

RESEARCH ARTICLE

Compound hydroclimatic extremes in a semi-arid grassland: Drought, deluge, and the carbon cycle

David L. Hoover¹  | Olivia L. Hajek²  | Melinda D. Smith²  | Kate Wilkins²  |
Ingrid J. Slette²  | Alan K. Knapp² 

¹USDA-ARS Rangeland Resources and Systems Research Unit, Crops Research Laboratory, Fort Collins, Colorado, USA

²Department of Biology and Graduate Degree Program in Ecology, Colorado State University, Fort Collins, Colorado, USA

Correspondence

David L. Hoover, USDA-ARS Rangeland Resources and Systems Research Unit, Crops Research Laboratory, Fort Collins, CO, USA.

Email: David.Hoover@usda.gov

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Abstract

Climate change is predicted to increase the frequency and intensity of extreme events including droughts and large precipitation events or “deluges.” While many studies have focused on the ecological impacts of individual events (e.g., a heat wave), there is growing recognition that when extreme events co-occur as compound extremes, (e.g., a heatwave during a drought), the additive effects on ecosystems are often greater than either extreme alone. In this study, we assessed a unique type of extreme—a contrasting compound extreme—where the extremes may have offsetting, rather than additive ecological effects, by examining how a deluge during a drought impacts productivity and carbon cycling in a semi-arid grassland. The experiment consisted of four treatments: a control (average precipitation), an extreme drought (<5th percentile), an extreme drought interrupted by a single deluge (>95th percentile), or an extreme drought interrupted by the equivalent amount of precipitation added in several smaller events. We highlight three key results. First, extreme drought resulted in early senescence, reduced carbon uptake, and a decline in net primary productivity relative to the control treatment. Second, the deluge imposed during extreme drought stimulated carbon fluxes and plant growth well above the levels of both the control and the drought treatment with several additional smaller rainfall events, emphasizing the importance of precipitation amount, event size, and timing. Third, while the deluge's positive effects on carbon fluxes and plant growth persisted for 1 month, the deluge did not completely offset the negative effects of extreme drought on end-of-season productivity. Thus, in the case of these contrasting hydroclimatic extremes, a deluge during a drought can stimulate temporally dynamic ecosystem processes (e.g., net ecosystem exchange) while only partially compensating for reductions in ecosystem functions over longer time scales (e.g., aboveground net primary productivity).

KEYWORDS

carbon flux, climate extremes, extreme precipitation, grassland, primary productivity

1 | INTRODUCTION

Intensification of the global hydrological cycle, driven by a warming atmosphere, is predicted to alter precipitation regimes in myriad

ways (Huntington, 2006; Trenberth et al., 2003). Larger precipitation events or “deluges,” more frequent anomalous wet and dry years, and increases in the severity of droughts are expected to become the “new normal” for many ecosystems (Donat et al., 2016; Fischer

et al., 2013; IPCC, 2013; Singh et al., 2013; Wang et al., 2017). Of the many manifestations of increasing climate variability, climate extremes are predicted to have the greatest impact on ecosystem structure and function (Jentsch et al., 2007; Kayler et al., 2015; Smith, 2011). Thus, it is not surprising that hydroclimatic extremes have already been linked to local-scale increases in exotic species (Concilio et al., 2015), regional-scale mortality in forests (Anderegg et al., 2013; Breshears et al., 2005), and global carbon cycle anomalies (Ahlström et al., 2015; Haverd et al., 2016; Reichstein et al., 2013; Zscheischler et al., 2014). Given that water availability limits or co-limits components of the carbon cycle (e.g., gross and net primary production; GPP and NPP) over much of Earth's land surface (Garbulsky et al., 2010; Nemani et al., 2003; Seddon et al., 2016), understanding how ecosystems respond to hydroclimatic extremes has relevance from local to global scales.

Although climate extremes are often studied as isolated events, most major environmental disasters result from compound climate extremes, defined as “the combination of multiple drivers and/or hazards” (Zscheischler et al., 2018). For example, a heat wave during a drought (e.g., a “hot drought”) can lead to widespread tree mortality (Breshears et al., 2005), or a storm surge combined with extreme rainfall can lead to damaging coastal floods (Wahl et al., 2015). While the effects of many compound climate extremes are often worse than either event individually, some may have contrasting effects, such as a deluge during a period of drought (IPCC, 2013; Zscheischler & Seneviratne, 2017). Both deluges and droughts are projected to become more frequent with climate change, and hence there is a growing likelihood for this compound climate extreme to be more prevalent in future climates. Deluges typically arise from mesoscale convective storms, and empirical evidence indicates that large convective storm complexes are growing in size and duration across the United States (Feng et al., 2016). As a result, the most extreme daily events (exceeding the 99% of probability distribution functions) have increased in frequency and their rate of increase is scaling faster than many other aspects of climate change (Bao et al., 2017; Fischer & Knutti, 2016). At the same time, widespread warming, regional precipitation declines, and hydroclimatic variability are projected to increase drought risk and severity throughout the subtropics and mid-latitudes (Cook et al., 2018).

