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Productivity responses to altered rainfall patterns in a C₄-dominated grassland

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Abstract Rainfall variability is a key driver of ecosystem structure and function in grasslands worldwide. Changes in rainfall patterns predicted by global climate models for the central United States are expected to cause lower and increasingly variable soil water availability, which may impact net primary production and plant species composition in native Great Plains grasslands. We experimentally altered the timing and quantity of growing season rainfall inputs by lengthening inter-rainfall dry intervals by 50%, reducing rainfall quantities by 30%, or both, compared to the ambient rainfall regime in a native tallgrass prairie ecosystem in northeastern Kansas. Over three growing seasons, increased rainfall variability caused by altered rainfall timing with no change in total rainfall quantity led to lower and more variable soil water content (0–30 cm depth), a ~10% reduction in above-ground net primary productivity (ANPP), increased root to shoot ratios, and greater canopy photon flux density at 30 cm above the soil surface. Lower total ANPP primarily resulted from reduced growth, biomass and flowering of subdominant warm-season C₄ grasses while productivity of the dominant C₄ grass *Andropogon gerardii* was relatively unresponsive. In general, vegetation responses to increased soil water content variability were at least equal to those caused by imposing a 30% reduction in rainfall quantity without altering the timing of rainfall inputs. Reduced ANPP most likely resulted from direct effects of soil moisture deficits on root activity, plant water status, and photosynthesis. Altered rainfall regimes are likely to be an important element of climate change

scenarios in this grassland, and the nature of interactions with other climate change elements remains a significant challenge for predicting ecosystem responses to climate change.

Keywords Climate change · Konza Prairie · Net primary productivity · Precipitation · Soil moisture

Introduction

Climate is a major factor controlling the structure and function of grassland ecosystems worldwide. In North America, grassland distribution and composition are determined primarily by regional temperature and rainfall gradients, soils, land use, and land management practices (Sala et al. 1988; Epstein et al. 1997; Hoch et al. 2002). Interannual variability in rainfall quantity affects productivity more in grasslands than in all other biomes in North America (Knapp and Smith 2001). Climate model predictions driven by expected increases in greenhouse gases suggest increased growing season drought and less frequent, but more energetic convective weather systems for Central Plains ecosystems (Groisman et al. 1999; Easterling et al. 2000). Such changes would result in larger per event rainfall inputs separated by longer dry intervals, which would be expected to lower the mean and increase the variability in soil water content compared to ambient rainfall patterns.

Grasslands are likely to exhibit strong and rapid structural and functional responses to these altered growing season rainfall patterns, even if mean soil moisture remains unchanged, because of inherent lags in plant responses to varying soil moisture conditions (Pearcy 1990; Wraith and Wright 1998), decreases in leaf photosynthetic carbon gain and water status (Volk et al. 2000; Fay et al. 2002) and altered resource pools and fluxes (BassiriRad et al. 1999). These underlying mechanistic responses may lead to shifts in community composition (Küchler 1974), and reduced net primary productivity (Silvertown et al. 1994; Briggs and Knapp

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1995). Many studies have examined net primary productivity in grasslands in relation to regional rainfall gradients (Lane et al. 1998), interannual variability in rainfall (Silvertown et al. 1994; Briggs and Knapp 1995), and seasonal rainfall distributions (Reynolds et al. 1999; Svejcar et al. 1999; Weltzin and McPherson 2000). Fewer studies have addressed the importance of the within growing season temporal distribution of rainfall events and per event rainfall amounts (Seagle and McNaughton 1993; Knapp et al. 2002).

We established a long-term rainfall manipulation experiment in a mesic tallgrass prairie known to be responsive to changes in water availability (Knapp et al. 2001; Knapp and Smith 2001) to evaluate the effects of growing season rainfall quantity versus within-season rainfall distribution on soil water content variability, aboveground plant productivity, belowground plant biomass, and cover of grasses and forbs. Because grasslands comprise 36% of terrestrial land cover (Sala 2001), their responses to altered rainfall patterns may have important consequences for global patterns of productivity and diversity under future climate scenarios.

