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The ecological role of small rainfall events in a desert grassland

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ABSTRACT

The frequency, magnitude and intensity of precipitation events are known to influence dryland ecosystems; yet, the majority of these rain events are small (<5 mm), and their role in driving biotic and abiotic processes remains unclear. To explore the effects of small rain events that occur between larger events on ecosystem processes, we experimentally manipulated small rainfall events in a mixed *Bouteloua eriopoda* and *Bouteloua gracilis* desert grassland. We experimentally removed all events <3.8 mm from treatment plots during a dry monsoon (2012), and to assess potential legacy effects, we added a similar magnitude of small rainfall events in 3.8-mm increments to the same treatment plots during a subsequent wet monsoon (2013). No difference in aboveground productivity occurred between ambient and treatment plots when small events were eliminated in 2012. However, soil moisture, soil organic carbon, available nitrogen and extracellular enzyme activity for phosphate mobilization were all lower in treatment relative to ambient plots. In 2013, treatment plots that received supplemental small events had lower aboveground productivity, soil moisture and soil N availability than ambient plots. We hypothesize that legacy effects from the removal of small events in 2012 limited the ability of these plots to respond to higher, supplemented rainfall in 2013. Therefore, a reduction in small precipitation events – which may be caused by changing rainfall properties or increasing rates of evaporation in a warming climate – may intensify some deleterious effects of dry monsoons, and inhibit grassland recovery in subsequent years with higher rainfall. Copyright © 2015 John Wiley & Sons, Ltd.

KEY WORDS aridland ecology; climate change; ecohydrology; precipitation; grasslands

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INTRODUCTION

Aridland ecosystem processes are driven by the frequency and magnitude of precipitation events (Fay *et al.*, 2000; Daly and Porporato, 2006; Fay *et al.*, 2008; Heisler-White *et al.*, 2008). A large proportion of these rain events is small, and it is unclear how small rain events may influence ecosystem processes. For example, vegetation productivity and soil respiration may be more responsive to a small number of large precipitation events compared with a larger number of smaller events that result in the same total amount of precipitation in arid and semi-arid grasslands (Heisler-White *et al.*, 2008; Thomey *et al.*, 2011; Vargas *et al.*, 2012), while mesic grasslands show decreased productivity in response to a precipitation pattern of a fewer number of large events (Heisler-White *et al.*, 2009). In contrast, Sala and Lauenroth (1982) determined that plants may also up-regulate photosynthesis in response to rain events as small as 5 mm day^{-1}. More recently, Lauenroth and Bradford (2012) found that events <5 mm were one of the most important controls on water balance processes in arid and semi-arid ecosystems. Together, these studies demonstrate the variable and inconsistent effects of small rain events on aridland ecosystem processes.

Projections of future climate in the southwestern United States call for greater temperature-driven aridity and possible small decreases in precipitation during all or part of the year (Seager *et al.*, 2007; Gutzler & Robbins, 2011). In a warming environment, increasing potential evaporation may reduce the residence time of precipitation-derived soil moisture, even if total precipitation remains unchanged (Rodriguez-Iturbe *et al.*, 1999; Robertson *et al.*, 2009; Petrie *et al.*, 2012). Although soil moisture derived from small rain events may be proportionally less influenced by increasing evaporation than that derived from large events (Lauenroth and Bradford, 2012), the effect will nonetheless be lower average soil moisture availability on key components of aridland ecosystems, such as biotic soil crusts (Belnap *et al.*, 2005). While small precipitation events may stimulate ecosystem metabolism (Lauenroth and Bradford, 2012) and nutrient mobilization (Ivans *et al.*, 2003), these moisture-dependent processes may be constrained by future evaporative demand. In the northern Chihuahuan Desert, the summer monsoon season from July to September may account for as much as 40–60% of total annual rainfall and drive more than 50% of annual vegetation net primary productivity (Muldavin *et al.*, 2008; Collins *et al.*, 2010). In this region, the average

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number of monsoon season precipitation events has increased over the past 100 years, while the average magnitude of these events has decreased from 3 to 2 mm (Petrie *et al*., 2014a). Thus, small rain events may play a significant but underappreciated role in aridland ecosystems. To evaluate the potential for climate change to impact aridland ecosystems, it is important to ascertain the relative role of small events for ecosystem functioning.

