Contrasting above- and belowground sensitivity of three Great Plains grasslands to altered rainfall regimes

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Abstract

Intensification of the global hydrological cycle with atmospheric warming is expected to increase interannual variation in precipitation amount and the frequency of extreme precipitation events. Although studies in grasslands have shown sensitivity of aboveground net primary productivity (ANPP) to both precipitation amount and event size, we lack equivalent knowledge for responses of belowground net primary productivity (BNPP) and NPP. We conducted a 2-year experiment in three US Great Plains grasslands – the C_4-dominated shortgrass prairie (SGP; low ANPP) and tallgrass prairie (TGP; high ANPP), and the C_3-dominated northern mixed grass prairie (NMP; intermediate ANPP) – to test three predictions: (i) both ANPP and BNPP responses to increased precipitation amount would vary inversely with mean annual precipitation (MAP) and site productivity; (ii) increased numbers of extreme rainfall events during high-rainfall years would affect high and low MAP sites differently; and (iii) responses belowground would mirror those aboveground. We increased growing season precipitation by as much as 50% by augmenting natural rainfall via (i) many (11–13) small or (ii) fewer (3–5) large watering events, with the latter coinciding with naturally occurring large storms. Both ANPP and BNPP increased with water addition in the two C_4 grasslands, with greater ANPP sensitivity in TGP, but greater BNPP and NPP sensitivity in SGP. ANPP and BNPP did not respond to any rainfall manipulations in the C_3-dominated NMP. Consistent with previous studies, fewer larger (extreme) rainfall events increased ANPP relative to many small events in SGP, but event size had no effect in TGP. Neither system responded consistently above- and belowground to event size; consequently, total NPP was insensitive to event size. The diversity of responses observed in these three grassland types underscores the challenge of predicting responses relevant to C cycling to forecast changes in precipitation regimes even within relatively homogeneous biomes such as grasslands.

Keywords: aboveground productivity, belowground productivity, carbon cycling, climate change, ecosystem function, ecosystem services, grassland, precipitation amount, precipitation pattern

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Introduction

Assessment of the regional-scale carbon (C) cycling consequences of forecast alterations in precipitation amount and pattern (Easterling *et al.*, 2000; IPCC, 2007) requires knowledge of the nature and range of responses of key ecosystem processes, such as net primary productivity (NPP), across multiple ecosystems (Luo *et al.*, 2011; Fraser *et al.*, 2012). While forecast changes in annual precipitation amounts vary widely among climate models and geographic location (IPCC, 2007; Zhang *et al.*, 2007), forecasts are more consistent for a general intensification of the global hydrological cycle leading to increases in interannual variation in precipitation amount (wetter wet and dryer dry years)

and a shift in rainfall patterns toward a greater frequency of larger (IPCC, 2007) and extreme (Jentsch *et al.*, 2007; Jentsch & Beierkuhnlein, 2008; Smith, 2011) events. Such changes have already been observed in North American grasslands; over the last 20 years in the Midwestern United States, precipitation inputs from storms 7.6 cm or larger have increased by 52% relative to long-term trends (Saunders *et al.*, 2012). In most terrestrial ecosystems, precipitation is a major driver of C dynamics, and this is certainly true for grasslands across the central US where a strong relationship exists between mean annual precipitation (MAP) and aboveground net primary productivity (ANPP; Sala *et al.*, 1988; Del Grosso *et al.*, 2008). Additionally, based on regional-scale analyses of long-term temporal relationships between precipitation and ANPP, productivity responses to altered precipitation amounts are expected to vary predictably across gradients of MAP and ANPP

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(Huxman *et al.*, 2004; Guo *et al.*, 2012). However, such inferences have been challenged by recent observational and experimental results showing a surprising degree of variability in productivity responses to altered rainfall amounts and patterns across several grassland types (Knapp *et al.*, 2002; Frank, 2007; Heisler-White *et al.*, 2009; Cherwin & Knapp, 2012; Byrne *et al.*, 2013; Zhang *et al.*, 2013a,b). Much less is known about belowground net primary productivity (BNPP) responses to variations in precipitation amount (Frank, 2007; Byrne *et al.*, 2013) and virtually all productivity responses to alterations in precipitation event size are limited to those aboveground (Knapp *et al.*, 2002; Heisler-White *et al.*, 2008, 2009; Muldavin *et al.*, 2008; Fay *et al.*, 2011; Thomey *et al.*, 2011; Cherwin & Knapp, 2012; Sponseller *et al.*, 2012). While information about ANPP responses is integral for predictions of changes in key ecosystem services such as forage production, BNPP measures are critical for assessments of ecosystem carbon sequestration.