Materials and methods

This study was conducted in the Rainfall Manipulation Plot (RaMPs) facility at the Konza Prairie Biological Station (KPBS) in the Flint Hills of northeastern Kansas, USA (39°05'N, 96°35'W). The vegetation of Konza Prairie consists of productive, perennial warm-season C₄ grasses and a diverse group of C₃ forbs (Freeman 1998). This region of the Central Plains experiences a temperate mid-continental climate, with a mid-growing season (July) mean temperature of 27°C (range 20 to 33°C), and mean annual precipitation of 835 mm year⁻¹. Mean growing season (May through September) rainfall totals 635 mm, with the driest period during July and August.

The RaMPs facility consists of 12 plots each located beneath a 14×9 m fixed-location rainout shelter covered during the growing season by a clear polyethylene roof. The shelters exclude natural rainfall from the plots and divert the excluded rainfall to storage tanks for experimental application using overhead sprinklers. Each shelter covers a 6×6 m sampling plot enclosed within a 7.6×7.6 m perimeter sheet metal barrier extending 0.1 m above ground to exclude overland flow and 1.1 m deep to limit lateral subsoil water movement (Fay et al. 2000).

The RaMPs are located on a typical lowland prairie site in terms of soil, vegetative composition, productivity, and land management. Soils are Irwin silty clay loams. The dominant grass species in the plots is *Andropogon gerardii*, accompanied by subdominant grasses *Sorghastrum nutans*, *Panicum virgatum*, and *Sporobolus heterolepis*, all warm season C₄ tallgrasses. Common forbs include *Solidago canadensis*, *Aster ericoides*, and *Salix missouriensis*. The plots and their surroundings have been burned each spring in late March. Frequent fire was historically common in this grassland and today is a preferred management practice (Knapp et al. 1998).

Four experimental rainfall treatments were implemented in 1998, each with three replicates. The treatments were factorial combinations of two growing season rainfall quantities (100% or 70% of natural ambient rainfall amounts) combined with two within-season temporal distribution patterns (ambient or altered rainfall timing), as follows.

Ambient

Each time a natural rainfall event occurred, the quantity of rain that fell was immediately (within 24 h) applied to the plots, replicating the naturally occurring rainfall regime.

Reduced quantity

Seventy percent of each naturally occurring rainfall event was applied immediately following the rain event.

Altered timing

Rainfall was accumulated and not applied until a dry interval 50% longer than the ambient dry interval had been imposed. Rainfall accumulated during the lengthened dry period was then applied as a single large event. The amount of rainfall applied in this treatment was identical to ambient, only the event size and temporal distribution of inputs was altered.

Reduced quantity and altered timing

Inter-rainfall dry intervals were lengthened by 50%, and only 70% of the accumulated rainfall was applied, which imposed both drought and altered temporal distribution of rainfall inputs.

Experimental rainfall applications were within 4% of target quantities, which were based on the ambient rainfall measured at on-site rain gauges. This incorporated naturally occurring interannual variability into the treatments, to avoid the need for supplemental water from domestic sources during dry years, with different chemistry than natural rainfall and to permit the use of unsheltered control plots to assess shelter effects. Shelter effects were reported previously (Fay et al. 2000); primary effects are reduced photosynthetic photon flux density (PPFD; 20% at midday), 1.2°C increased nighttime soil temperature (5 cm depth) caused by reduced nighttime re-radiation, a 17% increase in seasonal soil moisture, but no significant difference in aboveground net primary productivity (ANPP; 1998–2000 combined) in ambient treatment plots compared to unsheltered controls.

For the purposes of this study, our aim was to characterize soil moisture variability in the upper 30 cm of the soil profile, where most (75%) of the root biomass is located in this and many other ecosystems (Jackson et al. 1996). Soil water content was calculated from weekly time domain reflectometry measurements recorded with a Tektronix cable tester and paired 30 cm stainless steel rods permanently inserted at four locations per plot (Topp et al. 1980). Vertical profiles of PPFD were determined weekly during the 2000 growing season. Sampling was conducted at midday (1200–1400 hours CDT) on clear days at 10 cm increments in the canopy using a 1 m ceptometer (Decagon, Pullman, Wash., USA).

