RESEARCH ARTICLE

Deconstructing precipitation variability: Rainfall event size and timing uniquely alter ecosystem dynamics

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Abstract

1. Water-limited ecosystems are highly sensitive to not only precipitation amount, but also precipitation pattern, particularly variability in the size and timing of growing season rainfall events. Both rainfall event size and timing are expected to be altered by climate change, but the relative responses of dryland ecosystems to changes in rainfall event size versus timing have not been resolved. Here, we disentangle the effects of these different aspects of precipitation pattern on ecosystem dynamics.

2. We experimentally assessed how these two aspects of rainfall variability impacted a semi-arid grassland ecosystem by altering an ambient precipitation pattern to eliminate variability in (a) rainfall event size (all events were made the same size), (b) rainfall event timing (all events were uniformly spaced in time) and (c) both. Total precipitation amount was constant for all treatments. We measured responses of soil moisture, ecosystem carbon flux (e.g. net primary production and soil CO_2 flux), plant community composition and physiological responses of the dominant C_4 grass, *Bouteloua gracilis*.

3. Removing variability in rainfall event size altered ecosystem dynamics more than a pattern of uniform event timing, but the largest impact occurred when variability in both were removed. Notably, eliminating variability in both event size and timing increased above-ground net primary productivity by 23%, consistent with reduced water stress in the dominant C_4 grass, while also reducing seasonal variability in soil CO_2 flux by 35%, reflecting lower seasonal variability in soil moisture.

4. *Synthesis*. Unique responses to different aspects of precipitation variability highlight the complexity of predicting how dryland ecosystems will be affected by climate change-induced shifts in rainfall patterns. Our results provide novel support for the key roles of rainfall event size and timing, in addition to total precipitation amount, as determinants of ecosystem function.

KEYWORDS
ecosystem functioning, multifunctionality, net primary production, precipitation variability, pulse dynamics, semi-arid ecosystems, soil CO_2 flux, soil moisture

1 | INTRODUCTION

The distribution and functioning of terrestrial ecosystems are commonly related to climatic means, such as mean annual precipitation (MAP) or temperature (MAT; Whittaker, 1975). For example, the extent of grasslands across the central United States is well-constrained climatically (Borchert, 1950) and much of the spatial variation in grassland above-ground net primary production (ANPP) can be explained by differences in MAP (Sala et al., 1988). However, such broad-scale relationships between climate and ecosystem function can mask substantial variation in ecosystem functioning at individual locations, even when comparing years with similar total amounts of precipitation (Guo et al., 2006; Hsu et al., 2012; Knapp et al., 2018). Differences in intra-annual rainfall patterns are potentially a key factor driving this variation.

Precipitation variability during the growing season has been shown to play a substantial role in shaping ecosystem function, particularly in water-limited systems (Grant et al., 2014; Heisler-White et al., 2008, 2009; Knapp et al., 2002, 2008; Nielsen & Ball, 2015; Nippert et al., 2006; Wang et al., 2020). For example, alterations to the size and timing of rainfall events, two key aspects of rainfall patterns (Knapp et al., 2015), can lead to considerable differences in ANPP, even with no change in the total amount of precipitation (Fay et al., 2003; Felton et al., 2020; Heisler-White et al., 2008, 2009; Knapp et al., 2002). Given expected changes to rainfall patterns with climate warming (Groisman et al., 2012; Trenberth, 2011), it is important to understand the individual and combined effects of rainfall event size and timing on ecosystem function. Indeed, assessing the impacts of these different aspects of precipitation patterns will likely improve the near-term predictions of ecosystem responses to climate change (Estiarte et al., 2016).

In dryland ecosystems, where rainfall variability is typically high (Knapp & Smith, 2001), the importance of variation in precipitation patterns within the growing season (i.e. rainfall event size and timing) has been particularly well-documented (Collins et al., 2008; Heisler-White et al., 2008, 2009; Huxman, Snyder, et al., 2004; Muldavin et al., 2008; Petrie et al., 2016; Post & Knapp, 2019, 2020; Robertson et al., 2009). For example, results from Heisler-White et al. (2008) showed that increasing rainfall event size, without changing total growing season rainfall amount, could substantially increase ANPP in the semi-arid shortgrass steppe. However, in addition to altering event size and number, rainfall events in this study were spaced evenly throughout the growing season and thus there was an additional 'hidden treatment' of altered event timing in the experimental design (Heisler-White et al., 2008). Indeed, many rainfall experiments manipulate precipitation in a way that results in even event timing, though timing is not the manipulation of interest (e.g. Densmore-McCulloch et al., 2016; Felton, Knapp, et al., 2019; Felton, Zavislan-Pullero, et al. 2019; Liu et al., 2017). Studies with a 'hidden treatment' of even rainfall event size or timing could produce misleading results—a recent analysis comparing the response of ANPP to naturally variable versus evenly distributed precipitation event size and timing estimated that natural levels of rainfall variability can reduce ANPP by as much as 42% in a mesic tallgrass prairie (Felton et al., 2020). But to date, how variability in event size versus timing may differ in their impact on ecosystem functioning remains unresolved.

The objective of this study was to assess the impact of two key aspects of intra-annual rainfall variability, event size and event timing, on the dynamics and functioning of a semi-arid grassland ecosystem under field conditions. We selected a past growing season when precipitation amount and ANPP were average, and the intra-annual precipitation pattern was variable. We then experimentally reproduced the growing season precipitation (GSP) pattern for comparison with imposed treatments that modified this pattern by removing variability in rainfall event size, event timing or both. Thus, we eliminated these key aspects of variability, individually and in combination, to assess their relative importance in determining multiple dimensions of plant and ecosystem responses (e.g. soil moisture dynamics, leaf-level gas exchange and water stress, plant community composition, above- and below-ground net primary productivity and soil CO_2 flux).

We took the approach of reducing variability in event size and timing from a past ambient rainfall pattern rather than increasing variability because there are myriad permutations for increasing variability in both event size and timing. In contrast, by reducing variability in each to zero, we were able to alter both dimensions similarly and comparably. Moreover, this approach allowed us to not only equalize the number of days between events, but also dampen seasonal variation in rainfall inputs, with each growing season month receiving an equal amount of precipitation in the combined reduced variability treatment.

We predicted that each of these reduced precipitation variability treatments would affect soil moisture dynamics uniquely, and the combined effects of both dimensions of variability would be different than either individually. However, given that these dimensions of variability have not previously been assessed independently, we had no basis for predicting whether event size or timing would have a greater impact on this ecosystem, or if the responses to the combination of altered event size and timing would be larger or smaller than either individually.

