Frequency and Extent of Water Limitation to Primary Production in a Mesic Temperate Grassland

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ABSTRACT

The frequency and extent of water limitation to aboveground net primary production (ANPP) in a mesic grassland in NE Kansas (Konza Prairie, USA) was assessed with an 8-year irrigation experiment. Since 1991, transects spanning upland and lowland sites in annually burned, ungrazed tallgrass prairie were provided with supplemental water to satisfy evapotranspirational demands. This protocol minimized water limitations during the growing season, as well as interannual variability in water stress. Irrigation of this mesic grassland increased ANPP in 6 of 8 years by an average of 26% when compared to control transects. Although interannual variation in ANPP was greater in uplands than lowlands at nominal levels of precipitation, reducing interannual variability in water availability via irrigation eliminated topographic differences; the irrigation protocol also reduced interannual variability in ANPP by as much as 40%. The addition of supplemental water enabled us to extend the relationship

INTRODUCTION

Worldwide, net primary productivity in grasslands is constrained, to some extent, by water limitations in both temperate and tropical regions (Deshmukh 1984; Boutton and others 1988; Le Houerou and others 1988; Silvertown and others 1994; Briggs and Knapp 1995). Across the Great Plains of North America, there is a clear west–east gradient of inbetween annual precipitation and ANPP in grasslands to precipitation levels (average, 1153 mm; maximum, 1346 mm) similar to those experienced by more mesic grasslands that today exist only as remnants several hundred kilometers east of Kansas. This relationship was linear $(r^2 = 0.81)$, with maximum ANPP (738 g/m²) similar to values reported for sites in Illinois and Wisconsin. After 8 years of irrigation, production of the C3 forb component was twice that in control sites. These results indicate that water limitations in grasslands at the western edge of the presettlement extent of tallgrass prairie affect ANPP in most years and that this high frequency of water limitation may lead to greater dominance of the C₄ grasses than is seen in more eastern grassland sites.

Key words: *Andropogon gerardii*; C₄ grasses; forbs; grassland; irrigation; leaf water potential; primary production; tallgrass prairie; water limitation.

creasing precipitation and corresponding increases in primary production from the shortgrass steppes to the tallgrass prairies of the central United States (Sala and others 1988; Epstein and others 1998). At this regional scale, variation in annual precipitation can account for most of the spatial variability in productivity ($r^2 = 0.90$), (Sala and others 1988).

Within a grassland type, strong water limitation to productivity has been demonstrated, as expected, in the semi-arid shortgrass steppes of Colorado (Lauenroth and Sala 1992). At the eastern end of the precipitation gradient, however, in the more productive C_4 -dominated grasslands, higher annual

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rainfall amounts combined with nutrient and canopy light limitations may reduce the importance of water limitation to productivity (Briggs and Knapp 1995; Knapp and others 1998b). Indeed, Briggs and Knapp (1995) found no relationship between precipitation and productivity in tallgrass prairie sites protected from fire, perhaps due to the accumulation of detritus that shades emerging shoots and increases soil water availability (Knapp and Seastedt 1986). In burned sites, however, a significant precipitation–productivity relationship exists in both lowland and especially upland sites with shallow soils (Briggs and Knapp 1995).

Most grassland regions have inherently variable climates (Frank and Inouye 1994), and predicted changes in climate (rainfall amount, distribution or interannual variability), (Jones and others 1999; Plummer and others 1999) are likely to have strong impacts on temporal patterns of grassland productivity. By indirectly altering the availability of water, increases in atmospheric CO₂ are also expected to affect productivity, even in C₄-dominated grasslands (Knapp and others 1993; Owensby and others 1996, 1999). Because of the high temporal variability inherent in ecological processes in grasslands (Risser and others 1981; Knapp and others 1998c), short-term studies often lead to different conclusions from long-term experiments (Seastedt and Knapp 1993; Knapp and others 1998a). Unfortunately, past experimental manipulations of water availability in tallgrass prairie have been of short duration (Owensby and others 1970; Knapp 1984b) and have concluded that water limitations may be important in some years but not others. Clearly, a more robust assessment of the degree that water availability limits ecological processes under present climatic conditions is needed before predictions can be made about responses to future climatic scenarios.