ANPP was estimated annually by harvesting all aboveground biomass from ten 0.1 m² samples per RaMP in mid October. Since the plots were burned each spring and ungrazed, all aboveground biomass represented the current year's production. Samples were sorted into grasses and forbs, and in 1999 and 2000 the dominant warm season grass (*Andropogon gerardii*) was separated from the other grass species. Woody species comprised <2% of the aboveground biomass and were omitted from the analysis. All biomass components were dried at 65°C for at least 48 h prior to weighing. Plant community composition was assessed twice (May and August) each year by visual estimation of percent cover for each species present in four contiguous 1-m² subplots in a 2×2 m portion of each RaMP reserved for this purpose.

Root biomass was sampled during the winter following the 2000 growing season. Three 2.5 cm diameter cores per plot (minimum depth 1 m) were extracted using a hydraulic corer (Geoprobe 540 M Geoprobe, Salina, Kan., USA). The cores were divided into 10 cm increments, and the roots extracted by agitating the increments for 48 h in a 5% aqueous sodium metaphosphate solution to dissociate

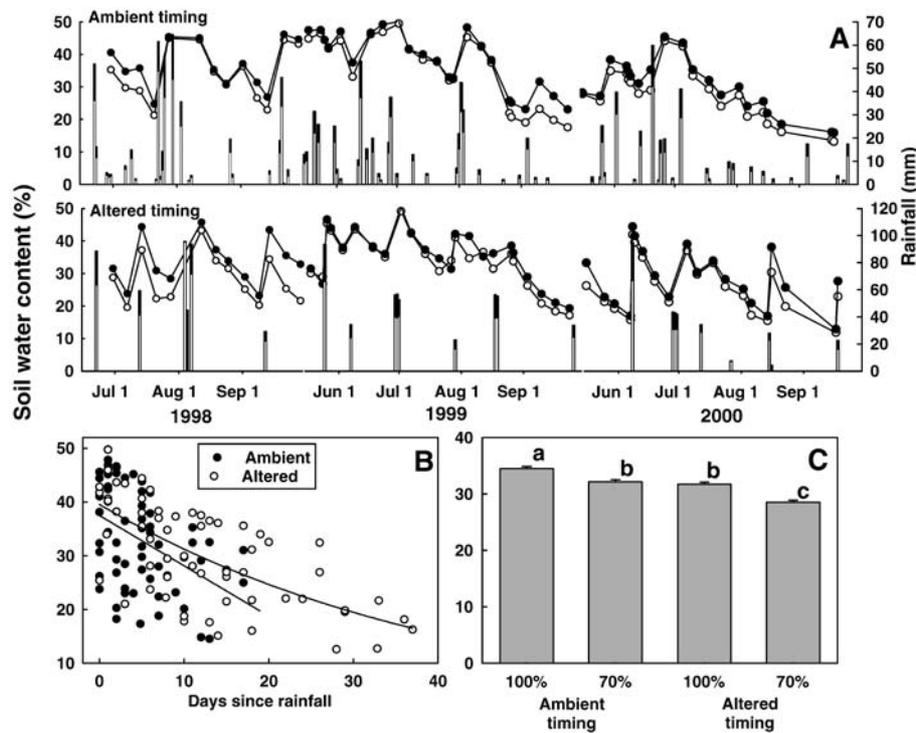


Fig. 1A–C Soil water content variability and means in the Rainfall Manipulation Plots for the 1998–2000 growing seasons. **A** Growing season time course of experimental rainfall inputs (bars) and soil water content (lines and symbols; 0–30 cm). Closed symbols and bars treatments receiving ambient rainfall quantities; open symbols and bars treatments receiving reduced rainfall quantities. The maximum sample date standard error in soil water content was

4.92%, during May 2000. **B** Soil water content versus dry interval length under ambient rainfall timing ($r^2=0.16$, $P=0.0008$) and altered rainfall timing ($r^2=0.45$, $P<0.0001$). **C** Three-year mean (\pm SE across sample dates) soil water contents by treatment. Significant terms from ANOVA: quantity $F_{1,8}=55.03$; timing $F_{1,8}=72.85$; both at $P<0.0001$

soil particles, followed by wet sieving. The washed roots were dried at 65°C to constant mass and weighed. Preliminary analyses found no treatment differences in root depth profiles, so the increment data were pooled for further analysis.