2 | MATERIALS AND METHODS

2.1 | Site description

We conducted this experiment at the Central Plains Experimental Range (CPER), a 6,280-ha tract of native shortgrass steppe in north-eastern Colorado, USA (40°49′N 104°46′W). Semi-arid ecosystems are critical drivers of variability in the global carbon cycle (Ahlström et al., 2015; Poulter et al., 2014) and their short stature and high sensitivity to precipitation make them ideal ecosystems for experimentally manipulating precipitation and testing hypotheses related to intra-annual temporal precipitation patterns. Indeed, precipitation manipulation experiments are more often conducted in grasslands

than any other ecosystem type (Knapp et al., 2017; Slette et al., 2019). Mean annual precipitation at the CPER is ~357 mm, >70% of which falls from April to September (Figure S1), and mean annual temperature is 9°C. The plant community is dominated (up to 90% of plant cover, Oesterheld et al., 2001) by the C_4 grass, *Bouteloua gracilis*, a widespread grassland species found throughout the US Great Plains and southwest as well as Mexico (Avendaño-González & Siqueiros-Delgado, 2021). We established our experiment in a site that had not been disturbed by large ungulate grazers since 1999. We performed our experiment in the absence of grazers to avoid grazer-induced damage to experimental infrastructure. Previous research at the CPER has shown that grazing has little impact on the sensitivity of production responses to precipitation amount (Irisarri et al., 2016; Varnamkhasti et al., 1995). Soils at this site are Ustollic Haplargids, characteristic of the shortgrass steppe (Petersen et al., 1993).

2.2 | Precipitation manipulation

We used precipitation data from the National Oceanic and Atmospheric Administration's (NOAA) National Centers for Environmental Information (https://www.ncdc.noaa.gov/) to identify a year with average growing season rainfall amount and substantial intra-annual rainfall variability (31-year record from Nunn, CO; Cooperative Observer Program [COOP] ID: 056023). We characterized precipitation patterns for each growing season (120-day period starting on May 1st) by the number of ecologically relevant rainfall events (>2 mm; Heisler-White et al., 2008), the size of each event, the length of each intervening dry period and the coefficient of variation (CV) of rainfall event size and of dry period length. We chose the 2005 growing season as the basis for our experiment because GSP was within the 95% confidence interval (CI) of the long-term mean (mean GSP = 102 mm; 2005 GSP = 114 mm), and ANPP was also near average (within the 95% CI) based on productivity data compiled from several previous studies conducted within the same locale (including Byrne et al., 2013; Cherwin & Knapp, 2012; Griffin-Nolan, Blumenthal, et al., 2019; Heisler-White et al., 2008, 2009; Scheintaub et al., 2009). The seasonal distribution of rainfall in 2005 matched general trends in the long-term record (i.e. precipitation falling mostly in the months of May and June; Hoover et al., 2021) and pre-growing season totals were typical for this site (Figure S1). Additionally, the number of ecologically relevant rainfall events in 2005 (*n* = 12) was near average for this site (Heisler-White et al., 2008). However, variability in rainfall event size *and* timing (quantified as the CV) were higher than average, which we considered desirable for assessing their relative impacts.

In early April 2016, we established twenty 1-m² plots in a topographically uniform area. We partially isolated plots from the surrounding soil matrix using aluminium flashing installed ~15 cm into the soil surrounding each plot to prevent overland and shallow soil flow of water into or out of the plots. We excluded all ambient precipitation from all plots beginning on May 1st using rainfall shelters consisting of large (2.4 × 3 m) roofs made of transparent polyethylene panels (Yahdjian & Sala, 2002). We installed the roofs at a height of ~1 m to allow airflow and established a 0.7-m buffer zone around all sides of each plot. We measured light interception by the panels using a 1-m linear quantum light sensor (Decagon AccuPAR, model LP-80) and found it to be minimal (~90% transmittance).

We assigned plots to the following treatments in a complete randomized block design: ambient rainfall pattern (AMB), even event size (E_{size}), even event timing (E_{timing}) and even event size and timing (EVEN). We applied water to the plots using a hose and flow metre attached to an on-site water source and pump. Previous analyses indicated that plant nutrient inputs from this water source (N, P and K) were low (Heisler-White et al., 2008) and met US EPA drinking water standards (Post & Knapp, 2020). Thus, water addition was not a significant source of N compared to atmospheric inputs (Burke et al., 2002, 2008) and was below the estimated levels of nitrogen critical loads for grasslands in this region (Symstad et al., 2019). We watered plots assigned to the AMB treatment on the exact days that it rained during the 2005 growing season, mimicking both the size and timing of rainfall events during that year. All other treatments involved modifications to that pattern (Figure 1). We watered the E_{size} treatment on the dates that it rained in 2005, but the size of all events was the 2005 average (~16 mm when all ≤2 mm events were excluded), creating a growing season with even rainfall event sizes and variable event timing. We watered the E_{timing} treatment according to the size and order of rainfall events that occurred in 2005, but we spaced the timing of all events evenly, creating a growing season with even rainfall event timing and variable event sizes. As our experiment lasted 120 days (the approximate length of the growing season), this resulted in rainfall events occurring every 10 days. Lastly, we watered the EVEN treatment with 16 mm every 10 days, creating a growing season with even rainfall event size and timing. We removed the roofs on September 13th. Precipitation in the months preceding our experiment (October 2015–April 2016) was higher than that in 2004–2005 and above the long-term average (Figure S1).

2.3 | Responses to precipitation manipulation

We measured soil moisture in the centre of each plot every 3 days as well as before and after each watering event, using a handheld 20-cm depth time-domain reflectometry (TDR) probe (Campbell Hydrosense II). This probe measures soil volumetric water content (vwc) in the top 20 cm of soil which corresponds to the primary rooting zone for *B. gracilis* (~90% of root biomass; Nelson et al., 2004). Because we could not visit the site every day throughout the growing season, we interpolated daily values of soil moisture using the linear approximation function (*approx*) in R.