Therefore, we established a long-term irrigation experiment in annually burned tallgrass prairie in 1991 (Knapp and others 1994) to assess the frequency and extent of water limitation to primary production in this grassland. Annually burned prairie was selected because of the historical role played by fire in this ecosystem (Axelrod 1985) and because frequent fire is necessary to eliminate forest encroachment (Bragg and Hulbert 1976; Knight and others 1994), reduce the number of exotic species (Smith and Knapp 1999), and maintain the biotic integrity of tallgrass prairie (Leach and Givnish 1996). Herein we present the responses of this system to the initial 8 years of supplemental water to address the following questions:

- 1. In what proportion of years does supplemental water (sufficient to minimize soil and plant water deficits) result in increased ANPP in tallgrass prairie relative to ambient precipitation?
- 2. Although interannual variability in ANPP is high in grasslands (Frank and Inouye 1994; Briggs and Knapp 1995), what proportion of this variability can be attributed to interannual variability in water availability? In other words, what is the degree of interannual variability in ANPP when water limitations are minimized by irrigation?
- Does the relationship between precipitation 3. and ANPP asymptote at high precipitation levels? This information is lacking because most of the remaining tallgrass prairie left in North America is at the western (drier) portion of this grassland's original extent (Samson and Knopf 1994), and comparative estimates of ANPP from the more mesic eastern tallgrass prairies are rare (Ehrenreich 1959; Old 1969; Peet and others 1975). Thus, extending the relationship between ANPP and precipitation to include precipitation levels more characteristic of eastern prairies (more than 1000 mm) will enable simulation models to predict responses more accurately in the remaining tracts of tallgrass prairie.
- How will a long-term increase in water avail-4. ability affect C₃ forb productivity? Forbs (primarily C₃ dicots) represent only a small proportion of ANPP in tallgrass prairie but account for a large proportion of plant species diversity (Turner and Knapp 1996; Collins and others 1998). Forbs, as C₃ dicots with greater water requirements than C₄ grasses, might be expected to increase in abundance and productivity as water limitation decreases. Indeed, more mesic eastern prairies have been described as being very diverse and species-rich in forbs (Havercamp and Whitney 1983; Reznicek and Maycock 1983). However, forb productivity has been negatively correlated with grass production in tallgrass prairie (Briggs and Knapp 1995), and if grass production increases in response to irrigation, forb productivity may decrease.

MATERIALS AND METHODS

Research was conducted at the Konza Prairie Biological Station (39°05′ N, 96°35′ W), a 3487-ha native (unplowed) tallgrass prairie site representative of the 50,000-km² Flint Hills region of eastern Kansas (Knapp and others 1998c). Konza Prairie

has a typical midwestern continental climate with warm wet summers and cold dry winters. Mean annual air temperature (30-year average) is 12.8° C with an average annual precipitation of 835 mm, but interannual climatic variability is high (Borchert 1950). The flora of Konza Prairie is dominated by warm season (C_4) grasses, including *Andropogon gerardii* and *Sorghastrum nutans* (Freeman 1998).

A long-term irrigation experiment was initiated at Konza Prairie in 1991. Details of the site and experimental protocol have been described previously (Knapp and others 1994), but briefly four parallel transects (alternating irrigated and control transects) span upland and lowland topographic positions. Each transect is approximately 140 m in length, and the topographic gradient from uplands to lowlands is approximately 7 m.

At 10-m intervals along each irrigation transect, 1.0-m tall high-impact rotating sprinkler heads (16 per transect) deliver water in a 30-m diameter circle. The maximum rate at which water can be applied is 8-mm/h in a 6-m wide strip centered on the line of sprinklers. This strip is where soil and plant responses are measured. Water is supplied to the irrigation transects from a groundwater well and storage reservoir.

Irrigation was scheduled to maintain the sum of ambient rainfall and supplemental water to satisfy estimated actual evapotranspiration (ET) during the growing season (May-September). Reference ET was estimated by a Penman combination equation (Lamm and others 1987) with input from a weather station located 8 km distant and a precipitation gauge within 200 m of the transects. Irrigation events typically occurred over a 2-day period, and uplands and lowlands were irrigated on consecutive days. Water was added in the early morning when winds are reduced. An average of about 25 mm was added to either uplands or lowlands in a given irrigation event. During very hot (air temperatures higher than 35°C) dry periods of the summer, as much as 50 mm of supplemental water was applied each week. The overall operational goal of the irrigation protocol was to maintain soil water (averaged from 0 to 30 cm) above 0.25 cm³/cm³ volumetric content throughout the growing season. This level of soil moisture typically corresponds to predawn leaf water potentials greater than 0.5 MPa in A. gerardii (Knapp and others 1994).