Over two growing seasons, we experimentally augmented water inputs to three major central US grasslands via the addition of many small events or a few large events and quantified responses of above- and belowground productivity to increased rainfall amount and altered input pattern. We used identical protocols at all sites to alleviate concerns that divergent results from past field experiments may reflect methodological differences that can confound comparisons among ecosystems (Fraser *et al.*, 2012). We tested predictions derived from conceptual models of production–precipitation relationships as well as inferences from recent field experiments. First, we tested the hypothesis that productivity responses to alterations in precipitation amount would vary inversely with MAP and site productivity (e.g., more arid grasslands will respond more to increased precipitation than more mesic grasslands; Huxman *et al.*, 2004). Alternatively, more arid sites may be less responsive to wet years than mesic sites because of reduced plant (meristem) density and low growth potential of individual plants in these ecosystems (Knapp & Smith, 2001). Second, we tested the stress threshold hypothesis (Knapp *et al.*, 2008), which predicts that in ecosystems with low annual precipitation and high evaporative demand, a shift to fewer but larger rainfall events will have a positive impact on NPP. This is because such ecosystems are chronically in a state of water stress due to low soil moisture and large events more effectively alleviate soil water stress than smaller events. Alternatively, in higher MAP ecosystems where soil moisture is usually less limiting, many small events will maintain soil water at nonstressful levels more consistently and a shift to fewer but larger events will have a negative impact on

productivity by increasing plant water stress, compared with the same amount of precipitation coming in smaller, more closely spaced events (Knapp *et al.*, 2008). Finally, we predicted that in all three grasslands, ANPP and BNPP would respond similarly to alterations in precipitation amount and pattern, consistent with previous grassland experiments (Xu *et al.*, 2013), but in contrast to results from forests where there is evidence that ANPP and BNPP may respond in opposing ways to changes in soil moisture (Newman *et al.*, 2006). Determining if aboveground productivity and belowground productivity respond similarly in direction and magnitude is key for predicting changes to carbon budgets under altered environmental conditions (Friedlingstein *et al.*, 1999; Wullschleger *et al.*, 2001).

Materials and methods

We examined above- and belowground vegetative responses to changes in precipitation pattern and amount in US tallgrass, northern mixed grass, and shortgrass prairies (Table 1). To incorporate natural rainfall variability into treatments, water additions occurred within the backdrop of natural rainfall patterns with amounts added based upon historical rainfall records from each site.

Experimental sites

We chose sites representative of three main ecosystem types spanning a productivity gradient within the North American grassland biome. These sites varied in their climatic regimes, soil properties, and composition of vegetation (Table 1), spanning many of the key gradients well documented across the central US grassland region.

The shortgrass prairie (SGP) site was located in Northern Colorado at the Central Plains Experimental Range in an area that had been protected from cattle grazing for 12 years at the start of the experiment. This site receives, on average, 321 mm of rainfall annually, much of which falls during the growing season (May–August), and has a mean annual temperature (MAT) of 8.6 °C (Lauenroth & Burke, 2008). ANPP in control plots during 2011 and 2012 was 47.5 g m^{-2} and vegetation is dominated by perennial, rhizomatous C$_4$ grasses, particularly *Bouteloua gracilis*. The northern mixed grass prairie (NMP) site was located in Eastern Montana at the Fort Keogh Livestock and Range Research Laboratory in an area ungrazed since 1999. This site receives only slightly more precipitation annually (342 mm) than SGP, but MAT is lower (7.8 °C; 1960–2010 USCRN data; Diamond *et al.*, 2013) and the region is more productive (ANPP from control plots 115.5 g m^{-2}). This site is dominated by perennial C$_3$ graminoids – primarily *Hesperostipa comata*, *Pascopyrum smithii*, and *Carex filifolia*. The tallgrass prairie (TGP) site was located in the Flint Hills region in Eastern Kansas at the Konza Prairie Biological Station in the upland portion of a watershed ungrazed for over 30 years. In contrast to the other two sites, this site was burned in each year of this study and historically has been burned frequently,

Table 1 Climate, soil, and vegetative characteristics of the Central Plains Experimental Range, Nunn, CO (SGP), Fort Keogh Livestock and Range Research Laboratory, Miles City, MT (NMP), and Konza Prairie Biological Station, Manhattan, KS (TGP). All vegetation characteristics except mean ANPP were calculated from species compositional measurements taken in 1 m^2 control plots in 2011 and 2012. ANPP values reflect average plot-level measurements in control plots over the 2 years of the experiment

	SGP	NMP	TGP
General			
Latitude	40°84′N	46°31′N	39°09′N
Longitude	104°76′W	105°98′W	96°55′W
Grassland type	Semiarid shortgrass	Northern mixed grass	Mesic tallgrass
Climate			
MAP (mm)*	321	342	835
Mean growing season precipitation (mm)*	204	193	428
MAT (°C)*	8.4	7.8	12.5
Soil			
A horizon texture†	Fine sandy loam	Loam	Silty clay loam
B horizon texture†	Sandy clay loam	Clay Loam	Silty clay loam
Pedon description†	Aridic Argiustoll	Aridic Argiustoll	Udic Argiustoll
Available water capacity†	Moderate – 17.5 cm	High – 28.7 cm	Moderate – 16.3 cm
Vegetation			
Mean ANPP (g m^{-2})	47.5	115.5	342.6
Species pool‡	35	36	38
Species richness (S)	6.4	13.4	9.5
Diversity (H′)	0.97	1.72	1.30
Evenness	0.54	0.67	0.58
C3 grass (%)	20.5	83.6	13.2
C4 grass (%)	70.7	3.1	81.0
Forb (%)	5.4	8.9	3.0
Annual (%)	2.5	13.5	0
Perennial (%)	96.5	86.4	100

