

Increasing precipitation event size increases aboveground net primary productivity in a semi-arid grassland

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Abstract Water availability is the primary constraint to aboveground net primary productivity (ANPP) in many terrestrial biomes, and it is an ecosystem driver that will be strongly altered by future climate change. Global circulation models predict a shift in precipitation patterns to growing season rainfall events that are larger in size but fewer in number. This “repackaging” of rainfall into large events with long intervening dry intervals could be particularly important in semi-arid grasslands because it is in marked contrast to the frequent but small events that have historically defined this ecosystem. We investigated the effect of more extreme rainfall patterns on ANPP via the use of rain-out shelters and paired this experimental manipulation with an investigation of long-term data for ANPP and precipitation. Experimental plots ($n = 15$) received the long-term (30-year) mean growing season precipitation quantity; however, this amount was distributed as 12, six, or four events applied manually according to seasonal patterns for

May–September. The long-term mean (1940–2005) number of rain events in this shortgrass steppe was 14 events, with a minimum of nine events in years of average precipitation. Thus, our experimental treatments pushed this system beyond its recent historical range of variability. Plots receiving fewer, but larger rain events had the highest rates of ANPP ($184 \pm 38 \text{ g m}^{-2}$), compared to plots receiving more frequent rainfall ($105 \pm 24 \text{ g m}^{-2}$). ANPP in all experimental plots was greater than long-term mean ANPP for this system (97 g m^{-2}), which may be explained in part by the more even distribution of applied rain events. Soil moisture data indicated that larger events led to greater soil water content and likely permitted moisture penetration to deeper in the soil profile. These results indicate that semi-arid grasslands are capable of responding immediately and substantially to forecast shifts to more extreme precipitation patterns.

Keywords Grasslands · Climate change · Precipitation variability · Rain event size · Pulse-reserve paradigm

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Introduction

Water availability is the primary constraint to plant productivity in many terrestrial biomes (Rosenzweig 1968; Webb et al. 1986; Le Houerou et al. 1988; Churkina and Running 1998), and it is an ecosystem driver that will be strongly affected by ongoing and future climate change (Houghton et al. 2001). Shifts in precipitation patterns, along with rising surface temperatures (Karl and Trenberth 2003), will have direct effects on the hydrologic cycle and the movement of water through the atmosphere-soil-biosphere continuum (McAuliffe 2003), whereas other global change drivers such as increases in CO_2 and N levels will indirectly

influence water demand and use by plants (Mooney et al. 1991; Owensby et al. 1996; Shaw et al. 2002). Even if the total precipitation inputs for a given system remain unchanged, predicted changes in the distribution of precipitation events (within or between seasons) will impact the timing and quantity of soil water available for plant uptake and biogeochemical processes (Weltzin et al. 2003).

Historically, precipitation data aggregated at annual or seasonal time scales were considered a suitable proxy for soil moisture and the metric most often used to relate water availability and aboveground net primary productivity (ANPP). At large spatial and temporal scales, abundant data support the strong predictive relationship between mean annual precipitation and ANPP (Rosenzweig 1968; Walter 1971; Sala et al. 1988). At more local scales, however, a considerable amount of variability in ANPP remains unexplained by annual precipitation alone (Lauenroth and Sala 1992; Knapp and Smith 2001), and both experimental and observational research suggest that the within-season distribution of precipitation events has significant effects on plant and soil processes (Novoplansky and Goldberg 2001; Knapp et al. 2002; Fay et al. 2003; Schwinning and Sala 2004; Sher et al. 2004; Harper et al. 2005; Sponseller 2007). The relative partitioning of a rainfall event to runoff, infiltration, and evaporation is complex and a function of soil characteristics and topography as well as antecedent soil water conditions and the magnitude and intensity of the event (Noy-Meir 1973). Ecological processes in arid and semi-arid ecosystems are particularly sensitive to within-season dynamics, due to intense water limitations and event-driven biological response patterns (Schwinning and Sala 2004).

In semi-arid grasslands, annual precipitation inputs are greatly exceeded by potential evapotranspiration, creating soil water conditions that are typically dry and only episodically relieved through discrete inputs of rainfall. Thus, chronic water limitation defines this ecosystem (Parton et al. 1981) and strongly influences the physiological characteristics and species composition of the biota (Sala et al. 1992; Chesson et al. 2004). Described originally by Noy-Meir (1973) and recently revisited by Reynolds et al. (2004), the “pulse-reserve” paradigm interprets individual rainfall events as rapidly recharging ecosystem resources, followed by the slow depletion of these resources through biological and physical processes. This perspective: (1) focuses on soil water as it becomes functionally available for plant and microbial processes; and (2) emphasizes the important contribution of these moisture pulses to biological activity, which occurs in the wake of rain events of sufficient size. The biological response, both in the long- and short-term, is tightly coupled to the amount, timing, and intensity of a given pulse (Schwinning and Sala 2004) and occurs in the context of the annual precipitation regime.

The highly variable precipitation regimes that characterize semi-arid grasslands (Noy-Meir 1973) are largely composed of precipitation events that are small in size but distributed with relatively short intervals between them. For example, in the shortgrass steppe of northeastern Colorado, 65% of daily precipitation events are <5 mm (Sala and Lauenroth 1982; Sala et al. 1992) with 90% of dry intervals less than 15 days in length (Wythers et al. 1999). This historical precipitation pattern of many frequent small events differs strongly from predicted global climate change scenarios, which emphasize a shift to larger events with longer intervening dry intervals (Groisman et al. 1999; Easterling et al. 2000; IPCC 2007).

