Effect of precipitation variability on net primary production and soil respiration in a Chihuahuan Desert grassland

M I C H E L L L . T H O M E Y *, S C O T T L . C O L L I N S *, R O D R I G O V A R G A S †, J E N N I F E R E . J O H N S O N *, R E N E E F . B R O W N *, D O N A L D O . N A T V I G * and M I C H A E L T . F R I G G E N S *
*Department of Biology MSC03-2020, University of New Mexico, Albuquerque, New Mexico 87131, USA, †Departamento de Biología de la Conservación, Centro de Investigación Científica y de Educación Superior de Ensenada (CICESE), BC 22860, México

Abstract

Precipitation regimes are predicted to become more variable with more extreme rainfall events punctuated by longer intervening dry periods. Water-limited ecosystems are likely to be highly responsive to altered precipitation regimes. The bucket model predicts that increased precipitation variability will reduce soil moisture stress and increase primary productivity and soil respiration in aridland ecosystems. To test this hypothesis, we experimentally altered the size and frequency of precipitation events during the summer monsoon (July through September) in 2007 and 2008 in a northern Chihuahuan Desert grassland in central New Mexico, USA. Treatments included (1) ambient rain, (2) ambient rain plus one 20 mm rain event each month, and (3) ambient rain plus four 5 mm rain events each month. Throughout two monsoon seasons, we measured soil temperature, soil moisture content (θ), soil respiration (R_s), along with leaf-level photosynthesis (A_{net}), predawn leaf water potential (Ψ_{pd}), and seasonal aboveground net primary productivity (ANPP) of the dominant C_4 grass, *Bouteloua eriopoda*. Treatment plots receiving a single large rainfall event each month maintained significantly higher seasonal soil θ which corresponded with a significant increase in R_s and ANPP of *B. eriopoda* when compared with plots receiving multiple small events. Because the strength of these patterns differed between years, we propose a modification of the bucket model in which both the mean and variance of soil water change as a consequence of interannual variability from 1 year to the next. Our results demonstrate that aridland ecosystems are highly sensitive to increased precipitation variability, and that more extreme precipitation events will likely have a positive impact on some aridland ecosystem processes important for the carbon cycle.

Keywords: carbon cycle, desert grasslands, leaf gas exchange, precipitation variability, primary production, soil respiration

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Introduction

As anthropogenic activities continue to influence drivers of global environmental change, novel abiotic conditions could shift terrestrial ecosystems outside their historical range of climate variability (Seastedt *et al.*, 2008). One consequence of such change is an increase in precipitation variability characterized by more extreme precipitation events punctuated by longer intervening dry periods (Wolters *et al.*, 2000; Kharin *et al.*, 2007). Recently, Knapp *et al.* (2008) developed a conceptual model (hereafter referred to as the 'bucket model') to predict the response of terrestrial ecosystems to increased intraannual precipitation variability characterized by extreme precipitation events and longer dry intervals. In this model, 'the bucket' represents the

uppermost soil layers with maximum root density and is characterized by upper and lower water stress thresholds. Projected changes in precipitation variability would alter soil water dynamics and biological processes depending on the existing water balance of an ecosystem. For example, in mesic systems where the bucket is moderately full, the model predicts that aboveground net primary productivity (ANPP) will decrease in response to less frequent extreme precipitation events because longer dry intervals between precipitation events increase the severity of soil water stress. In contrast, ANPP is predicted to increase in arid systems, where the soil water bucket is frequently empty, because extreme precipitation events would alleviate drought stress as deeper soil water infiltration will increase soil water content during the growing season.

Desert grasslands are distributed throughout the southwestern United States and climate models predict

that these ecosystems will be highly responsive to increased climate variability in the coming decades (Diffenbaugh *et al.*, 2008). These water-limited ecosystems are defined by highly variable seasonal and interannual precipitation, high rates of potential evapotranspiration, and pulsed precipitation events that drive biotic activity until available water is depleted (Noy-Meir, 1973; Reynolds *et al.*, 2004; Collins *et al.*, 2008). Climate variability and change within and between seasons will likely modify the frequency and intensity of current precipitation regimes influencing components of the carbon cycle in aridland ecosystems that may ultimately feedback to the regional climate system (Huxman *et al.*, 2004a, b; Chapin *et al.*, 2009).