In aridland ecosystems, small rain events temporarily wet the soil surface and stimulate activity in the upper few centimetres of soil, but it is unclear if these events influence longer-term ecosystem variables such as soil moisture availability and vegetation photosynthesis that is independent of the precipitation regime. One way that small rainfall events may affect ecosystems is through nutrient cycling. In the pulse-reserve model of nutrient cycling, small precipitation events do not percolate into the rooting zone to stimulate vegetation activity, but they can initiate microbial processes that result in a temporary reserve of resources (such as nitrogen, carbon and phosphorus) near the soil surface (Austin *et al*., 2004; Collins *et al*., 2014). These resources may then be made available to vegetation when larger precipitation events move nutrients and water into the rooting zone (Austin *et al*., 2004; Reynolds *et al*., 2004; Schwinning and Sala, 2004; Collins *et al*., 2008) or through plant–microbe interactions (Green *et al*., 2008; Kivlin *et al*., 2013). Most soil microbial activity occurs near the soil surface, and nutrient uptake and production by these microbes may often respond strongly to the patterns of small rain events (Belnap *et al*., 2004; Belnap *et al*., 2005). Thus, small rain events may ultimately play a large indirect role in ecosystem productivity by driving microbial processes even during periods when plants are inactive (Huxman *et al*., 2004).

Most precipitation experiments induce drought by passively making large events smaller (Yahdjian and Sala, 2010; Reichmann *et al*., 2013; Koerner and Collins, 2014). To determine the role of small rain events within the context of regional climate change projections for the southwestern USA, which call for a more variable precipitation regime, we experimentally eliminated only small rain events during the summer monsoon season to assess their effects on ecosystem processes in desert grasslands in the northern Chihuahuan Desert, Central New Mexico, USA. The main objective of our research was to determine the effect of small rainfall events ($<3.8\,\mathrm{mm\,day^{-1}}$) on desert grassland productivity, soil moisture availability, soil carbon (C) and nitrogen (N) content, and soil extracellular enzymatic activities (EEAs) during above-average and below-average monsoon seasons, and to assess their potential legacy effects from one year to the next. We also compared aboveground net primary productivity (ANPP) in this experiment with ecosystem carbon exchanges from eddy covariance in this grassland to explore productivity responses to patterns of rainfall events at daily and seasonal timescales. We hypothesized that small rainfall events would have little influence on primary productivity or soil moisture availability in wet and dry monsoons, but that microbially driven processes (e.g. EEA, soil C and N availability) would be negatively impacted by the removal of small rain events during a monsoon season with below-average precipitation.

SITE

Our research was conducted in a mixed *Bouteloua gracilis*-dominated and *Bouteloua eriopoda*-dominated desert grassland at the Sevilleta National Wildlife Refuge (SNWR), New Mexico, USA (34.359°N, 106.736°W). Elevation at this site is approximately 1615 m. Soils are classified as Turney loamy sand (a sandy clay loam), with a saturated hydraulic conductivity (K_{sat}) of 1.5–5.1 $\mathrm{cm\,hr^{-1}}$ and a field capacity $\sim\theta = 0.31$, averaged from 0-cm to 50-cm depth (United States Department of Agriculture, N. R. C. S., 2013; Petrie *et al*., 2014b). The upper 10 cm of this soil is classified as loamy sand (United States Department of Agriculture, N. R. C. S., 2013). The SNWR contains a broad ecotone between Chihuahuan Desert grassland dominated by *B. eriopoda* and semiarid shortgrass steppe dominated by *B. gracilis* (Gosz, 1993; Muldavin *et al*., 2008). Total annual precipitation was slightly lower than average in this grassland in the 5 years prior to our study (Petrie *et al*., 2014b).

METHODS

Experimental design

Based on daily precipitation totals from the Sevilleta Long Term Ecological Research meteorological network (7 sensors in 2006–2007 and 8 in 2008–2010, 38 total sensor years) located across a 50-$\mathrm{km^2}$ area of the SNWR (http://sev.lternet.edu/projects.php?meid=15), we determined that precipitation events of less than 3.8 $\mathrm{mm\,day^{-1}}$ during the monsoon season did not significantly reduce total seasonal precipitation (July–September) when removed from the precipitation record (paired *t*-test, $p > 0.05$). These small events accounted for 16 mm of monsoon-season precipitation on average, and 65% of precipitation events during this period.

In June 2012 prior to the start of the summer monsoon, we established 20 experimental plots in desert grassland with a 40 × 40-m area, ten of which were randomly assigned to the small rain event removal treatment and ten were left as ambient treatments. Removal treatments were covered by 2.2 × 2.4-m complete rainout shelters with a maximum height of 1.2 m angled to 0.9 m. Roofing consisted of clear polycarbonate panels (SuntufPlus, Palram Americas, Kutztown, PA, USA) that eliminated ultraviolet radiation but transmitted 90% of visible light.

While implemented from July to September 2012, these rainout shelters removed all rainfall from a centrally located 1-m^2 plot within the covered area in grassland co-dominated by *B. eriopoda* and *B. gracilis*, eliminating potential edge effects.