The site of the irrigation transects has been burned annually in April since 1991 (the site was burned intermittently prior to the initiation of the experiment) and has not been grazed by large ungulates for more than 20 years. Soils along the transects are silty clay loams (Ransom and others 1998), with finer textured soils with reduced infiltration rates in the lowlands (Knapp and others 1994). There are 14 sampling stations along each irrigated and control transect corresponding to the sprinklers on the irrigated transects (end sprinklers are not sampled). Five sites are at upland topographic positions, three at hillside sites, and six in the lowland. Only data from upland and lowland sites are presented.

Two estimates of water availability in irrigated and control transects were made each year. At each sampling station, soil moisture was measured at 1-2-week intervals with a time domain reflectometry (TDR) system using 15- and 30-cm rods (Topp and others 1980). Two pairs of rods were measured at each station. Midday (1300 h) leaf water potentials of the dominant grass, A. gerardii, were also measured at 10-day intervals each year. During the first 3 years of the experiment, mature leaves (n =7) were collected at each sampling station and stored in a humidified chamber; leaf water potential was then determined in a pressure chamber (PMS model 2000; PMS Inc., Corvallis, OR, USA). In the last 5 years of the study, sampling intensity was reduced to two upland and two lowland stations on each transect (n = 28 per treatment).

End-of-season (September) aboveground biomass harvests were used to estimated ANPP. Because the site is burned each spring (prior to plant growth), aboveground biomass represents the current year's production (Briggs and Knapp 1995). At each sampling station, all aboveground biomass was harvested in four 0.1-m² quadrats, sorted into graminoid and forb components, and oven-dried prior to weighing.

Statistical significance of responses within years was determined with ANOVA; irrigation treatment, topographic position, and transect were used as main effects. To assess overall effects of irrigation, we used repeated measures ANOVA because the transect locations were the same for each year. Linear regression analyses were used to relate long-term ANPP patterns to precipitation. All statistical analyses were performed using SAS procedures (Proc UNIVARIATE, Proc MIXED, and Proc REG) (SAS 1997). Statistical significance is expressed at $\alpha = 0.05$.

RESULTS

During the 8 years of the experiment, ambient annual precipitation levels at Konza Prairie varied almost twofold from 636 mm in 1991 to 1227 mm in 1993. The 8-year average annual precipitation



was 853 mm, a figure quite similar to the 30-year mean of 835 mm. The coefficient of variation (CV) of precipitation during this period was 24%; this figure is similar to the long-term (30-year) CV of 27% and is also typical of grasslands in the central United States (Knapp and others 1998c). The amount of supplemental water varied inversely to actual rainfall amounts; for example, 469 mm was added in 1991, whereas 85 mm was added in 1993. The 8-year average amount of supplemental water added to meet estimated evapotranspirational losses in this grassland was 299 mm. The total amount of water available to plants on the irrigation transects (ambient plus supplemental) varied from a low of 977 mm in 1994 to a high of 1346 mm in 1995. Interannual variation in total water inputs was caused by differences in air temperature, humidity, and the timing of ambient rainfall events. The 8-year average total water input to the irrigation transects was 1153 mm.

At Konza Prairie, air temperatures peak and growing season rainfall is lowest in July and August (Hayden 1998), so the greatest estimated ET demand occurred in these months. Thus, most irrigation was done at this time, and the maximum differences in soil moisture between control and irrigated transects were recorded during this period (Figure 1). Figure 1. Representative example (1996) of the seasonal dynamics of soil moisture (0-15 cm) along irrigated and control transects in annually burned tallgrass prairie. Each point is the mean of measurements from 10 upland and 12 lowland sites from replicate irrigated and control transects. Maximum differences in soil moisture between treatments occurred in most years from mid- to late summer. when frequent irrigation events (open bars, bottom panel) were necessary to meet the evapotranspirational demands of this grassland. The solid bars indicate natural rainfall events.

Effects of Topographic Position

In most years, ANPP was greater in upland control sites than in lowland sites (Figure 2); mean upland ANPP was about 10% higher (Table 1). However, irrigation resulted in equal ANPP in both uplands and lowlands (Table 1). It significantly increased ANPP in 6 of 8 years in uplands and 7 of 8 years in lowlands (Figure 2). Overall, irrigation increased ANPP by an average of 22% in uplands and 31% in lowlands.

