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Contingent productivity responses to more extreme rainfall regimes across a grassland biome

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Abstract

Climate models predict, and empirical evidence confirms, that more extreme precipitation regimes are occurring in tandem with warmer atmospheric temperatures. These more extreme rainfall patterns are characterized by increased event size separated by longer within season drought periods and represent novel climatic conditions whose consequences for different ecosystem types are largely unknown. Here, we present results from an experiment in which more extreme rainfall patterns were imposed in three native grassland sites in the Central Plains Region of North America, USA. Along this 600 km precipitation–productivity gradient, there was strong sensitivity of temperate grasslands to more extreme growing season rainfall regimes, with responses of aboveground net primary productivity (ANPP) contingent on mean soil water levels for different grassland types. At the mesic end of the gradient (tallgrass prairie), longer dry intervals between events led to extended periods of below-average soil water content, increased plant water stress and reduced ANPP by 18%. The opposite response occurred at the dry end (semiarid steppe), where a shift to fewer, but larger, events increased periods of above-average soil water content, reduced seasonal plant water stress and resulted in a 30% increase in ANPP. At an intermediate mixed grass prairie site with high plant species richness, ANPP was most sensitive to more extreme rainfall regimes (70% increase). These results highlight the inherent complexity in predicting how terrestrial ecosystems will respond to forecast novel climate conditions as well as the difficulties in extending inferences from single site experiments across biomes. Even with no change in annual precipitation amount, ANPP responses in a relatively uniform physiographic region differed in both magnitude and direction in response to within season changes in rainfall event size/frequency.

Keywords: climate change, environmental gradients, extreme events, grassland, plant productivity, precipitation variability

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Introduction

Enhanced radiative forcing, due to continued increases in greenhouse gas concentrations, is expected to raise the mean global surface temperature 1.1–6.4 °C by 2100 (IPCC, 2007). Climate models predict that this will result in greater inter- and intra-annual variability in precipitation patterns, and evidence is mounting that growing season precipitation regimes have become more extreme globally (Easterling *et al.*, 2000; Karl & Trenberth, 2003; Goswami *et al.*, 2006; Allan & Soden, 2008; Groisman & Knight, 2008). Such an intensification of hydrologic regimes will have important impacts on ecological processes and ecosystem services (Knapp *et al.*, 2008), but understanding and quantifying the impacts of these novel climate conditions remains a key challenge for ecologists (Weltzin *et al.*, 2003; Heisler & Weltzin, 2006; Williams *et al.*, 2007).

Characterized by larger individual events and extended periods of time between events, extreme rainfall

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regimes are expected to significantly alter the temporal supply of water to terrestrial ecosystems (Knapp *et al*., 2008). With no net changes in annual rainfall amount, these shifts in event frequency/magnitude may increase the severity of within-season drought, significantly alter evapotranspiration, and generate greater runoff from soils (Fay *et al*., 2003; MacCracken *et al*., 2003). How will ecosystems respond to these hydrologic changes? In spite of the increase in experimental studies demonstrating links between intra-annual precipitation patterns and biological processes in individual ecosystems (Knapp *et al*., 2002; Harper *et al*., 2005), a mechanistic understanding of the factors determining sensitivity *across* ecosystems is lacking. Ecosystems differ substantially in their sensitivity to interannual variation in precipitation, largely due to differences in vegetation structure, life history traits of dominant species, and biogeochemistry (Paruelo *et al*., 1999; Knapp & Smith, 2001; McCulley *et al*., 2005). These ecosystem attributes, which effectively determine potential responses to alterations in precipitation, are directly linked to long-term climatic averages and variability. We designed an experiment in natural grasslands arrayed across a strong precipitation–productivity gradient (600 km) in the Central Plains Region of North America, USA to evaluate the sensitivity of three distinct C_4-dominated grassland ecosystems to a shift to a more extreme within-season rainfall regime. Our primary objective was to develop a regional understanding of rain event frequency/amount as it influences grassland ecosystem function. We used a multisite experiment that included semiarid steppe, mixed grass prairie, and tallgrass prairie ecosystems to evaluate the null hypothesis that ecosystem-level patterns and mechanisms would be similar across a broad region and major biome. Reducing storm frequency and increasing rain event intensity led to a reduction in soil CO_2 flux, carbon fixation, and aboveground net primary productivity (ANPP) in tallgrass prairie (Knapp *et al*., 2002), and we hypothesized that similar reductions in carbon cycling processes would be observed across this gradient. To our knowledge, this is the first multisite experiment designed to test the generality of ecosystem response to changes in precipitation event frequency/intensity, which are expected to accompany rising [CO_2] concentrations and warmer surface temperatures (IPCC, 2007).

The Central Plains Region is an ideal location to test the generality of ecosystem responses to predicted shifts to more extreme rainfall patterns because it is characterized by a relatively uniform geomorphic template and contains three moisture-driven ecosystems, which share a common physiognomy but differ in their dominant species, diversity, and average soil moisture levels (Burke *et al*., 1991; Table 1). The region covers ca. 1.8 km × 10^6 km (Sims, 1991) and is characterized by a gradual west–east gradient in precipitation, which controls the distribution of plant life forms (Borchert, 1950; Weaver & Albertson, 1956). Precipitation increases from ca. 300 mm in the west, in the rain shadow of the Rocky Mountains, to over 1000 m in the east and ANPP (Sala *et al*., 1988) and plant cover (Vinton & Burke, 1997) similarly increase along this dry to wet gradient (Sala *et al*., 1988). Mean annual temperature remains approximately constant for a given latitude (Lauenroth *et al*., 1999) and as such, precipitation is the most important climatic variable for this region (Burke *et al*., 1991). Whereas water availability limits ANPP in semiarid steppe in nearly all years, the availability of other resources (such as nitrogen or light) may interact with water availability to determine ANPP in mesic tallgrass prairie in years of average or above-average precipitation (Knapp *et al*., 1998).

