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Responses of *Bouteloua eriopoda* and Soil Stability to Precipitation Extremes in Chihuahuan Desert Grassland

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Responses of *Bouteloua eriopoda* and Soil Stability to Precipitation Extremes in Chihuahuan Desert Grassland

Laura K. Sadorf¹*

ABSTRACT—Climate change is expected to increase the frequency and duration of extreme dry and wet years. As water is the most limiting resource in these semi-arid deserts, it is important to understand how semi-arid plants respond to precipitation changes, given that climate change will alter desert ecosystems in the future. To study these responses, I applied an extreme precipitation treatment (10 mm water twice per week) to a *Bouteloua eriopoda*-dominated desert grassland preceding the 2018 monsoon season. I measured soil moisture, soil stability, and vegetative growth of *B. eriopoda* within treatment and control plots, which received no water addition. While two natural rain events increased *B. eriopoda* growth in all plots, growth was significantly increased in response to the extreme precipitation treatment. Yet, control plots responded more quickly to natural rain pulses than continuously watered plots. Soil stability was not correlated with total cover of *B. eriopoda*. Soil stability was also measured at two adjacent long-term precipitation manipulation experiments. In comparison with this experiment, soils were more stable at watered plots in a long-term monsoon rainfall addition experiment and control plots in a long-term drought experiment. These results indicate that extreme precipitation events are beneficial for *B. eriopoda*-dominated grasslands, and *B. eriopoda* is especially responsive to rain pulses between dry periods. Further investigation is needed to determine the interaction between *B. eriopoda* and soil stability, which may provide insight for future success of this dominant desert grass.

KEYWORDS—*black grama*, *Bouteloua eriopoda*, phenology, soil stability, precipitation, semi-arid, pulse-dynamics, productivity

INTRODUCTION—Global climate models predict a more variable climate in the future, including increased frequency of extreme wet and dry years (Knapp et al. 2015). Currently, extreme wet years are rare, and their impacts should be documented through means other than modeling, such as experimental approaches (Knapp et al. 2015; Knapp et al. 2017). Many studies describe sporadic rainfall events via the pulse-dynamics paradigm (Ogle & Reynolds 2004; Reynolds et al. 2004; Thomey et al. 2011; Báez et al. 2013; Collins et al. 2014; Petrie et al. 2014; Thomey et al. 2014). Noy-Meir (1973) first described pulse-dynamics in arid land ecosystems as the biological processes that result after a rainfall event. This refers to sporadic rain events that drive biological responses of plants, such as growth and reproduction (Ogle & Reynolds 2004). More recently, the pulse-reserve paradigm is defined as rain pulses that drive biological activity resulting in a resource reserve, such as biomass or available nutrients (Collins et al. 2014). This reserve is important for driving plant responses well after a rain event (i.e. pulse) has

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occurred (Collins et al. 2014). According to Reynolds et al. (2004), a “pulse” is categorized as a collection of events that are capable of recharging soil water for a significant portion of the season. For example, plant productivity in semi-arid ecosystems responds rapidly to rainfall pulses, and thus is driven by pulse dynamics. Productivity during the growing season is therefore a function of the frequency and intensity of precipitation events (Reynolds et al. 2004; Collins et al. 2014), which are predicted to become more extreme under climate change (Knapp et al. 2015).

Many studies have looked at pulse-reserve dynamics

across varying lengths and degrees of precipitation treatments (Thomey et al. 2011; Báez et al. 2013; Thomey et al. 2014). Báez et al. (2013) compared plant community dynamics of *Bouteloua eriopoda* and *Larrea tridentata* dominated sites after 4–5 years of experimental drought and precipitation. This long-term rainfall manipulation experiment showed that *B. eriopoda* is sensitive to drought—the response is similar to shallow-rooted grasses despite the fact that *B. eriopoda* is a C_4 plant, which typically thrives in hot, dry climates (Báez et al. 2013). Thomey et al. (2011) conducted a rainfall manipulation experiment and compared aboveground net primary productivity (ANPP) of *B. eriopoda* after small, large, and ambient rainfall treatments over two monsoon seasons. Large rainfall treatments were found to have a greater effect on plant growth than small rainfall treatments, suggesting that *B. eriopoda* maximizes carbon gain during advantageous periods (Thomey et al. 2011). Extreme precipitation experiments are important in *B. eriopoda*-dominated grasslands because this C_4 grass is sensitive to drought (Báez et al. 2013; Thomey et al. 2014), and water is the most limiting resource for plant productivity in all grass-dominated ecosystems (Wilcox et al. 2017).