Semi-arid regions, which encompass some of the world's most extensive grasslands, are well known for having highly variable precipitation regimes—within and among years (Knapp & Smith, 2001; Lauenroth & Bradford, 2009; Schwinning et al., 2004; Snyder & Tartowski, 2006). Ecosystem functions, such as net primary productivity and other facets of the carbon cycle, are particularly sensitive to precipitation variability in these regions (Gherardi & Sala, 2015; Maestre et al., 2016; Sala et al., 1988), which play a dominant role in the global land CO₂ sink (Ahlström et al., 2015; Haverd et al., 2016; Poulter et al., 2014). To date, research on hydroclimatic extremes in semi-arid grasslands has often focused on individual extremes, such as drought (Cherwin & Knapp, 2012; Evans & Burke, 2013; Evans et al., 2011) or deluges (Post & Knapp, 2020, 2021), but there has been little attention on their combined effects.

In this study, we evaluated the effects of compound hydroclimatic extremes—a deluge during drought—on production and carbon cycling in a semi-arid (shortgrass steppe) grassland in Colorado (USA). The North American shortgrass steppe extends from Mexico through Texas and as far north as Wyoming and has highly variable responses to both precipitation amount and patterns (Heisler-White et al., 2008; Hoover et al., 2021; Lauenroth & Sala, 1992). In this region, most extreme droughts are short term (<2 years; Felton et al., 2021); thus, we decided to focus on a single year, extreme “flash drought” for this experiment. We imposed an extreme drought and then interrupted this drought with either a single extreme deluge event or the equivalent amount of precipitation provided in several smaller events. We examined how a deluge during drought might uniquely affect the spatial and temporal availability of soil water and, consequently, plant growth, and carbon fluxes.

2 | METHODS

2.1 | Site description

Research was conducted at the 6500 ha USDA-Central Plains Experimental Range located in the shortgrass steppe of north-central Colorado, USA (40°50'N, 104°43'W, 1645 m above sea level) and part of the Long-Term Agroecosystem Research network (2012-present; <https://ltar.ars.usda.gov/>). Mean annual precipitation is 342 mm (Hermance et al., 2015) with ~75% falling during the growing season (May–August) and mean annual temperature is 8.6°C (Lauenroth & Sala, 1992). Long-term ANPP averages ~74 g m⁻² and consists largely of perennial C₄ grasses (~75%) with the rest of the plant community including perennial C₃ grasses, cool-season annual grasses, forbs, and cacti (Hoover et al., 2021). Soil texture at the study site is sand clay loam (61% sand, 17% silt, and 22% clay) with 6.4% organic matter (Post & Knapp, 2020). The study site was relatively flat with a history of moderate cattle grazing (0.6 animal unit months ha⁻¹ stocking rate) but was enclosed by a fence during the experiment to protect infrastructure.

2.2 | Experimental design

During the 2019 growing season (May–August), four precipitation treatments were randomly assigned to forty 1 m² plots spaced 2 m apart ($n = 10$ per precipitation treatment). Plots were hydrologically isolated by installing aluminum flashing (5 cm aboveground and 10 cm belowground) 0.25 m beyond the extent of the plot. Given the strong influence of ambient precipitation on drought severity when using a passive rainfall reduction approach (Hoover et al., 2018), we excluded precipitation by installing clear plastic rainout shelters (2.2 × 2.2 m) 1 m over each plot and then added water. Similar studies suggest that the rainout shelters have minimal effects on light, microclimate, and plant responses (Loik et al., 2019; Post & Knapp, 2020). We added water under the rainout shelters to simulate four

precipitation treatments: (1) a control treatment ("CON"; based on the exact precipitation event pattern and amount that occurred at the site in 1989, see below for more details), (2) a drought treatment ("DRT"; a 77.5% reduction in each event added to the control plots), (3) a drought plus deluge treatment ("DRT+DEL"; the DRT treatment with a 60 mm deluge added mid-July), and (4) a drought plus small events treatment ("DRT+SE"; the DRT treatment, with a total of 60 mm of precipitation added to nine events from mid-July through mid-August; Table S1).

All precipitation treatments were based on long-term precipitation records from the site (1980–2016; Hoover et al., 2021) and derived from the daily precipitation amount and pattern of the year 1989, which we determined as the "most average" year on record (Table S1). We selected this year by calculating the following precipitation metrics: growing season total amount, monthly total amount (May, June, July, and August), mean daily total, the number of events, and the number of consecutive dry days between events, following the methods of Knapp et al. (2015). Next, for each of the precipitation metrics, we calculated the percentile of each year based on the distribution of the entire period and then determined the absolute deviation from average (i.e., the 50th percentile). For example, if a given year's seasonal total precipitation was in the 65th percentile for the historical record, then the absolute percentile deviation from average was 0.15. We then eliminated years where any metric's percentile deviation from average was "extreme," defined as values <10th or >90th percentiles (thus, greater than 0.4). We then summed the absolute percentile deviation from average across all metrics and further examined the 7 years with the lowest summed values. From these 7 "average years," we selected 1989 after careful consideration of the timing of precipitation events during the period around the deluge, specifically there were no large precipitation events (>25.4 mm) or exceptionally long consecutive dry days (>21 days) in July.