Globally, the grassland biome covers 1/3 of the earth's terrestrial surface and provides important ecosystem services that include forage land for livestock and carbon sequestration. In temperate regions, the grassland biome displays some of the greatest interannual variability in ANPP under current precipitation patterns (Knapp *et al*., 2001) and may be among the most responsive to future climate changes. As documented by the intense droughts of the 1930s and 1950s, this formerly extensive but now largely fragmented grassland region is both socioeconomically and ecologically vulnerable to extremes in climate variability (Weaver & Albertson, 1944). Assessing responses across such large-scale gradients permits more powerful inferences to be made regarding both the short- and long-term implications of climate change and at scales relevant to policymakers (Burke *et al*., 1991; Weltzin *et al*., 2003; Emmett *et al*., 2004).

Materials and methods

This experiment was directly designed to evaluate the interaction between means and extremes of a key limiting resource (water) that is likely to change in novel ways during the next century (Williams *et al*., 2007). We defined extreme precipitation regimes from an intra-annual perspective as a shift from extant rainfall patterns to regimes characterized by fewer, but larger events with extended intervening dry periods between events. Using long-term climatic data, we first characterized the historic frequency of growing season rainfall events for each of three grassland sites along a productivity gradient and selected experimental treatment scenarios that were in the more extreme tails of long-term rainfall records (Fig. 1). While mean annual precipitation (MAP) increases nearly threefold

Table 1 Key plant, soil, and climate characteristics of three grassland ecosystem types located within the Central Plains Region of North America (USA)

	SGS Shortgrass steppe LTER Nunn, CO	HYS Saline experimental range Hays, KS	KNZ Konza prairie LTER Manhattan, KS
Climate and vegetation			
Latitude	40°49′N	38°53′N	39°05′N
Longitude	104°46′W	99°23′W	96°35′W
MAP (mm)	321	576	835
MAT (°C)	8.6	11.9	13
Vegetation type	Semiarid steppe	Mixed grass prairie	Mesic tallgrass prairie
Dominant plant species	*Bouteloua gracilis*	*Bouteloua curtipendula/ Schizachyrium scoparium*	*Andropogon gerardii/ Sorghastrum nutans*
Long-term mean ANPP ($\mathrm{g\,m^{-2}}$)	97	300	425
Soil physical and mineralogical properties			
A horizon texture (% sand–silt–clay)	14–58–28	6–69–25	8–60–32
Bulk density ($\mathrm{g\,m^{-3}}$)	1.2	1.2	1.4
Pore space (%)	50–55	50–55	47–53
Clay mineralogy	Mica and smectite	Mica and smectite	Kaolinite and smectite
B horizon Texture (% sand–silt–clay)	12–54–34	7–50–43	4–46–50
Bulk density ($\mathrm{g\,m^{-3}}$)	1.4	1.5	1.5
Pore space (%)	47–53	44–49	44–49
Clay mineralogy	Smectite	Smectite	Smectite
Pedon Classification	Aridic Argiustoll	Typic Argiustoll	Typic Argiustoll

The sites are SGS, the Shortgrass Steppe Long-Term Ecological Research (LTER) site; HYS, the Saline Experimental Range, under the management of the Kansas State University Western Agricultural Research Center; and KNZ, the Konza Prairie Biological LTER site. MAP, mean annual precipitation; MAT, mean annual temperature. Plant species nomenclature follows that of the Great Plains Floral Association (1986). Soils data are adapted from Blecker (2005) and Blecker *et al.* (2006). Soil taxonomy follows that of the USDA. ANPP, aboveground net primary productivity.

(320–830 mm) across this gradient, a similar number of rainfall events (16–18 events) occur during the growing season for all three ecosystems (Fig. 1). We chose experimental treatments of 12-, 6-, or 4- events and imposed the long-term average precipitation amount to experimental plots in each grassland type according to average seasonal trends.

Experimental protocol

We manipulated the temporal distribution of growing season rainfall within 15 rainout shelters per site in the semiarid shortgrass steppe (NE Colorado), mixed grass prairie (central KS), and mesic tallgrass prairie (eastern KS) of the Central Plains Region. All ambient rainfall was excluded from experimental plots beneath rainout shelters, and the 30-year mean quantity of growing season rainfall appropriate for each site was added to each experimental plot and distributed as 12-, 6-, or 4-events ($n = 5$ replicate shelters per regime within each grassland ecosystem). Events were applied based on the historical seasonal course of rainfall inputs for each site. Duration of the dry interval between events was 10-, 20-, or 30-days, respectively.

Grassland sites

The experimental sites were the Konza Prairie Long-Term Ecological Research site (tallgrass prairie; Manhattan, KS, USA), and the saline experimental range (SER) (mixed grass prairie; Hays, KS, USA) and the Shortgrass Steppe Long-Term Ecological Research site (shortgrass steppe). Details for each site are described below and summarized in Table 1.