From 1 July through 30 September 2012, we used a gas pump and sprayer hose to apply a total of seven watering treatments equal to ambient rain event size, distributed evenly to the entire 2.2 × 2.4-m area shortly after each ambient rain event >3.8 mm (Figure 1). Thus, these plots only received ambient precipitation events >3.8 mm, and larger events were not manipulated in this experiment. Prior to taking end-of-season measurements, we added an additional 3.8-mm event at the end of the monsoon season in 2012 to both ambient and treatment plots to facilitate soil enzyme analysis in conditions that would otherwise have been too dry. We used deionized water, stored in an onsite tank, for watering applications. This watering application technique increases rainfall intensity (magnitude per unit time) compared with ambient rainfall and, although the effects of higher rainfall intensity that occur in this technique are not well documented, this technique is widely used in precipitation manipulation experiments and has the benefit of not resulting in significant plot run-off during water application. Because precipitation in 2012 was lower than average, our design resulted in a total of 87 mm of rain in ambient plots and 71 mm in treatment plots (Figure 1).

In 2013, we reversed the rainfall treatment during a large monsoon when scattered small events were likely to be less important than in a dry year. In this year, all plots received ambient precipitation, and rainout shelters were not implemented. Treatment plots also received four 3.8-mm rainfall additions applied approximately once every 18 days. Thus, total added rainfall in 2013 was nearly equal to the amount of precipitation removed in 2012 (−16 mm in 2012, +15.2 mm in 2013). Because precipitation in 2013 was higher than average, our design resulted in a total of 143 mm of rain in ambient plots and 158 mm in the treatment plots (Figure 1).

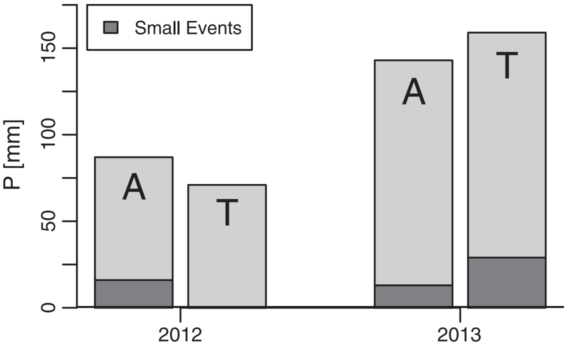

Figure 1. Total rainfall in ambient precipitation (A) and precipitation treatment (T) plots in 2012 and 2013. The experimental treatment in 2012 removed small rainfall events (<3.8 mm day^{-1}). In 2013, four small 3.8-mm rainfall events were added incrementally to treatment plots (15.2 mm total).

To account for higher evaporation on watering days (when ambient rainfall did not occur), we used the FAO-56 Penman–Monteith equation (Suleiman and Hoogenboom, 2007) to determine how higher temperature and lower relative humidity on these days increased potential evaporation (mm day^{-1}). Using meteorological data, we determined that days without rainfall at the SNWR experienced 12% higher potential evaporation, on average, from 2007 to 2011, and this determination was corroborated by water flux data from eddy covariance. Therefore, all watering treatments were increased by 12% in our study to account for daily potential evaporation. This method indirectly accounts for lower cloud cover and higher incident solar radiation during days that did not experience rainfall.

Measurements and data analysis

Aboveground net primary productivity (ANPP: g C m^{-2} y^{-1}) was measured at the beginning (late June) and end (early October) of the monsoon season in 2012 and 2013. ANPP was measured using a nondestructive allometric sampling method and linear regression based on species volume units developed using total standing biomass measurements (Huenneke *et al.*, 2001; Muldavin *et al.*, 2008). Volumetric soil moisture content (θ: m^3 m^{-3}) was measured continuously using soil water content probes (ECH2O EC-5, Decagon Devices, Inc., Pullman, WA, USA). Probes were buried horizontally at a 5-cm depth under vegetation in five replicates each of ambient and treatment plots.

Soil nitrogen content (μg 10 cm^{-2}) was measured using plant root simulator probes (Western Ag Global, Saskatoon, SK, Canada). One pair of cation and anion probes was located in each experimental plot (20 total pairs) at the interface of vegetation and bare soil. Plant root simulator probes provide estimates of plant available NH_4–N and NO_3–N during the monsoon season. Soil samples were taken from 0-cm to 10-cm depth at the beginning and end of each monsoon season from each treatment plot (a total of 20). Oxidizable soil organic carbon (SOC: %) was measured using the loss on ignition technique, where 5 g of sieved soil was oven dried at 450 °C to determine C loss by weight, and SOC percentages were converted to g C m^{-2} using the bulk density for sandy loam (1.5 g cm^{-3}) (United States Department of Agriculture, N. R. C. S., 2013).

The net seasonal change in extracellular enzyme activity of soil interspaces was analyzed following Stursova *et al.* (2006). Shortly before the beginning and shortly after the end of the monsoon season (late June and early October, respectively) in 2012 and 2013, we measured extracellular enzymatic activities in ambient and treatment soils (0–10-cm depth) for three enzymes: (1) β-D-glucosidase; (2) alkaline phosphatase; and (3) alanyl aminopeptidase.