While individually small, these events represent a consistent source of water with little interannual variability in their contribution to annual moisture inputs in many semi-arid systems (Sala et al. 1992; Golluscio et al. 1998; Loik et al. 2004). Events as small as 5 mm elicit biological activity and are effective in improving water status and subsequently production processes in *Bouteloua gracilis*—the dominant plant and graminoid species in the shortgrass steppe. Considered collectively, small events account for ca. 25% of growing season precipitation and are hypothesized to have a relatively larger impact (activity/mm) on ecosystem dynamics than large events (Sala and Lauenroth 1982). The rapid physiological response time of *B. gracilis* (<12 h; Sala and Lauenroth 1982) to rainfall events characteristic to this growing season rainfall pattern enables this species to maximally utilize small pulses of moisture before they are lost to bare soil evaporation.

Although small events contribute considerably to eco-physiological activity of plants during the growing season, analyses of long-term data for precipitation and ANPP suggest that the single most important explanatory variable for interannual variability in ANPP is the amount of precipitation received in large events (≥ 30 mm, Lauenroth and Sala 1992). Indeed, in semi-arid grasslands, the difference between wet and dry years is related to the presence or absence of large storms, which result in greater growing season and annual moisture inputs (Parton et al. 1981; Sala et al. 1992). Because total precipitation and the number of large events are highly correlated historically, it is difficult to assess the importance of large events (independent of annual precipitation amount) on ecosystem function. Consequently, predicted scenarios that emphasize an increase in large but less frequent events, without any increase in annual precipitation totals, represent conditions that are novel to this ecosystem (Williams et al. 2007). Thus, it is important to understand the impact of this forecast shift in precipitation regime on overall ecosystem function as well as responses of the dominant grass *B. gracilis*, particularly given this species' role in providing the primary economic-

based ecosystem service derived from shortgrass steppe— forage production.

To address this knowledge gap, we paired an analysis of growing season precipitation patterns during the past 65 years (1940–2005) with an experimental manipulation of growing season rainfall patterns that contrasted small, frequent events with large, infrequent events while maintaining total growing season precipitation amounts as equal. The focus of this experiment was growing seasonal rainfall (May–September) because precipitation inputs during this time account for greater than 70% of annual precipitation totals and large events most frequently occur during this time. Our primary goal was to determine the relative importance of small and large events during the growing season as they contribute to ecosystem function in this semi-arid shortgrass steppe ecosystem. Specific research questions included the following:

1. What trends in event size and dry interval length characterize the semi-arid shortgrass steppe in recent history (past 65 years)?
2. How do event size and frequency influence ANPP in a growing season of average precipitation?
3. What is the role of event size and frequency in influencing pulse-related ecophysiological responses of the dominant grass species, *B. gracilis*, to predicted changes in precipitation patterns?

Materials and methods

Site description

Research was conducted at the Central Plains Experimental Range (CPER) in northeastern Colorado, USA (40° 49' N 104° 46' W). The CPER is located within the Shortgrass Steppe Long-Term Ecological Research site, which is a partnership between Colorado State University and the United States Department of Agriculture—Agricultural Research Service and Forest Service. The shortgrass steppe region is a semi-arid grassland and receives an average of 321 mm of precipitation annually (Lauenroth and Sala 1992), 70% of which occurs during the May–September growing season. Mean annual temperature is 8.6°C and ranges from –5°C in January to 22°C in July (Milchunas and Lauenroth 1995). The plant community is dominated by the C₄ grass *B. gracilis* (blue grama), with other major species including *Bucloe dactyloides* (buffalo grass), *Artemisia frigida* (fringed sagewort), *Sphaeralcea coccinea* (scarlet globemallow) and *Opuntia polyacantha* (plains prickly pear). Average ANPP for the site is 97 g m⁻² (Lauenroth and Sala 1992) and *B. gracilis* comprises up to 90% of total aboveground grass biomass (Lauenroth et al. 1978).

While site management is focused on the varying intensities of cattle grazing in shortgrass steppe, the study site was located in a large enclosure from which cattle were removed in 1999. The soils of the study site are considered representative of the shortgrass steppe ecosystem and classified as Ustollic Haplargids (Petersen et al. 1993).

Analysis of the historical precipitation record

We obtained daily precipitation data from the CPER for the time period of 1940–2005 in order to characterize the recent historical precipitation record. Measured daily precipitation that was greater than or equal to 2 mm was considered biologically effective and included in our analyses. To make these data comparable to the period of experimental manipulation, we classified precipitation from 26 May–11 September of each year into rain events. In many cases, an individual day of recorded precipitation constituted a rain event; however, where consecutive days of measured precipitation were identified, these were collectively considered as one rain event. In order to avoid overestimating event size or underestimating the number of rain events in a given year, we divided cases of >3 days of consecutive measured precipitation into two events and assigned an event date according to the day in which the greatest quantity of precipitation was received.

We characterized the growing season of each year (1940–2005) according to cumulative precipitation, number of events, mean event size, mean dry interval length, and maximum event size. In addition, we analyzed separately only those years in which growing season precipitation was ±15% of the long-term mean (190 mm, or 161–218 mm). This allowed us to characterize the precipitation regime of these years for specific comparison with our experimental manipulation, which was based on average growing season rainfall amounts. To provide important context for the year in which this experiment occurred, we also calculated winter/early spring (January–April) precipitation for 2005 as well as long-term mean, maximum, and minimum values.

Rainout shelter design and construction

We erected fifteen 5.1-m² rainout shelters, which were designed to exclude ambient rainfall in experimental plots and were located in a relatively flat grassland site with spatially homogeneous cover and no obvious signs of past disturbance. Shelter construction began with trenching the perimeter of all plots to >1 m below ground surface and lining the trench with 6-mil plastic to minimize sub-surface water flow and prevent root and rhizome penetration into or out of the plot. The barrier enclosed a 2.25 × 2.25-m area to a depth of 1 m, which we refer to as the “sheltered area”. To eliminate surface water flow into plots, metal

flashing was also installed on three sides, extending ca. 0.3 m below ground surface and ca. 0.1 m above ground surface. Metal flashing was not installed on the remaining downhill side to allow for surface runoff to occur during the application of precipitation events. Dimensions for the sheltered area were selected so that natural rainfall would be excluded from a central 1.25×1.25 -m core plot designated for plant and soil sampling. The core plot was surrounded by a 0.5-m buffer. For rainout shelters of comparable size, Yahdjian and Sala (2002) estimated a 0.20-m edge effect associated with ambient rainfall, and our 0.50-m buffer effectively isolated core plots from nearly all ambient precipitation (J. Heisler-White, personal observation).