Mesic tallgrass prairie (KNZ)

The Konza Prairie Biological Station (KNZ) is a native C_4-dominated mesic grassland in the Flint Hills of northeastern Kansas (39°05′N, 96°35′W), an area that remains the largest continuous expanse of unplowed tallgrass prairie in North America (Samson & Knopf, 1994). MAP is 835 mm, 75% of which falls during the April–September growing season (Hayden, 1998). The

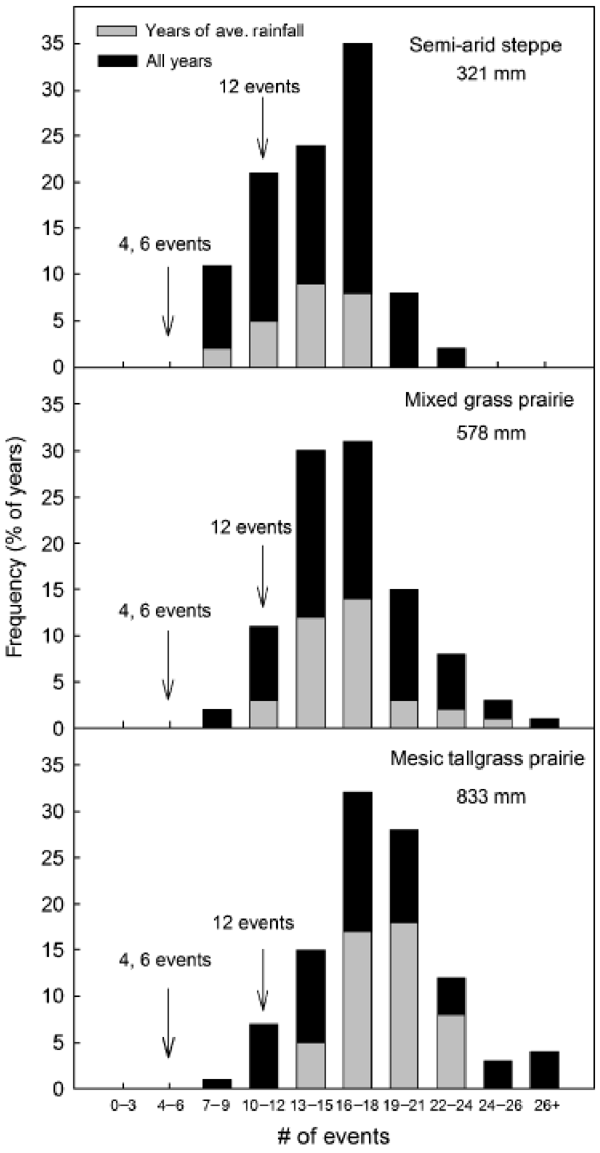

Fig. 1 Distribution patterns for growing season rainfall events across the Central Plains Region. Data are from the National Climate Data Center from 1907 to 2006 for Hays, KS (mixed grass prairie) and Manhattan, KS (tallgrass prairie). For the semiarid steppe (Nunn, CO), data were available only for 1948–2006. Long-term average annual rainfall is included for reference.

climate is considered temperate midcontinental and characterized by periodic droughts and large seasonal and interannual variability in rainfall. Mean annual temperature is 13 °C. The plant community is dominated by relatively few native perennial C_4 grasses including *Andropogon gerardii* (big bluestem) and *Sorghastrum nutans*, (Indiangrass) but considered floristically diverse, due to the abundance of C_3 herbaceous forb species (Freeman, 1998). The management of KNZ, and tallgrass prairie in general, includes frequent fire, and the site in which experimental plots were located was burned in early April 2006. All 15 rainout shelters were located in a gently sloping, typical lowland prairie, where the soils are Udic Argiustolls with a soil texture of 8% sand, 60% silt, and 32% clay (Blecker, 2005).

Mixed grass prairie (HYS). The SER (38°53′N, 99°23′W) is a 2400 acre contiguous tract of native mixed grass prairie that has been managed by the Agricultural Research Center-Hays (Kansas State University) since 1994. It is located in the Saline River Watershed, ca. 25 miles northeast of Hays, Kansas. The SER consists of a variety of upland, lowland, and breaks range sites and is managed for cattle grazing. In 2005, an electric fence was installed to exclude cattle from experimental plots. The plant community is dominated by the C_4 graminoids *Bouteloua curtipendula* (sideoats grama) and *Shizachyrium scoparium* (little bluestem), but C_3 forbs such as *Ambrosia psilostacyha* (cuman ragweed), *Dalea purpurea* (purple prairie clover) and *Psoralea tenuiflora* (slimflower scurfapea) are abundant in cover. This mixed grass prairie site contains a diverse plant community in which species from its western (more arid) and eastern (more mesic) grassland neighbors coexist. MAP (long term average) is 576 mm (Harmoney, 2007). The soils in this area are Typic Argiustolls with a composition of 6% sand, 69% silt, and 25% clay (Blecker, 2005).