Although the majority of extreme precipitation and drought studies measure ANPP as an indicator of grass production in response to rainfall treatments, plant vegetative growth can be a better indicator of plant growth on a short time scale, which can represent a more accurate depiction of when plants are fixing carbon (Wang et al. 2018). Precipitation pulses, and thus pulse-reserve dynamics, are biologically important because they can affect plant phenology by stimulating growth of vegetative and reproductive structures (Noy-Meir 1973; Ogle & Reynolds 2004). Ogle & Reynolds (2004) elaborated on pulse-reserve dynamics by noting that the response (i.e. growth rate) of a plant depends on its prior state before rainfall. The prior state refers to antecedent conditions, such as activity level of roots or enzymes, which influence the water uptake and photosynthetic rate of plants (Ogle & Reynolds 2004). This elaboration included thresholds that govern plant responses, such as the maximum growth rate a plant exhibits after precipitation pulses (Ogle & Reynolds 2004). An increase in the growth rate of a plant depends on the size of the pulse. If the growth rate was near the plant's maximum threshold before a pulse, then additional pulses would have no effect on its growth, as the plant's growth rate is already at a maximum. Vegetative growth is a good indicator of

plant response to pulses, because it visually demonstrates the uptake of water and nutrients from the soil (Adair & Blake 2010; Wang et al. 2018). Even small rain events can stimulate resource pulses by supporting activity of biological soil crusts (“biocrusts”) and only a slight increase in rain events can stimulate plant nutrient uptake and photosynthesis (Adair & Burke 2010).

According to Collins et al. (2008), there are important interactions and feedbacks of biotic and abiotic processes that assist in governing pulse-reserve dynamics. These biotic and abiotic processes include biocrust processes, soil moisture dynamics, and soil stability (Collins et al. 2008; Collins et al. 2014). Soil stability is defined as the degree to which soils resist erosion and is affected by biotic and abiotic processes, though biological components contribute the most to stability (Chaudhary et al. 2009; Fernandes et al. 2018). Soil stability tests are considered important for assessing ecosystem health according to Rangeland Monitoring Procedures (Eldridge & Greene 1994; Herrick et al. 2015). Biocrusts provide soil stabilization services through filamentous cyanobacteria located in the upper 2 mm soil layer (Ferrenberg et al. 2015; Fernandes et al. 2018). The link between soil stability and plant vegetative growth may be drawn from the ability of biocrusts to regulate soil hydrology and nutrient cycling through their rapid response to rain pulses (Ferrenberg et al. 2015).

This study was designed to elucidate possible connections between *B. eriopoda* vegetative growth and soil stability after a precipitation treatment to represent pulse-dynamics, via the experimental replication of summer monsoon events. The precipitation treatment was designed to represent summer storm events because precipitation in the Chihuahuan Desert is highly variable and summer monsoons produce 53% of the average annual precipitation (Reynolds et al. 2004; Thomey et al. 2011). This study set out to test the following questions: (i) what effects do extreme precipitation additions have on the vegetative growth of *B. eriopoda*; (ii) what are the effects of these same treatments on soil stability; and (iii) how does soil stability differ in response to a short-term monsoon in comparison to long-term monsoon and drought experiments?

Specifically, this study hypothesizes that: (i) extreme precipitation treatments will increase the total biomass of *B. eriopoda*, which will be evident in the presence of new foliage; (ii) increasing water to the system will increase soil stability; (iii) high soil stability will retain water longer, allotting more time for *B. eriopoda* roots to uptake

water, thus causing an increase in foliar cover; and (iv) low soil stability will retain water in the soil for a shorter period of time, causing low water uptake in *B. eriopoda* roots, resulting in no change in vegetative growth.