Grasslands are known to be highly sensitive to precipitation variability (Knapp & Smith, 2001; Huxman *et al.*, 2004a, b). In mesic tallgrass prairie, increased precipitation variability decreased seasonal leaf-level photosynthesis (A_{net}), ANPP, and soil respiration (R_s; the CO_2 efflux from soils to the atmosphere) (Knapp *et al.*, 2002; Fay *et al.*, 2003; Harper *et al.*, 2005). Contrary to mesic grasslands, A_{net} and ANPP increased in semiarid short grass steppe under experimentally altered precipitation patterns (Heisler-White *et al.*, 2008). Yet, few studies in aridland ecosystems expand beyond single-pulsed events or seasonal changes in precipitation regimes (Huxman *et al.*, 2004a, b; Ignace *et al.*, 2007; Patrick *et al.*, 2007; Cable *et al.*, 2008) to include the effects of increased growing season intraannual precipitation variability (but see Heisler-White *et al.*, 2009).

To determine the effects of altered precipitation regimes on an arid ecosystem, we experimentally altered precipitation frequency and intensity without changing the total amount of precipitation added in Chihuahuan Desert grassland during the summer monsoon in 2007 and 2008. Based on the bucket model, we hypothesized that a small number of large storm events would increase soil moisture availability over the growing season leading to higher A_{net}, increased ANPP and an increase in soil respiration relative to a large number of small storm events.

Materials and methods

Study site

Our study was conducted at the Sevilleta Long Term Ecological Research (LTER) site on the Sevilleta National Wildlife Refuge (SNWR) located 80 km south of Albuquerque, New Mexico, USA (latitude 34°20′20″, longitude 106°43′30″). Livestock have been excluded from the Refuge since 1973. Climate at the SNWR is arid to semiarid with dry cool winters and springs. Mean annual temperature is 13.2 °C with an average low of 1.6 °C in January and a high of 25.1 °C in July. Precipita-

tion is highly variable within and between years (Pennington & Collins, 2007), averaging approximately 250 mm yr^{-1} with 53%, on average, falling during the summer monsoon (July–September). More information about the site can be found at http://sev.lternet.edu/.

Experimental design

We manipulated rainfall event size and timing using a repeated experimental design within the Monsoon Rainfall Manipulation Experiment (MRME). Vegetation at the experimental site is characterized as Chihuahuan Desert grassland dominated by *Bouteloua eriopoda*. From 1999 to 2008 ANPP ranged from 17 to 180 g m^{-2} yr^{-1} (Muldavin *et al.*, 2008; Xia *et al.*, 2010). The MRME consists of thirteen 8 m × 13 m plots that were established in 2006 of which 10 plots were randomly assigned to one of two rainfall variability treatments ($n = 5$ per treatment). Three ambient rain plots served as reference for comparison to treatment plots. Throughout the 2007 and 2008 monsoon seasons (July–September), each treatment plot was irrigated using an overhead system with raindrop quality sprinkler heads that delivered water in a 360° pattern with a total flow rate of 148.20 L min^{-1}. Water used for irrigation was obtained from a reverse-osmosis system and contained 0.67 ppm NO$_3$–N and 1.01 ppm NH$_4$–N. Rainfall treatments included: (1) large treatments that received ambient rainfall plus one 20 mm rainfall event each month ($n = 5$; receiving three rainfall events July–September) and (2) small treatments that received ambient rainfall plus four 5 mm rainfall events each month ($n = 5$; receiving 12 rainfall events July–September). Thus, we added the same amount of precipitation (20 mm) per month over the monsoon season but we varied the size (20 and 5 mm) and frequency (monthly vs. weekly) of applied precipitation events. In this study, 20 mm rainfall events simulated more extreme precipitation inputs and 5 mm rainfall events represented average precipitation inputs at the Sevilleta LTER site where 71.3% of events are ≤ 5 mm and 11.6% are between 10 and 20 mm (1988–2008). Throughout this manuscript, 'pulse-response' refers to measurements collected 24 h following an applied rainfall event (or water pulse), and 'seasonal' refers to measurements that were integrated over each monsoon season.