Treatments were implemented in May with daily precipitation amounts for the DRT treatment reduced by 77.5%, which is equivalent to the 1st percentile of the long-term precipitation record (i.e., a 1 in 100-year drought; Table S1). The DRT+DEL and the DRT+SE treatments received the same rainfall as the DRT treatment through July 15. On July 16, the DRT+DEL treatment received an additional 60 mm event (Table S1), equivalent to the 98th percentile event size for the site (Post & Knapp, 2021). For the DRT+SE treatment, a total of 60 mm was added across the nine remaining events in the growing season (Table S1). For all treatments, water was added by hand using a sprayer attached to a pump and digital flow meter (01N31GM 1" nylon water meter, Great Plains Industries, Inc.). Water was applied evenly at a rate that prevented overland flow. Due to above-average April precipitation (+37.2 mm), when there were no rainout shelters over the plots (due to risk of shelter-damaging snowstorms), we delayed water additions until the end of the May to achieve an average season precipitation total. As a result, our drought treatment received 28.8 mm more precipitation during that period than if the drought treatments were active, and thus was in the 3rd percentile (based on historic precipitation in May–August), rather than our

target 1st percentile over the whole growing season. Overall, the four treatments resulted in three different precipitation amounts (May–August): CON treatment = 175.3 mm, which is equal to the 43rd percentile of historic precipitation record (long-term May–August mean = 186.6, SD = 63.3); DRT treatment = 68.3 mm (3rd percentile); and both DRT+DEL and DRT+SE = 128.3 mm (18th percentile). Therefore, the DRT treatment was an extreme drought (<5th percentile) while the DRT+DEL and DRT+SE received total precipitation (May–August) equivalent to a moderate drought (<20th percentile).

2.3 | Soil moisture

Soil moisture was measured weekly from 0 to 90 cm at 10 cm increments using a Sentek Diviner probe (Diviner 2000, Sentek Pty Ltd.) on a subset of plots ($n = 3$ per treatment), using a site-based calibration (Jabro et al., 2005), to calculate volumetric water content (VWC). Measurements were collected weekly (and more frequently after the deluge) and integrated by depth (5 cm resolution) and over time (daily) using linear interpolation (R package *imputeTS*; Moritz & Bartz-Beielstein, 2017).

2.4 | Phenology measurements

To assess plant growth and phenology, weekly plot canopy greenness was estimated using repeat digital photography (adapted from Post & Knapp, 2020, 2021). Previous research has demonstrated that plot-level responses in canopy greenness scale well to landscape-level measurements (e.g., satellite-derived greenness via normalized difference vegetation index, or NDVI; Post et al., 2021). For each photograph, a digital camera was positioned directly over a marked region of interest (50 × 50 cm frame in the corner of each plot) at a 90° angle relative to the ground surface. Each image was cropped to the interior region of the 50 × 50 cm frame prior to analysis with the R package *EBImage* (Pau et al., 2010), which calculated the average green chromatic coordinates (GCCs) of the pixels in each photograph. The GCC index calculated greenness relative to total brightness of each pixel (Filippa et al., 2016), thus accounting for variation in image lighting, such as shading from experimental infrastructure.

2.5 | Carbon flux measurements

Carbon flux measurements were conducted on a subset of plots ($n = 5$) using a custom portable flux chamber (0.5 × 0.5 × 0.5 m) attached to a LI-6400 (LiCOR, Inc.) using methods adapted from Hopping et al. (2018) and Hu et al. (2013). A 0.5 × 0.5 m aluminum base was placed in each plot for carbon flux measurements to assure a good seal with the ground. Measurements were taken mid-day between 8:30 and 14:00 (MST) throughout the growing season, although sampling frequency varied. During each

measurement, the chamber was first vented for 7 s then placed over the aluminum base with two fans running to circulate air. Data were logged over a 2 min period to collect the first light measurement (net ecosystem exchange; NEE). The chamber was then vented for 7 s and the measurement was repeated for a second light measurement. The chamber was vented again for 7 s and another measurement was taken during a 2 min period of darkness imposed by an opaque chamber cover (ecosystem respiration; ER). After collection, the data were processed, and the last 30 s of the measurement were averaged to produce a single value for NEE and ER per measurement. Finally, GPP was calculated as $GPP = NEE - ER$.

2.6 | Net primary production measurements

Aboveground net primary production (ANPP) was measured in all plots ($n = 10$ per treatment) at the end of the growing season (mid-September). In each plot, all plant material from two 0.1 m^2 subplots was harvested to ground height, dried at 60°C for 48 h sorted to remove previous year biomass, and weighed to the nearest 0.01 g . Belowground net primary production (BNPP) was estimated as fine root mass production using root ingrowth cores. At the start of the growing season, a soil core (5 cm diameter, 30 cm deep) was taken from every plot. We placed a cylindrical mesh basket (5 cm diameter, 30 cm deep, $2 \times 2 \text{ mm}$ mesh openings) filled with sieved, root-free soil (collected adjacent to the experiment) and packed to approximate field density into each core hole and filled any space between the ingrowth core and intact soil with sieved, root-free soil. At the end of the growing season, we removed the ingrowth cores and stored them at 4°C . We washed all roots free of soil by wet sieving (0.5 mm sieve) each ingrowth core under low water pressure and then submerging the remaining sample in a shallow bowl of water, picking out roots with forceps and removing attached soil by hand. We dried roots at 60°C for 48 h and then weighed them. We calculated BNPP as fine root mass production per m^2 ground area. NPP was estimated by summing ANPP and BNPP from each plot.