MATERIALS & METHODS—Study area. This study was conducted on McKenzie Flats in the Sevilleta National Wildlife Refuge (SNWR), located 80 km south of Albuquerque, New Mexico, USA (34°20'37.73" N, 106°43'38.45" W). Within the SNWR, the study site lies in Chihuahuan Desert grassland dominated by *B. eriopoda* (Poaceae), which is found on homogeneous soils (Buxbaum & Vanderbilt 2007). *Bouteloua eriopoda* is a warm-weather, stoloniferous perennial grass and typically thrives at elevations of 3,500 to 5,500 ft (U.S. Department of Agriculture Natural Resources Conservation Service [NRCS] 2005). New vegetation grows from basal axillary buds and from axillary buds at nodes on stolons (NRCS 2005). The climate at the SNWR is semi-arid with an average annual temperature of 13.2°C, mean low of 1.6°C in January and high of 25.4°C in July (Thomey et al. 2011; Báez et al. 2013). Summer monsoon rainstorms occur July–September with an average annual precipitation of 250 mm (Thomey et al. 2011; Báez et al. 2013).

Experimental design. To test the effects of an extreme precipitation treatment on *B. eriopoda*, I conducted a rainfall manipulation experiment for four weeks during June and July 2018 in a semi-arid grassland. Fourteen 1 m² plots were randomly selected from a 40 x 15 m area located 30 m east of a dirt road. Seven plots received a precipitation treatment of 10 mm of water two times per week for four weeks, while seven plots received no treatment. This represented above-average monsoon events, in contrast to the average of < 5 mm of water per event (Petrie et al. 2014). The water treatment was applied with a watering can to a 1.2 m² area so that the water treatment for each 1 m² plot extended 0.2 m beyond each plot, assuring that the plant rooting zone within plots received the same amount of water throughout. Treatment water was obtained through reverse-osmosis and contained 0.67 ppm NO³-N and 1.01 ppm NH⁴-N (Thomey et al. 2011). I chose to apply 10 mm of water to each plot since few precipitation inputs (11.6%) are between 10 and 20 mm in the SNWR (Thomey et al. 2011; Petrie et al. 2014). Although 10 mm rainstorms are not the most extreme precipitation events to this ecosystem, the frequency of this treatment (biweekly) is not common and thus, is considered

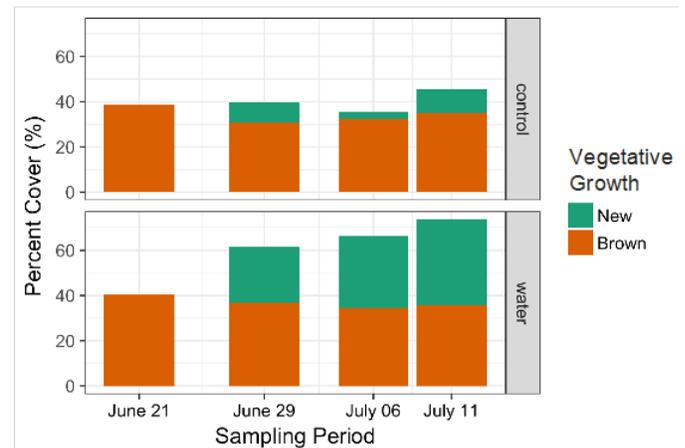


FIGURE 1. Vegetative growth was sampled in 14 plots, 7 control and 7 watered, within one site in *Bouteloua eriopoda*-dominated grassland in the Northern Chihuahuan Desert, New Mexico, USA. Vegetative growth was sampled four times throughout the experiment. Percent cover of new foliage and brown foliage of *B. eriopoda* was recorded during each sampling date when present. Brown foliage remained constant across all sampling dates for control and water (t-stat = -1.56, df = 48, $P = 0.12$). New foliage differed between watered and control plots (t-stat = -13.0, df = 32, $P < 0.001$). Total cover (new and brown) differed between the treatment and control plots across all sampling dates (t-stat = -5.13, df = 65, $P < 0.001$).

extreme (Petrie et al. 2014). This treatment simulated increases in both rainfall frequency and size. Response variables included vegetative growth, soil moisture, and soil stability.