Semiarid shortgrass steppe (SGS). The Shortgrass Steppe Long-Term Ecological Research (SGS) site is a semiarid shortgrass steppe site that is located in northeastern Colorado, USA (40°49′N, 104°46′W). SGS is located within the Central Plains Experimental Range and represents a partnership between Colorado State University and the United States Department of Agriculture – Agricultural Research Service and Forest Service. MAP for this region is 321 mm (Lauenroth & Sala, 1992), 70% of which occurs in the May–September growing season. Mean annual temperature is 8.6 °C. The plant community is dominated by the C_4 grass species, *Bouteloua gracilis* (blue grama), with other major C_3 forb species including *Artemisa frigida* (fringed sagewort), *Sphaeralcea coccinea* (scarlet globemallow) and *Opuntia polycantha* (plains pricklypear). The study site was located in a large exclosure from which cattle were removed in 1999. The soils of this site are considered representative of the shortgrass steppe ecosystem and are Aridic Argiustolls (14% sand, 58% silt, 28% clay; Blecker, 2005).

In selecting the locations for rainout shelters, we intentionally chose experimental sites in which plant community structure was representative of a given grassland type and key physical properties of the soil that regulate water holding capacity (e.g. texture, porosity, and mineralogy) as constrained by soil parent materials (residual sedimentary rocks and loess) were similar (Table 1).

Shelter design and rainfall application

Rainout shelters ($n = 15$ per grassland type) were erected in May–June 2005 and designed to exclude ambient rainfall in 5.1 m^2 experimental plots. The perimeter (2.25 m × 2.25 m) of each shelter was trenched to ≥1 m below ground surface and lined with 6 mil plastic to minimize subsurface water flow and prevent root and rhizome penetration into or out of the plot. Dimensions for the sheltered area were selected so that natural rainfall would be excluded from a central 1.25 m × 1.25 m core plot designated for plant and soil sampling. The core plot was surrounded by a 0.5 m buffer. Shelter roofs were installed ca. May 1, 2006 and covered the plots for the duration of the growing season (120 days). The aboveground structure consisted of four wooden corner posts anchored in the soil to a depth of 1 m. Inset roofs (clear corrugated polycarbonate sheeting) were elevated ca. 1.1 m above the ground surface and sloped slightly towards subtle topographic gradients to allow for quick drainage of ambient rainfall. Ambient plots were included in the experimental design as a reference, but are not true controls because they received ambient rainfall amounts at ambient intervals. Rainfall events were manually applied to sheltered plots and followed seasonal distribution trends for event quantity. The total amount of water applied to sheltered plots was 191 mm for semiarid steppe, 340 mm for mixed grass prairie, and 450 mm for tallgrass prairie. Ambient rainfall in 2006 was 123 mm, 251 mm, and 436 mm, respectively. Large events were applied over 2–3 day intervals to ensure that plots never received greater than ca. 25 mm in a single day in semiarid steppe, 38 mm in mixed grass prairie, or 50 mm in tallgrass prairie.

ANPP

ANPP was estimated by harvesting all plant material in two 0.25 m^2 quadrats from within the core plot of each sheltered area. In these grasslands dominated by herbaceous perennials, a single harvest was sufficient to capture peak biomass (Knapp *et al.*, 2007). In March–April 2006, all previous years' dead aboveground plant biomass was cleared from experimental plots via clipping or fire. The purpose of this pregrowing season harvest was to remove all previous years' standing dead so that all aboveground plant material harvested in 2006 could easily be identified as current year's growth and to mimic historic management in this region (fire and/or grazing). Harvesting of ANPP occurred in September 2006 at ca. 20 days following the final simulated rainfall event. Harvested plant material was oven dried at 60 °C for 72 h, sorted, and weighed to the nearest 0.1 g.

Plant water relations

Water relations of the dominant species were estimated via plant water potential (Ψ) measurements, which were taken at mid-day using a Scholander-type pressure chamber (PMS Instruments, Corvallis, OR, USA). The species sampled were *B. gracilis* (SGS), *A. gerardii* (KNZ), and *S. nutans* (KNZ). Leaves ($n = 3$ per shelter) were collected between 1100 and 1300 h MST on four to five sampling dates throughout the growing season.

Within each shelter, three leaves of each of the dominant plant species were collected, measured, and averaged for a shelter-level value. Since 'shelter' was considered the experimental unit, $n = 5$ for each water manipulation treatment. At KNZ, Ψ was measured on June 22, 23, 26, 28, and July 25. At SGS, Ψ was measured on July 12, 14, 17, and 21. At both sites, measurements were clustered around the mid-point of the experiment (day 60 of 120) and captured both pre- and postrainfall Ψ. For the purpose of this multisite experiment, we averaged Ψ across sampling dates to estimate a mean value for the mid-point of the experiment and growing season.

Leaf tissue N

A composite sample of leaf tissue from five tillers of the dominant grass species was taken from within each core plot at the mid-point of the growing season. The species sampled were *B. gracilis* at SGS, *S. scoparium* and *B. curtipendula* at HYS, and *A. gerardii* and *S. nutans* at KNZ. Samples were dried at 60 °C for 3 days, ground on a Wiley Mill, and analyzed for total percentage C and N on a Leco elemental CHN analyzer (St Joseph, MI, USA).