We established a 0.25-m² subplot in each plot to assess the treatment effects on the physiology and growth of the dominant C_4 grass species, *B. gracilis*. We measured midday and predawn leaf water potential (ψ_{mid} and ψ_{pre} respectively) of *B. gracilis* approximately every 2 weeks beginning in June. We were unable to sample in May, as leaves were not fully emerged (due to the late-season
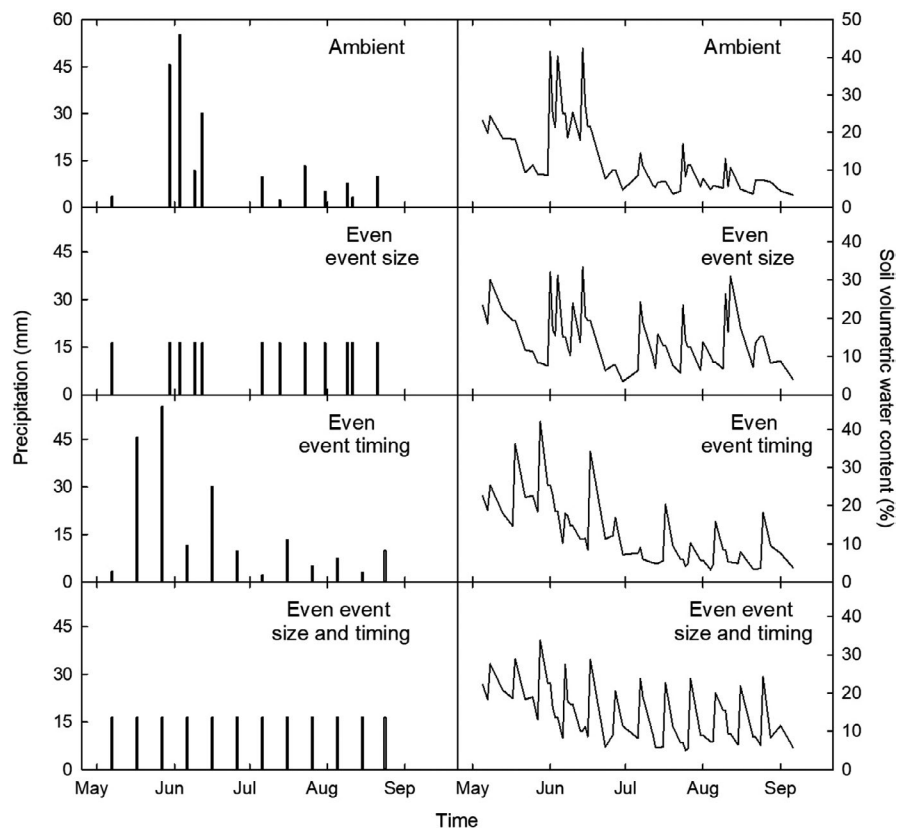
FIGURE 1 Precipitation treatments applied and mean soil moisture (% volumetric water content) responses to each treatment throughout the growing season. The ambient treatment matched the rainfall pattern (i.e. timing and size of each rainfall event >2 mm) of 2005. The 'even event size' treatment matched the timing of rainfall events in 2005 but each rainfall event was uniform in size (~16 mm). The 'even event timing' treatment was watered every 10 days (i.e. even timing) but matched the size and order of rainfall events that fell in 2005. Lastly, the 'even event size and timing' treatment was watered perfectly uniformly, with the same amount of rain (~16 mm) falling every 10 days. Tick marks on the x-axis represent the 1st day of every month

phenology of *B. gracilis*). We clipped two leaves per plot at the base and placed them in a plastic bag with a moist paper towel to avoid desiccation. We then placed each leaf in a Scholander-style pressure chamber (PMS Instruments) to measure leaf water potential. We compared measurements of leaf water potential to leaf turgor loss point (π_{TLP}), the leaf water potential at which average cell turgor is lost and leaf wilting occurs, which we estimated by osmometry (Griffin-Nolan, Ocheltree, et al., 2019). Briefly, we collected a single tiller from each plot in mid-July and rehydrated it in the laboratory for ~12 hr. Using a biopsy punch, we sampled leaf tissue from a single leaf per tiller (n = 5 per treatment). We wrapped this leaf disc in tin foil and submerged it in liquid nitrogen for ~60 s to rupture cell walls. To ensure cell lysis, we punctured each disc ~15 times using forceps, and quickly placed it in a vapor pressure osmometer (VAPRO 5520, Wescor) within 30 s of freezing. Following a 10-min equilibration time, we recorded osmolarity every 2 min until stability was reached (<5 mmol/kg change in osmolarity between measurements). We converted osmolarity to leaf osmotic potential at full turgor (π_o) (π_o = osmolarity × −2.3958/1,000) and further converted π_o to π_{TLP} using a linear model developed specifically for grass species of this region (Griffin-Nolan, Blumenthal, et al., 2019): $\pi_{TLP} = 0.944\pi_o − 0.611$.

We measured field net photosynthetic rates of tagged individuals in each plot during the warm growing season months when the grasses were actively growing (June and July). Photosynthesis was measured within 1–2 weeks of watering using a LiCOR-6400XT infrared gas analyser (LiCOR). We measured leaf gas exchange at ambient humidity levels with environmental conditions inside the sample chamber standardized across measurements (leaf

temperature = 25°C; Flow rate = 500 μmol/s; Reference chamber CO_2 = 400 ppm; photosynthetically active radiation = 1,500 μmols of photons m^{-2} s^{-1}). We selected the youngest fully expanded leaf for each measurement and allowed 2–5 min of equilibration time in the leaf chamber prior to recording net photosynthetic rate (average of 3 logged values). As leaves of *B. gracilis* did not fill the sample chamber, we estimated leaf area from leaf width and chamber length. To avoid periods of high vapour pressure deficits that might reduce stomatal opening, we measured photosynthesis between 9:00 and 11:00 hr. We also monitored the growth (e.g. height and # of green leaves) of the same tagged individuals approximately every 2 weeks.

We assessed species composition in each 1-m^2 plot during both the spring and the fall. We used the highest relative cover value in the final analysis (Koerner & Collins, 2014). At the end of the growing season (mid-September), we estimated ANPP by harvesting all above-ground biomass from two quadrats (0.1 m^2) randomly placed in separate 0.25-m^2 subplots designated for destructive measurements. We removed biomass produced the previous year before drying (48 hr at 60°C) and weighing the biomass produced in 2016. Biomass was sorted into estimates of productivity for *B. gracilis*, all other grasses and forbs separately.

We estimated below-ground net primary production (BNPP) using root ingrowth cores to measure fine root mass production. At the start of the growing season, we took two soil cores (5 cm diameter, 30 cm deep) from each plot and placed a mesh cylinder filled with root-free soil (previously collected from near the study plots and sieved in the laboratory) packed to approximate field density into the core holes. We then filled any space between the ingrowth

core and the intact soil with sieved soil. The majority of root production at our study site occurs in the top 20 cm of the soil (Nelson et al., 2004), much like other grassland and savanna ecosystems (Jackson et al., 1996; Nippert et al., 2012; Schenk & Jackson, 2002; Sun et al., 1997; Weaver & Darland, 1949). Furthermore, previous research has linked changes in root production within this depth to changes in ecosystem function even though maximum rooting depth may be much deeper (Nippert & Holdo, 2015). Thus, sampling to a depth of 30 cm reasonably approximates BNPP. Ingrowth cores were monitored throughout the growing season, and no plant establishment from the inserted soil was ever observed. We removed ingrowth cores at the end of the growing season and cut each core to yield three depth increments, 0–10, 10–20 and 20–30 cm below the soil surface, which we processed individually (samples were stored at 4°C until processing). We washed soil off the roots (via wet sieving and then submerging in a shallow bowl of water and picking out roots) before drying (48 hr at 60°C) and weighing them.