Foliar cover and vegetative growth were measured once per week over four weeks to track responses of *B. eriopoda* to increased rainfall. Foliar cover was determined by estimating the percent of 1 dm² quadrant squares occupied by each plant. Vegetative growth was measured by visually estimating the percent of new and brown foliage from the total percent cover, which was derived from the foliar cover measurements. Before treatment began, *B. eriopoda* accounted for 30–50% of total cover within all plots. Other subdominant species included *Gutierrezia sarothrae*, *Plantago patagonica*, and *Chamaesyce lata*. Vegetative growth was only described for *B. eriopoda* within the 1 m² plots because this dominant grass displayed the most growth and cover change compared to all other species during this experiment.

Soil stability was not correlated with vegetative growth of *B. eriopoda*, so this study compared soil stability between short-term and long-term experiments. Soil

stability was quantified at three different sites located on McKenzie Flats, SNWR: (i) a short-term monsoon experiment (this study); (ii) a long-term monsoon experiment (Monsoon Rainfall Manipulation Experiment, MRME); and (iii) a long-term drought experiment (Extreme Drought in Grassland Experiment, EDGE). Monsoon Rainfall Manipulation Experiment was located 52 m E from this experiment and EDGE was located 703 m SW from this experiment. Soil stability was tested and ranked using the method described by Herrick et al. (2015) in the Monitoring Manual for Grassland, Shrubland and Savanna Ecosystems. Soil stability was ranked on a scale from 1 to 6 after dipping the soil sample in water. A ranking of 1 (low stability) indicates that < 10% of the soil sample remained after 30 sec after dipping the sample in water five times. A ranking of 6 (high stability) indicates that 75–100% of the soil sample remained after five water dips.

Soil moisture was measured as volumetric water content (%VW) using a handheld soil moisture probe, Moisture Meter type HH2 (Delta-T Devices Ltd., Cambridge, UK). Soil moisture was measured immediately before and after each watering treatment and the consecutive 1–2 days after each watering treatment. Soil moisture measurements were recorded at the edge and center of each plot at a depth of 16 cm, within the recognized rooting zone of *B. eriopoda* (Thomey et al. 2011). The edge and center soil moisture measurements were averaged for each plot before analysis.

Data analysis. Data analysis was completed in Microsoft Excel (version 16.15, Redmond, WA, USA). Two-sample t-tests were used to compare the differences in vegetative cover between control and watered plots. These t-tests analyzed brown and new foliage separately to find differences in those variables between control and watered plots (FIG 1). Analysis of variance (ANOVA) with

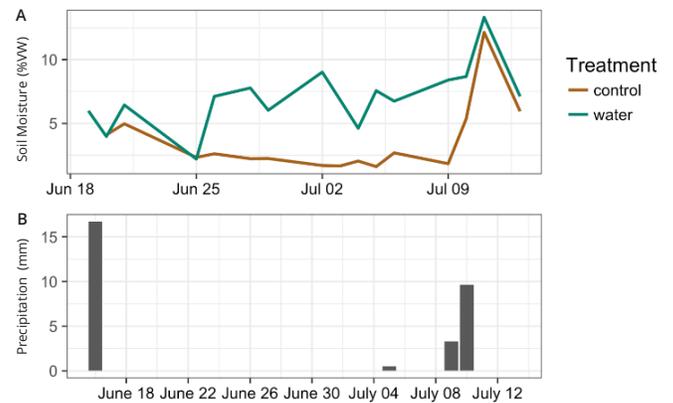


FIGURE 2. Daily record of soil moisture content and natural precipitation throughout the four-week simulated monsoon treatment period during June–July 2018. (A) Average soil moisture (% VW) was recorded at 160 mm depth for each water and control plot and then averaged across each treatment. (B) Two natural rain events occurred on 16 Jun 2018 and 10 Jul 2018.

replication was used to analyze the total foliar cover between the first and last sampling dates, June 21 and July 11, for control and watered plots (TABLE 1). The α was set to 0.05 for all analyses. All figures were created in R, version 3.5.0 (R Core Team 2018).