Soil N availability

Available N in soils was measured from May to September using mixed cation–anion resin bags. Resin bags were made from sheer nylon stockings filled with equal measures (5 g each) of strong anion and cation exchangers. Intact bags were soaked in 0.6 N HCl to clean them and preload the resins with H^+ and Cl^- ions. Three resin bags were placed 5 cm deep in both treatment and ambient plots at all sites in May 2006 and collected in September. In the lab, resin bags were rinsed with deionized water and extracted with 2 $\mathrm{mol\,L}^{-1}$ KCl solution. Available N concentrations were determined on an Alpkem Autoanalyzer (OI Corporation, College Station, TX, USA).

Soil water content

Soil moisture probes were installed in July 2005 and remained in place for the duration of the experiment. Soil moisture was measured ca. every 3 days from May–September to capture dynamics associated with simulated rainfall events. We measured soil moisture just before a simulated rain event and at days 1, 3, and 5 postevent. Volumetric water content was estimated via sensors that measured dielectic permittivity of the soil (ECH_2O soil moisture sensors, Decagon, Pullman, WA, USA). Each sensor integrated soil moisture for the top 20 cm of soil and was placed within the core plot of both sheltered and ambient plots at all sites (one probe per shelter, $n = 5$ probes per treatment).

Plant species richness

Plant species richness was assessed by inventorying all species present in two 0.25 m^2 quadrats per rainout shelter at each grassland site. Inventories were conducted in both June and August, and we characterize species richness as the total number of species/quadrat for the 2006 growing season. Replicate measurements within a shelter were averaged to determine a shelter-level value.

Statistical analyses

Statistical analysis of ANPP, water relations, leaf tissue N, soil N availability, and species richness were conducted using a general linear model (PROC GLM) in which the main effects were site and treatment (SAS 9.1, Cary, NC, USA). Treatments were assigned at random to the 15 shelters within a site. Each sheltered plot was an experimental unit, so replicate measurements at the subplot level were averaged by plot for analysis ($n = 5$ per treatment per grassland site). For both water relations and leaf tissue N, data were collected for the dominant plant species from within site, and we tested the main effect of species in these analyses. Mid-day leaf water potential measurements occurred on multiple sampling dates and we tested for both the main effect of time and the treatment by time interaction. Repeated measures analyses were not used because we sampled different individuals on each date. The LSMEANS procedure was used to test for significant differences among means according to preplanned comparisons of treatments or species within a site. Values presented are means ± 1 SE and the level of significance for all statistical tests was $P \leq 0.05$ unless otherwise noted. For both foliar N and Ψ, the main effect of species was not significant, and we combined these data according to the main effect of treatment and report mean responses in the text and figures.

Results

ANPP

A shift to fewer but larger events, with no change in total rainfall amount, significantly altered total ANPP in all three grassland ecosystems (Fig. 2). The main effect of site was significant ($P < 0.01$), as was the site-by-treatment interaction ($P < 0.01$). Together, these results indicate that the response pattern to more extreme rainfall events was not consistent across the different grassland types. At the most arid end of the moisture gradient (semiarid steppe; Fig. 2a), a redistribution of rainfall from 12- to 4- events resulted in a 30% increase in ANPP from 97 to 126 g m^{-2} ($P = 0.05$). The largest increase (70%) in ANPP occurred in mixed grass prairie (located intermediate within the precipitation gradient), where ANPP was increased from 113 to 193 g m^{-2} in response to the shift from 12- to 4- events ($P = 0.02$; Fig. 2b). These positive ANPP responses to a more extreme rainfall regime were reversed in the most mesic grassland (tallgrass prairie); here, an 18% reduction ($P = 0.06$) in ANPP was measured (579–488 g m^{-2}; Fig. 2c).

Across this biome, we noted two treatment responses that were consistent among different grassland types. First, ANPP in plots exposed to ambient rainfall did not significantly differ from the 12-event rainfall scenario (Fig. 2; this was in spite of considerable variation in both rainfall amount and distribution during the 2006 growing season). Second, plots receiving six vs. four events did not significantly ($P > 0.10$) differ from one another in their ANPP responses, regardless of the magnitude or direction of their response in comparison to the 12-event scenario.

Dynamics of soil water content

Soil water content, a proximal driver of ANPP in grasslands (Briggs & Knapp, 1995), was strongly influenced by altered rainfall patterns (Fig. 3). The semiarid steppe and tallgrass prairie, endpoints in the precipitation gradient, exhibited clear inverse responses to extreme rainfall regimes, with the mixed grass prairie intermediate (data not shown). In the upper 20 cm of the soil profile [where a significant fraction of root biomass is located, (Singh *et al.*, 1998)], mean soil water content in the semiarid steppe increased by 19%, as the number of events decreased from 12 events (8.3%) to 4 events

