre-grazing treatment in 2007, grazing treatment in 2008 (red arrow), recovery year 1 in 2009 and recovery year 2 in 2010. Significant differences within each year are denoted by "*". Error bars represent ±1 SE. See Table 1 for split-plot ANOVA results for each year.

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, total ANPP in the grazed treatment remained 39%, 37% and 42% below control values (Fig. 3a). Furthermore, in the ungrazed plots in 2009, the altered rainfall treatment significantly reduced total ANPP by 19%. Grazing significantly reduced grass ANPP (Table 1). In 2008 (grazing year), grazing decreased grass ANPP by 43%. In the recovery years, grass ANPP in the grazed treatment remained 93%, 78% and 74% below control values (Fig. 3b). Altered rainfall also decreased grass ANPP by 31% in 2011, but no significant interaction with grazing occurred. Grazing significantly increased forb ANPP during the grazing year (57%) and in the first year of recovery (78%) (Table 1), but by 2010 and 2011, forb ANPP was not significantly affected by the grazing treatment (Fig. 3c).
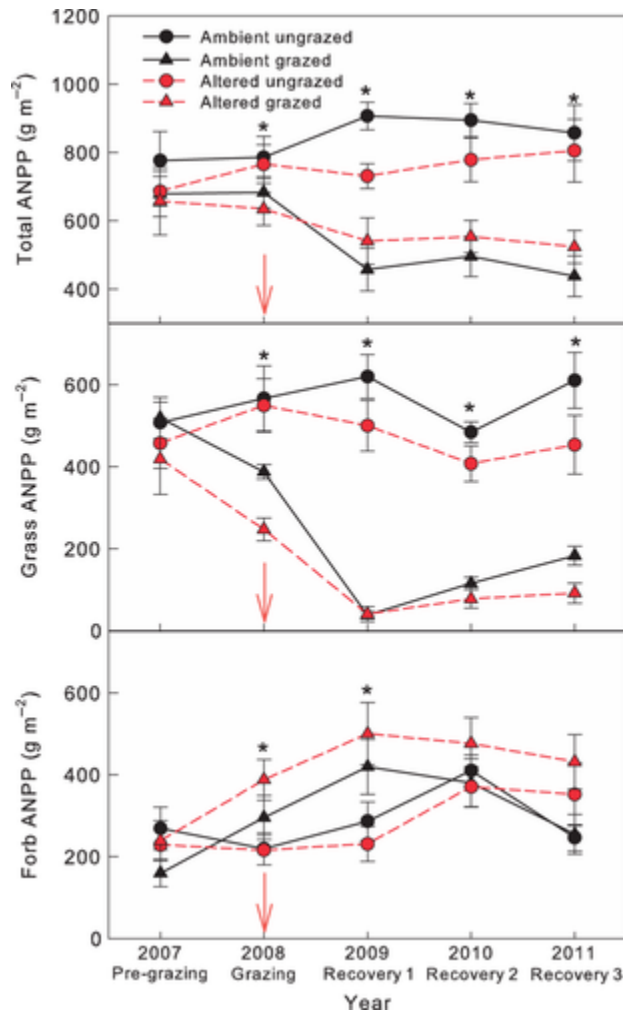

Figure 3. (**a**) Total, (**b**) grass and (**c**) forb annual net primary production (ANPP) for ambient (black with solid lines) and altered rainfall treatments (red with dashed lines) in ungrazed (circles) and grazed (triangles) tallgrass prairie. The 5 yr of data correspond to pre-grazing treatment in 2007, grazing treatment in 2008 (red arrow) and recovery years 1–3 (2009–2011). Significant differences within each year are denoted by "*". Error bars represent ±1 SE. See Table 1 for split-plot ANOVA results for each year.

Table 2. Split-plot ANOVA F-statistics (P-value) for grass, forb and total stem densities responses to ambient and altered rainfall regimes in grazed and ungrazed tallgrass prairie. 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 ($0.1~\text{m}^{-2}$)

| 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)
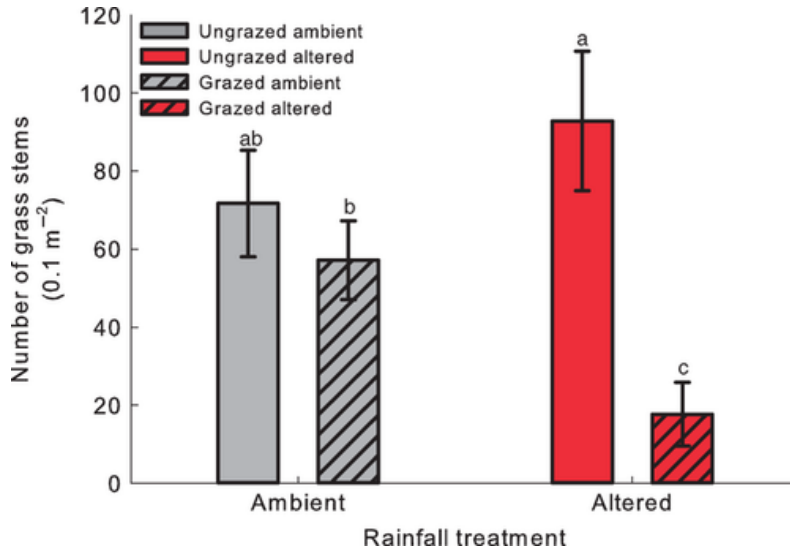
Figure 4. Number of grass stems for late season 2010 in ambient (grey) and altered (red) rainfall treatments in ungrazed (solid) and grazed (hashed) tallgrass prairie 2 yr following the grazing treatment. Letters denote significant differences between the treatments ($P \leq 0.05$). Error bars represent ±1 SE.