*Obtained from NOAA climate data from Miles City, MT, Nunn, CO, and Manhattan, KS.
†Soil Survey Staff (2013).
‡Total number of species encountered in all control plots within a site.

reflecting historical and managed fire regimes for the region (Knapp, 1998). The TGP site receives an average of 835 mm of rainfall annually. ANPP in control plots was 342.6 g m^{-2}, and consisted mostly of perennial, rhizomatous, C$_4$ grasses – namely *Andropogon gerardii*, *Sorghastrum nutans*, and *Schizachyrium scoparium* (See Table 1 for additional information about each site).

Experimental treatments

We added water to the experimental plots in two different patterns while keeping total rainfall amount constant between treatments. We added either numerous (11–13) small events spaced relatively evenly throughout the growing season (Many-Small treatment) or larger amounts of water were added to naturally occurring large storms a few times (3–5) over the course of the growing season (Few-Large treatment). Control plots received ambient precipitation (with one exception – see section 'Treatment effects on precipitation regimes' below), which permitted us to assess the effects of increases in total precipitation as well as alterations in event size and number. The treatments were applied based on three criteria: (i) If

no natural large rain event (see paragraph below for 'large' event size categorization details) occurred in a 7-day period, a small water addition was applied to the Many-Small treatment; (ii) when a natural large precipitation event occurred, the sum of all water previously added to the Many-Small treatment since the last large event was then added to the Few-Large treatment; and (iii) if there were no large precipitation events for 28 consecutive days, a water application was added to the Few-Large treatment.

Natural precipitation regimes vary substantially among these three grasslands, so we based the size of the small water additions and the timing of large events on simulations of different combinations of these two variables using historical data from each site. The goal of these simulations was to identify treatment regimes that would consistently manipulate precipitation pattern and amount among the three sites while maintaining total precipitation amounts within historical ranges of variability. Based on our simulations, we added 5.6 mm of water every 7 days for the Many-Small treatment at the SGP and NMP grasslands and 10.3 mm at TGP. We designated 'large' rainfall events (i.e., events that triggered the additions to the Few-Large treatment) as those of a size

greater than or equal to: 9.9 mm (85th percentile event size) at SGP, 9.1 mm (85th percentile) at NMP, and 19.8 mm (80th percentile) at TGP.

Treatments (local aquifer water) were applied with a garden watering wand in the morning or evening to minimize evaporative loss during watering events. Large event additions were applied as 5–10 mm portions separated by ca. 5 min to allow water to penetrate into the soil and avoid aboveground lateral flow.

Treatment effects on precipitation regimes

From late May through August of 2011 and 2012 at each site, precipitation was manipulated so that total growing season (May–August) rainfall was increased 15–50% in the Many-Small and Few-Large treatments relative to control plots. For both years, this precipitation increase required 11–13 events in the Many-Small treatment and 3–5 events in the Few-Large treatment (Fig. 1). The size of added events across sites and the 2 years ranged from 5.6 to 10.3 mm in the Many-Small treatment and from 12.3 to 37.8 mm (added on top of large ambient storms) in the Few-Large treatment (Table S1). The mean size of rainfall events, the proportion of precipitation from large events (defined as precipitation events in the 80th percentile), the number of and proportion of rainfall from extreme events (95th percentile), and the average length of dry periods were all increased in the Few-Large treatment relative to the Many-Small treatment in both years and at all sites while the number of events was decreased (Table S1). All Few-Large events (i.e., the sum of ambient and added rainfall during a treatment application) fell within the natural range of large rainfall events at each site such that, (i) treatment events were never larger than the long-term maxima; and (ii) the average size of treatment events were similar to the long-term mean of large event sizes (Table S1). In 2011, control plots received ambient precipitation, but due to low levels of growing season precipitation at all sites in 2012, one water addition corresponding to the 90th percentile event size at each site (SGP: 15.7 mm; NMP: 15.6 mm; TGP: 37.4 mm) was added to all plots when the cumulative growing season precipitation dropped below the historical 25th percentile.

Experimental design

At each site, ten 25 m^2 (5 × 5 m) blocks were established as a randomized complete block design in a relatively flat area with plant communities representative of the larger area. Within these, 4 m^2 (2 × 2 m) subplots (two watering pattern treatments, one control, and one empty) were randomly assigned with 0.5 m between subplots. In the center of each subplot, 1.96 m^2 (1.4 × 1.4 m) sampling plots were established with a 0.8 m buffer between the edge of sampling plots and adjacent treatment subplots. Soil moisture measurements indicated that this buffer was sufficient to avoid any influence of adjacent water applications. Due to inherently low levels of green biomass in SGP, mesh wire fencing (1 m tall) was installed around each block to minimize small mammal herbivory in watered plots.