Respectively, these enzymes reflect the magnitude of the ability of soil microbes and fungi to (1) break down plant cellulose to mobilize carbon; (2) break down phosphates to mobilize phosphorus; and (3) break down the bond in alanine amino acids to mobilize nitrogen. Collectively, these assays show the net potential of soil enzymes from various sources to mobilize limiting nutrients at the beginning and end of the monsoon season (Stursova *et al.*, 2006; Collins *et al.*, 2008).

We explored the relationship between ecosystem carbon exchange and precipitation using data from an eddy covariance instrument located in desert grassland <1 km from our experimental site. Fluxes of surface CO_2 were measured from this eddy covariance instrument from 2007 to 2011 (Anderson-Teixeira *et al.*, 2011). We used three-axis sonic anemometers (Campbell Scientific CSAT-3, Campbell Scientific, Logan, UT, USA) to measure vertical wind speed at 10 Hz and calculate covariance. We compiled 30-min averages of covariance, corrected for temperature and water vapour fluctuations (Webb *et al.*, 1980) and frequency responses (Massman, 2000). Gas exchange was measured using open-path gas analyzers (LiCor LI-7500, LICOR Biosciences, Lincoln, NE, USA). We gap filled net ecosystem exchange (NEE) and estimated ecosystem respiration (RE) using the Max Planck Institute (Open MPI) procedure (Falge *et al.*, 2001; Reichstein *et al.*, 2005) (http://www.bgc-jena.mpg.de/~MDIwork/eddyproc/index.php). We calculated gross primary productivity (GPP) as NEE + RE.

To explore the relationship between precipitation events and vegetation productivity at daily timescales, we compared daily GPP measured by the nearby eddy covariance instrument with statistics of average precipitation event timing (λ: events day^{-1}) and average event magnitude (α: mm event^{-1}). Using daily data during the summer monsoon from 2007 to 2011, we compared GPP measurements with λ and α at the grassland site over the prior 14 days to quantify the average GPP response to short-term precipitation history, and used linear interpolation technique to estimate GPP for all possibilities of λ and α over this time interval. Thus, our state-space analysis illustrates the average relationship between daily GPP in this grassland and varying combinations of λ and α from precipitation that occurred over the 14 days prior to the GPP measurement. Varying the window from 8 to 20 days did not affect the results of this analysis.

RESULTS

At the time of establishment, total vegetative cover, as well as the cover of *B. eriopoda* and *B. gracilis*, did not differ between ambient and treatment plots (two-tailed, unpaired *t*-test; $p > 0.05$). Precipitation during the 2012 monsoon season was 22% lower than the 2001–2010 average (87 and 110 mm average), and the experimental treatment was 36% lower (71 mm; Figure 1) than average. Removing small precipitation events resulted in significantly lower daily average soil moisture (0–10 cm) in treatment plots (3.3% treatment, 6.9% ambient, $p < 0.001$), and this difference was especially notable after day 20, when treatment plots showed a sharp decline in soil moisture retention following all rain events (Figure 2a). Ambient plots had significantly higher SOC at the end of the 2012 monsoon season (4.1 g C m^{-2} ambient, 3.3 g C treatment, $p < 0.03$; Figure 3) and significantly higher total soil NO_3–N and NH_4–N (79.8 μg 10 cm^{-2} ambient, 54.6 μg treatment, $p < 0.03$; Figure 4a) compared with treatment plots. We observed significantly higher alkaline phosphatase (phosphate enzyme) activity in ambient plots at the end of the 2012 monsoon ($p < 0.05$; Figure 5a) and nearly significant differences in alanyl aminopeptidase (alanine enzyme) ($p < 0.09$), suggesting that ambient plots had a higher potential for nutrient mobilization at the end of the monsoon season. ANPP did not differ between ambient and treatment plots in 2012 (Figure 4b). During the 2012 period, the cover of *B. gracilis* decreased 15.4% in ambient plots (one-tailed, paired *t*-test; $p < 0.03$) and decreased 45.8% in treatment plots (one-tailed, paired *t*-test; $p < 0.002$), and these reductions in cover were proportionally greater in treatment relative to ambient plots (one-tailed *t*-test, $p < 0.004$). We observed no additional differences in cover or ANPP for *B. eriopoda* or for *B. gracilis* in 2012.