RESULTS—Change in vegetative growth over time. This study was influenced by two ambient rain pulses. The first ambient rain pulse occurred on 16 Jun 2018, before the first sampling date, and the second ambient rain pulse occurred on 9–10 Jul 2018, before the last sampling date (FIG 2). On the first sampling date, 21 Jun 2018, soil moisture (%VW) was similar between control and watered plots, which averaged between 5–6%VW. Throughout the experiment, watered plots maintained the same average soil moisture while control plots had low soil

TABLE 1. Analysis of total foliar cover between control and watered plots of the first (21 Jun 2018) and last (11 Jul 2018) sampling days. Calculations were determined with a two-way ANOVA with replication.

Source of Variation	SS	df	MS	F	P-value	F crit
Sample	2735.37	1	2735.38	28.9615	1.5687 × 10 ⁻⁵	4.2597
Columns	1586.27	1	1586.27	16.7950	0.0004	4.2597
Interaction	1192.77	1	1192.77	12.6288	0.0016	4.2597
Within	2266.77	24	94.4487			
Total	7781.19	27				

moisture of 2%VW. On the last sampling date, 11 Jul, both control and watered plots increased soil moisture to 8 and 10%VW, respectively, due to the second ambient rain pulse. Throughout this experiment, brown foliage remained constant in both watered and control treatments ($t\text{-stat} = -1.56$, $df = 48$, $P = 0.12$). On the second vegetative growth sampling day, 29 Jun, both control and watered plots showed new foliage on all *B. eriopoda* plants. Percent cover of new foliage increased slightly in watered plots for the remainder of the experiment (FIG 1 & 3). New foliage increased in control plots on the last vegetative growth sampling day, which occurred one day after the second natural rain-pulse to the experimental site (FIG 1, 3, & 4). Total foliar cover in both treatment and control plots increased over the course of the experiment (TABLE 1; $F = 28.96$, $df = 1$, $P < 0.001$), although the total cover of watered and control plots differed at the end of the experiment (TABLE 1; $F = 12.63$, $df = 1$, $P = 0.0016$). Change in vegetative growth and total foliage cover were not correlated with soil stability.

Soil stability at three sites. Soil stability was measured at three different sites to determine the differences in soil stability between a short-term monsoon treatment, a long-term monsoon treatment, and a long-term drought treatment in *B. eriopoda*-dominated grassland. This experiment, a short-term monsoon treatment, found no difference in soil stability between watered and control treatments (FIG 5; $t\text{-stat} = 0.15$, $df = 11$, $P = 0.89$). In MRME, a long-term monsoon experiment, there were no significant differences among all treatments (FIG 5; $F = 1.17$, $df = 2$, $P = 0.35$). In EDGE, a long-term drought experiment, soil stability was significantly higher in control plots compared to drought treatment (FIG 5; $t\text{-stat} = 5.66$, $df = 11$, $P = 0.0001$).

DISCUSSION—Change in vegetative growth over time.

The results of this study support the hypothesis that an extreme precipitation treatment will have a positive effect on total foliar cover and vegetative growth change of *B. eriopoda*. Total foliar cover and new foliage increased in all plots. There were two natural rain pulses that influenced the study system, one on 16 Jun and the other on 9–10 Jul (FIG 2 & 3). The first natural rain pulse caused a noticeable change in vegetative growth in both treatments on the second sampling day, 29 Jun 2018 (FIG 1). There is some discrepancy in FIG 2 where the heavy spike in ambient rainfall on 16 Jun did not increase soil moisture to a similar degree as the ambient rainfall on 9 Jul did.