Data collection

Throughout the 2011 and 2012 growing seasons (May–September), hourly measurements of volumetric soil water content integrated over 0–20 cm were made at each site (ECH_2O probes, Decagon Devices Inc., Pullman, WA, USA) and averaged to obtain daily means in three blocks at each site. Probes were calibrated using soil bulk density values and gravimetric soil moisture measurements over a range of soil moisture conditions.

Site community composition at each site was assessed by estimating plant species abundances visually to the nearest 1% in a 1 m^2 area within each control plot in 2011 and 2012.

Aboveground net primary productivity (ANPP) of herbaceous vegetation was estimated at each site by harvesting all aboveground biomass at the end of the growing season (September) in 3, 0.1 m^2 subplots per sampling plot in 2011 and 2, 0.1 m^2 subplots per sampling plot in 2012. Samples were dried at 60 °C for 48 h, sorted to remove any previous year's plant material, and weighed.
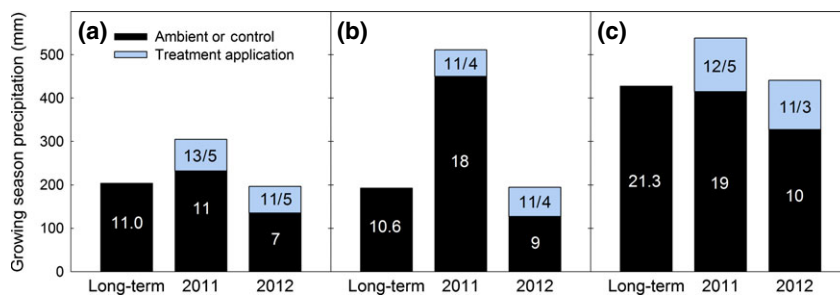

Fig. 1 Long-term and treatment growing season (May–August) precipitation characteristics at all sites – (a) Central Plains Experimental Range (SGP; 1969–2010), (b) Fort Keogh Livestock Range and Laboratory (NMP; 1960–2010), and (c) Konza Prairie Biological Station (TGP; 1960–2010). Numbers within the black bars indicate the average number of events >5 mm in historical records in the Long-term bars or the number of events >5 mm experienced by the control plots in the 2011 and 2012 bars. The first number within the lightly shaded or blue bars indicates the number of water additions added to the Many-Small treatment and the second indicates the number added to the Few-Large treatment.

Belowground net primary productivity (BNPP) was estimated using root ingrowth cores (Persson, 1980) in one subplot in 2011 and two subplots in 2012 (the latter were pooled) at each site. Mesh cylinders 5 cm in diameter made from 2 mm fiberglass screen were inserted 30 cm deep into the ground in May to sample the majority of root growth (Jackson *et al.*, 1996). These cores were filled with native soil sieved with a 2 mm screen to remove pre-existing root biomass, and then packed to a density approximate of natural soil conditions. Root ingrowth cores were removed in September and separated into 0–15 ($BNPP_{0-15}$) and 15–30 cm ($BNPP_{15-30}$) depths. Roots were removed from the soil using a hydropneumatic root elutriator (Smucker *et al.*, 1982) for SGP and NMP sites and by hand washing for the TGP site (due to high soil clay content). Roots were dried at 60 °C for 48 h, and weighed. Ash mass of samples was obtained by heating samples in a muffle furnace at 450 °C for 4 h and then subtracted from ash-inclusive dry mass. ANPP and BNPP estimates for each plot were summed to calculate total NPP per plot.

Statistical analyses

Soil moisture measurements for each site and treatment were compared over the entire growing season using repeated-measures ANOVA with an autoregressive heterogeneous covariance structure (proc MIXED in SAS, Version 9.3, Cary, NC, USA). Least squared means were compared among treatments when the site-based model showed the treatments had a significant overall effect. The response variables ANPP, BNPP, NPP, BNPP:ANPP, and $BNPP_{0-15} : BNPP_{15-30}$ were natural log transformed to satisfy normality assumptions and analyzed using repeated-measures ANOVA with heterogeneous compound symmetry covariance structure over both years of the experiment (MIXED procedure in SAS). Years were combined in a repeated-measures ANOVA because of nonsignificant interactions between treatment and year (Table S4), different

variances between the 2 years, and a lower corrected Akaike information criterion (AICc) in the repeated-measures model allowing for different variances between years than the model keeping the variances constant. To assess differences between ANPP and BNPP sensitivity within a site, we calculated differences between watering treatment and control productivity (for both ANPP and BNPP) pairing plots within a block and then divided this by the amount of precipitation that treatment plots received throughout the growing season. We then analyzed these sensitivity values using a repeated-measures ANOVA with heterogeneous compound symmetry covariance structure over both years of the experiment. Differences in above- and belowground sensitivity to watering pattern were assessed by comparing ANPP and BNPP responses in each treatment to control plots (i.e., did the treatments cause a significant response?).