We measured in situ soil CO_2 flux weekly at approximately midday using a LICOR 6400-09 portable gas exchange system with soil CO_2 flux attachment. We installed one polyvinyl chloride (PVC) collar in each plot, between plants, and removed litter and vegetation from within each collar (via clipping at the soil surface with scissors, or by hand if loose) prior to each measurement so that only CO_2 flux from the soil was included. We averaged measurements across the season to estimate mean soil CO_2 flux per plot. We also estimated the temporal variability of soil CO_2 flux as the CV of measurements within each plot. Note, this is different from estimates of between-plot variation around the mean for each treatment.

2.4 | Statistical analysis

To assess the treatment effects on leaf water potential, photosynthesis, plant growth and soil CO_2 flux, we ran linear mixed effects models with treatment, time and their interaction as fixed effects and plot as a random effect nested within block. We investigated significant treatment × time interactions with pairwise comparisons using the *emmeans* function and adjusted p-values for multiple comparisons (Tukey method). We used R version 3.6.1 (R Core Team, 2019) to perform this analysis and those described below.

We used linear mixed effects models to assess the treatment effects on ANPP, relative cover of *B. gracilis*, BNPP, fine root depth distribution, BNPP:ANPP ratio, total NPP (ANPP + BNPP), species richness, mean and CV of soil CO_2 flux and π_{TLP} using the *lmer* function in the LME4 package (Bates et al., 2014), with treatment as a fixed effect and block as a random effect. We averaged within-plot replicates prior to all analyses. We used similar mixed effects models to assess differences in median soil moisture (we used median, rather than mean, because the data were highly skewed, making the median a better indicator of common soil moisture conditions in our plots) and several indices of soil moisture variability—the CV, consecutive disparity index (D), skewness (a measure of lack of symmetry) and kurtosis (a measure of how heavy tailed data are) of soil moisture.

The CV is highly sensitive to rare events and does not account for the chronological order of events in a time series, whereas the D is a temporal variability index that measures the average rate of change between consecutive values. We calculated D as follows:

$$D = \frac{1}{n-1} \sum_{i=1}^{n-1} \left| \ln \frac{p_{i+1}}{p_i} \right|,$$

where p_i is the series value at time i and n is the series length (Fernández-Martínez et al., 2018). Skewness and kurtosis were measured using the TSA package (Chan et al., 2020).

We further quantified soil moisture pulse dynamics by recording the number of days soil moisture fell below a threshold corresponding to leaf turgor loss point, which was identified from the nonlinear relationship between predawn leaf water potential and volumetric water content (Figure S2). Recovery from this threshold (TLP recovery) was quantified as the number of days soil moisture rose above the 95% CI of the mean across treatments (mean vwc = 13.6%) after being below π_{TLP}. Lastly, we recorded the number of soil moisture pulses (SMPs), which we defined as an increase in soil moisture of at least 10% vwc after being below the 95% CI of the mean (e.g. from 8% to 18% vwc). We assessed treatment differences in these parameters using mixed effects models with treatment as a fixed effect and block as a random effect. We transformed data when necessary to meet model assumptions of normality and homoscedasticity.

To assess multivariate responses to the treatments, we used a probabilistic principal component analysis (PCA). We ran two PCAs, one for biotic variables and the other for abiotic variables. The abiotic variables included all metrics of soil moisture variability and pulse dynamics and represent a broad range of impacts that rainfall variability may have on soil moisture. Biotic variables included the estimates of ANPP and BNPP, soil CO_2 flux (mean and temporal CV), % cover of *B. gracilis* and all physiological parameters related to water stress and photosynthesis, together providing a multifunctional perspective on plant and ecosystem responses to rainfall variability. When necessary, we log-transformed data to meet the assumptions of normality. We scaled and centred all data prior to analyses and conducted the PCAs using the PCAMETHODS package (Stacklies et al., 2007). To test for significant differences between treatments in multivariate space, we extracted plot scores for each axis of each PCA and used an analysis of variance (ANOVA) followed by pairwise comparisons using Tukey HSD.

3 | RESULTS

3.1 | Soil moisture

Each precipitation variability treatment uniquely altered the temporal dynamics of soil moisture (Figure 1; Table S1). Overall, seasonal-average soil moisture was higher, and soil moisture variability was lower in both the EVEN and E_{size} treatments compared to the E_{timing} and AMB treatments (Figure 2). Specifically, median soil moisture in

the EVEN treatment was significantly higher than both the AMB and E_{timing} treatments ($p = 0.0001$), and soil moisture in the E_{size} treatment was significantly higher than the AMB treatment ($p < 0.001$; Figure 2A). Soil moisture CV was significantly higher in the AMB and E_{timing} treatments than in the E_{size} and EVEN treatments ($p < 0.01$; Figure 2B). The D was lower in the AMB treatment compared to the EVEN treatment ($p = 0.013$), with no significant difference among other treatments (Figure 2C). The AMB treatment had the highest skewness and kurtosis in soil moisture ($p < 0.01$), and the EVEN treatment resulted in lower kurtosis ($p = 0.04$) and skewness ($p = 0.007$) than the E_{timing} treatment (Figure 2D–E).

The volumetric water content corresponding to leaf turgor loss point was 7.35% vwc (Figure S2), and there were no treatment differences in π_{TLP} ($p = 0.69$). Soil moisture in the AMB and E_{timing} treatments was below wilting point more often than in either the EVEN or E_{size} treatments ($p < 0.01$; Figure 2F), with limited recovery from wilting in the AMB treatment ($p < 0.05$; Figure 2G). Lastly, the EVEN and E_{size} treatments experienced more frequent SMPs than the AMB treatment ($p < 0.01$; Figure 2H).

3.2 | Plant growth and physiology

By late July, ψ_{pre} of *B. gracilis* in the AMB treatment fell below π_{TLP} (−2.77 MPa) and was significantly lower than that measured in the E_{timing} ($p = 0.037$) and EVEN ($p = 0.0035$), but not E_{size}, treatments. We did not observe recovery from below wilting in the AMB treatment for the remainder of the experiment. In early August, ψ_{pre} of E_{timing} also fell below π_{TLP} and was significantly lower than E_{size} ($p = 0.0015$) and EVEN (marginally significant; $p = 0.0654$), but not AMB. By the end of August, ψ_{pre} of both E_{timing} and AMB were far below π_{TLP} and significantly lower than EVEN ($p < 0.05$) and E_{size} ($p < 0.001$), which were not significantly different from each other. Notably, ψ_{pre} of E_{size} and EVEN never fell below π_{TLP} during the measured time periods (Figure S3).