Shelter roofs were installed on 26 May 2005 and covered the plots for the duration of the growing season. The above-ground structure consisted of four wooden corner posts anchored in the soil to a depth of 1 m. Each roof was detachable and consisted of a wooden frame covered in clear corrugated polycarbonate sheeting (Green-Lite). Roofs 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. Shelter sides and ends remained open in order to maximize air movement and minimize temperature and humidity effects. While this design was chosen to minimize chronic microclimatic effects, such effects are unavoidable and so we report effects on both photon flux density and soil temperature. This experiment was not directly tied to ambient rainfall conditions for the 2005 growing season; therefore, no unsheltered control plots (no shelter but similar rainfall patterns) were possible. We established additional plots and collected similar measurements in adjacent “nonsheltered areas”. These plots were equivalent in size to the sheltered areas and contained core plots for sampling. All senesced plant material from previous years was removed (clipped) from sheltered areas in early May to ensure that all aboveground growth was produced during the 2005 growing season.

Experimental treatments and protocol

The experimental period consisted of 120 days (26 May–11 September 2005). Because the experimental objective was solely to alter the frequency of events and the dry interval duration, all sheltered plots received 190 mm of precipitation—the 30-year mean for the experimental period. The shelters were randomly assigned to one of the following treatments with five replicates each: (1) 12 events, (2) six events, or (3) four events. Rain events were spaced at 10-, 20-, or 30-day intervals, respectively, but event sizes were not constant throughout the growing season. Instead, the quantity for a given rainfall event was based on the 30-year

mean for the time period preceding it in order to follow seasonal distribution patterns. For example, a rainfall event on 14 June for a sheltered plot with a 20-day dry interval length would be based on the 30-year mean for the period of 26 May up to and including 14 June, and this event size would be larger than one in July, a month with much less rainfall historically. Water was applied from a tank stored onsite, which was stocked from a nearby groundwater well. Chemical analysis of the groundwater revealed that key plant nutrients (N, P, K) were below detectable levels. Rain events were applied manually through the use of 8-l watering cans at a rate of <25 mm/h to simulate fast-moving storm systems that characterize this region during summer months. Large events were applied over 2- to 3-day intervals to ensure that plots never received greater than ca. 25 mm in a single day, which also minimized run off. We chose 25 mm as the maximum daily rain event size based on a long-term data analysis by Lauenroth and Sala (1992) that identifies events >25 mm as relatively infrequent in occurrence.

Shelter effects on microclimate

We examined shelter effects on microclimate through a series of paired measurements inside and outside the plots. Using a 1-m linear quantum light sensor (Decagon, Pullman, Wash.), photosynthetically active radiation (PAR) was measured both above and below all shelter roofs ($n = 15$) at 0900, 1200, and 1400 hours MST on 21 July 2006 under full sun conditions. Four paired measurements were taken per shelter, and percent transmittance was calculated as a fraction of below roof PAR compared to the immediately above roof value. Percent transmittance was not significantly different at any of the time intervals and averaged $87 \pm 3\%$, which is similar to values observed in other permanent structures used to deflect ambient rainfall (Fay et al. 2000; Yahdjian and Sala 2002). Soil temperature was measured at 15-min intervals during July and August 2006 using soil temperature probes attached to multi-channel Hobo dataloggers (Onset, Bourne, Mass.). Measurements were taken at 5-cm depth both inside and outside the shelters ($n = 2$ temperature sensors per location) to allow for temperature to be directly analyzed in a pair-wise manner. This configuration was established in three shelters and included one shelter per treatment type. We detected a significant difference ($P < 0.01$) in daily mean, maximum, and minimum soil temperatures underneath the shelters as compared to the adjacent environment. Mean daily temperature was reduced by 1.8°C inside the shelters; however, this was likely due to shading effects of increased plant production inside the shelters rather than due to the shelters themselves. Maximum daily temperatures were also

reduced inside the shelters (ca. 3.4°C), but daily minimum temperatures were only affected slightly (ca. 0.8°C). These values are similar to those reported in other rainout shelters located in arid and semi-arid environments (Yahdjian and Sala 2002).

Soil moisture measurements

Soil moisture was measured ca. every 8 days from June to September. Volumetric water content was estimated via sensors that measured dielectric permittivity of the soil (ECH₂O soil moisture sensors, Decagon). Each sensor integrated soil moisture over the top 20 cm of soil and was placed within the core plot (ca. 0.75 m from the sheltered edge) of four shelters per treatment type and in all of the ambient plots. Sensor accuracy is estimated at ±4%. Measurement dates were selected to track soil moisture dynamics in response to the most frequent experimental precipitation regime (12 events). We measured soil water content just prior to a rain event and within 2–3 days post-rain event.

Field measurements of C and water relations in the dominant grass *B. gracilis*

In order to minimize investigator impacts in the plots, we limited our measurements of plant C and water relations to a mid-season water addition that occurred on 25–26 July 2005. This water addition occurred on days 60–61 of the experiment and all plots received a water addition at this time. Gas exchange (net photosynthesis) of *B. gracilis* was measured post-event on 27 July 2005 at 1100–1300 hours MST under high light conditions (fixed at 2,000 μmol m⁻² s⁻¹) using an LI-6400 portable photosynthesis system (Li-Cor, Lincoln, Neb.). In each of the 15 shelters, two measurements were taken on leaves of *B. gracilis*. Water relations of *B. gracilis* were estimated via midday xylem pressure potentials (XPP) using a Scholander-type pressure chamber (PMS instruments, Corvallis, Ore.). Leaves ($n = 3$ per shelter) were collected between 1100 and 1300 hours MST on 24 July 2005 (pre-event) and 27 July 2005 (post-event).