Results

Soil moisture responses

Soil moisture was measured in both years at all three sites, but we report only the 2012 data set due to two several-week periods of probe malfunctions at two of the sites in 2011. For periods of data overlap between the 2 years, 2011 responses to treatments were consistent with 2012 data, as expected given that treatments were applied with the same protocol each year. In 2012, growing season average soil moisture levels in control plots were significantly different among sites (Table S2). At all sites, small and large water additions resulted in increased soil moisture (Fig. 2), but despite obvious differences among control and treatment plots in soil moisture after water additions, season-long soil moisture averages were not significantly different
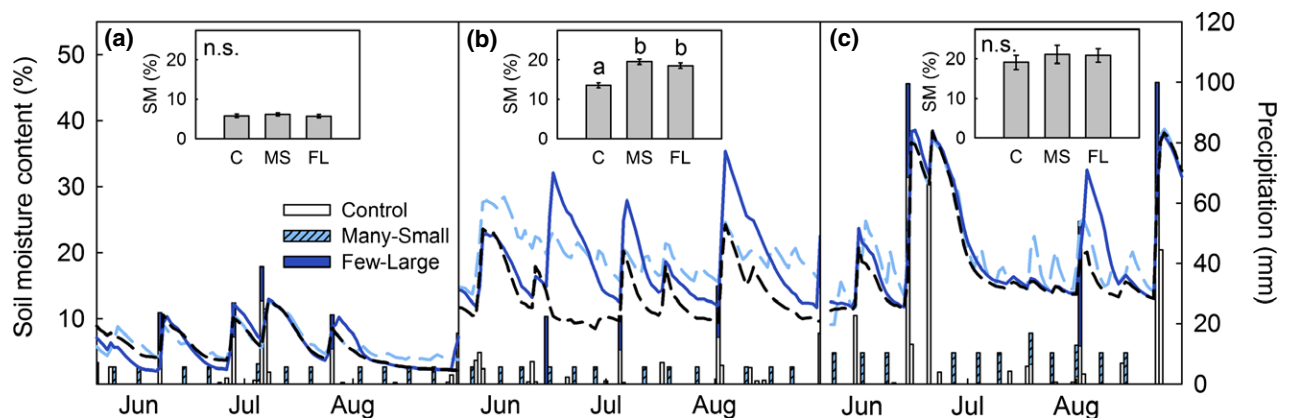

Fig. 2 Daily soil moisture and precipitation measurements during the 2012 growing season for all treatments – Many-Small (light, dashed lines and light, hashed bars), Few-Large (dark, solid lines and bars), and Control (black dashed lines and unfilled bars) – at the (a) Central Plains Experimental Range (SGP), (b) Fort Keogh Livestock and Range Laboratory (NMP), and (c) Konza Prairie Biological Station (TGP). Insets: Growing season averages (May 23–August 31, 2012) of soil moisture in Control (C), Many-Small (MS), and Few-Large (FL) treatments. Different letters represent significant differences of least squared means between treatments within a site. *P* values were adjusted for multiple comparisons using Tukey honest significant difference method.

among treatments in SGP or TGP (Table S2). Conversely, both patterns of water addition treatments led to significantly higher average soil moisture levels at NMP (Table S2; Fig. 2).

Productivity

Treatment effects on all direct productivity measures varied by site (i.e., significant Site*Treatment interactions; Table S3), so sites were examined independently. We show productivity responses in three ways: (i) as