2.7 | Statistical analyses

To assess the effects of the precipitation treatments on phenology, carbon fluxes, and biomass, we built linear mixed effects models using the "lme" function in the R package "nlme" (Pinheiro et al., 2021). Models for phenology (greenness) and carbon fluxes (GPP, NEE, and ER) included precipitation treatment and date as fixed effects, with plot as a random effect. Models for biomass (ANPP, BNPP, and NPP), included precipitation treatment as a fixed effect and plot as a random effect. To assess significant differences among groups, we calculated post-hoc Tukey's pairwise differences. All analyses were performed in R v. 3.6.0 (R Foundation for Statistical Computing, Vienna, Austria).

3 | RESULTS

3.1 | Precipitation and soil moisture dynamics

All precipitation treatments started with similar soil moisture profiles in May, with high VWC (35% VWC) in the 0–30 cm and lower soil moisture levels (18% VWC) in the deeper layers (35–80 cm; Figure 1). Divergence in soil moisture levels among the CON and DRT treatments initially occurred in early June (Figure 1). Throughout June and early July, shallow soil moisture decreased across all treatments (Figure 1). On July 16, all treatments received precipitation with 13.7 mm in the CON treatment, 3.1 mm in the DRT treatment, and 63.1 mm in the DRT+DEL treatment to simulate the 60 mm deluge event added to the 3.1 mm the DRT treatment received (Figure 1; Table S1). Additionally, on July 16, the DRT+SE treatments began receiving additional precipitation to each event through August (Figure 1; Table S1). The differences in daily precipitation amounts led to divergence in soil moisture among all precipitation treatments. As expected, there was a large pulse in soil moisture following the 60 mm additional water added in the DRT+DEL treatment (Figure 1; Figure S1). The soil moisture pulse remained above pre-deluge soil moisture (13% VWC) for 21 days, until it started drying from the surface downward (Figure 1). The DRT+SE treatment maintained slightly elevated soil moisture through August, although never increasing to the same magnitude or depth of wetting observed in the DRT+DEL treatment (Figure 1). Meanwhile the DRT treatment continued a drying trend throughout the rest of the growing season (Figure 1).

3.2 | Greenness

Greenness dynamics mirrored soil moisture across the precipitation treatments (Table 1; Figures 1 and 2). All treatments had similar levels of greenness during May with the effects of the drought appearing in early June while the CON treatment increased relative to the other treatments, peaking in late June (Figure 2). Greenness in the CON treatment was significantly greater than in the DRT treatment until mid-August (August 8; Figure 2). There was a rapid response in greenness just 2 days after the deluge was added in mid-July with the DRT+DEL treatment briefly exceeding the CON treatment 10 days after the deluge (Figure 2). The increase in greenness relative to the DRT treatment lasted for approximately 1 month after the deluge event (Figure 2). For the DRT+SE treatment, greenness increased gradually and to a much lesser degree, requiring several weeks to diverge from the DRT treatment (Figure 2).

3.3 | Carbon fluxes

The DRT treatment reduced growing season GPP (51%), ER (56%), and NEE (47%) relative to the CON precipitation treatment, while the DRT+DEL and DRT+SE treatments were intermediate to CON and DRT treatments (Table 2; Figure 3). As with canopy greenness, GPP

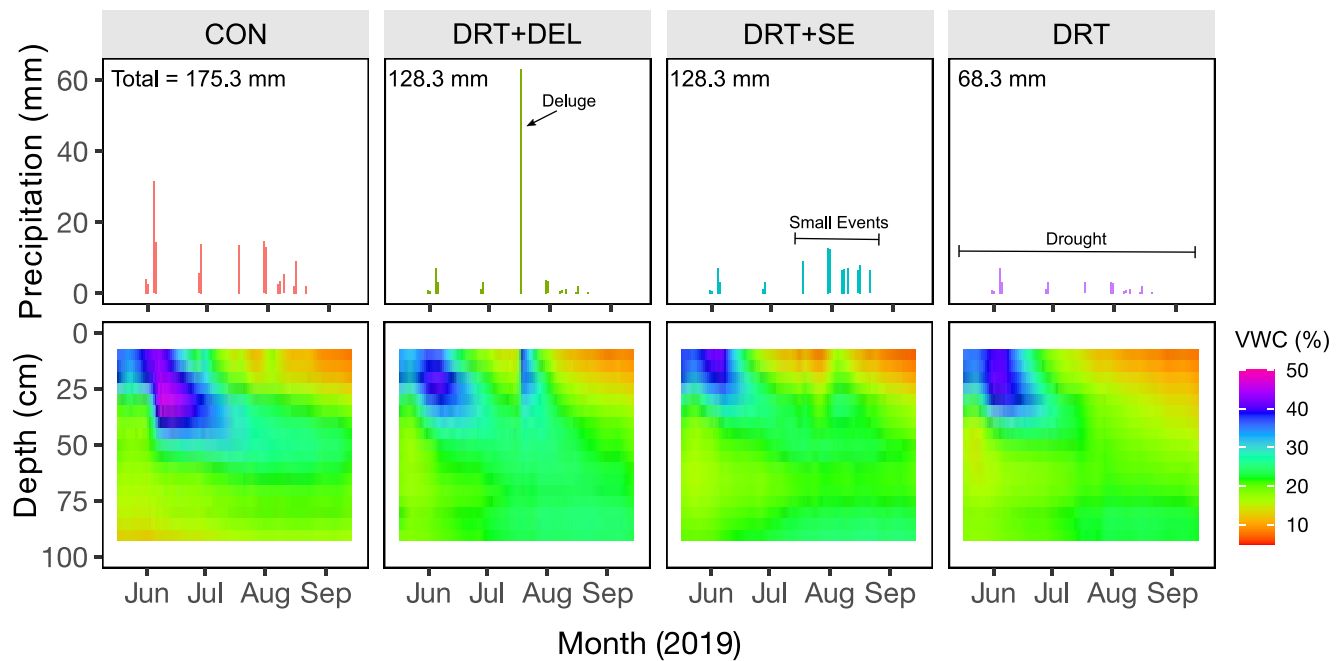


FIGURE 1 Precipitation inputs and soil moisture. (Top) Precipitation inputs for control (CON), drought with deluge (DRT+DEL), drought with small events (DRT+SE), and drought (DRT) treatments, with total values in top left corners. (Bottom) Soil moisture with depth and time. VWC, volumetric water content