As expected in annually burned grassland, ANPP was strongly related to precipitation in both upland and lowland sections of control transects (Figure 3). Although ANPP was similar in uplands and low-lands in years with average (835 mm) or less than average rainfall, during wet years ANPP was substantially higher in uplands than in lowlands (Figure 3). Moreover, both the range and CV of ANPP over the 8-year period was greater for uplands than lowlands (Table 1). Irrigation substantially reduced the range of ANPP and particularly the CV for uplands.

Transect Level Responses

When data from upland and lowland sites were combined, irrigation increased ANPP by an average



Figure 2. Responses in aboveground net primary production (ANPP) to irrigation in upland and lowland tallgrass prairie sites in NE Kansas over an 8-year period. Solid bars (bottom panel) indicate annual precipitation for control sites; open bars indicate rainfall plus supplemental water added via irrigation. Error bars denote ± 1 standard error of the mean (n = 10 sites in uplands and 12 in lowlands); * indicates significant differences (P < 0.05) between irrigated and control ANPP.

of 26% during the experiment, and statistically significant increases were detected in 6 of 8 years (Figure 4). Indeed, the relationship between precipitation and ANPP for all data combined was linear, robust, and showed no tendency toward reaching an asymptote (Figure 5). The maximum amount of precipitation input to this grassland (1346 mm, 61% above the 30-year average) led to an increase in ANPP to 738 g/m², or 50% above the control average of 491 g/m².

In 6 of 8 years, average midday leaf water potentials in *A. gerardii* were significantly lower in control than in irrigated plants (Figure 4). But overall differences in seasonal means were small (0.17 MPa) over the 8-year period. Despite these small differences, leaf-level measures of plant water status in *A. gerardii* provided two important insights into the degree of water limitation to ANPP in this grassland. First, leaf water potential measurements on individual dates were rarely lower than –1.9 MPa in the irrigation transect (data not shown). This is important because at leaf water potentials below –2.0 MPa, net photosynthesis in *A. gerardii* decreases rapidly to less than 50% of maximum (Knapp and others 1993). Second, seasonal differences in water potential, though small, had substantial power in predicting responses in ANPP to irrigation (Figure 5), reflecting the sensitivity of growth processes to small changes in leaf-level plant water status.

Finally, forb ANPP was similar in both irrigated and control transects at the beginning of the experiment (Figure 6), but annual burning led to a 53% reduction in forb ANPP in the control sites after 8 years. Conversely, no reduction in forb ANPP was evident along irrigated transects. In 5 of the last 6 years of the study, forb ANPP was significantly increased by irrigation (Figure 6). Similar patterns were evident when uplands and lowlands were analyzed separately (data not shown).

DISCUSSION

The grasslands of the Flint Hills of eastern Kansas represent the largest remaining tract of unplowed tallgrass prairie in North America (Samson and Knopf 1994; Knapp and others 1998c). Konza Prairie lies at the mesic end of the west-east precipitation gradient across the central grassland region, but it is near the xeric edge of the presettlement extent of tallgrass prairie. The increase in precipitation inputs to the irrigation transects (8-year average, 1153 mm) essentially placed these sites under an annual precipitation regime that was more similar to that experienced by the presettlement (and extant remnant) prairies at the same latitude in Indiana and Ohio. Thus, this irrigation experiment can provide us with some insight into the range of water limitation that may have occurred historically across the tallgrass prairie region.

Results from this experiment are presented separately for upland and lowland sites and then combined into a transect-level response for these sites. Although focusing on topographic position would provide more information, there are two reasons for our choice of a transect-level approach. First, the upland sites at this location have relatively deeper soils than most upland sites on Konza Prairie, which tend to have shallow rocky soils (Schimel and others 1991). Perhaps as a result of the deeper, well-drained soils in the uplands in this study, ANPP was about 10% higher in upland control transects than in lowlands. By contrast, the longterm average of upland ANPP at annually burned sites on Konza Prairie is about 28% lower than in lowland sites (Briggs and Knapp 1995). A 10%

Soil	Mean (SE)	CV	Max (SE)	Year	Min (SE)	Year
Up	514.9 (9.82) ^b	18.13	698.0 (34.99)	1993	376.8 (12.07)	1997
Low	466.6 (8.13) ^c	11.23	530.1 (23.50)	1993	330.2 (23.21)	1991
Up	628.8 (9.84) ^a	8.86	738.2 (25.97)	1995	542.0 (20.57)	1997
Low	614.0 (10.00) ^a	9.25	675.0 (24.16)	1998	474.4 (23.58)	1992
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Table 1. Summary of Responses in Aboveground Net Primary Production (ANPP) at Sites along Irrigation and Control Transects in Tallgrass Prairie for the Period 1991–98

CV = coefficients of variation of ANPP for the 8-year period. Years indicate when maximum and minimum ANPP occurred. Means are shown in g/m² for upland and lowland soils with standard errors in parentheses.