Late season total stem density showed similar patterns in 2009 and 2010 (Table 2); thus, 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 SE stems; ungrazed: mean = 81 ± 13 stems), while in the altered rainfall plots, grazing reduced stem density by 67% (grazed: mean = 34 ± 8 stems; ungrazed: mean = 103 ± 17 stems). The decrease in total stem density was driven primarily by a decrease in grass stem density. 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% (Fig. 4). 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 ± 1 and 11 ± 2 for grazed and ungrazed plots, respectively.

Discussion

We found that altered rainfall regime alone had no impact on plant community structure, yet repeated simulated grazing throughout 2008 altered community structure and ANPP for 3 yr after grazing occurred (Figs 2 and 3). As predicted, grazing under ambient rainfall patterns increased plant community diversity, a widely documented response in mesic tallgrass prairie (Damhoureyeh & Hartnett 1997; Knapp et al. 1999; Towne et al. 2005; Collins & Smith 2006). However, grazing under ambient conditions did not have the predicted minimal impact on grass ANPP. Instead, grazing reduced grass ANPP during the treatment year by >40% and increased forb ANPP regardless of the rainfall treatment.

Compensation or over-compensation can occur if grazing increases resource availability (Turner et al. 1993). Defoliation increases light and potentially soil moisture availability by reducing transpiring leaf area. In addition, grazing can increase soil N availability via root mortality, along with faecal and urine deposition (Frank & Groffman 1998), a mechanism not mimicked by clipping. Nevertheless, under-compensation occurred in our study, which is a common response under repeated moderate to heavy defoliation in tall and mid-height grasses (Holland & Detling 1990; Knapp et al. 2012). For example, Woodis & Jackson (2008) found that clipping *A. gerardii* monthly throughout the growing season caused a ca. 70% decrease in production. Preferred forage species like *P. virgatum* and *A. gerardii* decrease under heavy grazing or if plants are not allowed adequate recovery time between defoliation events (Vinton & Hartnett 1992; Vinton et al. 1993). Mousel et al. (2003) found that grazing in August after a June grazing event decreased basal cover of *A. gerardii*. They recommended a grazing system with a minimum 40-d rest period to maintain a viable population of *A. gerardii*. Our simulated grazing treatment included a 30-d rest period with an August grazing event following grazing in June and July, a grazing regime from which these grasses were unable to recover.

The grazing effects carried over in the following years, even though no further grazing occurred. 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 & Hartnett (1992) found that *A. gerardii* tillers that had been grazed repeatedly in 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 below-ground biomass (Biswell & Weaver 1933; Hartnett 1989).

Carbon limitation may explain the long-term (3 yr) decrease in grass ANPP due to a single year of severe grazing. Although the response of below-ground biomass to grazing varies globally (Pandey & Singh 1992; Milchunas & Lauenroth 1993; McNaughton et al. 1998; Frank et al. 2002), studies from Konza have found that grazing decreases below-ground biomass (Vinton & Hartnett 1992; Turner et al. 1993; S. E. Koerner and S. L. Collins, unpubl. data),

likely due to reallocation of resources above-ground to compensate for shoot removal. Therefore, repeated grazing may have depleted below-ground reserves in the grasses, leaving individuals unable to accumulate enough carbon to replenish above-ground tissue. The presence of grazers has been shown to decrease bud banks (Archer & Detling 1984; Vinton & Hartnett 1992) resulting in fewer tillers in the following year (Dalgleish & Hartnett 2006). In addition, repeated grazing or clipping has been shown to alter root:shoot ratios in *A. gerardii*, eventually leading to lower mycorrhizal root colonization (Hetrick et al. 1990). 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 tiller biomass in subsequent seasons.

Grass stems were less dense in the altered rainfall plots that were grazed, but not in the grazed ambient rainfall plots. Reduced overall carbon gain from grazing would be exacerbated by low soil moisture, and might result in grasses producing fewer buds and ultimately fewer stems (Dalgleish & Hartnett 2009). Even though fewer grass stems were found in the altered plots, grass biomass was equal in the two rainfall treatments. Grasses compensated by increasing tiller size, creating no net effect on ecosystem function in response to grazing–rainfall interactions. Similar results were found in a semi-natural planted meadow in Germany, where mowing neither buffered nor amplified the adverse effect of rainfall variability on productivity (Walter et al. 2012). Thus, grass tiller size compensates for reduced tiller number following severe grazing.