Aboveground net primary productivity

We estimated ANPP at the conclusion of the experiment by clipping all plant material in two 0.25-m² quadrats from within the core plot of each sheltered area. Harvested plant material was oven dried at 60°C for 72 h, sorted, and weighed to the nearest 0.01 g. Sorted classes included *B. gracilis*, other grasses, and forbs (including sub-shrubs). Cacti were not harvested and were estimated to cover no more than 5% of the sampling area.

Statistical methods

All analyses of historical and experimental data were conducted in SAS version 9.1, with the level of significance for all statistical tests set at $P < 0.05$. Pearson product-moment correlations were used to test for a significant relationship between growing season mean event size, maximum event size, and mean dry interval length, and ANPP. We used a single-factor generalized linear model (PROC GLM) with precipitation event number as the main effect to test for significant differences in ANPP. Because of the difference in sample size between ambient plots and experimental plots ($n = 3$ vs. $n = 5$), the LSMEANS procedure was used to contrast group means after significant ANOVA results.

For midday water potentials, a two-factor generalized linear model (PROC GLM) was used to evaluate the effect of time and treatment as well as their interaction. Factor levels for time were pre-event and post-event XPP. A single-factor ANOVA was used to compare leaf-level gas exchange measurements. For all statistical analyses, each shelter was considered an individual experimental unit ($n = 5$ per treatment).

To assess minor microclimatic effects associated with the shelters, we compared PAR levels and soil temperature based on paired measurements taken inside and outside the shelters. For the light environment, we used a single-factor ANOVA to compare PAR above and below all shelter roofs ($n = 15$). Soil temperature data were characterized based on the daily mean, maximum, and minimum value measured for each of three shelters. Temperature data were analyzed using an ANOVA that compared values inside and outside of the shelters across the growing season.

Results

Summary of historical precipitation trends

For the 65-year period (1940–2005), the mean rain event size during the growing season was 12.9 ± 0.4 mm, while the mean dry interval length was 8.4 ± 0.3 days. During this period, an average of 14 rain events occurred annually and the mean maximum rain event for a given year was 18.2 mm.

The number of growing season rainfall events varied from a low of seven events (1959–1960) to a high of 23 events (1996) while total seasonal rainfall ranged from a low of 53.8 (1964) to 370.6 mm (1997). The most common frequency of events was 16, which occurred in 10 years of the 65-year period (Fig. 1). There were no years in which six or four events occurred, but 12 events occurred in 4 years (Fig. 1). The 2005 growing season comprised nine rain events. It is important to note that less than one-third of

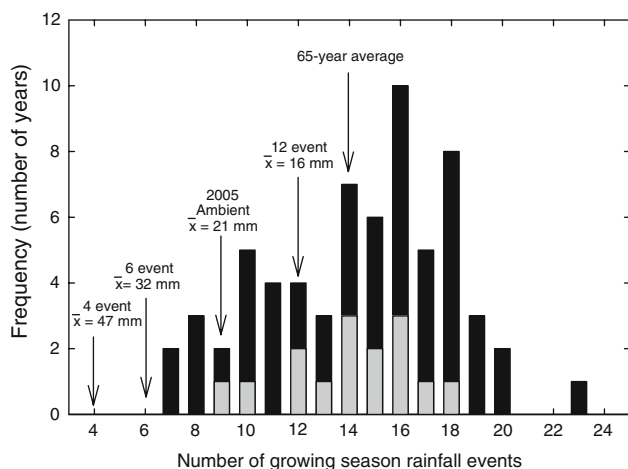


Fig. 1 Distribution of rainfall from 1940 to 2005 ordered according to the total number of growing season rainfall events and the frequency of years in which a given number of events occurred. *Black bars* indicate all years from 1940–2005, whereas *gray bars* indicate the number of rain events for only those years in which growing season precipitation was considered average ($190 \text{ mm} \pm 15\%$). For referencing the measured plots to this historical pattern, the number of rainfall events that occurred during the 2005 growing season (ambient) and the experimental treatments (12, six, and four events) are indicated

the years in the most recent past (1940–2005) were characterized by 12 or fewer events (the focus of this experimental manipulation) and greater than 50% of the years experienced 14–18 rainfall events (Fig. 1).

All years (1940–2005) of this analysis were characterized by at least one event that was $\geq 15.8 \text{ mm}$ —the mean event size for the 12 event precipitation treatment. In 45/65 years (70%), a rain event occurred that was $\geq 31.7 \text{ mm}$

(the average event size for the six event precipitation regime) whereas in 20/65 years (31%), at least one rain event in a given year exceeded 47.5 mm (the average event size for the four event precipitation regime).

Winter/early (January–April) spring precipitation averaged $56 \pm 3.6 \text{ mm}$ in the semi-arid steppe during the past 65 years but was highly variable ($\text{CV} = 52.5\%$). The maximum and minimum winter/early spring precipitation amounts for 1940–2005 were 154.9 and 16.8 mm, respectively, with ca. 70% of years falling within $\pm 50\%$ of the long-term mean (28–84 mm). In 2005, 78 mm of precipitation were received in winter/early spring.