In contrast to ψ_{pre}, leaf water status at midday (ψ_{mid}) regularly fell below π_{TLP} for all treatments. The general response of ψ_{mid} mirrored that of ψ_{pre} with water stress being highest in the E_{timing} and AMB treatments by the end of the growing season compared to both E_{size} and EVEN ($p < 0.001$; Figure S3). While most *B. gracilis* individuals
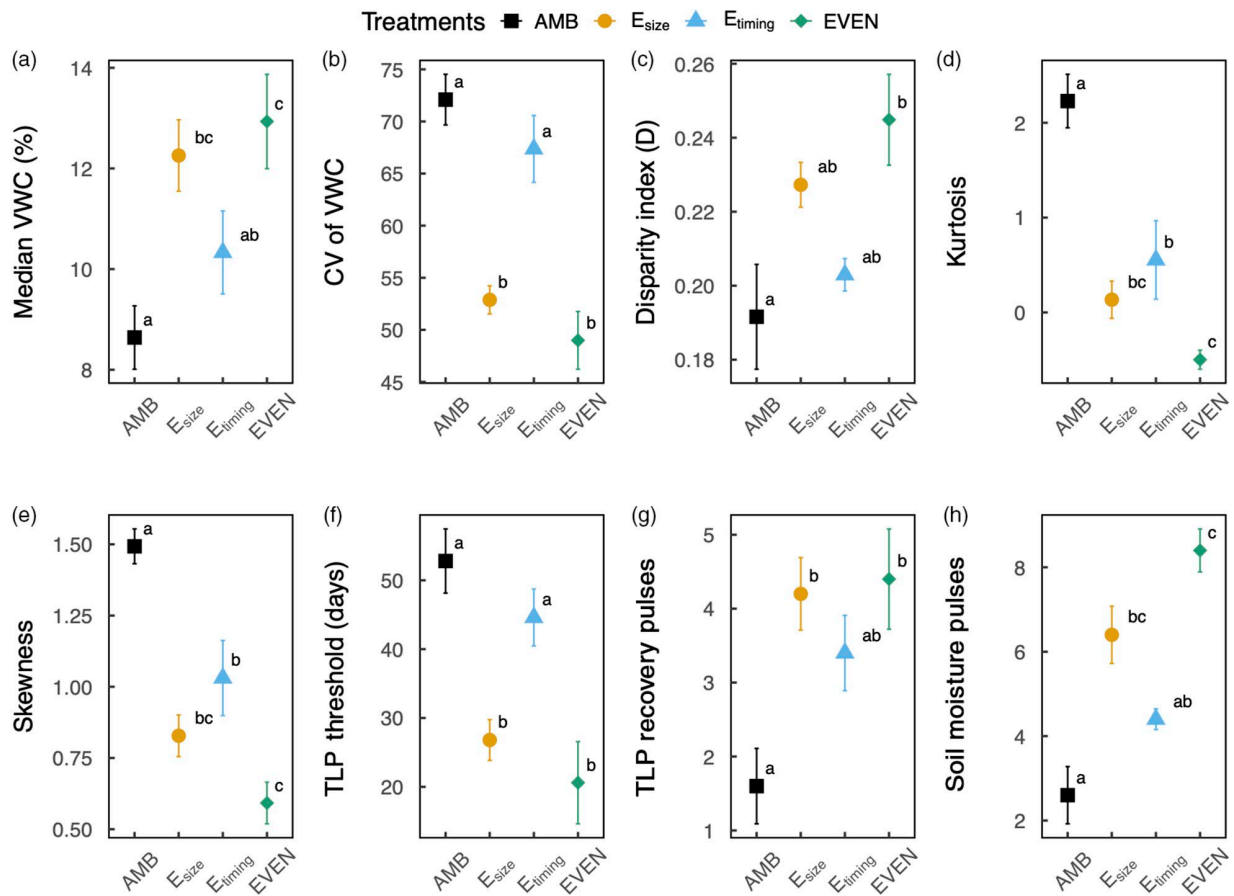

FIGURE 2 Treatment effects on multiple indices of soil moisture including median soil moisture (a), coefficient of variation (CV) of soil moisture (b), the consecutive disparity index of soil moisture (c), soil moisture skewness (d) and soil moisture kurtosis (e). Also shown are the number of days each treatment spent below the soil moisture threshold corresponding to leaf turgor loss point (f) as well as the number of times soil moisture recovered from below that threshold (g). Lastly, the number of large soil moisture pulses (SMPs) are shown for each treatment (h). Data points depict mean values ($\pm SE$) averaged across plots per treatment. Significant differences among treatments ($p < 0.05$) are indicated by different lettering. AMB, ambient treatment; E_{size}, even event size treatment; E_{timing}, even event timing treatment; EVEN, even event size and timing treatment

lost turgor by midday across treatments, *B. gracilis* maintained turgor in late July in the EVEN treatment (higher ψ_{mid} than any other treatment; $p < 0.05$) and in both EVEN and E_{timing} treatments in early August (Figure S3).

We observed significant treatment effects on the net photosynthetic rate of *B. gracilis*, depending on the time of measurement (time × treatment interaction, $p = 0.019$; Table S1). Specifically, we observed significantly higher photosynthetic rates for *B. gracilis* in the EVEN treatment compared to the AMB and E_{timing} treatments in July (Figure S4). The treatments also altered the height and leaf phenology of these same individuals (Table S1). Notably, *B. gracilis* in the AMB and E_{timing} treatments were taller and had a lower proportion of green leaves compared to the E_{size} and EVEN treatments by the end of the growing season (albeit not always significantly different; Table S2).