the response to watering pattern treatments relative to the control (Fig. 3a–c); (ii) as the absolute response to watering treatments regardless of watering pattern (i.e., Many-Small and Few-Large treatments were pooled) relative to the control (Fig. 3d–f); and (iii) as the productivity response to water addition standardized by the amount of precipitation added in a particular site/ year relative to the control (Huxman *et al.*, 2004; Fig. 3d–f insets). Precipitation additions significantly increased ANPP, BNPP, and Total NPP in both TGP and SGP, but had no effect in NMP (Fig. 3; Table S4). In
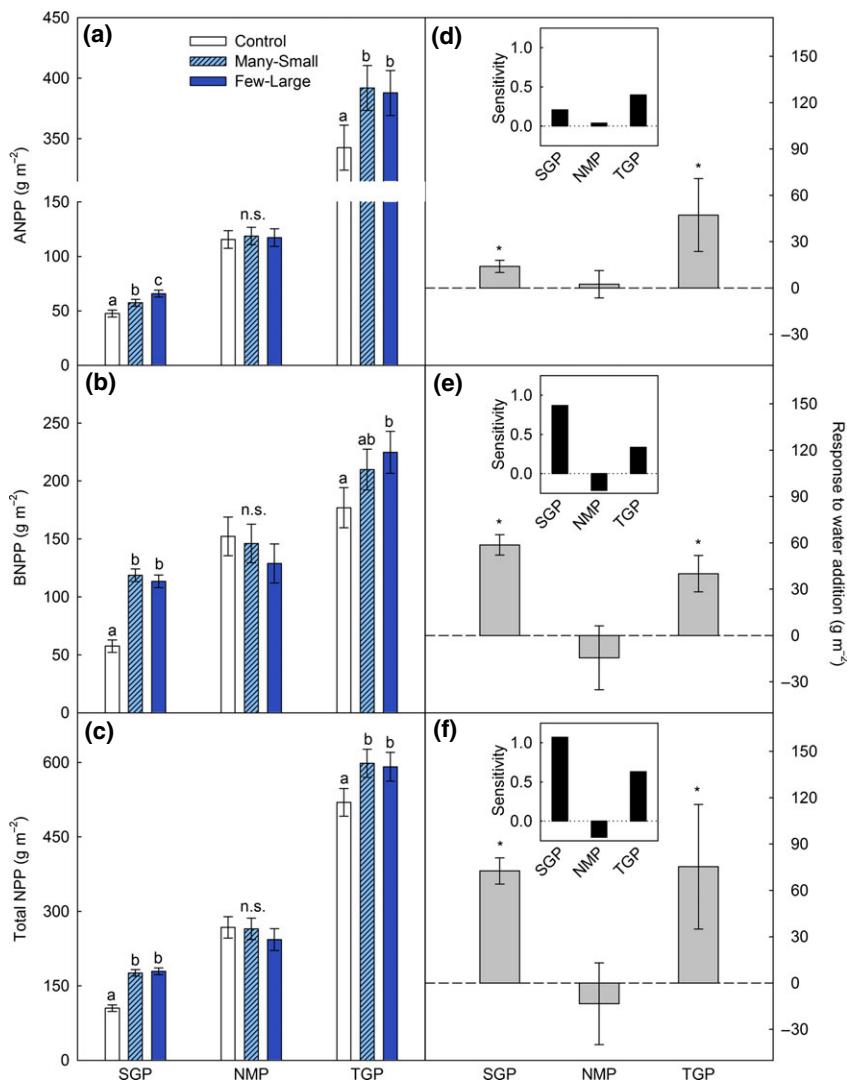

Fig. 3 Productivity responses to altered precipitation regimes at all sites – Central Plains Experimental Range (SGP), Fort Keogh Livestock and Range Laboratory (NMP), and Konza Prairie Biological Station (TGP). Responses are organized into those resulting from water added in different patterns (a–c) and overall response to water addition regardless of pattern (d–f). Productivity is partitioned into aboveground (a, d), belowground (b, e), and total (c, f) categories. Different letters indicate a significant difference based on multi-comparison of least squared means. Asterisks in panels d–f indicate that responses due to water addition are significantly different than control plots (dashed line) at the $\alpha = 0.05$ level. Insets: Sensitivity calculated as the change in productivity (g m^{-2}) per unit change in precipitation (mm) in pooled water addition treatments relative to control plots at each site.

TGP, both the Many-Small and Few-Large treatments led to significant increases of ANPP, but there was no difference between the watering pattern treatments (Fig. 3a; Table S5). Conversely, BNPP in TGP was significantly higher than in the control only in the Few-Large treatment (Fig. 3b). Regardless of watering pattern at the TGP site, water addition increased ANPP and BNPP by 47.2 ± 23.6 g m^{-2} ($\mu \pm$ SE) and 40.0 ± 11.8 g m^{-2}, respectively, which corresponded to 13.8% and 22.6% increases (Fig. 3d, e). In SGP, both the Few-Large and Many-Small treatments increased ANPP relative to the control and ANPP in the Few-Large treatment was higher than in the Many-Small treatment (Fig. 3a; Table S5). BNPP in the Many-Small and Few-Large treatments in SGP was significantly higher than in the control, but there was no effect of event size/number (Fig. 3b; Table S5). Regardless of watering pattern, water addition led to a 14.0 ± 3.9 g m^{-2} and 58.6 ± 6.6 g m^{-2} increase in ANPP and BNPP (Fig. 3d, e), respectively, or 29.4% and 102.0% increases relative to the control at SGP (Fig. 3d, e). In SGP and TGP, total NPP in the Many-Small and Few-Large treatments was significantly higher than the control, yet there was no significant difference between the two treatments. Overall, water addition caused a 72.6 ± 8.6 g m^{-2} increase in total NPP in SGP and a 75.28 ± 40.3 g m^{-2} increase in TGP (Fig. 3f) corresponding to 69.1% and 14.5% increases, respectively (Fig. 3f).

We compared sensitivity of different productivity types (i.e., ANPP and BNPP) and found that the relationship between ANPP and BNPP sensitivity differed significantly across sites (Table S6), so we analyzed sensitivity individually at each site. In TGP and NMP, ANPP and BNPP sensitivities were not significantly different from each other while in SGP, BNPP sensitivity was almost fourfold greater than that of ANPP (Fig. 3d, e insets; Table S6).

The ratio of belowground to aboveground net primary productivity (BNPP : ANPP) varied significantly among sites with the highest ratio in SGP (1.78 ± 0.18), followed by NMP (1.34 ± 0.11), and TGP (0.55 ± 0.02). Neither precipitation pattern nor precipitation amount affected BNPP : ANPP and treatment effects did not vary significantly by site ($F = 1.79$, $P = 0.14$, Figure S1).