ANPP trends during years of average rainfall

In only 15 years within the 65-year record was growing season precipitation within $\pm 15\%$ of the average (Fig. 1) and years in which 14–16 events occurred accounted for 8 of these years. We were able to identify only a single year in the 1940–2005 time period in which growing season precipitation was ca. average and 12 events occurred (Fig. 1, Table 1). This occurred during the 1975 growing season in which 12 events occurred and 177.5 mm of rainfall were recorded. ANPP in 1975 was estimated to be 94 g m^{-2} , which was similar to ANPP in the 12-event plots of the experimental manipulation (see below). In years of average precipitation and comparable event frequency to the 12-event plots in our experimental manipulation, ANPP varied from a low of 63 g m^{-2} to a high of 118 g m^{-2} (Table 1). Neither mean event size nor mean dry interval length was significantly correlated with ANPP in the historical climate record.

Table 1 Years in which growing season precipitation was $\pm 15\%$ of the long-term mean (1940–2005) for the Central Plains Experimental Range. CV Coefficient of variation calculated for the growing season, ANPP aboveground net primary productivity

Year ^a	ANPP ^b (g m^{-2})	Precipitation (mm)	No. of events	Mean event size ^c (mm)	Max. event size (mm)	CV for event distribution (%)	CV for event size
2005	105 ^d	189.7	9	21.1 ± 5.8	49.3	114.5	96.5
1974	63	168.1	10	16.8 ± 6.8	73.7	33.3	127.7
1975	94	177.5	12	14.8 ± 3.3	39.9	70.4	69.9
1955	70	167.1	13	12.9 ± 2.9	34.8	250.7	80.6
1946	97	161.3	14	11.5 ± 2.4	34.0	252.3	78.4
1953	102	190.5	14	13.6 ± 3.9	53.8	47.6	105.2
1990	90	172.0	14	12.3 ± 2.4	32.8	109.0	66.5
1952	118	210.6	15	14.0 ± 3.1	36.6	90.3	85.6
1983	115	189.2	15	12.6 ± 1.5	20.3	56.8	49.2

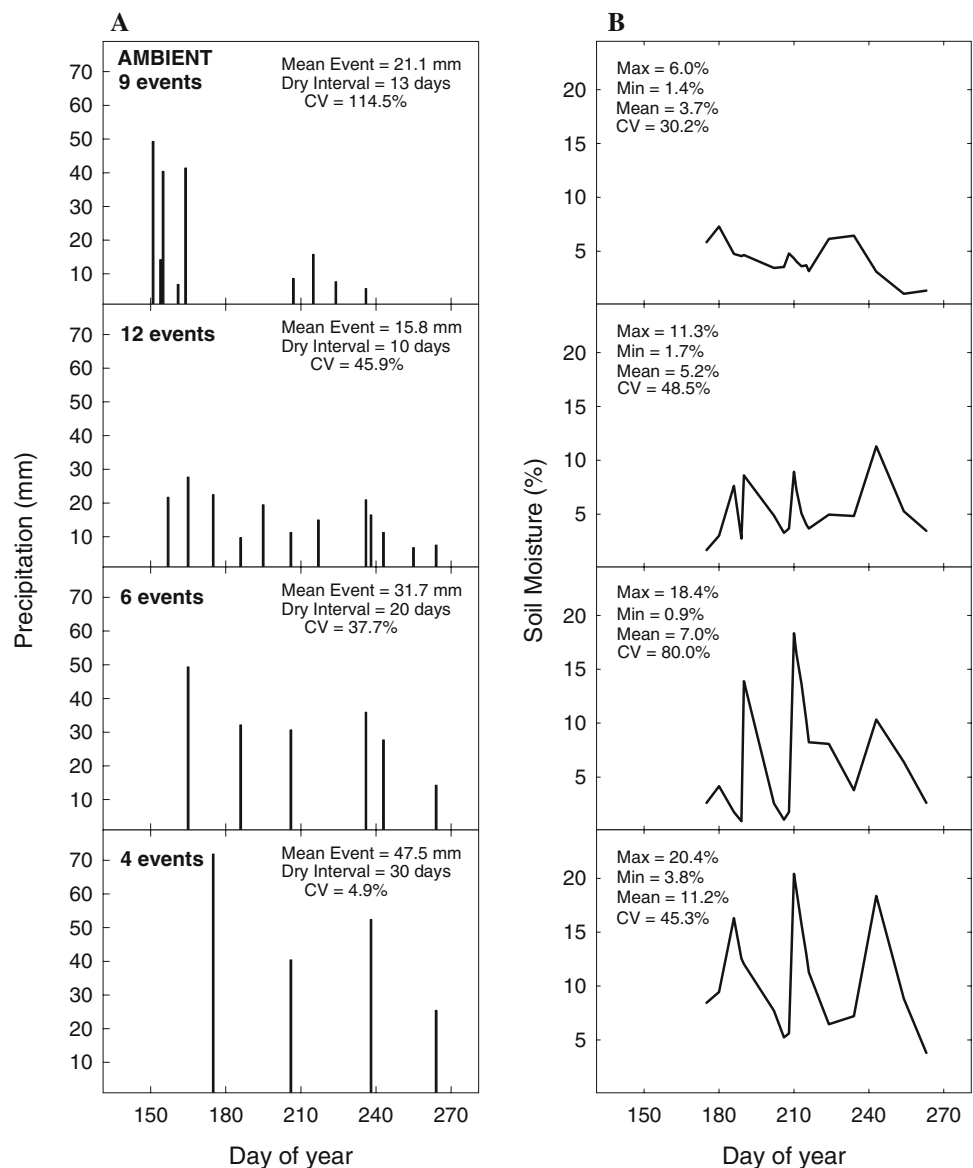
^a Years are ordered according to increasing number of events

^b Data for ANPP are from Lauenroth and Sala (1992)

^c Mean event size includes the SEM

^d In 2005, ANPP was estimated by clipping ambient plots at the end of the growing season