During the period between monsoon seasons (October 2012–June 2013), total precipitation was 42% below the 2001–2011 average (114.7 mm average, 66.2 mm in 2012–2013), and the April of 2013 was the only month during this period with an above-average rainfall (+203%;

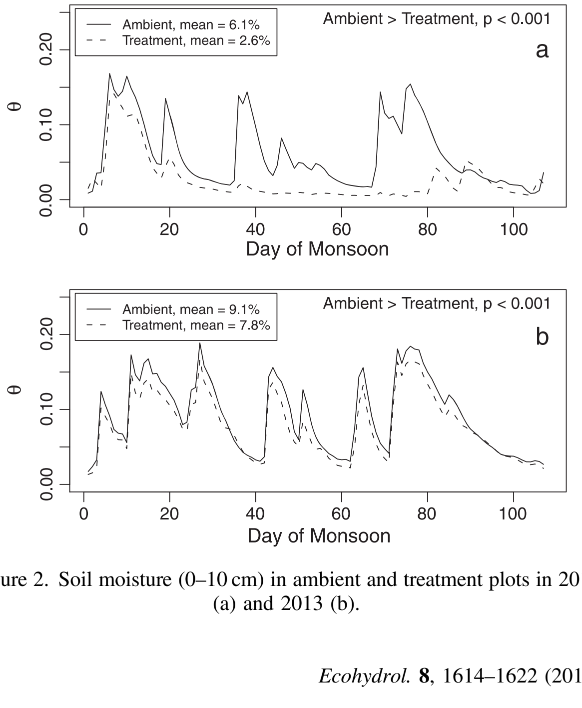

Figure 2. Soil moisture (0–10 cm) in ambient and treatment plots in 2012 (a) and 2013 (b).

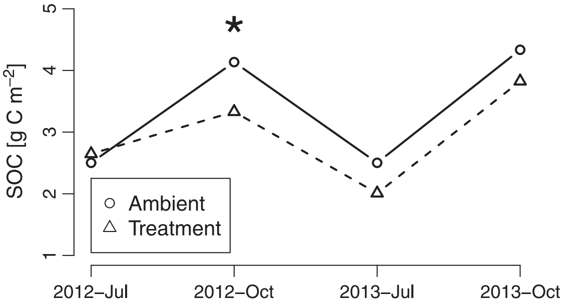

Figure 3. Soil organic carbon (SOC: g C m^{-2}) in ambient and treatment plots at the beginning and end of the monsoon season in 2012 and 2013. SOC was significantly higher in ambient plots at the end of 2012 ($p < 0.03$).

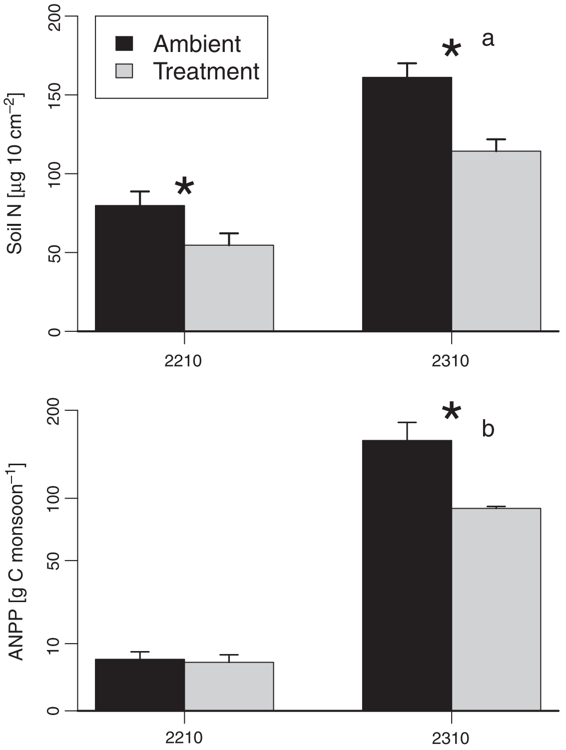

Figure 4. Net soil nitrogen content (µg N 10 cm^{-2}) in ambient and treatment plots (a) and aboveground net primary productivity (ANPP: g C m^{-2} monsoon^{-1}) in ambient and treatment plots in 2012 and 2013 (b). Soil N was significantly higher in ambient compared with treatment plots in 2012 ($p < 0.03$) and 2013 ($p < 0.05$), and ANPP in 2013 was significantly higher in ambient plots in 2013 ($p < 0.02$).