Gas exchange measurements

Leaf-level gas exchange (A_{net}) was measured using a Li-6400 portable photosynthesis system (Li-Cor, Lincoln, NE, USA) with a standard leaf chamber. Throughout both monsoon seasons, weekly field campaigns in all plots occurred 24 h following a scheduled rainfall event (i.e. pulse-response). During each field campaign, all plots in the experiment were sampled in random order. A_{net} measurements were recorded on one to two fully expanded leaves from three individual plants in each plot and averaged to obtain mean pulse-response A_{net} for treatment and reference plots. Irradiance (red/blue LED light source) was set to saturating light conditions (1000 μmol m^{-2} s^{-1}) that had been determined by light

response curves. The CO_2 concentration (400 μmol mol^{-1}) and block temperature were set to ambient conditions before the first measurement and held constant across all plots in order to maintain consistent chamber conditions throughout the measurement period (09:00–14:00 hours). Leaf area was determined by multiplying the measured width of each leaf by the length of the chamber. Rates of A_{net} were corrected for leaf area using Li-6400 simulator software (OPEN V5.3).

Following A_{net} measurements, leaf samples were collected and returned to the laboratory to determine leaf nitrogen concentration (% N/dry mass). For each measurement date, leaves obtained from individual plots were combined by treatment, oven dried at 60 °C for 24 h, and ground for nitrogen analysis. Leaf nitrogen concentration was determined by high temperature combustion and gas chromatography. All analyses were preformed using a ThermoQuest CE Instruments NC2100 Elemental Analyzer (ThermoQuest Italia S.p.A., Rodano, Italy).

Leaf water potential

Predawn leaf xylem pressure potentials (Ψ_{pd}) were measured on five to six leaves collected from distinct *B. eriopoda* tillers in each plot. Mean Ψ_{pd} is reported for treatment and reference plots. Leaves were collected (predawn) and put immediately into plastic bags and then stored in a cooler. Predawn leaf water potentials were measured within 1–2 h of collection with a Scholander-type pressure chamber (PMS, Model 1000, PMS Instrument Co., Corvallis, OR, USA).

ANPP

Across all plots, *B. eriopoda* accounted for ∼70% of plant cover. Additional subdominant species included *Sphaeralcea wrightii*, *Sporobolus* spp., and *Gutierrezia sarothrae*. ANPP was measured in two 1 m^2 subplots permanently located in each plot starting in 2007. ANPP measurements were recorded in the spring and fall of 2007 and 2008 when plant species had reached peak biomass. For every subplot, the biomass of each individual of each species was determined from cover and height size classes. Regressions of weight-to-volume were developed by harvesting various sized individuals of each species from adjacent areas. A positive change in green biomass (current season's growth) from spring to fall in each subplot was used as a measure of mean seasonal ANPP (for all species) (for detailed methods, see Muldavin *et al.*, 2008).

Soil moisture and soil respiration

Nearly 8 months before the start of the experiment, soil sensor nodes were installed in all plots to ensure soil equilibrium after installation of environmental sensors. Each sensor node consisted of ECH$_2$O soil temperature and soil moisture sensors (EC-TM Decagon Devices Inc., Pullman, WA, USA) and Vaisala CARBOCAP soil CO_2 sensors (GMM 222, Vaisala, Helsinki, Finland) that were placed under the canopy and within the rooting zone of *B. eriopoda* at three depths (2, 8, and 16 cm) as described in Vargas & Allen (2008). The CO_2 sensors were protected with Gore-Tex® fiber to avoid possible wetting during rainfall events while allowing free gas exchange. Soil temperature (T_s), soil moisture content (θ), and soil CO_2 concentration were measured continuously at 30 min intervals throughout both monsoon seasons. Values of soil CO_2 concentration (ppm) were corrected for temperature and pressure using the ideal gas law according to the manufacturer. We calculated soil respiration (R_s, μmol CO_2 m^{-2} s^{-1}) using the flux-gradient method as has been described for multiple ecosystems (Vargas *et al.*, 2010). Briefly, we used Fick's law of diffusion where the diffusivity of CO_2 was corrected for temperature and pressure (Jones, 1992) and calculated as a function of soil moisture, soil porosity, and soil texture (Moldrup *et al.*, 1999). Soil porosity is 0.43 m^3 m^{-3} and bulk density was 1.51 g cm^{-3}. Soils are Typic Haplargids derived from piedmont alluvium. Soil texture in the upper 20 cm is 68% sand, 22% silt, and 10% clay, with 2% calcium carbonate (Kieft *et al.*, 1998). Across all treatment and reference plots, we used daily mean values, calculated on a 24 h basis, to report seasonal R_s. Mean daily soil θ, calculated as the average soil θ for measurements from 2 to 16 cm depth, was used to determine pulse-response and seasonal soil θ. Similarly, daily mean soil temperature (T_s) was calculated on a 24 h basis and averaged over all depths to obtain seasonal T_s.