Each sheltered plot was an experimental unit, so sample date, treatment, and growing season means for all response variables were calculated and analyzed using plot mean values in mixed model ANOVAs. Rainfall manipulations were fixed effects, sample date or year were repeated measures. Means separations were performed using t -tests of least squares means.

Results

The 1998 growing season was slightly wetter (694 mm) than the long-term average, while below-average rainfall characterized the growing seasons of 1999 (519 mm) and 2000 (410 mm). In total, the ambient rainfall pattern during the three growing seasons produced 79 rainfall events, averaging 15.6 mm, with temporal variability similar to the natural long-term ambient rainfall pattern (CV =312%, SD =9.5 mm day⁻¹, 15-year SD for KPBS =8.9 mm day⁻¹). The altered timing treatment reduced the number of events (24), and increased their mean size (49.7 mm) and temporal variability (CV =449 and 480% for altered and altered/reduced, respectively).

Rainfall manipulations caused several consistent changes in soil water dynamics during each growing

season. The ambient rainfall pattern produced generally high soil water contents through May, June, and early July each year (Fig. 1a), followed by declining soil water contents through August and early September, when rain fell less frequently and temperatures reached their growing season maxima. When rainfall quantities were reduced but applied at ambient timing, the temporal pattern in soil water content closely tracked that of the ambient treatment (Fig. 1a), with expected reductions in mean soil water content on individual sample dates. In contrast, in the altered timing treatments, soil water content exhibited strong peaks after experimental applications, followed by pronounced declines during the lengthened dry intervals (Fig. 1a, b). The seasonal mean soil water content declined by 8% in the altered timing treatment, almost identical to the reduction in mean soil water content in the reduced quantity treatment (Fig. 1c) even though the altered timing treatment received 100% of the ambient rainfall quantity. When rainfall timing was altered and quantities reduced, temporal variation in soil water content remained high (Fig. 1a) and the 3-year mean soil water content was 17% below ambient (Fig. 1c).

ANPP was reduced by rainfall manipulations, with the 3-year mean total ANPP reduced by 10% (~75 g/m²) below ambient by both the reduced quantity and the

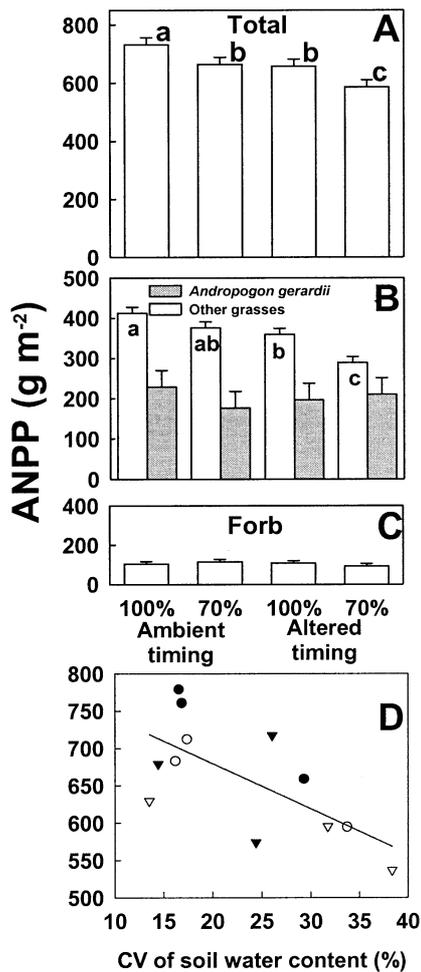


Fig. 2A–D Above net primary productivity (ANPP) in the RaMPs. **A** Mean total ANPP for 1998 through 2000, \pm SE (across years). Significant ANOVA terms: quantity $F_{1,8}=8.07$, $P=0.0218$; timing $F_{1,8}=9.67$, $P=0.0145$. **B** Graminoid ANPP from *Andropogon gerardii* and other graminoids (mostly C_4 grasses, see text); other graminoids quantity $F_{1,8}=13.20$, $P=0.0067$; timing $F_{1,8}=22.71$, $P=0.0014$. **C** Forb ANPP. **D** Mean total ANPP separated by treatment and year versus the CV of July soil water content. $r^2=0.40$, $P=0.015$