Fig. 2 a Distribution of growing season rainfall events for the ambient (unsheltered) and experimental plots during the 2005 growing season. **b** Soil moisture dynamics (0–20 cm) for the 2005 growing season. Descriptive statistics in each panel refer to just the time period of the experiment. CV Coefficient of variation



Precipitation for the 2005 growing season (ambient and experimental)

Precipitation for the 2005 growing season was 189.7 mm, which was distributed in nine rain events (Fig. 2). The total amount received was nearly identical to the 30-year mean (189.9 mm) and the amount that was applied to all sheltered plots. While completely fortuitous, this allowed us to make direct comparisons between sheltered and unsheltered plots with regard to precipitation amount. However, the distribution of precipitation events across the 2005 growing season was quite uneven, with 103.9 mm falling in the first 10 days of the experiment (Fig. 2a). Thus, the coefficient of variation (CV) for dry interval length was highest in ambient plots (114.5%) as compared to sheltered plots, where a CV

of 45.9, 37.7, and 4.9% was calculated for the 12-, six-, and four-event treatments, respectively (Fig. 2a). Two extended dry intervals occurred during the 2005 growing season, the first of which was 40 days in length and occurred from mid-June through late July. The second dry interval occurred during the final 30 days of the experiment (August–September). The majority of precipitation during the 2005 growing season fell in three large events, which were 49.3, 40.4, and 41.4 mm, respectively.

For the experimental plots, mean event size increased from 15.8 mm (12 events, range 6.7–27.7 mm) to 31.7 mm (six events, range 14.2–49.4 mm) to 47.5 mm (four events, range 25.4–71.8 mm), which resulted in a two-fold difference in mean event size between the 12- and four-event precipitation regimes (Fig. 2a). It is important to note that

the largest event for the 12-event treatment (27.7 mm) was similar in amount to the smallest event in the four-event treatment (25.4 mm), and that the largest event for the four-event treatment (71.8 mm) was exceeded just 5 times in the 65-year period. This large event was applied over a 3-day period in our experimental plots.

Soil moisture dynamics

Mean soil moisture for the 2005 growing season was lowest in the ambient plots (3.7%) and varied between a minimum value of 1.4% and a maximum value of 6.0% (Fig. 2b). In the experimental plots, mean soil moisture was inversely related to the number of rainfall events, with mean soil moisture values increasing from 5.2% to 7.0% to 11.2% for the 12-, six-, and four-event treatments, respectively (Fig. 2b). Soil moisture data for the 2005 growing season begins on day 30 of the experiment and does not capture the soil moisture associated with the large rain events in the ambient plots during the early part of the growing season. Maximum values for soil moisture were observed in the six- and four-event plots (18.4 and 20.4%, respectively), which were nearly two-fold higher than in the 12-event plots (11.3%). Variability in soil moisture dynamics peaked in the six-event plots (CV = 80.0%) and was lowest in the ambient plots (CV = 30.2%).

Aboveground net primary productivity

For the 2005 growing season, the number of precipitation events had a significant effect on ANPP. In the 12-event plots, total ANPP was $105.1 \pm 24.1 \text{ g m}^{-2}$ (Fig. 3). This was significantly lower than the six-event and four-event plots, where total ANPP was $177.7 \pm 37.7 \text{ g m}^{-2}$ and $183.7 \pm 37.2 \text{ g m}^{-2}$, respectively (Fig. 3). Unsheltered plots exposed to ambient conditions had the lowest total ANPP, which was $67.3 \pm 8.9 \text{ g m}^{-2}$ (Fig. 3). Forbs comprised 5–10% of the total biomass within all rainfall treatments (both experimental and ambient) and no significant treatment effect could be identified (data not shown). The total ANPP response was driven primarily by *B. gracilis* in all treatments.

Plant C-water relations

We focused our measurements of plant C-water relations on a precipitation event at the mid-point of the experiment (day 60; 25 July 2005) in which all treatments experienced a water application on the same day and had cumulatively received similar total precipitation inputs for the growing season. The mid-season precipitation event was applied as 11.2, 30.7, and 40.4 mm for the 12-, six-, and four-event plots, respectively. Midday water potentials measured pre-

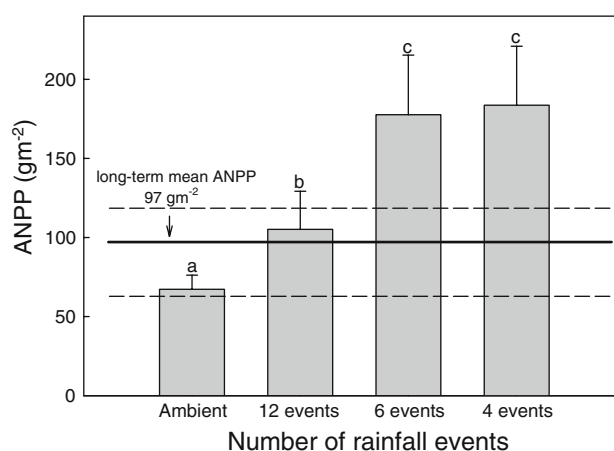


Fig. 3 Total aboveground net primary productivity (ANPP; g m^{-2}) for ambient and experimental plots in 2005. Error bars denote 1 SEM and different letters indicate significant differences ($P < 0.05$) among treatments. The solid horizontal line indicates the long-term (52 year) mean ANPP for the Central Plains Experimental Range. The dashed horizontal lines indicate the long-term maximum (118 g m^{-2}) and minimum (63 g m^{-2}) values for ANPP in growing seasons characterized by average precipitation