and NEE were not significantly different until June when the CON treatment had greater carbon uptake than the other three treatments (Figure 3). Differences in ER between the CON and other precipitation treatments were slower to develop, emerging in mid-July

(Figure 3). It is important to note that there were no significant differences in any carbon fluxes among precipitation treatments on the day prior to the deluge (Figure 3). After the mid-July deluge, there was an immediate pulse in ER, but not GPP, which increased ER in the DRT+DEL treatment over the growing season relative to the DRT (53% increase) and DRT+SE (45% increase) treatments (Figure 3). GPP peaked 1 week after the deluge, while ER decreased, leading to a net uptake of carbon for the DRT+DEL treatment. The deluge affected carbon fluxes for 1 month (Figure 3), similar to the pattern observed with greenness (Figure 2). The additional water in the DRT+SE treatment took 2 weeks to significantly affect carbon fluxes, with higher rates of carbon gain than loss, relative to the DRT treatment, leading to net carbon uptake (NEE; Figure 3). As soil moisture and carbon

TABLE 1 Greenness ANOVA

Term	Greenness		
	df	F	p
Precipitation treatment	3	65.0	<.001
Date	16	2445.8	<.001
Precipitation treatment × date	48	1345.4	<.001

FIGURE 2 Canopy greenness. Average canopy greenness for a 0.5×0.5 m plot area using the green chromatic coordinate (GCC) color index for control (CON), drought with deluge (DRT+DEL), drought with small events (DRT+SE), and drought (DRT) treatments. Deluge timing (July 16, 2019) indicated by dashed line. Points represent means ± 1 SE, asterisks indicate significant differences among treatments for a given date

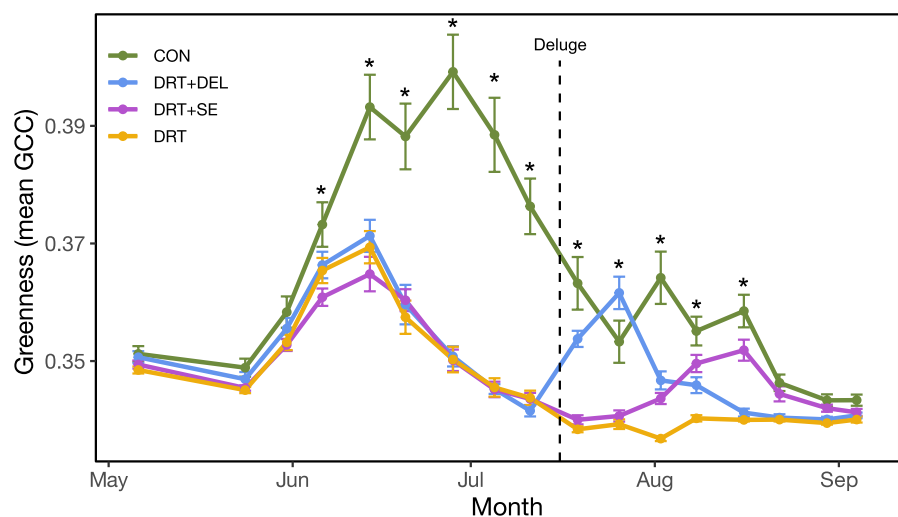


TABLE 2 Carbon fluxes ANOVAs

Term	GPP			NEE			ER		
	df	F	p	df	F	p	df	F	p
Precipitation treatment	3	35.9	<.001	3	16.7	<.001	3	36.4	<.001
Date	11	1154.2	<.001	11	1031.5	<.001	11	418.7	<.001
Precipitation treatment × date	33	412.8	<.001	33	294.6	<.001	33	270.0	<.001

Abbreviations: ER, ecosystem respiration; GPP, gross primary production; NEE, net ecosystem exchange.