3.3 | Carbon cycle processes

Treatments with lower temporal variation in precipitation resulted in higher ANPP, following the order AMB < E_{size} < E_{timing} < EVEN, although treatment differences were only marginally significant ($p = 0.067$; Figure 3A). Removing variability in both rainfall event size and timing in the EVEN treatment led to a 23% increase in ANPP relative to the AMB treatment (Tukey-adjusted p-value = 0.07). We observed similar trends for both grasses and forbs, and for *B. gracilis*, although no significant differences were observed among treatments (Table S1). Treatments had no effect on species richness (Table 1); however, relative cover of *B. gracilis* was significantly higher in the EVEN treatment compared to that of both the AMB and E_{timing} treatments (Table 1). While *B. gracilis* co-occurs with other less abundant C3 forbs and grasses at our study site, relative cover of
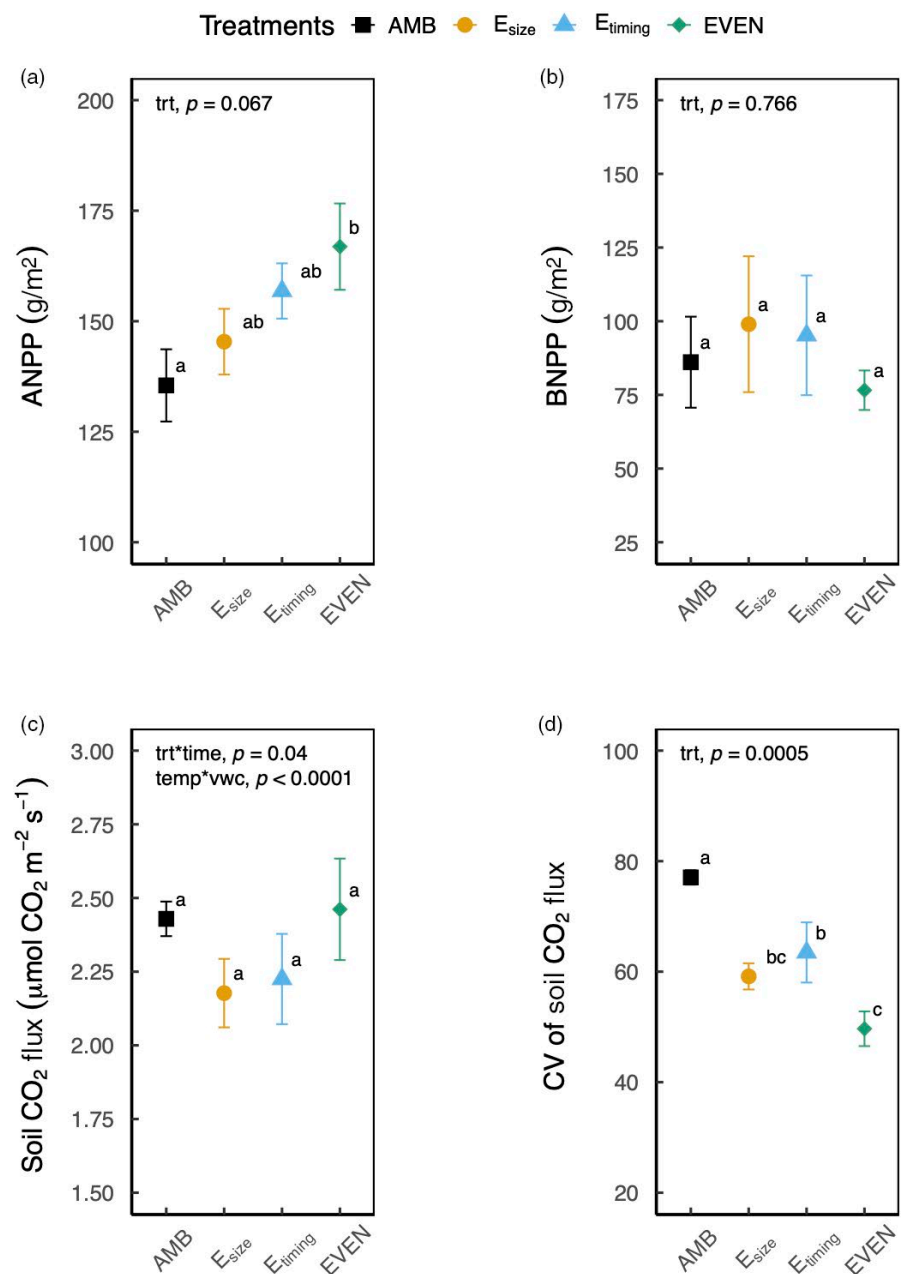

FIGURE 3 Treatment effects on above-ground net primary production (ANPP) (a), below-ground net primary productivity (BNPP) (b), mean soil CO_2 flux (c) and temporal variability in soil CO_2 flux, expressed as the coefficient of variation (CV) (d). Data points depict mean values (±*SE*) averaged across plots per treatment. Importantly, the CV of soil CO_2 flux represents temporal variability within plots, which is different from the error bars around mean soil CO_2 flux, which represents variation among plots in mean soil CO_2 flux. Significant differences among treatments ($p < 0.05$) are indicated by different lettering. AMB, ambient treatment; E_{size}, even event size treatment; E_{timing}, even event timing treatment; EVEN, even event size and timing treatment

TABLE 1 Mean (*SE*) species richness and relative cover of *Bouteloua gracilis* for each treatment, along with the *F*-statistic and *p*-value from each statistical model. Superscript lettering denotes statistically significant ($p < 0.05$) differences between treatments

Dependent variable	AMB	E_{size}	E_{timing}	EVEN	F	p
Species richness	9.0 (0.4)[a]	9.2 (0.5)[a]	8.6 (1.1)[a]	7.0 (0.89)[a]	1.85	0.19
Bouteloua gracilis cover	21.8 (1.5)[a]	29.3 (2.7)[ab]	26.1 (1.6)[a]	34.4 (1.4)[b]	7.99	0.002

these species was less affected by the rainfall variability treatments (Table S4). Relative cover of *Carex eleocharis*, a C_3 sedge, was slightly higher in AMB plots compared to the EVEN plots (6.7 vs. 1.2% cover; $p = 0.08$). Neither total BNPP ($p = 0.77$; Figure 3B) nor BNPP depth distribution (Table S3) varied among the treatments. Additionally, we observed no significant difference among treatments in total NPP (BNPP + ANPP; $p = 0.48$) or the BNPP:ANPP ratio ($p = 0.61$).

Average growing season soil CO_2 flux did not differ among treatments (Figure 3C), but there was a significant interaction between time and treatment, and between soil moisture and temperature (Table S1). Indeed, treatments did significantly alter the seasonal CV of soil CO_2 flux, which was lower with lower rainfall variability (Figure 3D; $p < 0.001$). Specifically, temporal variability in soil CO_2 flux was lower in the E_{size}, E_{timing} and EVEN treatments compared to the AMB treatment. Soil CO_2 flux was strongly positively correlated with soil moisture ($R^2 = 0.72$), and pulses in soil CO_2 flux followed pulses in soil moisture, leading to transient differences among treatments throughout the growing season (Figure S5). Soil CO_2 flux was only slightly (negatively) correlated with soil temperature ($R^2 = 0.16$; Figure S5), demonstrating the dominant role of soil moisture in determining carbon fluxes in this water-limited system.

3.4 | Principal component analysis

The first axis of the abiotic PCA explained 77% of the variability in soil moisture variables across plots (Figure 4A), with clear treatment separation along this axis (Figure 4C). Notably, the EVEN and E_{size} treatments were not significantly different from each other (Figure 4C). Both treatments were associated with higher soil moisture, lower soil moisture variability, more frequent SMPs and greater recovery from leaf wilting than the other two treatments (Table S5). The AMB treatment was associated with more frequent days below wilting, lower soil moisture and higher soil moisture variability than any other treatment (Figure 4A). We observed no significant treatment separation along the second principal component of the abiotic PCA (Figure S6).