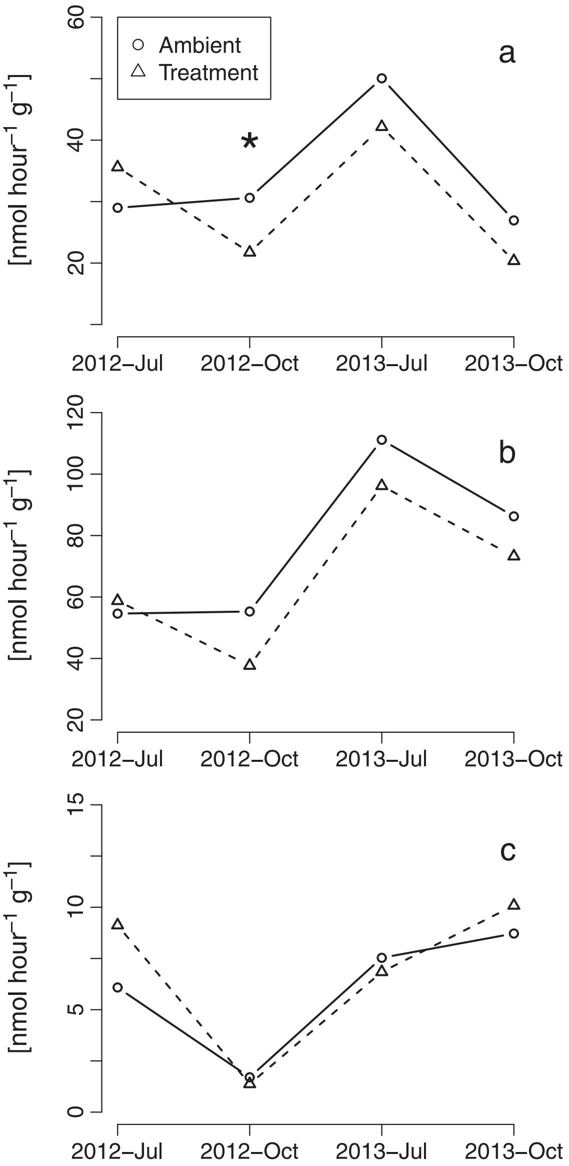

Figure 5. Net extracellular enzyme activity (EEA: nmol hour^{-1} g soil^{-1}) of soil interspaces (0–10 cm depth) in ambient and treatment plots at the beginning and end of the monsoon season in 2012 and 2013. EEA data includes analysis of alkaline phosphatase (a), alanyl aminopeptidase (b) and β-D-glucosidase (c). Extracellular activity of alkaline phosphatase was significantly higher in ambient plots at the end of the 2012 monsoon ($p < 0.05$; a).

11.6 mm average, 23.5 mm in April 2013). During the 2013 monsoon, rainfall was 29% higher than the 2001–2010 average (143 and 110 mm average), and treatment plots received 43% higher rainfall (159 mm; Figure 1). We observed significantly higher daily average soil moisture (0–10 cm) in ambient plots (7.8% and 9.1% ambient, $p < 0.001$), although the difference between treatment and ambient plots was not as large as in 2012 (Figure 2b). SOC did not differ between ambient and treatment plots at either the beginning or end of the 2013 monsoon (Figure 3), nor did soil enzyme activities (Figure 5). Soil NO_3–N and NH_4–N was significantly higher in ambient compared with treatment plots (161.1 µg 10 cm^{-2} ambient, 114.3 µg treatment, $p < 0.05$; Figure 4a). We observed significantly higher ANPP in ambient compared with treatment plots (161.8 g m^{-2} ambient, 90.7 g m^{-2} treatment, $p < 0.02$; Figure 4b). The cover of *B. eriopoda* increased 97.4% in ambient plots (one-tailed, paired *t*-test; $p < 0.05$), which was a significantly larger increase than that of *B. eriopoda* in treatment plots (one-tailed *t*-test, $p < 0.03$), which showed

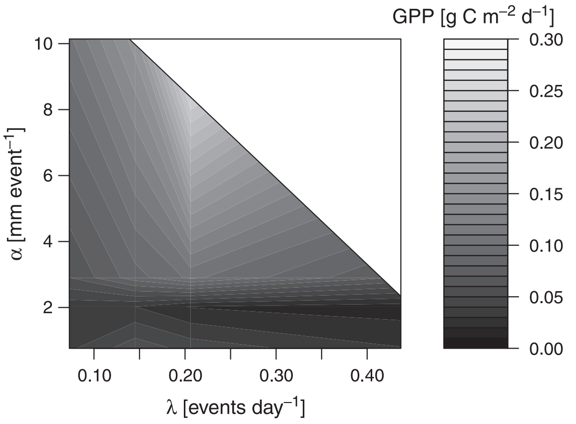

Figure 6. Response of daily gross primary productivity (GPP: g C m^{-2} day^{-1}) during the summer monsoon season, illustrated on the colour ramp, to average precipitation timing (λ: events day^{-1}) and magnitude (α: mm event^{-1}) statistics over the 14 days prior to measurement of GPP. The rate of change in GPP as α increases from approximately 2 to 3 mm event^{-1} suggests that GPP may be sensitive to precipitation as it crosses this threshold.

no significant increase or decrease in cover. ANPP for *B. eriopoda* was higher in ambient compared with treatment plots as well (84 g C ambient, 19 g C treatment; one-tailed *t*-test, $p < 0.02$). We observed no additional differences in cover or ANPP for *B. eriopoda* or for *B. gracilis* in 2013.