Different letters (a, b, c) after mean values indicate significant differences (P < 0.05).



Figure 3. The relationship between aboveground net primary production and annual precipitation for upland and lowland sites in control (nonirrigated) transects in tallgrass prairie. Both relationships were significant (P < 0.05), but they diverged at high levels of precipitation.

reduction in lowland ANPP at the irrigation site relative to other lowland sites on Konza Prairie (Briggs and Knapp 1995) may also have contributed to this atypical (inverse) pattern of upland/ lowland productivity. Thus, a topographic approach could be misleading because the uplands at the irrigation study site may not be representative of the surrounding grassland.

The second reason for combining data from both topographic positions was that average control ANPP at the transect level (491 g/m²) was similar to the long-term average of ANPP from annually burned upland and lowland sites across Konza Prairie (480 g/m²) (Knapp and others 1998b). Thus, transect-level ANPP at the irrigation site is representative of watershed-level ANPP for Konza Prairie.

The first of the four objectives of this study was to determine how often growing-season rainfall limits ANPP in this grassland. Our expectation was that water limitations to productivity would be much



Figure 4. Responses in aboveground net primary production (ANPP) (top panel) to irrigation (upland and lowland sites combined) in NE Kansas tallgrass prairie. Solid bars (middle panel) denote annual precipitation for control sites; open bars denote rainfall plus supplemental water added via irrigation. The bottom panel shows average midday leaf water potential (Ψ) in A. gerardii in irrigated and control transects (upland and lowland sites combined). Mean values (± 1 SE) over the 8-year period are in parentheses; * indicates significant differences (P < 0.05). Error bars in the top panel denote ± 1 standard error of the mean; bars are smaller than the symbols in the bottom panel.

less pronounced in tallgrass prairie than in semiarid grasslands, where it is likely that water is limiting every year (Lauenroth and Sala 1992). However, when supplemental water was applied to minimize water deficits in this mesic grassland,



Figure 5. Relationship between aboveground net primary production (ANPP) in tallgrass prairie and annual precipitation inputs (PPT) (top panel). Data are from both irrigated and control transects over an 8-year period, with upland and lowland sites combined for each treatment. Linear model: ANPP = 154.5 + 0.405 PPT. The bottom panel shows the relationship between the difference in ANPP for the irrigated and control transects (upland and lowland sites combined) and the difference in seasonal average midday leaf water potential (Ψ) in *A. gerardii* for irrigated and control transects. Linear model: Δ ANPP = 49.9 + 568.7 $\Delta \Psi$.

ANPP increased in 6 of 8 years at the transect level (7 of 8 years in the lowlands) (Figures 2 and 4). Thus, despite well-documented limitations of light (Knapp 1984a) and nitrogen (N) (Seastedt and others 1991; Blair 1997) to ANPP in this grassland, water appears to limit (or at least colimit) annual productivity 75% of the time. Annually burned tallgrass prairie is very sensitive to N addition (Blair 1997). The extent to which increased N availability, due to greater N mineralization in irrigated sites, interacted with increased moisture to contribute to this production response remains to be evaluated.