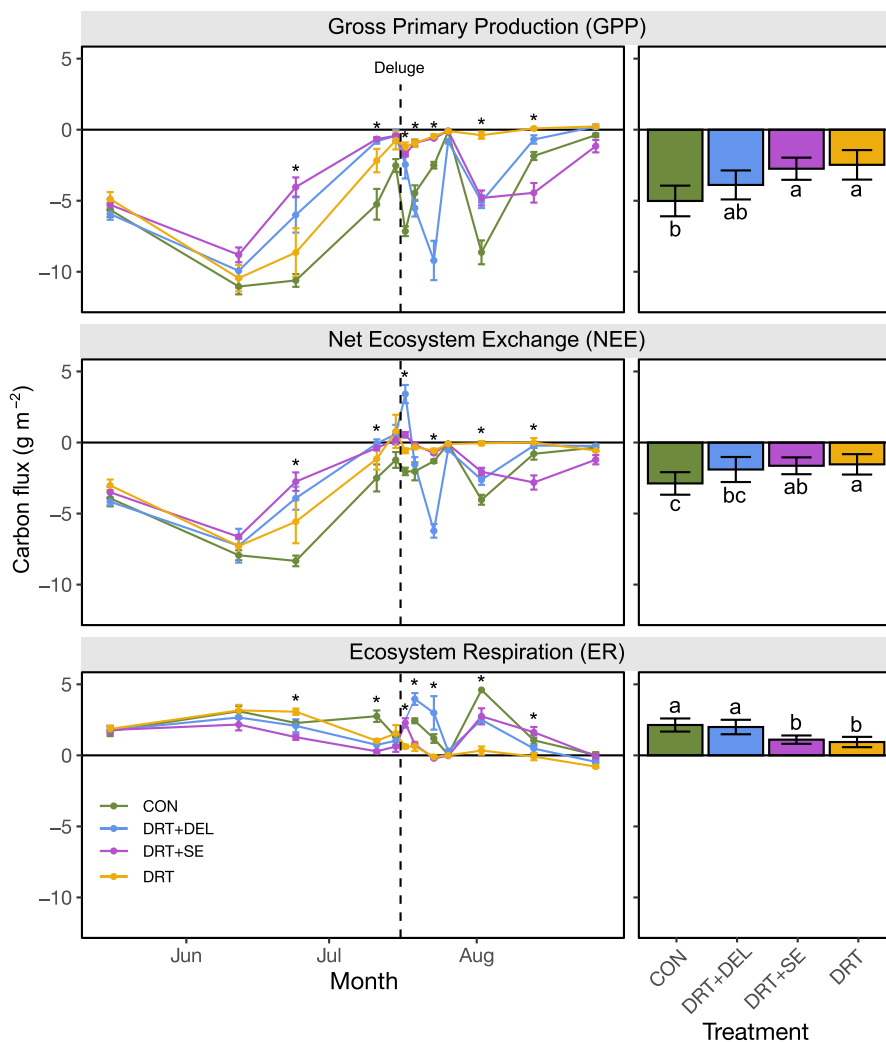


FIGURE 3 Carbon Fluxes. Carbon fluxes for control (CON), drought with deluge (DRT+DEL), drought with small events (DRT+SE), and drought (DRT) treatments. (LEFT) Carbon fluxes through time. Points represent means ± 1 SE, asterisks indicate significant differences among treatments for a given date. (RIGHT) Carbon flux means by treatment during the growing season. Bars represent means ± 1 SE, letters indicate significant differences among treatments

fluxes declined seasonally in the CON treatment, GPP and NEE in the DRT+SE treatment increased and were significantly different from the CON for only one observation in mid-August (Figure 3). Averaged over the growing season, the DRT+DEL treatment had greater carbon uptake than the DRT treatment but was not significantly different than the CON or DRT+SE (Table 2; Figure 3).

3.4 | Productivity

Relative to the CON, the DRT treatment significantly reduced ANPP (by 44%), BNPP (by 36%), and NPP (by 38%; Table 3; Figure 4). The

TABLE 3 Productivity ANOVAs

Production metric	Term	df	F	p
ANPP	Precipitation treatment	3	22.0	<.001
BNPP	Precipitation treatment	3	12.3	.017
NPP	Precipitation treatment	3	18.8	<.001

Abbreviations: ANPP, aboveground net primary production; BNPP, belowground net primary production; NPP, net primary production.

DRT+SE treatment was also significantly lower than the CON treatment but was not significantly different from the DRT+DEL or DRT treatment for any productivity metric (Figure 4). Meanwhile, the DRT+DEL treatment had intermediate effects on all productivity metrics and did not differ significantly from the CON treatment but was 24%, 10%, and 15% lower for ANPP, BNPP, and NPP, respectively (Figure 4). Next, we compared the ANPP in the experimental treatments to the long-term (36-year) historical record of precipitation (May–August) and ANPP from this site (Figure 5). The CON and DRT treatments fall very close to the predicted line in this linear regression (Figure 5). Meanwhile the DRT+DEL treatment falls within the 95% confidence interval with the DRT+SE treatment just below this interval.

4 | DISCUSSION

In this study, we focused on the ecological effects of compound hydroclimatic extremes—a deluge during a drought—which are both increasing in frequency and intensity but may have contrasting

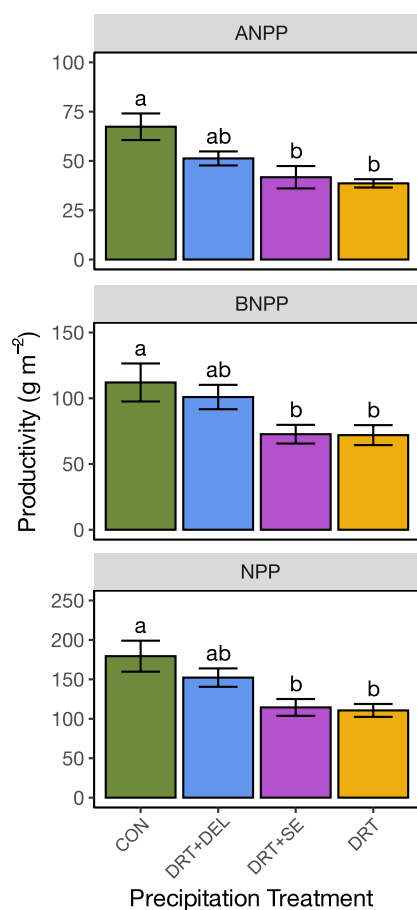


FIGURE 4 Productivity. Aboveground (ANPP), belowground (BNPP), and net primary production (NPP = ANPP + BNPP) for control (CON), drought with deluge (DRT+DEL), drought with small events (DRT+SE), and drought (DRT) treatments. Bars represent means $\pm$ 1 SE, letters indicate significant differences among treatments