altered timing treatments (Fig. 2a). As with soil water content, the reduced quantity and altered timing treatments were additive, together causing a 20% decrease in total ANPP. The maximum reduction in ANPP in response to rainfall manipulations (165 g m^{-2}) occurred in the combined treatment in 2000, the driest year of the study. Mean ANPP separated by treatment and year was negatively correlated with July soil water variability ($r^2=0.40$, $P=0.015$, Fig. 2d). Higher soil water variability in the altered timing treatments was also associated with a 35% higher ratio of root mass to peak shoot mass ($P=0.03$, Table 1).

Canopy PPFD at 30 cm above the soil surface increased over ambient with rainfall manipulations (Fig. 3a). In mid-July, PPFD in the ambient timing treatments abruptly decreased, suggesting rapid biomass

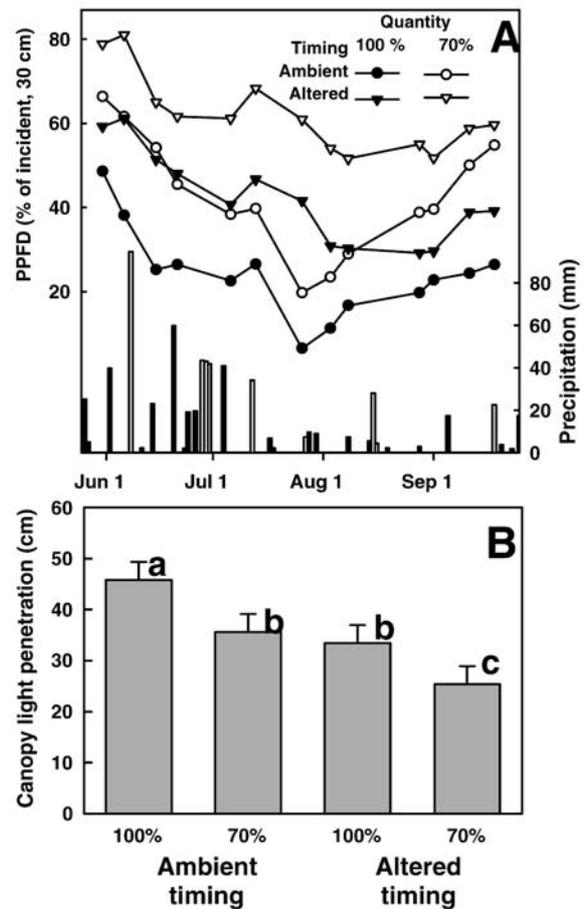


Fig. 3A–B Canopy PPFD levels under experimental rainfall manipulations in the RaMPs. **A** Seasonal changes in PPFD in the plant canopy (symbols and lines), measured at 30 cm above ground during 2000. SEs omitted for clarity; the maximum SE (across plots) was 17% on 15 June. Temporal pattern of rainfall inputs under ambient (black bars) and altered timing (white bars) treatments are also shown. **B** Growing season mean light penetration into the canopy, expressed as the height above ground in the canopy at which PPFD is at 50% of incident. Means \pm SE (across sample dates). Significant ANOVA effects: quantity $F_{1,8}=6.73$, $P=0.0319$; timing $F_{1,8}=10.25$, $P=0.0126$

accumulation. In the altered timing treatments, this PPFD decrease was both attenuated and delayed. From peak biomass (mid-August) through the remainder of the growing season, canopy PPFD increased as plants senesced, most rapidly in the reduced quantity treatments. These seasonal patterns in canopy PPFD translated into a 22–45% increase in growing season mean canopy PPFD caused by rainfall quantity and timing manipulations (Fig. 3b).