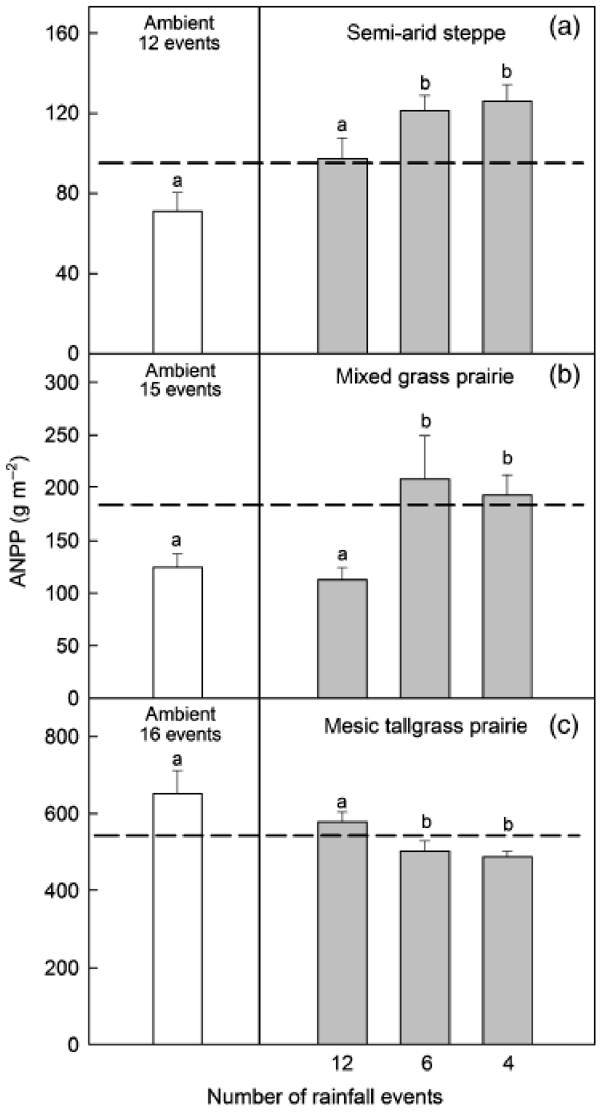

Fig. 2 ANPP response to a shift in rainfall regime (reduced event number and corresponding increases event size) in three grasslands across a Central Plains, USA precipitation gradient. Panels for each grassland ecosystem include ANPP under ambient rainfall conditions (white bar) in addition to the three experimental rainfall regimes (grey bars). For reference, long-term mean ANPP for each ecosystem is depicted by a horizontal dashed line. Mean event size for the 12-, 6-, and 4-event scenarios was 16, 32, and 48 mm in semiarid steppe; 28, 57, and 85 mm in mixed grass prairie; and 38, 75, and 113 mm in tallgrass prairie. Significant ANPP differences between rainfall scenarios for a given grassland ecosystem are indicated by different letters. Error bars represent ± 1 SE. ANPP, aboveground net primary productivity.

(10.2%). In contrast, mean soil water content was reduced by 20% (17.2% vs. 13.5%) with a shift from 12- to 4-events in mesic tallgrass prairie.

Concurrently, more extreme rainfall regimes (four events) along this precipitation gradient led to elevated soil moisture in semiarid steppe (Fig. 3a) and lower soil moisture in tallgrass prairie (Fig. 3b). In semiarid steppe, large rain events resulted in considerable increases in soil water content and were observed to rapidly elevate soil moisture to a mean maximum value of 103% above the seasonal average. In the dry intervals between events, soil water was maintained at a mean minimum of −24% of seasonal average soil water content. Moisture reductions (due to less frequent rainfall events) were comparatively greater in the mesic grassland, where a mean minimum of −55% of seasonal average soil water content characterized periods between events. While large rain events consistently increased soil moisture content above the seasonal average (mean maximum = 30%), both the duration and magnitude of these moisture pulses was less than in semiarid steppe.

Plant water relations and tissue chemistry

Analyses of leaf water potential (Ψ) revealed that the main effect of site was significant ($P<0.01$) in addition to the treatment-by-site interaction ($P<0.01$). It is important to note that Ψ measurements were taken only at SGS and KNZ. At the mid-point of the growing season, Ψ were significantly increased ($P<0.01$) in response to more extreme rainfall (four events) in semiarid steppe (from −4.3 ± 0.2 to −3.0 ± 0.1 MPa; Fig. 3a *inset*). Mid-season foliar N concentrations were similarly increased (from 2.0 ± 0.08 to 2.3 ± 0.08 $\mu g\, g^{-1}$; Fig. 3a *inset*). In the mesic grassland site, more extreme rainfall (four events) significantly ($P<0.01$) reduced mid-day Ψ at the mid-point of the growing season, suggesting relatively greater plant water stress in response to this treatment (Fig. 3b *inset*). A concomitant reduction ($P<0.01$) in leaf tissue N (from 1.0 ± 0.03 to 0.9 ± 0.02 $\mu g\, g^{-1}$) was also observed with a shift from 12- to 4-events (Fig. 3b *inset*). As expected, leaf tissue N was significantly lower ($P<0.01$) in mesic tallgrass prairie compared with semiarid steppe. In the mixed grass prairie, the main effect of rainfall treatment was not significant ($P>0.05$).