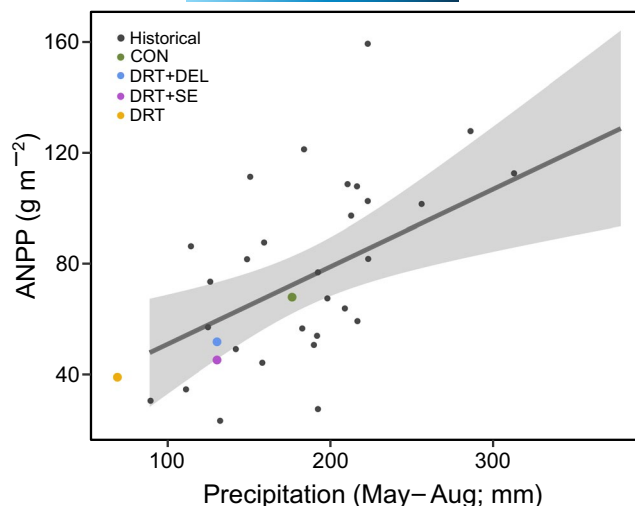


FIGURE 5 Precipitation versus productivity. The relationship between aboveground net primary production (ANPP) and precipitation for the historical record (1983–2018) and the control (CON), drought with deluge (DRT+DEL), drought with small events (DRT+SE), and drought (DRT) experimental treatments. Gray line indicates a linear regression between precipitation and total ANPP for the historical record ($r^2 = .28$; $p = .0003$), with gray shaded area representing the 95% confidence interval. Treatment means for experimental treatments were laid on top of this long-term relationship for reference

ecological impacts. We experimentally examined the effects of these precipitation extremes in a semi-arid grassland, which is highly sensitive to variation in precipitation amount and pattern (Heisler-White et al., 2008; Hoover et al., 2021; Lauenroth & Sala, 1992; Wilcox et al., 2015). There were three key results from this experiment. First, the effects of extreme drought alone were consistent across all measured variables, with large reductions in greenness, carbon fluxes, and productivity, relative to the CON treatment. Such responses are in agreement with a large body of past drought research in semi-arid grasslands. Second, the deluge during drought immediately stimulated carbon fluxes and plant growth, with effects persisting for one month post-deluge. Overall, the effects on the DRT+DEL treatment on productivity were intermediate to the CON and DRT treatments. Third, precipitation delivered as one extreme event during drought stimulated plant growth and carbon fluxes more than the equivalent amount delivered as several smaller events, and although these two treatments seldom differed significantly on growing season time scales, values of greenness, carbon cycling-, and productivity were always higher for the DRT+DEL than the DRT+SE treatment. Overall, these results showed that contrasting hydroclimate extremes, such as a deluge during a drought, can have unique off-setting effects on temporally dynamic processes (e.g., NEE and greenness), but may not be able to fully compensate for reductions in longer term ecosystem variables (e.g., ANPP). The latter is expected given that precipitation inputs to the DRT+DEL treatment were 25% below the CON treatment and

precipitation totals equated to a moderate drought (<20th percentile of long-term precipitation).

4.1 | Ecological effects of a single hydroclimatic extreme—Drought

In this study, extreme drought had strong effects on all measured variables, relative to the CON treatment, which received the same precipitation pattern and amount as the most average year on record (1989). As observed in other studies at this site (e.g., Lauenroth & Bradford, 2009), there was tight coupling between the precipitation inputs and soil moisture availability, particularly in the 0–30 cm depths (Figure 1). Ecosystem processes, including greenness and carbon fluxes closely mirrored soil moisture dynamics across the four precipitation treatments (Figures 1–3). Over the course of the growing season, the DRT treatment resulted in early senescence and reduced NEE by 46% relative to the CON (Figures 2 and 3). As soil moisture reached limiting levels in mid-July, both GPP and ER fluxes approached zero, suggesting both carbon uptake from plants and respiration (autotrophic and heterotrophic) had been severely limited. These results are similar to droughts observed across the Great Plains; this region can switch from a net sink to a net source of carbon during drought with the drier, western extent particularly sensitive (Petrie et al., 2016; Zhang et al., 2011). As with greenness and carbon fluxes, extreme drought had large effects on productivity in this experiment. Drought significantly reduced ANPP and NPP relative to the CON with marginal effects on BNPP ($p = .08$; Figure 4). The magnitude of reduction in ANPP was consistent with the long-term record (Figure 5) but greater than other drought experiments at this location (Byrne et al., 2013; Cherwin & Knapp, 2012).