The PCA of biotic variables revealed significant separation among treatments along the first component axis, which explained 36% of the variability and was primarily associated with ANPP, CV of soil CO_2 flux and physiology and relative cover of *B. gracilis* (Figure 4B; Table S5). Specifically, the mean PC1 score for the AMB treatment was significantly lower than all other treatments (Figure 4D; Tukey $p < 0.05$), indicating high temporal variability in soil CO_2 flux, low ANPP, greater physiological stress and lower relative cover of *B. gracilis*. In contrast, the EVEN treatment had a significantly higher

PC1 score than both the AMB and E_{timing} treatment and was associated with higher relative cover and physiological performance of *B. gracilis*, higher ANPP and lower temporal variability in soil CO_2 flux (Figure 4D). Notably, the E_{size} and E_{timing} treatments did not differ significantly from one another along the first component of the biotic PCA, nor did the E_{size} and EVEN treatment. We observed no treatment separation along the second component of the biotic PCA (Figure S6), which explained 29% of variation and was primarily associated with below-ground processes (BNPP, root:shoot ratio and mean soil CO_2 flux) as well as total NPP.

To test whether multivariate biotic responses were associated with the multivariate abiotic response to treatments, we extracted the plot scores from the first axis of each PCA (those axes that separated plots by treatment) and ran a linear regression predicting biotic PC scores from abiotic PC scores. Overall, 62% of variation along the biotic PC (which was associated with ANPP, soil CO_2 flux variability and performance of the dominant C_4 grass) was explained by the abiotic PC scores ($R^2 = 0.62$; $p < 0.0001$; Figure S7). We also determined Pearson's *r* correlation values for relationships between all variables included in the PCA (Figure S8). Leaf water potential and relative cover of *B. gracilis* were strongly correlated with soil moisture parameters, as was the temporal CV of soil CO_2 flux. Additionally, ANPP was positively correlated with SMPs ($r = 0.47$) and negatively correlated with kurtosis ($r = 0.48$) and skewness ($r = 0.51$) of soil moisture.

4 | DISCUSSION

Using a variable growing season rainfall pattern as a 'control' treatment in this semi-arid grassland, we experimentally altered this naturally occurring precipitation pattern, and reduced precipitation variability in the following three ways: (a) by making all precipitation events the same size, (b) distributing all events uniformly in time and (c) making all events equal in size and uniformly distributed. Overall, the combination of reduced variability in both precipitation event size and event timing had a larger impact on ecosystem dynamics than either individually. Specifically, removing variability in rainfall event size *and* timing led to reduced leaf water stress, increased carbon assimilation, increased relative cover of the dominant grass species (*B. gracilis*), higher ANPP and lower variability in soil CO_2 flux. However, this treatment did not affect BNPP or seasonally averaged soil CO_2 flux. Increased ANPP and reduced temporal variability in soil CO_2 flux were both associated with higher soil moisture, reduced soil moisture variability and increased frequency of SMPs as indicated by a strong correlation between
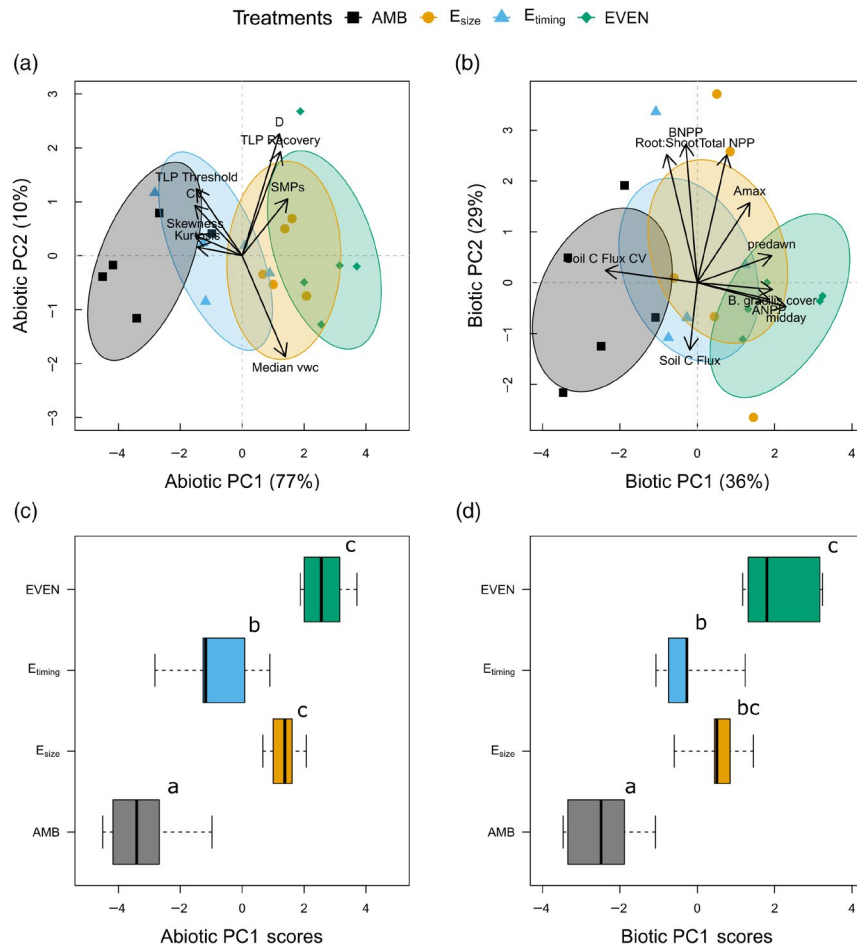
FIGURE 4 Principal component analysis (PCA) biplots showing the multivariate abiotic (a) and biotic (b) response to altered precipitation variability treatments. Abiotic variables include the estimates of soil moisture dynamics, and biotic variables include all measures of ecosystem function, community structure and physiology. Ellipses represent 95% confidence intervals centred at the mean for each treatment. The distribution of plot scores along the first component of the abiotic (c) and biotic (d) PCA is shown as boxplots with differences in letters denoting significance differences ($p < 0.05$) among treatments. BNPP, below-ground net primary production; ANPP, above-ground net primary production; Root:Shoot, BNPP:ANPP ratio; Total NPP, ANPP + BNPP; A_{max}, maximum assimilation rate for *Bouteloua gracilis*; midday, midday leaf water potential; predawn, predawn leaf water potential; Soil C flux, soil CO_2 flux; Soil C flux CV, CV of soil CO_2 flux; D, consecutive disparity index; CV, coefficient of variation for soil moisture; Kurtosis, soil moisture kurtosis; Skewness, soil moisture skewness; TLP threshold, number of times soil moisture fell below turgor loss point; TLP recovery, number of times soil moisture recovered from below turgor loss point; SMPs, soil moisture pulses; Median vwc, median volumetric water content; AMB, ambient treatment; E_{size}, even event size treatment; E_{timing}, even event timing treatment; EVEN, even event size and timing treatment

the first components of the biotic and abiotic PCAs (Figure S7). Importantly, the effects of rainfall event size and timing were not offsetting, making the impact of removing variability in both larger than removing variability in either one individually. Thus, by deconstructing rainfall patterns, we now have direct evidence that these two aspects of climate variability are both independently important for understanding how semi-arid ecosystems respond to changes in precipitation variability.