Plant species richness

We did not detect any significant changes in plant species richness or community structure in response to altered precipitation patterns (data not shown). However, plant species richness did vary considerably between the three grasslands types (Fig. 4). Mixed grass prairie was characterized by greatest total plant species richness (8.8 ± 0.4 species/0.25 m^2) whereas semiarid steppe had the lowest total species richness (4.9 ± 0.3 species/0.25 m^2). Mixed grass prairie also had the greatest species richness for both grass (4.3 ± 0.2

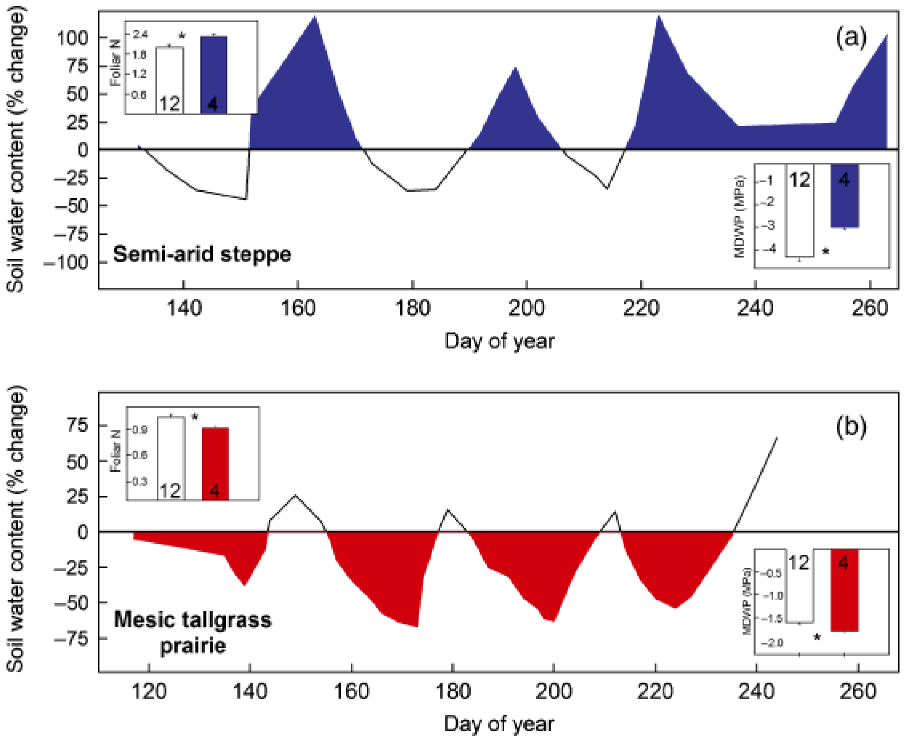

Fig. 3 Temporal dynamics of soil water content under extreme rainfall patterns (4 large events per year) in semiarid steppe (a) and mesic tallgrass prairie (b), which represent the endpoints of the Central Plains gradient. Data for soil water content (%) are for the four-event scenario and expressed as the percent difference from seasonal average soil moisture for the 12-event scenario. For the semiarid steppe, the time periods of above-average soil water content are indicated by blue shading. For tallgrass prairie, the time periods of below-average soil water content are indicated by red shading. *Right Insets*. Average mid-day water potential (MDWP; MPa) for the dominant grass species in the 12- and 4-event scenarios. *Left Insets*. Mid-season foliar N levels for the dominant grass species in the 12- and 4-event scenarios. Statistically significant results are indicated by an asterisk (*). The dominant species in semiarid steppe is *Bouteloua gracilis* while mesic tallgrass prairie is codominated by *Andropogon gerardii* and *Sorghastrum nutans*. Error bars represent ± 1 SE.

species/0.25 m^2) and forb (4.5 ± 0.3 species/0.25 m^2) functional groups.

Soil N availability

Soil N availability was strongly influenced by the frequency and magnitude of simulated rainfall events (supporting information Fig. S1). The main effects of site and treatment were significant, as was the treat-by-site interaction ($P < 0.01$ for all tests). In both semiarid steppe and mesic tallgrass praire, soil N availability increased ($P < 0.01$) with a shift to more extreme rainfall (a shift from 12- to 4- events). In mixed grass prairie, there was no significant difference ($P > 0.05$) in available soil N in response to the different rainfall treatments.

Discussion

Climate models forecast an increase in extreme precipitation events in response to an anthropogenically warmed climate. Because such changes in the distribution of rainfall represent novel changes for many ecosystems, both the short- and long-term effects of these changes remain largely unknown. We used a natural resource gradient within the Central Plains grassland region to evaluate the relative responsiveness of three distinct grassland types to this expected shift in rainfall pattern. While our results demonstrate strong sensitivity of all grassland types to more extreme rainfall regimes, both the magnitude and direction of the ANPP response differed from semiarid steppe to mesic tallgrass prairie. The dynamic changes in soil water content that accompanied large rain events and extended dry intervals provide evidence that hydrologic changes that accompany more extreme precipitation regimes can strongly influence plant and soil processes (even in the absence of any change to seasonal amounts).

The responses in soil water content, plant physiology/leaf chemistry, and ANPP along this precipitation and average soil water gradient, highlight the relative importance of two key aspects of extreme rainfall regimes (larger event size vs. greater dry interval

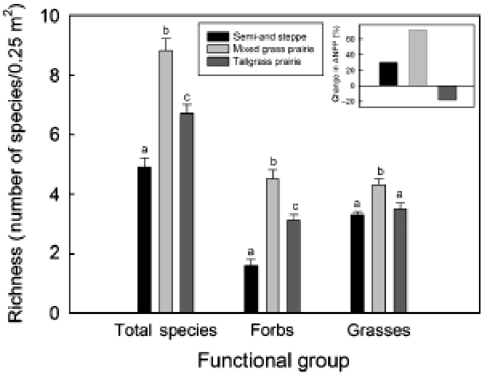

Fig. 4 Plant species richness (number of species/0.25 m^2) in three temperate grassland ecosystems within the Central Plains Region of the US. Data for both grass and forb functional types are included. Significant differences within a functional group are indicated by different letters. *Inset*. Change in total ANPP (%) with a shift to more extreme rainfall patterns for semiarid steppe, mixed grass and tallgrass prairie ecosystems. The greatest change in NPP (+ 70%) occurs in mixed grass prairie, which is characterized by greatest total plant species and functional group diversity. Error bars represent ± 1 SE. ANPP, aboveground net primary productivity.