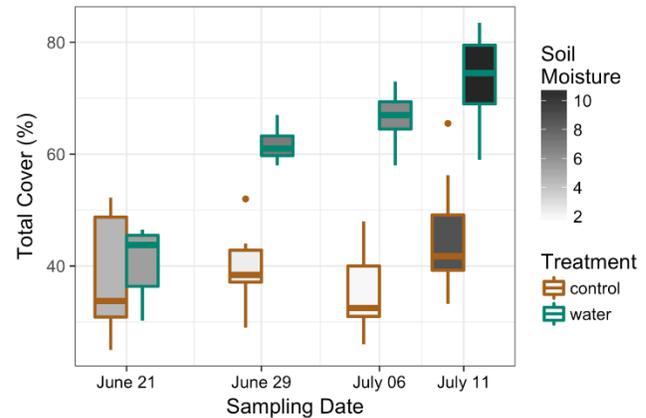


FIGURE 3. Comparison of total foliage cover of *B. eriopoda* between watered and control plots across four sampling periods. Brown box plots represent control plots that received ambient rainfall. Teal box plots represent watered plots that received 10 mm water biweekly plus ambient rainfall. Shading within each box plot represents the average soil moisture (%VW) of each treatment, white for low soil moisture and black for high soil moisture.

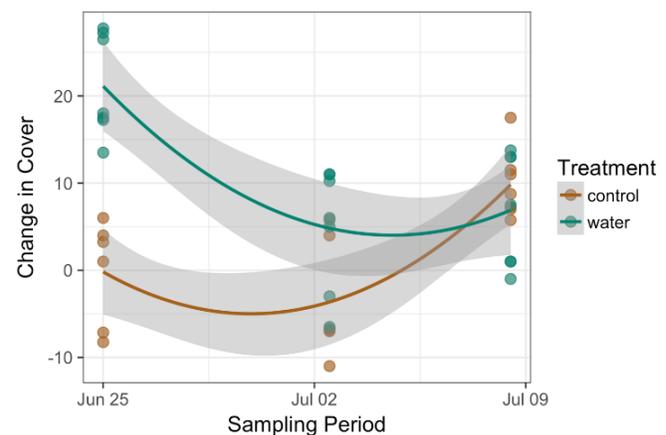


FIGURE 4. Change in cover of *B. eriopoda* compared among four sampling periods. Change in cover was calculated for each consecutive sampling period and is shown for each mid-date between each sampling period. The blue line represents plots that received weekly watering treatments and the red line represents control plots that received no treatment. Points represent cover measured for each individual plot. Upper and lower limits of best fit lines are \pm SE.

Since precipitation data were collected from a rain gauge located at MRME, 53 m from this study site, there may have been unequal rainfall to this experimental site since monsoons are known to unevenly distribute rain across the landscape due to localized cells (Petrie et al. 2014). The second natural rain pulse caused a more noticeable effect in control plots than watered plots (FIG 3 & 4).

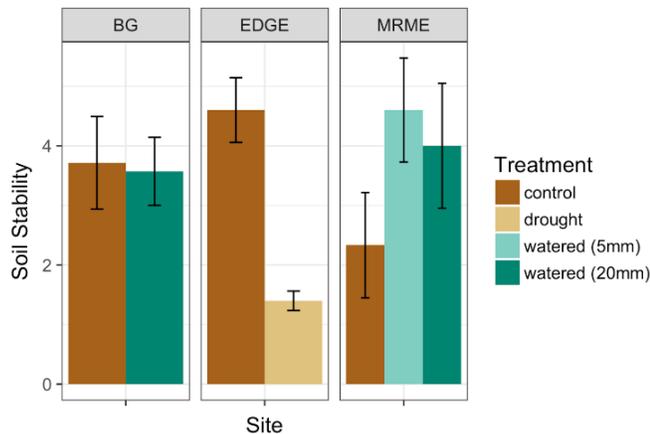


FIGURE 5. Comparisons of soil stability at three different sites in *B. eriopoda*-dominated grassland in the Northern Chihuahuan Desert, New Mexico, USA. The sites are labeled as follows: short-term monsoon treatment (BG), long-term drought treatment (EDGE), and long-term monsoon treatment (MRME). Legend labels are associated with separate treatments within each site. In BG, soil stability did not differ between ambient rainfall and 10 mm biweekly waterings (t -stat = 0.15, $df = 11$, $P = 0.89$). In EDGE, soil stability significantly differed between ambient rainfall and drought treatment (t -stat = 5.66, $df = 11$, $P = 0.0001$). In MRME, soil stability did not differ between ambient rainfall and the two watering treatments ($F = 1.17$, $df = 2$, $P = 0.35$). Soil stability is ranked on a scale from 1 to 6; 1 is low stability and 6 is high soil stability. Error bars are \pm SE.