The dominant grass *Andropogon gerardii* showed no productivity response to either rainfall quantity or timing (Fig. 2b), while the subdominant C_4 grasses (primarily *Sorghastrum nutans*, *Panicum virgatum*, *Sporobolus heterolepis*) showed strong decreases in productivity with changes in both quantity and timing of rainfall. Grass stem densities and *Sorghastrum nutans* flowering stem densities responded in parallel with grass productivity

Table 1 Root biomass, above-ground biomass and the root: shoot ratio at the end of the 2000 growing season for the ambient and altered timing treatments (averaged across rainfall quantity treatments). Means (SE)

	Ambient timing	Altered timing	<i>t</i>	<i>P</i> -value
Root mass 0–100 cm (g m ⁻²)	1,109.0 (70.7)	1,330.6 (137.2)	1.44	0.1816
Aboveground biomass (g m ⁻²)	736.4 (33.4)	656.2 (38.2)	1.58	0.1453
Root: shoot ratio	1.51 (0.08)	2.05 (0.20)	2.52	0.0305

Table 2 Vegetative and flowering stem responses to rainfall manipulations in the RaMPs, means (SE). ANOVAs: Graminoids quantity × timing $F_{1,6}=5.38$, $P=0.059$; *Sorghastrum nutans* timing $F_{1,8}=10.00$, $P=0.013$

	Ambient timing		Altered timing	
	100	70	100	70
Rainfall quantity (%)				
Vegetative stems (per m ²)				
Graminoids	578.6 (30.1)a	460.9 (30.1)b	464.5 (30.1)b	484.5 (30.1)b
Forbs	60.5 (12.2)	44.1 (12.2)	39.5 (12.2)	50.0 (12.2)
Flowering stems (per m ²)				
<i>Sorghastrum nutans</i>	71.8 (9.0)a	57.8 (9.0)a	40.0 (9.0)b	32.8 (9.0)b
<i>Andropogon gerardii</i>	15.8 (6.8)	4.8 (6.8)	9.0 (6.8)	14.5 (6.8)

(Table 2). Also, *S. nutans* cover during the 2000 growing season decreased 12% from 1997 pre-treatment values in the altered timing treatments while increasing 60% from pre-experiment cover in the ambient timing treatments ($F_{1,6}=10.63$ $P=0.02$).

Discussion

Changes in the temporal pattern and packaging of growing season rainfall inputs strongly affected variability in 0–30 cm soil water content. Other studies have reported similar temporal changes in soil moisture in response to changes in the temporal pattern of rainfall inputs (Volk et al. 2000). The similar growing season mean soil moisture values found in the altered timing and reduced quantity treatments likely resulted from the extended dry intervals of the altered timing regime. While the larger rain events were likely more efficient than smaller ambient events in terms of lower canopy interception and evaporative losses and greater soil infiltration, the longer dry intervals led to greater soil moisture depletion. Thus, repackaging growing season rainfall into fewer, larger events, a prediction of many climate change models, was as important as reducing the total quantity of rainfall in terms of effects on ANPP. This was most evident in the driest year of the study, when altered rainfall patterns reduced ANPP by 165 g/m², a reduction in ANPP equivalent to a 17% reduction in rainfall on an interannual basis (Briggs and Knapp 1995).

Temporal patterns of canopy development were altered throughout the growing season by rainfall manipulations, but the mid-season attenuation in canopy growth found in the altered timing treatments may be most important in terms of productivity. At mid-season, several crucial factors converge, including increasing summer temperatures, decreasing mid summer rainfall, and heavy transpirational demand from high canopy leaf area. When soil moisture variability (and associated water deficits) were

increased in the altered timing treatments, the mid-season gap between soil moisture supply and evaporative demand was increased, diminishing plant performance relative to ambient timing (Percy 1990; Wraith and Wright 1998). Since variability in precipitation and soil moisture is generally greater than variability in evaporative demand (Oesterheld et al. 1999), biomass accumulation would be expected to be regulated mainly by variation in inputs rather than outputs of water.

Altered rainfall timing increased plant root to shoot ratios, because of both reduced aboveground biomass and a trend toward increased root biomass (Table 1). Hayes and Seastedt (1987) reported decreased total root length and root production during extended drought in this grassland, but increased root biomass in response to water stress is consistent with predictions for forest systems (Joslin et al. 2000). The periodic episodes of high soil water content that occurred in the altered timing treatment may have stimulated root growth sufficiently to compensate for the intervening soil moisture deficits, potentially preventing even larger reductions in aboveground plant productivity.