4.2 | Ecological effects of compound hydroclimatic extremes—Drought and deluge

We evaluated the effects of compound hydroclimatic extremes—a deluge during a drought—in two ways. First, we examined how the DRT+DEL treatment compared to the CON and DRT treatments for a given response variable. If the DRT+DEL treatment was significantly different from the DRT but equal to the CON, it would suggest that the deluge pulse “rescued” key ecosystem functions from drought (Post & Knapp, 2020, 2021). This was observed in both greenness and carbon cycling. The DRT+DEL treatment resulted in a large, short-term pulse in greenness and carbon fluxes in the DRT+DEL treatment relative to the DRT treatment, (Figures 3 and 4). Over the course of the growing season, the addition of the 60 mm deluge to the DRT increased NEE by 23% and ER by 112% (Figure 3). Conversely, if the DRT+DEL treatment was significantly different from the CON but equal to the DRT, it would suggest that the deluge pulse did not alleviate the effects of drought. This was not the case for any measured variables in the DRT+DEL

treatment. It should be noted that ANPP, BNPP, and NPP in the DRT+DEL treatment were not significantly different from either DRT or CON, suggesting that the deluge had intermediate effects on productivity (Figure 4). These results are consistent with observations in other semi-arid ecosystems indicating that these grasslands are very sensitive to pulses of moisture, particularly during periods of water limitation (Huxman et al., 2004; Reynolds et al., 2004).

A second way we evaluated the compounded effects of a deluge during drought, was to compare the DRT+DEL with the DRT+SE treatments, which differed only in precipitation pattern, not amount. This allowed us to determine if delivering the precipitation as a single deluge rather than the same precipitation amount in multiple smaller (normal) events during drought resulted in an enhanced response. We observed several differences between the DRT+DEL and DRT+SE treatments in the continuously monitored variables. First, greenness and carbon fluxes had faster and larger responses to the DRT+DEL treatment compared to the DRT+SE treatment (Figures 2 and 3). One possible mechanism for this difference is related to spatial and temporal differences in soil moisture between the two treatments. The DRT+DEL treatment recharged soil moisture through the primary rooting zone (0–30 cm), while the equivalent amount of precipitation delivered in smaller events in the DRT+SE treatment had smaller recharging effects, which were closer to the surface (Figure 1; Figure S1). In the shortgrass steppe, and dryland ecosystems more broadly, evaporative demand is quite high, and therefore, infiltration of water from larger events to deeper soil layers can reduce the proportion lost to evaporation and increase the number of days when available soil water is above critical thresholds for plant and microbial function (Knapp et al., 2008; Lauenroth et al., 2014; Schwinning et al., 2004). Despite the strong, but transient effects on carbon cycling, there were no significant differences between DRT+DEL and DRT+SE treatments for seasonally averaged carbon fluxes (except ER) or production (Figures 3 and 4). Overall, these results suggest that precipitation delivered as one extreme event during drought stimulates plant growth and carbon cycling more than the equivalent amount delivered as smaller events, but has smaller impacts on season-long variables, such as productivity.

4.3 | Implications

Semi-arid ecosystems are “hot spots” for the global carbon sink, driving variability in the dynamics of the terrestrial carbon cycle due to their sensitivity to water availability and highly variable precipitation regimes (Ahlström et al., 2015; Haverd et al., 2016; Poulter et al., 2014). Results from this study highlight the tight coupling between precipitation, soil moisture, and carbon cycling in these ecosystems, as a single deluge event stimulated large pulses in carbon fluxes and plant growth, despite experiencing an extreme drought. The impacts of the compound effects of these hydroclimatic extremes likely depend on the magnitude of the deluge relative to the drought in terms

of precipitation amount, timing, and spatial extent. The sensitivity of plant growth and carbon cycling to deluges depends on seasonal timing and event size in this semi-arid grassland (Post & Knapp, 2020, 2021). If we imposed a larger deluge earlier in the growing season, this may have resulted in greater compensation for drought. Furthermore, droughts typically have large spatial extents (regional to continental; Andreadis et al., 2005; Sheffield et al., 2009), while extreme precipitation events occur at smaller scales, with deluges originating from individual cumulonimbus clouds or complexes of mesoscale convective systems (Houze, 2004). Thus, while a deluge may result in a large pulse in carbon uptake locally, the effects of drought will likely dominate regional carbon cycling. Overall, these results showed that a deluge during a drought has unique effects on the carbon cycle, stimulating a "hot moment" in plant growth and carbon cycling. However, ecosystem responses to an extreme precipitation event (a deluge) during a drought were not significantly greater (i.e., statistically) than responses to the equivalent addition of water via several smaller events across the growing season. Finally, the increase in precipitation in the DRT+DEL and the DRT+SE treatments (relative to the drought treatment) increased most ecosystem response variables in proportion to the amount of water added but did not fully compensate (or "rescue," Post & Knapp, 2020, 2021) reductions in annual plant production compared to CON treatment levels.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data used in this manuscript are publicly available through the US Department of Agriculture's Ag Data Commons (<https://doi.org/10.15482/USDA.ADC/1524422>).

ORCID

David L. Hoover  <https://orcid.org/0000-0002-9326-9791>

Olivia L. Hajek  <https://orcid.org/0000-0003-0352-7660>

Melinda D. Smith  <https://orcid.org/0000-0003-4920-6985>

Kate Wilkins  <https://orcid.org/0000-0002-9875-1149>

Ingrid J. Slette  <https://orcid.org/0000-0002-7707-3246>

Alan K. Knapp  <https://orcid.org/0000-0003-1695-4696>

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