Even though watered plots maintained higher total cover than control (t -stat = -5.13, $df = 65$, $P < 0.001$), control plots responded slightly faster to the second natural rain pulse than did watered plots (FIG 4). This can be related to previous findings at MRME where *B. eriopoda* responded more favorably to rain pulses that are separated by dry periods (20 mm water/mo) rather than continuous watering cycles (5 mm water/wk; Thomey et al. 2011).

These results show the importance of coupling short-term experiments with long-term experiments. Even though long-term studies like MRME (Thomey et al. 2011) and EDGE (unpublished data) found that *B. eriopoda* responds more favorably to rain pulses separated by dry periods across the growing season, short-term experiments are able to examine the more immediate responses of *B. eriopoda*. Oftentimes, long-term experiments only focus on species composition or aboveground primary productivity. This broad focus of long-term experiments may show that plants respond to climate change, but they do not focus on the underlying mechanisms of plant responses, such as the rapid foliar response of *B. eriopoda*,

as this short-term experiment demonstrated. Referring to Ogle & Reynolds' (2004) elaboration on pulse-dynamics, the watered plots were probably operating near their maximum growth rate threshold whereas control plots were operating near their minimum growth rate threshold (FIG 4). This is inferred by the slightly higher increase and steeper trajectory of percent cover in control plots compared to watered plots (FIG 4). Longer monitoring of this experiment, coupled with natural rainfall events, would lead to a more deterministic conclusion.

Soil stability at three sites. The results do not support the hypothesis that increasing water to the system would increase soil stability. Soil stability was not correlated to soil moisture, nor the change in *B. eriopoda* vegetative growth. Since soil stability was not correlated with vegetative growth in this experiment, soil stability was analyzed at a long-term monsoon experiment (MRME) and a long-term drought experiment (EDGE) to determine differences between short-term treatments and long-term treatments. This experiment and MRME showed no difference in soil stability between their respective treatments, whereas EDGE did have significant differences in soil stability between treatments. The soil stability results from MRME are most likely due to small sampling size and a range of soil stability results within each treatment. However, there is an important trend within MRME. I found that the soil was slightly more stable within the 5 mm water/wk plots compared to the 20 mm water/mo plots. Since biocrusts are sensitive to changes in pulse sizes (Fernandes et al. 2018), biocrusts may favor consistent soil moisture contrary to *B. eriopoda*, which had more biomass at the 20 mm water/mo plots at MRME (Thomey et al. 2011), although further experimentation is needed to draw a more solid conclusion. When comparing soil stability rankings from MRME to this study, the watered treatments at MRME had higher soil stability than either treatment in this experiment.

CONCLUSIONS—Because climate change is predicted to lead to an increase in the magnitude and frequency of wet and dry years (Knapp et al. 2015), understanding how semi-arid plants respond to precipitation extremes is pertinent to how plant dynamics may be altered in the future. This study showed that precipitation extremes increase the total cover and new foliage of *B. eriopoda*, though the magnitude of that change depends on the amount of precipitation *B. eriopoda* receives (FIG 1, 3, & 4). Soil stability differed between short-term and

long-term precipitation manipulation experiments. Long-term experiments had more stable soils, suggesting that long-term treatments may be necessary for sustaining growth of biocrusts (Fernandes et al. 2018). This study is a stepping stone for long-term experiments to determine the effects of climate change in a semi-arid ecosystem. Although there was no relationship between total foliar change and soil stability, long-term experiments can incorporate a range of soil stability testing to determine that relationship, such as analyzing soil stability on a gradient from open interspaces to under plant canopies. Future investigation of the minute changes to semi-arid grasslands due to extreme precipitation will help expand our understanding of how semi-arid ecosystems will change within a varying arid climate.

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