Finally, we tested for differences between BNPP at 0–15 and 15–30 cm depths. At all sites, BNPP$_{0-15}$ was higher than BNPP$_{15-30}$ (Fig. 4; Table S2), but the mean ratio of BNPP$_{0-15}$: BNPP$_{15-30}$ differed among sites ($F = 4.25$, $P = 0.02$). The ratio in NMP was significantly lower than both SGP (46.8% reduction; $t = 2.66$, $P = 0.01$) and TGP (44.2% reduction; $t = 2.35$, $P = 0.03$) while the ratios did not significantly differ between SGP and TGP ($t = 0.26$, $P = 0.80$). We found
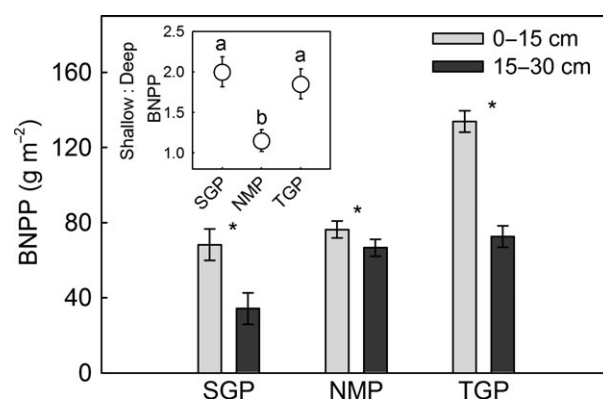

Fig. 4 Belowground net primary productivity in 0–15 cm and 15–30 cm soil layers at all three sites – the Central Plains Experimental Range (SGP), Fort Keogh Livestock and Range Research Laboratory (NMP), and Konza Prairie Biological Station (TGP). Because there was no treatment effect on rooting depth, values shown are averaged over treatments at each site. Asterisks denote significant differences ($\alpha = 0.05$) between rooting depths within a site. Inset: Ratio of shallow (0–15 cm) to deep (15–30 cm) BNPP for each site. Data are presented in the original scale, but analyses used log-transformed values to meet normality assumptions for analysis of variance. Different letters denote significant differences between rooting depth ratios at different sites.

no significant treatment effects at any site concerning the distribution of BNPP in the soil.

Discussion

There is now abundant experimental evidence that forecast alterations in precipitation event size and number, in addition to amount, will probably affect C cycling processes in terrestrial ecosystems (Knapp *et al.*, 2002; Heisler-White *et al.*, 2008, 2009; Chen *et al.*, 2009; Hao *et al.*, 2013; Kulmatiski & Beard, 2013; Zhang *et al.*, 2013a,b). Indirect evidence is also emerging that increases in event size may interact with drought, muting reductions in productivity in water-limited ecosystems (Cherwin & Knapp, 2012; Raz-Yaseef *et al.*, 2012). Here, we extend this body of research by assessing the impact of altered event size and number during years with above-average precipitation. Unlike the studies above, we also measured BNPP, which is especially important in grasslands where BNPP often exceeds ANPP (Weaver, 1954; Sims & Singh, 1978; Milchunas & Lauenroth, 2001). We conducted identical experiments in shortgrass, northern mixed grass, and tallgrass prairie sites in the central US to test three hypotheses: (i) that both ANPP and BNPP sensitivities to increased precipitation amount would vary inversely with MAP (Huxman *et al.*, 2004); (ii) that increased event size would affect high and low MAP sites differently

(Knapp *et al.*, 2008); and (iii) that belowground responses to increases in precipitation would be consistent with aboveground responses.

Responses to increases in precipitation

Huxman *et al.* (2004) estimated sensitivity of ANPP to changes in precipitation based on slopes of production–precipitation relationships in sites spanning a wide range of MAP. When looking at ANPP responses to water additions that were proportional to each site's average rainfall (ca. 30%) in both of the C$_4$-dominated grasslands, we found that although ANPP in the most productive site with the highest MAP (TGP) responded the most to increases in precipitation and the driest site (SGP) responded the least (Fig. 3d), this response pattern was reversed for BNPP (Fig. 3e) resulting in no absolute difference between these two sites in the response of total NPP to increased precipitation (Fig. 3f). When responses were expressed as sensitivity (change in productivity/unit change in precipitation; Huxman *et al.*, 2004; Fig. 3 insets), contrary to the general trend reported by Huxman *et al.* (2004), sensitivity of ANPP was greatest in TGP (highest MAP) and lower in SGP. This pattern is consistent with the meristem limitation hypothesis, which predicts that more arid low productivity ecosystems have limited capacity to respond to increases in precipitation due to existing traits of resident species (Lavorel & Garnier, 2002) and the inherent trade-off between drought tolerance and growth potential (Chapin, 1980). However, our findings that BNPP and NPP sensitivities to increased precipitation were greater in SGP (Fig. 3e, f insets) do provide support for the Huxman *et al.* (2004) model of sensitivity to alterations in precipitation.