The dominant grasses and forbs did not respond to periods of decreased soil water content associated with increased soil moisture variability as might be expected based on their leaf physiological attributes. The warm season grasses contributing the bulk of the biomass in this system possess the C₄ photosynthetic metabolism, which generally confers higher photosynthetic water use efficiency via higher carbon uptake and lower transpiration rates than with the C₃ photosynthesis found in most forbs (Knapp and Medina 1999). Lower production of the grass functional group despite their more efficient leaf physiology could have resulted from several factors.

Root activity may have declined under the altered timing treatment because of the prolonged soil moisture deficits in the top 30 cm. Drought reduces root activity most strongly in near-surface roots (Wraith et al. 1995), and grasses concentrate a high proportion of their roots in

the upper part of the soil profile (Weaver 1968; Sims et al. 1978). As a result, grass water status and N uptake might be expected to be directly affected by increased soil moisture variability, with recovery of root activity requiring days or weeks (BassiriRad and Caldwell 1992; Casper and Jackson 1997; Wraith and Wright 1998). Since resin extractable soil N increased in the altered rainfall timing treatments (Harper 2002), N limitation is not a likely factor causing reduced grass production (Turner et al. 1997). Altered rainfall timing causes lower leaf water potential and photosynthesis in *Andropogon gerardii* and *Sorghastrum nutans* (Fay et al. 2002; Knapp et al. 2002; P. Fay, unpublished data), suggesting that lower root activity due to increased soil moisture variability leading to lower plant water status and carbon gain is a likely mechanism causing lower grass ANPP.

While the warm-season C₄ grasses as a group are frequently found to be important drivers of ANPP responses in grasslands (Sala et al. 1989; Silvertown et al. 1994; Briggs and Knapp 1995), the two most abundant warm season grasses in the ecosystem exhibited contrasting cover and flowering responses to altered rainfall patterns despite their widespread co-occurrence and similar photosynthetic physiology and life histories. The greater response to moisture in *S. nutans* and the other grasses relative to *A. gerardii* is consistent with previous studies (Knapp 1984; Senock and Ham 1995; Cuomo et al. 1998; Silletti and Knapp 2001). Thus, the subdominant grasses may be more strongly impacted by rainfall variability than the dominant species, and a key attribute of dominant plant species in grasslands may be their greater tolerance of rainfall variability. Williams et al. (1998) also found that increased water variability had no effects on biomass or leaf area of *Themeda triandra*, the dominant graminoid in the Serengeti.

The forbs potentially benefit from the factors apparently limiting grass production. Forbs may avoid the detrimental effects of increased soil moisture variability because their deeper root distributions relative to the grasses allow them access to deeper, less temporally variable soil water supplies. As a group, C₃ forbs require higher soil N than the C₄ grasses, and would likely benefit from higher soil N under the altered rainfall timing treatment. Many forbs are active early and late in the growing season, avoiding the midseason period when rainfall variability has the greatest consequences. Moreover, forbs active during the later portions of the growing season may benefit from increased PPFD transmittance through the grass canopy resulting from altered rainfall timing.

Conclusion

Increased temporal variability in growing season rainfall patterns led to increased soil moisture variability and reduced ANPP in this grassland ecosystem. Thus, the well-established responsiveness of ANPP to water availability in this grassland (Knapp et al. 2001) arises from

both the quantity of rainfall inputs and variability in the temporal distribution of rainfall during the growing season. Our results suggest that the sensitivity of ANPP to changes in water availability may be due more to direct effects of soil moisture deficits on root growth and activity resulting in lower plant water status and carbon gain, and not from effects on soil N. Traditional groupings of C₄ grasses versus forbs did not fully explain productivity responses to rainfall variability. The low diversity, high productivity and rapid growth of C₄ grasses at mid-season are reminiscent of many crop species, where frequent irrigation often boosts yields by minimizing soil moisture variability (Hillel 1987; Saeed and El-Nadi 1998). Altered rainfall regimes are thus an important element of climate change scenarios in this grassland, with the potential to magnify the effects of predicted atmospheric warming, and to offset any increased water use efficiency of grassland plants due to elevated CO₂ (Knapp et al. 1993; Owensby et al. 1997). Understanding these interactions among climate change elements remains a significant challenge for predicting ecosystem responses to climate change.

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