Throughout the study period, we used the mean absolute difference in soil θ to quantify how ambient rainfall patterns vs. ambient rainfall patterns plus small or large rainfall additions altered soil θ variability (Knapp *et al.*, 2002). These values were determined using mean daily soil θ in reference ($n = 3$) and treatment plots ($n = 5$ each treatment). Within each plot type (reference or treatment), soil water variability was calculated as the absolute difference in mean daily soil θ between consecutive days. Data for this study are located in data sets SEV188, 191, 206, 223, 224, and 225 at http://sev.lternet.edu.

Data analysis

Data analysis was completed using SAS (v 9.1, Cary, NC, USA). For each measured variable, data obtained from a single plot were averaged daily such that each plot represented an experimental unit ($n = 3$ for ambient rainfall and $n = 5$ for 5 and 20 mm rainfall addition plots, respectively). When the data were analyzed collectively, year × treatment interactions were not significant ($P > 0.05$); however, there was a significant ($P < 0.05$) difference between years. Therefore, years were analyzed separately rather than combined. In each year, the main effects were divided into two groups: (1) pulse-response (i.e. post wetting measurements) of A_{net}, Ψ_{pd}, soil θ, and % leaf N/dry mass and (2) seasonal measurements (i.e. across the monsoon season per year) of R_s, T_s, ANPP, soil θ, and soil θ variability. Values were compared between treatments and reference plots. Data that did not meet the assumptions of analysis of variance (ANOVA) were log or square root transformed and analyzed using a single-factor General Linear Model (PROC GLM). Significant treatment effects were followed by LS Means for multiple comparisons with unbalanced designs. Data that failed to meet the assumptions of ANOVA,

despite transformation, were analyzed using a single-factor Kruskal–Wallis test (PROC npar1way; Wilcoxon's) for treatment effects and multiple comparisons between treatments. For all analyses, α was set to 0.05.

Results

In 2007, small and large treatment plots received 152.2 mm of rainfall (ambient + applied). Reference plots received 92.2 mm of ambient precipitation (Table 1) which measured 36% below the long-term monsoon mean (125.8 mm) at the SNWR (1988–2008). In 2008, small and large treatment plots received 239.6 mm of rainfall (ambient + applied). Reference plots received 179.6 mm of ambient precipitation (Table 1) which measured 30% above the long-term mean. For both years, the majority of ambient rainfall events were <5 mm, but the number of large rainfall events (>20 mm) more than doubled in 2008 (Table 1).

Pulse-response after experimental rain events

Both rainfall addition treatments increased mean daily soil θ but this response was contingent on ambient rainfall (Fig. 1a, b, d, e). In 2007 and 2008, large monthly rainfall additions significantly increased pulse-response soil θ and for 6 consecutive days thereafter when compared with plots that received small weekly rainfall additions (Year 2007: $H = 13.22$, $P = <0.001$; Year 2008: $H = 6.83$, $P = 0.009$) and reference plots (Year 2007: $H = 32.91$, $P = <0.001$; Year 2008: $H = 10.28$, $P = 0.001$) (Fig. 1b and e). Mean daily soil temperature reached peak values early in the monsoon season (July–August) and decreased as the season progressed (Fig. 1c and f).