Our second objective was to estimate the proportion of interannual variability in ANPP that can be



Figure 6. Responses in aboveground net primary production (ANPP) of forbs (C_3 dicots) to irrigation (upland and lowland sites combined) in NE Kansas tallgrass prairie over an 8-year period; * indicates years in which forb production was significantly greater (P<0.05) in irrigated sites than in control sites.

attributed to variability in water availability. This was assessed by comparing the temporal CV for irrigated and control transects. Irrigation reduced interannual variability (CV) in ANPP to less than half the level of control ANPP in uplands, with smaller reductions of the CV in lowlands (Table 1). This finding is consistent with the stronger relationship between precipitation and ANPP in uplands vs lowlands noted in this study (Figure 3) as well as in previous analyses (Briggs and Knapp 1995). Overall, a comparison of the temporal variation in ANPP in control (CV = 14.8%) and irrigated (CV = 9.0%) sites suggests that interannual differences in water availability may account for as much as 40% of the temporal variability in ANPP in annually burned tallgrass prairie. The remaining variability may be due to interannual variations in nutrient availability, temperature, growing-season length, solar radiation, and other climatic factors that have been related to production in this grassland (Risser and others 1981). There are no comparable data on interannual variability from more mesic (eastern) prairies to contrast with the CV for irrigated transects. However, ANPP in irrigated transects (mean, 621 g/m²; maximum, 738 g/m²) was well within the range of ANPP measured in Illinois and Wisconsin $(513-865 \text{ g/m}^2)$ (Old 1969; Peet and others 1975). Thus, it is likely that the interannual variability in ANPP was historically lower in more mesic tallgrass prairies further to the east.

A third objective was to extend the ANPP-precipitation relationship to include higher precipitation levels than normally occur in NE Kansas. Both increases in precipitation and atmospheric CO₂ can lead to improved water relations in grasslands (Owensby and others 1996); therefore, extending this relationship has predictive value. But extrapolating the relationship between present-day precipitation amounts and ANPP will lead to erroneous predictions if the relationship is nonlinear and asymptotes. Lauenroth and Sala (1992) constructed a regional (linear) relationship between annual precipitation and ANPP that predicted an increase of 60 g/m^2 per 100 mm increase in precipitation. The linear relationship from this irrigation study predicts a lesser increase in ANPP ($40 \text{ g/m}^2 \text{ per } 100 \text{ mm}$ precipitation); (Figure 5). This discrepancy is consistent with the findings of Lauenroth and Sala (1992), who concluded that regionally based relationships between ANPP and precipitation will overestimate responses at a single site. Of course, these predictions are contingent on the continued dominance of C₄ grasses and the lack of substantial changes in plant community composition.

As a fourth objective, we addressed plant community changes and increased water availability. In shortgrass steppe, irrigation led to dramatic shifts in plant species composition (Lauenroth and others 1978) in a relatively short period of time. In our study of tallgrass prairie, we focused on responses in the C_3 forbs because they are a critical component of plant species diversity (Turner and Knapp 1996; Collins and others 1998). Forbs typically comprise only about 10% of the biomass in annually burned prairie, and plant diversity is lower in these sites than in those burned less frequently (Knapp and others 1998c). But our results suggest that forb ANPP may increase in response to greater water availability (Figure 6). The temporal decrease in forb ANPP in control sites reflects the shift in fire regime from less frequent burning to annual fire. Such a reduction in forbs might be expected if there is direct fire-induced mortality of some forb species (Briggs and Knapp, forthcoming). However, in 5 of the last 6 years, forb ANPP was significantly higher in the irrigation transects. If one of the mechanisms by which C_4 grasses outcompete the C_3 forbs is related to their higher water use efficiency (Knapp and Medina 1999), then an increase in the success of C₃ plants would be expected in wetter sites. Overall, plant species richness was also higher in irrigated than control transects in each of the last 5 years (data not shown). These results are consistent with the view that more mesic grasslands have greater forb biomass.

In summary, an 8-year assessment of the frequency and extent of water limitation to ANPP in annually burned grassland indicated that water limits ANPP 75% of the time by an average of 26%. This mesic grassland was quite responsive to changes in water availability across a broad range of precipitation levels, and it was even more responsive to changes in leaf water status of the dominant species, A. gerardii (Figure 5). Indeed, as much as 40% of the characteristically high interannual variability in ANPP in this grassland may be attributed to interannual differences in precipitation. Finally, a long-term increase in water availability led to a significant increase in C₃ forb biomass relative to sites experiencing only nominal rainfall. This finding suggests that the forb-rich remnant prairies at the eastern edge of the distribution of tallgrass prairie may be a product, in part, of higher levels of water availability. Conversely, greater water limitations in grasslands at the western edge of the presettlement extent of tallgrass prairie may lead to greater dominance of the C₄ grasses than is seen in more eastern grassland sites. The overall sensitivity of ANPP to the manipulation of water availability in this mesic grassland indicates that predicted changes in climate will have a directly measurable impact on grasslands throughout the Great Plains.

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