   In contrast to the SGP and TGP, the lack of sensitivity of productivity (ANPP, BNPP, and NPP) at NMP (intermediate productivity and MAP) to added growing season precipitation and altered soil moisture levels (Fig. 2) suggests that northern mixed grasslands are relatively insensitive to wet growing seasons as well as droughts (Heitschmidt *et al.*, 1999; Frank, 2007; White *et al.*, 2014). Although colimiting resources can control productivity when one resource is overly abundant (Tilman, 1982) as in NMP in 2011 (Fig. 1), the lack of evidence of greater nitrogen limitation in NMP relative to other sites (Dodd & Lauenroth, 1979; Haferkamp *et al.*, 1993; Collins *et al.*, 1998) and an identical response during relatively low ambient precipitation inputs and soil moisture levels in 2012 (Fig. 2b) lead us to suggest that colimitation by nitrogen is not the primary factor controlling the minimal response in NMP. Instead, we posit that the lack of sensitivity to growing season precipitation inputs reflects the early-season

growth dynamics of this C$_3$-dominated system (Table 1; Ehleringer, 1978; Pearcy *et al.*, 1981; Vermeire *et al.*, 2008, 2009) as well as much greater reliance on soil moisture inputs from winter and early spring precipitation (Vermeire *et al.*, 2008), including snow melt. Indeed, our results showing that root production in NMP tended to occur more evenly throughout the upper 30 cm of the soil relative to the other two grasslands (Fig. 4) are consistent with regional rooting depth patterns (Schenk & Jackson, 2002) and the notion that NMP relies less on summer rains (which tend to wet soil layers closer to the surface) than the more shallowly rooted SGP and TGP. Only when early-season moisture inputs are low has BNPP been shown to decline in these grasslands (Frank, 2007). Overall, the lack of response of this grassland to the precipitation treatments imposed (both amount and pattern; Fig. 3) suggests that this widespread grassland type is likely to respond uniquely – relative to the C$_4$ grasslands of the central and southern US – to climatic changes that occur during the summer.

Responses to altered precipitation patterns

In contrast to NMP, both TGP and SGP responded to watering pattern, but in opposing ways above- and belowground (Fig. 3a, b). A shift from the Many-Small to the Few-Large precipitation pattern had no effect on ANPP in TGP, contrary to previous studies in this grassland (Knapp *et al.*, 2002; Heisler-White *et al.*, 2009; Fay *et al.*, 2011), whereas the Few-Large watering pattern significantly increased ANPP in SGP, as predicted by Knapp *et al.* (2008) and confirmed by several other studies (Heisler-White *et al.*, 2009; Thomey *et al.*, 2011; Sponseller *et al.*, 2012). Watering pattern had less impact belowground for SGP, yet more for TGP. These incongruent effects above- and belowground resulted in a lack of sensitivity of NPP to alterations in precipitation pattern in both grasslands (Fig. 3a–c).

Are BNPP responses to changing precipitation regimes consistent with ANPP?

Across these three grassland types, responses of ANPP and BNPP were not consistent with regard to changes in precipitation amount and pattern. In SGP, the differential sensitivities of ANPP and BNPP to precipitation amount contrasted with the similar ANPP and BNPP sensitivities in TGP (Fig. 4d–f insets). In NMP, there were no differences between responses of ANPP and BNPP as both were insensitive to changes in precipitation regimes. Although other studies have shown discordant responses of BNPP and ANPP to reductions in precipitation (Frank, 2007; Byrne *et al.*, 2013), most

sensitivity theory is based on ANPP (Knapp & Smith, 2001; Huxman *et al.*, 2004; Knapp *et al.*, 2008) not BNPP. This pattern of above- and belowground sensitivities across the two C$_4$-dominated sites suggests that increases in rainfall may impact the ecosystem service, forage production, more in the higher rainfall regions of the central US, whereas total vegetative biomass inputs (potentially affecting carbon sequestration rates) will be more responsive to precipitation inputs in more arid regions.

As annual precipitation amounts and patterns are altered via global change, predictions of ecosystem responses are needed to help inform policy and land management decisions. We show here that ecosystems within a single biome can vary greatly in their responses (ANPP, BNPP, and NPP) to increases in precipitation amount and altered pattern. Although several predictions of ecosystem sensitivity or resistance to climate change have been based on gradients in resource levels (Huxman *et al.*, 2004; Cleland *et al.*, 2013) or the inherent productivity of the ecosystem (Grime *et al.*, 2008; Hudson & Henry, 2010), the unique lack of response to either increased precipitation amount or altered pattern in the C$_3$-dominated NMP suggests that other ecosystem attributes such as vegetative functional composition (Table 1), root depth distribution (Fig. 4), and the timing of precipitation inputs may be important in modifying ecosystem sensitivity to an intensification of the hydrological cycle.

Acknowledgements

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Supporting Information

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

Data S1. Long-term and treatment calculations of precipitation regime characteristics.

Data S2. Model results showing treatment effects on soil moisture, ANPP, BNPP, NPP, BNPP:ANPP, and comparing ANPP and BNPP sensitivity within and among sites.

Data S3. Figure showing BNPP:ANPP responses among treatments and sites.