Forbs benefitted from the decreased abundance of the dominant grasses in the grazing treatment. Forb abundance and richness are generally negatively correlated to ANPP and grass cover in tallgrass prairie (Hartnett & Fay 1998; Collins & Calabrese 2012). In addition, altered rainfall may not have impacted the forbs as strongly as the grasses. The forbs in this grassland are primarily cool season C_3 species, which have been shown to exhibit niche differentiation in timing and soil water use strategies (Weaver 1954; Nippert & Knapp 2007). Many forbs initiate growth early in the spring, with maximum growth occurring from mid-March to early June (Weaver 1954). In our experiment, the two treatments had similar soil moisture levels in early spring, as the manipulation does not begin until approximately mid-April, and treatments diverge gradually as the rainfall manipulation is imposed. The dominant grasses, on the other hand, are warm season C_4 species that begin active growth later in the spring and continue growing through early autumn, with maximum biomass produced in mid-summer (Weaver 1954) when soil moisture differences between the treatments are maximized. Forbs may also avoid competition for water with C_4 grasses by utilizing deeper water sources when this resource is limiting and leaf water stress is high (Nippert & Knapp 2007).

Grazing decreased grass ANPP by over 40% and increased forb ANPP by almost 60%, and these effects persisted for 2 yr 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, although 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, altered rainfall patterns slow recovery of grass stem density, with little effect on grassland ecosystem function. Overall, we found grazing had a much stronger influence on grassland productivity and structure compared to increased precipitation variability, and that both grazed and ungrazed grasslands were resilient to more variable precipitation regimes.

Acknowledgements

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Supplementary Information
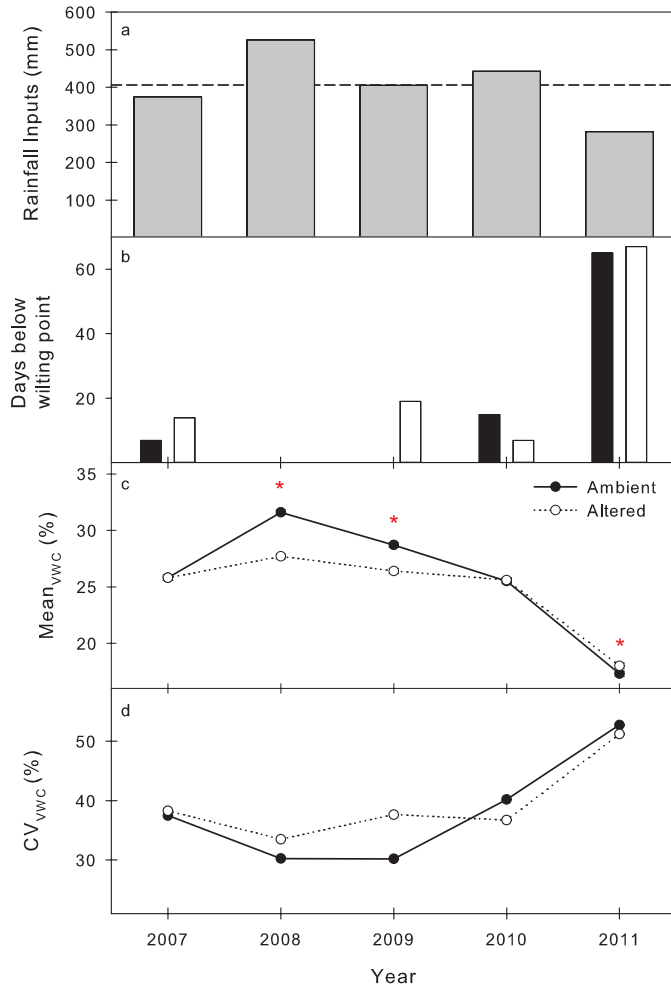
Fig. S1. Environmental effects from rainfall treatments. The five years of data correspond to pre-grazing treatment in 2007, grazing treatment in 2008, and recovery years 1-3 (2009-2011). a) Growing season rainfall and five year average during the study period (black dashed reference line). b) Number of days below -1.5 MPa for the ambient (black bars) and the altered (white bars) rainfall treatments (13% soil volume water content) (Zeglin et al. unpublished data). c) Mean soil volumetric water content (VWC) for 0-15 cm for the ambient (filled symbols solid line) and altered (open symbols, dotted line) rainfall treatments. Red asterisks indicate significant differences ($p<0.05$) between the treatments within a year. Mean soil moisture was significantly

11   decreased (F=54.52, p<0.0001) by the altered rainfall treatment across all years, but rainfall

12   treatment significantly interacted with year, yielding a significant decrease in soil VWC in only

13   two out of the 5 years. However, these were two of the focal years of the study – the grazing

14   treatment year and the first year of recovery. c) Coefficient of variation (standard error/mean) of

15   mean soil VWC for 0-15 cm for the ambient (filled symbols, solid line) and the altered (open

16   symbols, dotted line) rainfall treatments. Again the grazing treatment year and the first recovery

17   year has the strongest increase in soil moisture variability.