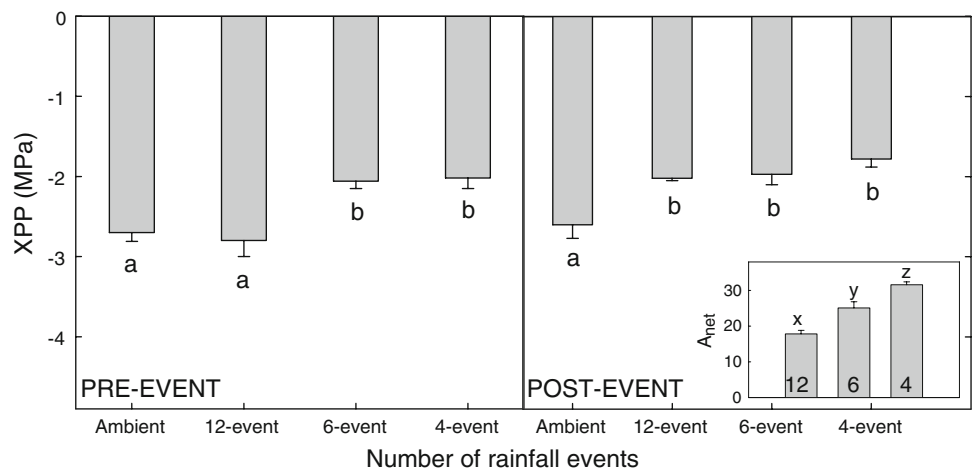
event (24 July 2005) revealed that both the ambient and 12-event plots ($-2.7 \pm 0.1 \text{ MPa}$ and $-2.8 \pm 0.02 \text{ MPa}$, respectively) were significantly more water-stressed than the six- and four-event plots ($-2.1 \pm 0.09 \text{ MPa}$ and $-2.0 \pm 0.1 \text{ MPa}$, respectively; Fig. 4). Midday water potentials were measured again post-event on 27 July 2005 and revealed that the 12-, six-, and four-event plots were no longer significantly different. Thus, while there was no significant change in midday water potential for the six- and four-event plots, water relations in the 12-event plots significantly increased ($-2.0 \pm 0.03 \text{ MPa}$; Fig. 4). Midday water potentials for the ambient plots remained unchanged, as no rainfall occurred during the time period between pre- and post-event measurements.

Post-event measurements of leaf-level gas exchange revealed an inverse relationship between rain event frequency and A_{net} . Sheltered plots that had received the second of four events had the highest photosynthetic rates ($31.6 \pm 0.8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; Fig. 4 inset). In contrast, the 12-event plots (which had just received event six of 12) had the lowest photosynthetic rates ($17.8 \pm 1.0 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; Fig. 4 inset).

Discussion

In semi-arid grasslands, the temporal distribution of precipitation events strongly regulates periods of biological activity, which integrate across the growing season to determine annual rates of ANPP. While annual and seasonal precipitation patterns are key drivers of ecosystem processes, the

Fig. 4 Midday leaf water potentials for *Bouteloua gracilis* before and after a mid-season precipitation event. *Inset* Post-event measurements of leaf-level gas exchange in *B. gracilis* in the experimental plots. For each precipitation frequency, presented values are treatment means \pm 1 SE. Significant treatment differences are indicated by different letters. Units for A_{net} are $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. *XPP* Xylem pressure potentials



timing, extent, and duration of precipitation pulses most directly influence how rainfall is translated into soil water that is available for plant uptake (Loik et al. 2004). In 2005, we manipulated the number of growing season rainfall events (while holding total precipitation constant) and determined that larger, less frequent rainfall events resulted in greater ANPP and mid-season photosynthetic rates in the dominant grass, *B. gracilis*. Our goal was to expose treatment plots to predicted precipitation regimes that are largely absent from the historical record and our analyses of long-term data confirmed this. In years in which growing season precipitation was considered average, event number varied between nine and 18, with the 2005 growing season being characterized as having the fewest number of events in the last 65 years. While a growing season precipitation pattern of 12 events (with average growing precipitation) occurred twice during the last 65 years, years with four or six events did not occur during this time period.

Given the variability that exists in event number and mean event size during growing seasons of average precipitation, it is not surprising that annual precipitation amount accounts for only 39% of the interannual variability in ANPP within this semi-arid grassland (Lauenroth and Sala 1992). In this study, all experimental plots received ca. 190 mm of rainfall, but total ANPP varied by ca. 75% from $105.1 \pm 24.1 \text{ g m}^{-2}$ to $183.7 \pm 37.2 \text{ g m}^{-2}$. Including ambient plots in the analyses further increased variation in ANPP to 173%. These results from ambient plots highlight the importance of the regularity in event distribution, and the dry interval length. Clearly this grassland is quite sensitive to rainfall event timing and amount, and a directional change in precipitation regime to fewer events that are larger in size or alterations in the timing of those events will have immediate and direct consequences on plant C and water relations and ecosystem function (Sala and Lauenroth 1982).

Interannual variability in winter/early spring precipitation may interact with growing season rainfall to influence

annual ANPP patterns. While a relatively minor (30%) contributor to total annual precipitation, winter/early spring precipitation establishes soil moisture content at the onset of the growing season and frequently represents a peak in annual soil moisture dynamics (Lapitan and Parton 1996). In 2005, winter/early spring precipitation was 78 mm, which was slightly above the long-term mean of $56 \pm 3.6 \text{ mm}$. Exceptionally dry or wet winter/early spring conditions, even if followed up by average growing season precipitation inputs, may modify annual rates of ANPP.