The 23% increase in ANPP that resulted from removing variability in both rainfall event size and timing is equivalent to increasing growing season precipitation by 25% in this semi-arid grassland, based on the temporal relationship between ANPP and GSP for this site (13-year record; Figure S9). We posit that this increase in ANPP

with reduced rainfall variability is a consequence of the increasingly pulsed nature of soil moisture throughout the growing season. There were several large storms in 2005 (>25 mm), which were replicated in the AMB treatment (Figure 1); however, these events all occurred early in the growing season, which is typical for this ecosystem. Each of the reduced precipitation variability treatments distributed this precipitation more evenly throughout the growing season with the EVEN treatment increasing the pulsed nature of soil moisture most consistently (Figure 1). In dryland ecosystems, soil moisture pulses are important drivers of plant growth and ecosystem function (Noy-Meir, 1973). Indeed, the EVEN treatment resulted in more frequent SMPs (Figure 2H) and higher ANPP (Figure 3A), and the higher consecutive disparity in soil moisture observed in the EVEN treatment

(Figure 2C) is an indication that this pulsed nature was maintained throughout the growing season. Additionally, the EVEN precipitation treatment equalized the timing between events and variation in seasonal rainfall distribution, which are directly related to each other, thereby removing the formidable challenge that seasonal rainfall environments pose to organisms (Moore et al., 2020). Previous studies in the shortgrass steppe have indicated that large rainfall events falling before mid-season are more important for ANPP than late-season rainfall (Parton et al., 2012; Post & Knapp, 2019). However, large rainfall events may affect ANPP less if they are temporally clustered.

In the central United States, evidence suggests that C_4 grasses benefit from proportionally more precipitation falling in warmer months (Knapp et al., 2020; Paurelo & Lauenroth, 1996). Similarly, we observed reduced water stress and increased abundance of the dominant C_4 grass, *B. gracilis*, in treatments that redistributed precipitation to the warmer, later months in the growing season. However, our results suggest that uniformity in the size, rather than timing, of rainfall events is more important for maintaining leaf turgor (Figure 2F), carbon assimilation (Figure S4) and overall abundance of this C_4 grass (Table 1). Shortgrass prairie is an ideal ecosystem for linking plant eco-physiology with ecosystem function because of the high degree of species dominance. Indeed, we found positive associations between the physiological responses of *B. gracilis* and ANPP (Figure 4B), supporting the assertion that dominant species physiology is an important driver of ecosystem function in the shortgrass steppe (Avolio et al., 2019).

Several studies have addressed grassland root dynamics in response to experimental changes in precipitation amounts (e.g. Chou et al., 2008; Dukes et al., 2005; Mueller et al., 2018; Xu et al. 2013; Zhang et al., 2019; Zhou et al., 2012) but few have studied root responses to changing precipitation patterns in a field setting (Fay et al., 2003; Williams et al., 1998), pointing to a need for such studies. Contrary to above-ground responses, we found that BNPP was unaffected by reduced variability in precipitation. This suggests that there is a greater stability of production below-ground in response to intra-annual precipitation variability, which could help buffer this system against forecast precipitation changes. The difference in ANPP versus BNPP in our study suggests that below-ground dynamics cannot always be reliably predicted based on above-ground measurements and highlights the importance of quantifying below-ground impacts directly.

Consistent with previous studies (Bremer et al., 1998; Harper et al., 2005; Knapp et al., 1998; Mielnick & Dugas, 2000), we found that grassland soil CO_2 flux was highly correlated with soil moisture (Figure S5). It is thus not surprising that the CV of soil CO_2 flux (a major contributor to biotic PC1) was associated with soil moisture dynamics (Figure S7). This supports previous findings that pulses in soil moisture lead to pulses in soil CO_2 flux (Chen et al., 2008, 2009; Huxman, Cable, et al., 2004; Huxman, Snyder, et al., 2004; Liu et al., 2002; Sponseller, 2007). However, growing season-average soil CO_2 flux rates did not differ among treatments (Figure 3C), despite significant differences in median soil moisture content (Figure 2A). We also did not detect an impact of these precipitation treatments on total NPP (despite ANPP responses); thus, our results suggest

that the overall balance of ecosystem C exchange may be less sensitive to variability in precipitation pattern than some of its individual components, at least in the short term (one growing season).

Several questions emerge from our study that could motivate future research on how intra-annual precipitation variability influences ecosystem dynamics. Our results can be used to 'bookend' the predictions of ecosystem functioning with changing precipitation patterns as we selected a year with high rainfall variability; we would assume that precipitation patterns might influence ecosystem dynamics less in low rainfall variability years but sensitivity across multi-year periods remains unresolved. Our experimental approach also warrants replication in more mesic ecosystems and in wet or dry years (*cf.* Zhang et al., 2021). In a mesic prairie, for example, the impact of high rainfall variability on ecosystem dynamics was more pronounced in dry years relative to wet years (Felton et al., 2020). Additionally, the legacy effects of antecedent precipitation on grassland productivity are well-documented (Griffin-Nolan et al., 2018; Petrie et al., 2018; Sala et al., 2012), yet few studies have explored the interactive effect of antecedent precipitation and growing season precipitation pattern on productivity. Here, we replicated the exact rainfall pattern and growing season precipitation amount recorded in 2005 yet measured much higher ANPP (135.48 g/m^2) than that observed in 2005 in the same location (67.3 g/m^2; Heisler-White et al., 2008), which could be due, in part, to the wet fall and spring preceding our experiment (Figure S1).

The ecological impact of climate variability is often assessed using individual metrics of ecosystem function, such as ANPP. However, this approach can be misleading, given that ecosystem functioning is inherently multidimensional (Manning et al., 2018). If we had only measured ANPP, for example, we would have concluded that evenness in rainfall event timing, rather than size, is more important for semi-arid ecosystem function (Figure 3A). However, our combined measure of ecosystem functioning, including below-ground processes, community dynamics and dominant species physiology indicates that rainfall event size has a greater multidimensional effect than timing, and that these two dimensions of climate variability are not offsetting in their combined effects on ecosystem functioning (Figure 4).

In summary, we found that precipitation event size and timing uniquely alter ecosystem dynamics and that removing variability in both has a larger effect than removing variability in either one individually. The unique impacts of variability in precipitation size versus timing mean that predictions of ecosystem responses to precipitation pattern need to account for both, as well as their combined effect. Further, when designing future experiments, ecologists must be cognizant of how rainfall manipulations alter either or both of these key aspects of precipitation variability.

AUTHORS' CONTRIBUTIONS

R.J.G.-N., I.J.S. and A.K.K. contributed to the design of the experiment; R.J.G.-N. and I.J.S. collected the data; R.J.G.-N. conducted all the analyses and wrote the initial draft of the manuscript. All the authors contributed substantially to revisions.

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DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.kkwh70s4q (Griffin-Nolan et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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