Using 5 years of eddy covariance data (2007–2011), we found that daily GPP (g C m^{-2} day^{-1}) at a nearby grassland site was more sensitive to the average magnitude of rainfall events (α: mm event^{-1}) over a prior period of 14 days than it was to the average number of events (λ: events day^{-1}) over the same period (Figure 6). Furthermore, GPP responded strongly as α increased from 2 to 3 mm, suggesting that even a small number of these events were sufficient to stimulate grassland carbon uptake.

DISCUSSION

In this study, we experimentally removed small rainfall events from grassland plots during a dry monsoon in 2012 and added a similar magnitude of precipitation in four small events to treatment plots during a wet monsoon the following year. In 2012, treatment plots experienced lower θ, soil NO_3–N and NH_4–N, SOC and alkaline phosphatase enzyme activity compared with ambient plots, but did not experience lower ANPP. In 2013, seasonal averaged θ was higher in treatment and control plots compared with 2012, but treatment plots experienced somewhat lower seasonal averaged soil NO_3–N and NH_4–N, and ANPP than ambient plots, despite receiving supplemented precipitation in the form of small rain events.

Eddy covariance data from 2007 to 2011 show that daily GPP in this grassland was more sensitive to increasing magnitude of precipitation events than to increasing number of precipitation events during the summer monsoon season. For both GPP and ecosystem respiration (not shown), measured fluxes increased substantially at ~1.5–3.5 mm day^{-1} (Figure 6). While our results from eddy covariance are approximate and limited by the spatial and temporal scale of evaluation, studies by Schwinning and Sala (2004) and Reynolds *et al.* (2004) have observed similar patterns of C and N fluxes in the Chihuahuan Desert. Therefore, we hypothesize that the nutrient status of ambient plots was increased relative to treatment plots in 2012 by at least three events between 1.5 and 3.8 mm. Once water limitation has been removed, N and P are the most limiting nutrients in this ecosystem (Mueller *et al.*, 2008; Turnbull *et al.*, 2011; Yandjian *et al.*, 2011), and nitrogen addition in SNWR grassland has been shown to increase aboveground productivity during wet years (Ladwig *et al.*, 2012).

Compared with average or wet years, below average precipitation in the northern Chihuahuan Desert may result from a similar number of small rain events but fewer large rain events (Petrie *et al.*, 2014a). In dry years, ANPP is limited by water availability rather than soil nutrients, which likely explains the similar ANPP between treatment and ambient plots in 2012 in our study, when total precipitation between treatment and ambient plots was very low and differed by only 16 mm. Available soil N may accumulate during dry years because small events stimulate microbial mineralization, but this N is not taken up by plants (Huxman *et al.*, 2004; Collins *et al.*, 2008). Reichmann *et al.* (2013) found lower available soil N in irrigated plots compared with drought treatments as a function of higher leaching and immobilization by plants and microbes. In contrast, we found lower plant available N in plots where small rain events were removed during a year of below-average precipitation. These are the events that would otherwise stimulate microbial mineralization as well as N fixation by crusts (Belnap, 2002; Austin *et al.*, 2004). As a consequence, plants in treatment plots had access to lower available soil nitrogen at the end of the 2012 monsoon, which may have limited their ability to respond to higher rainfall in the following monsoon season, and perhaps also in spring, 2013, when April rainfall was 203% higher than average. Furthermore, while we did not observe differences in SOC between ambient and treatment plots in 2013 (Figure 3), our analysis did not measure soil labile carbon, which may often be more highly utilized by soil microbes in semi-arid ecosystems and follow a similar availability pattern to that of soil N (Austin *et al.*, 2004).

We hypothesize that the reason for higher ANPP in ambient compared with treatment plots in 2013 is that the small event removal treatment in 2012 – which significantly reduced nutrient pools – hindered the ability for vegetation in treatment plots to respond to a subsequent monsoon season with high rainfall. During 2012, vegetative cover in treatment plots decreased from 21.4% to