Large versus small events

Biological effects

The dominant grass species at the short-grass steppe (*B. gracilis*) has been shown to respond rapidly to events as small as 5 mm through improved water relations (Lauenroth and Sala 1982). A similar result was observed in this experiment, where midday water potential of *B. gracilis* significantly increased following a mid-season water pulse of 11.2 mm. Our experimental results also revealed the importance of pulse intensity and antecedent conditions as primary drivers of the physiological response of *B. gracilis*. Prior to the mid-season soil moisture pulse that we monitored, XPP of *B. gracilis* in the 12-event plots was significantly lower than in the six- and four-event plots, respectively. This was in spite of the fact that the 12-event plots had most recently received precipitation—only 9 days before. After the precipitation event, significant responses in XPP were only observed in the frequent, small pulse event treatments (12-events), where soil moisture was considerably less prior to the pulse. This suggests that water relations of this species are (1) very dynamic in growing seasons that are dominated by small pulses with few or no large events and (2) that under such conditions *B. gracilis* episodically alternates between stressed and non-stressed

conditions. Post-event measurements of A_{net} revealed somewhat different results, as leaf-level gas exchange remained considerably lower in grasses in the frequent, small event plots as compared to those in the infrequent, large event plots. This mismatch between water status and A_{net} suggests that the more water stressed history of these plots reduced the photosynthetic capacity of *B. gracilis* and its ability to recover when water status improved (Sala et al. 1982). The relative unresponsiveness of the six- and four-event plots to the mid-season water event also provides insight. Prior to the event, soil moisture was greatest in the six event plots and sufficient to sustain high levels of photosynthetic activity. The overall greater availability of soil moisture that resulted from the previous precipitation events likely maintained higher photosynthetic capacity in these grasses. Unfortunately, we do not have data for A_{net} prior to the pulse, so it we could not determine if *B. gracilis* in any of the plots responded with an increase in leaf-level gas exchange. Nonetheless, the ability of *B. gracilis* to maintain relatively high photosynthetic rates when there was a history of large precipitation events (within the context of average growing season amounts) is a trait consistent with the increase in ANPP in the six- and four-event treatments.

Hydrology

Two key characteristics drive the ecohydrology of semiarid grasslands: (1) evaporative demand exceeds precipitation inputs at both short- (i.e., daily) and long-term (i.e., annual) time scales (Noy-Meir 1973; Sala et al. 1992) and (2) plant cover is typically less than 50%, which results in substantial bare soil evaporation (Burke et al. 1998). Consequently, nearly all precipitation inputs during the growing season are returned to the atmosphere by plant processes (transpiration) and/or purely physical processes (evaporation; Noy-Meir 1973; Sala et al. 1992). For this reason, the spatial and temporal availability of soil moisture for biological processes is directly linked to event size and frequency. The major consequence of a precipitation regime that is dominated by frequent, small events (semi-arid grasslands) is that the water input by individual events remains in the uppermost soil layers, which are most vulnerable to bare soil evaporation (Sala and Lauenroth 1985; Wythers et al. 1999). This results in very dynamic soil moisture patterns (Lauenroth and Bradford 2006). Growing season estimates of evaporation for the shortgrass steppe are 5–8 mm/day following a rain event (Wythers et al. 1999; Lauenroth and Bradford 2006); thus it is reasonable to assume that precipitation applied experimentally at ca. 10-day intervals (the 12-event treatment) was entirely lost to the atmosphere prior to the next event. This is consistent with the pulse-reserve paradigm. In the frequent, but small event plots,

mean soil moisture was ca. 5% and never exceeded 11%. In contrast, large precipitation events (applied at 30-day intervals—four events) recharged soil moisture to the extent that it rarely dropped below 5%. Certainly, a considerable percentage of the water from large events would also be rapidly lost to the atmosphere via both evaporation and transpiration; however, two conditions result that make these large pulses more biologically effective between precipitation events. First, large events likely led to increased soil moisture at greater depths (not measured in this study, but see Sala et al. 1992; Parton et al. 1981) where the influence of evaporative demand is negligible. Second, large events resulted in a greater number of growing season days in which soil moisture at 0–20 cm was elevated in contrast to the 12-event plots. It is this depth in the soil profile in which ca. 50% of total fine root biomass is located (Sala et al. 1992), allowing *B. gracilis*, in particular, to utilize both shallow and deeper soil moisture resources. This translates into important immediate effects on plant ecophysiology, which integrate into greater ANPP when considered across the time span of the growing season.

An additional aspect of hydrology not quantified in this experiment is that of hydraulic redistribution, which has been documented for several species in arid and semi-arid ecosystems (Caldwell et al. 1998). Ryel et al. (2003) demonstrated that roots of *Artemisia tridentata* can effectively move water from rainfall events <8 mm to deeper zones in the soil profile and later use this water for transpiration. This mechanism of efficient water use by plants merits further study under conditions of forecast altered rainfall regimes.

Uniform versus stochastic precipitation events

In semi-arid ecosystems, precipitation events are rarely evenly spaced in time (Loik et al. 2004), and it is unlikely that they will be in the future. For this reason, dichotomous questions addressing “frequent, small events versus infrequent, large events” encompass only one key aspect of precipitation variability while ignoring another one—stochasticity. In our analysis of the precipitation record (1940–2005), we identified 9 years in which total precipitation for the growing season was ca. average ($\pm 15\%$ of the long-term mean). While considered “average” at the aggregate temporal scale of the growing season, these 9 years differed considerably in the total number of events, mean event size, maximum event size, and the variability in event distribution. As a result, ANPP varied more than twofold, from a low of 63 g m^{-2} to a high of 184 g m^{-2} across this range of “average amount” years. Curiously, the year in which ANPP was lowest had the largest maximum event size (73.7 mm), during which >40% of the growing season precipitation was received. Additionally, the remaining

90 mm was divided into nine events with fewer than 10 mm each. In contrast, the year in which ANPP was highest had a maximum event size of 36.6 mm, with the remaining 14 growing season events sharing 180 mm. Similar to analyses in other grasslands, we were not able to identify a significant relationship between mean event size or dry interval length and ANPP (Nippert et al. 2006; Swemmer et al. 2006). Nonetheless, our results suggest that the relative evenness of event size in combination with event number may have important effects on ecosystem function. Future research focusing on these other aspects of precipitation regimes is needed to elucidate the relative importance of event size and distribution in this and other ecosystems.

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