length) in semiarid vs. mesic grasslands. Semiarid steppe is characterized by chronically low soil water availability and extended periods of intense water stress (Sala *et al.*, 1992). Plant traits associated with stress tolerance (i.e. reduced leaf area, high WUE efficiency; Sala *et al.*, 1992) allow the dominant species to persist. While small rain events can intermittently alleviate chronic water stress and improve plant water relations (Sala & Lauenroth, 1982), high atmospheric evaporative demand rapidly depletes soil water after these small precipitation inputs (Wythers *et al.*, 1999). This historic pattern of small precipitation inputs contrasts sharply with the forecast shift to larger, less frequent events. Because soil water content and actual evapotranspiration are already chronically low, the semiarid steppe is not particularly sensitive to increases in the interval between events. However, when larger rain events occur, deeper penetration of soil water into the profile and less proportional loss to evaporation (as long as runoff is not increased dramatically; Knapp *et al.*, 2008) increases the amount and duration of water in the soil for plant uptake. Indeed, we measured midday Ψ in *B. gracilis* (the dominant plant species) at the mid-point of the growing season and found significant reductions in plant water stress with fewer but larger events (Fig. 3a). The combination of improved plant water relations and greater foliar N content (Fig. 3a), perhaps due to increased soil microbial activity or N release from enhanced wetting/drying cycles, is consistent with greater leaf level carbon fixation and ultimately greater ANPP across the growing season.

In contrast, mesic systems are defined by relatively high soil water availability and low water stress for substantial portions of the growing season. Here, frequent events consistently recharge soil water and therefore maintain most ecosystem processes in a relatively unstressed state. Extending the dry intervals between events results in long periods of soil water depletion – to levels that result in relatively greater leaf-level water stress. Plant traits related to high production potential (rapid growth rates, high leaf area, and low WUE) are consistent with strong demands for soil water and high sensitivity of the dominant plant species *A. gerardii* and *S. nutans* to reduced soil water availability (as evidenced by a reduction in Ψ and foliar N concentration; Fig. 3b). This contrasting sensitivity of semiarid and mesic grassland ecosystems to different aspects of more extreme rainfall regimes (event size vs. interval between events) is supported by recent experiments in arid steppe and mesocosm studies (Fay *et al.*, 2008; Heisler-White *et al.*, 2008; Jankju, 2008).

We found no evidence to link responses in ANPP to changes in soil N availability with altered rainfall patterns along the precipitation gradient. Indeed, higher amounts of N were recovered from ion-exchange resin bags in treatments with fewer and larger events, which is consistent with pulsed releases of mineral N in response to soil wetting and drying (Fierer & Schimel, 2002; Miller *et al.*, 2005). N availability over the growing season was greatest in response to extreme rainfall patterns (four events) in both semiarid steppe and mesic tallgrass prairie (see supporting information Fig. S1). Thus, while the temporal mismatch between limiting resources (N and water) may be an important constraint to ecosystem function over the long-term, it did not appear to influence ANPP or plant uptake in this experiment.

The 70% increase in ANPP in mixed grass prairie (Fig. 4 *inset*) in response to more extreme rainfall patterns is consistent with predictions regarding the sensitivity of this grassland to variability in precipitation (Paruelo *et al.*, 1999; Knapp & Smith, 2001). Such ecosystems have been found to be most responsive to altered precipitation regimes, largely due to their history of extreme climatic variability and the range of plant species traits present. Plant species diversity was highest in the mixed grass prairie (Fig. 4), where a greater abundance of both C_4 graminoids and C_3 forb species comprise the plant community. Although ecological theory and empirical evidence from other grasslands suggests that greater diversity should lead to greater temporal stability in ecosystem processes (Naeem *et al.*, 1996; Tilman & Downing, 1996), this pattern was not evident at this regional scale.

Our results have several important implications for predicting the magnitude and direction of change in temperate grasslands specifically, and terrestrial biomes in general, under future climates. First, it is clear that responses to extreme rainfall regimes can be rapid and independent of any change in annual precipitation amount. In this experiment, we focused on ANPP because it integrates important ecological processes that range from plant ecophysiology and microbial activity to community structure. Second, we have shown that even structurally similar ecosystems within the same biome can show dramatically different responses to forecast shifts in rainfall patterns, with some regions of the biome experiencing greater water limitations while water stress in others will be alleviated. As a result, well known regional-scale relationships between ANPP and MAP that have been considered strongly linear (Sala *et al*., 1988) may change substantially under future climates. Given the importance of ANPP as a provider of key ecosystem services (forage production) as well as its role in the global C cycle, the contingent nature of its response to this forecast climate change highlights the need for a deeper understanding of the sensitivities of ecosystems to alterations in extremes as well as means in future climates.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Analysis of historic precipitation record and rationale for experimental rainfall manipulations.

Figure S1. Available soil N in grassland ecosystems of the Central Plains Region in response to a within-season shift in rainfall regime.