16.4% (paired, one-tailed *t*-test; $p < 0.035$). Early senescence in dry years has previously been observed in this grassland (Petrie *et al*., 2014b), and bare soil evaporation is the largest component of θ losses from upper soil horizons in many semi-arid grasslands (Lauenroth and Bradford, 2012). We attribute lower average daily θ in treatment plots in 2012 (Figure 2a) to lower total precipitation and also to this loss of vegetative cover and increase in bare soil fraction, which likely decreased infiltration and increased evaporation in treatment plots compared with ambient plots (Bhark and Small, 2003). At the beginning of the 2013 monsoon season, neither vegetative cover (18.6% ambient, 15.9% treatment, $p > 0.14$) nor spring biomass ($5.3\,\mathrm{g\,m^{-2}}$ ambient, $3.9\,\mathrm{g\,m^{-2}}$ treatment, $p > 0.53$) was greater in ambient compared with treatment plots. By the end of the season, however, both vegetative cover (41.0% ambient, 26.3% treatment, $p < 0.02$) and ANPP were significantly higher in ambient plots (Figure 4b). The emerging difference in growth and vegetative cover during the 2013 monsoon is consistent with higher θ in ambient compared with treatment plots (Figure 2b), and also the potential for ecosystem C exchanges to respond to the small differences in precipitation inputs that occurred in 2012 (Figure 6). Because of these differences, we attribute ANPP differences in 2013 to higher soil nutrient availability in ambient plots, and possibly lower meristem density in treatment compared with ambient plots, which allowed grasses in ambient plots to respond more favourably to higher rainfall than those in treatment plots in 2013. Meristem density, as well as the production potential of aboveground and belowground plant biomass, may not be fully captured by measurements of ANPP, especially at the low biomass values observed at the beginning of the 2013 monsoon. Although ANPP was higher in treatment plots in 2013 compared with 2012, both *B. gracilis* and B. *eriopoda* percent cover declined in treatment plots during the 2013 monsoon season, suggesting that the 2012 monsoon had a strong legacy effect on vegetation in treatment plots in 2013.

Previous research has shown that grassland productivity at the SNWR is meristem limited (Dalgleish and Hartnett, 2006), and meristem density is hypothesized to be a key mechanism by which ANPP responds to interannual variability in rainfall (Knapp and Smith, 2001) and nitrogen availability (Dalgleish *et al*., 2008). Sala *et al*. (2012) reported that interannual variability in ANPP at a site over time is often poorly correlated with mean annual precipitation, suggesting that legacy effects are prominent in arid grasslands. Indeed, Reichmann *et al*. (2013) found strong legacy effects on ANPP in a northern Chihuahuan Desert grassland. Specifically, the ANPP response in plots during a wet year that followed 2 years of experimental drought was lower than the ANPP response in plots that did not experience drought. This legacy was explained by lower tiller density, a function of meristem availability, following the drought treatments. Our results are consistent with these findings and suggest that small rain events may be important sources of shallow soil moisture for production and maintenance of meristems in this desert grassland, and are corroborated by the sensitivity of grassland C exchanges observed via eddy covariance (Figure 6). Furthermore, the differing responses of dominant vegetation that we observed suggest that *B. eriopoda*, a Chihuahuan Desert species, may be more suited to the periodicity of wet and dry monsoon seasons than *B. gracilis*, which is a semi-arid shortgrass steppe species. *B. eriopoda* cover and ANPP were not significantly affected by the removal treatment in 2012, but *B. eriopoda* cover and ANPP were higher in ambient compared with treatment plots in 2013. Conversely, in 2012, *B. gracilis* showed reduced cover in ambient plots and to a greater degree in treatment plots. *B. gracilis* also had lower vegetative cover in ambient plots compared with *B. eriopoda* at the end of the 2013 monsoon (11.0% *B. gracilis*, 25.3% *B. eriopoda*; $p < 0.04$). Over the past 25 years, cover of *B. eriopoda* in this grassland has been increasing at a much greater rate than the cover of *B. gracilis* (Collins and Xia, 2015). Changes in the size and frequency of rain events may contribute to this pattern by altering the competitive dynamics between these two long-lived perennial grasses.

The legacy effects of small events may facilitate grassland recovery in the year following a dry monsoon season, and conversely, the lack of small events may hinder grassland recovery under the same conditions. At the SNWR, the average monsoon season from 2001 to 2010 produced 110 mm of precipitation, and drier than average monsoons like in 2012 (71 mm) are a common occurrence in the Chihuahuan Desert region, and dry years may occur more frequently in the future (Gutzler and Robbins, 2011). In a warming climate, higher evaporative demand is likely to reduce the soil moisture residence time of small precipitation events (Laio *et al*., 2002; Austin *et al*., 2004; Porporato *et al*., 2004), making them less effective. The magnitude of monsoon season rainfall events has decreased across the northern Chihuahuan Desert (Petrie *et al*., 2014a), and small events are likely to constitute a larger proportion of the total number of events in the future. In our study, the loss of small events promoted more frequent grassland senescence and loss of vegetative cover, lower availability of soil C, soil NO_3–N and NH_4–N, and P mobilization potential, and reduced ANPP response in years following a dry monsoon. Based on eddy covariance data, the threshold between effective and ineffective rainfall events may be very small. The loss of soil nutrients or biotic potential is a precursor to grassland degradation in this region (Turnbull *et al*., 2011), and may contribute to the state transition of grassland to shrubland in dryland ecosystems (D'Odorico *et al*., 2013). Overall, our results show that small precipitation events may have significant legacy effects on productivity of desert grassland following dry years, and the increased rate of evaporation of these events in a warmer climate may further influence how desert grassland responds to and recovers from moisture limitation in the future.

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