Throughout the 2007 monsoon season, plots receiving small weekly or large monthly rainfall additions significantly increased pulse-response soil θ by 89.1% and 84.7% compared with reference plots (Fig. 2a). The significant increase in pulse-response soil θ in treatment plots (small: $H = 8.80$, $P = 0.003$; large: $H = 21.56$, $P = <0.001$) also corresponded with less negative Ψ_{pd} (small: $F = 15.35$, $P < 0.01$; large: $F = 15.35$, $P < 0.01$; Fig. 2b; Supporting Information, Fig. S1) and a significant increase in A_{net} (small: $H = 6.74$, $P = 0.01$; large: $H = 7.74$, $P < 0.01$; Figs 2c and S1) when compared with

Table 1 Total monsoon precipitation (July through September) and the total number of events in each rainfall event size category as observed at the Monsoon Rainfall Manipulation Experiment site at the SNWR in central New Mexico, USA

Year	Total precipitation (mm)	Rainfall event size class (mm)			
		<5	5–10	10–20	>20
2007	92.2	18	4	1	1
2008	179.6	15	2	3	4

Average long-term monsoon precipitation at the SNWR is 125.8 mm (1988–2008).

B. eriopoda in reference plots. In contrast, pulse-response soil θ had no affect on leaf nitrogen concentrations from leaves collected throughout the study period ($H = 3.92$, $P = 0.14$). Among the two rainfall addition treatments, the magnitude and frequency of rainfall additions did not significantly affect pulse-response soil θ, Ψ_{pd}, or A_{net} (Fig. 2a–c).

During 2008, pulse-response soil θ increased across all treatment and reference plots (Fig. 2a) likely as a result of the 95% increase in ambient precipitation compared with 2007 (Table 1). Nevertheless, plots receiving small or large rainfall additions maintained higher pulse-response soil θ than reference plots (small: $H = 5.50$, $P = 0.02$; large: $H = 7.75$, $P < 0.01$; Fig. 2a). While there was no difference in A_{net} between reference and small rainfall addition plots, A_{net} in large rainfall addition plots was significantly higher than in the reference plots ($F = 2.55$, $P = 0.03$; Fig 2c; Fig. S1). Throughout the 2008 season, there was no treatment effect on leaf nitrogen concentrations ($F = 2.84$, $P = 0.07$) and Ψ_{pd} ($F = 2.27$, $P = 0.11$). However, leaves sampled from rainfall addition plots consistently maintained less negative Ψ_{pd} when compared with reference plots (Fig. 2b; Fig. S1).

Seasonal responses

Across the 2007 monsoon season, small weekly and large monthly rainfall additions increased seasonal soil θ relative to reference plots (small: $H = 8.25$, $P = 0.004$; large: $H = 32.91$, $P < 0.001$; mean soil θ: 0.06 ± 0.003, 0.07 ± 0.003, 0.08 ± 0.003 m^3 m^{-3} reference, small, and large, respectfully; Fig. 2d). In contrast to pulse-response measures of soil θ, seasonal soil θ in large rainfall addition plots increased by 20% when compared with seasonal soil θ in small rainfall addition plots. Furthermore, seasonal soil θ measured at 16 cm in large rainfall addition plots was significantly higher when compared with reference ($H = 47.49$, $P = <0.001$) and small rainfall addition plots ($H = 24.25$, $P = <0.001$) (Supporting Information, Fig. S2).

Over the growing season, large monthly rainfall additions increased R_s 30.3% and small weekly rainfall additions increased R_s 13.5% ($F = 37.22$, $P < 0.01$; Fig. 2e) when compared with reference plots. Overall, R_s reflected differences in seasonal soil θ (Fig. 2d and e) and treatment differences in total seasonal R_s occurred throughout the study period (838, 726, and 638 g C m^{-2} large, small, and reference, respectively; Fig. 3a). Average diel patterns of R_s were always higher in large monthly rainfall addition plots compared with small weekly rainfall addition, and reference plots (Fig. 3c–e) and are consistent with the seasonal R_s results. Precipitation treatments had no significant effect on seasonal T_s (2007: $F = 4.38$, $P = 0.11$; mean seasonal T_s: 27.66 ± 0.36, 26.73 ± 0.34, 27.00 ± 0.34 °C reference, small, and large, respectively; Fig. 1c).

Throughout the 2008 monsoon season, seasonal soil θ increased across treatment and reference plots (mean seasonal soil θ: 0.09 ± 0.004, 0.10 ± 0.004, 0.11 ± 0.004 m^3 m^{-3} reference, small, and large, respectively) when compared with 2007 (Fig. 2d). This increase in precipitation along with several large (>20 mm) natural rainfall events (Table 1) diminished the difference in seasonal soil θ between reference and small
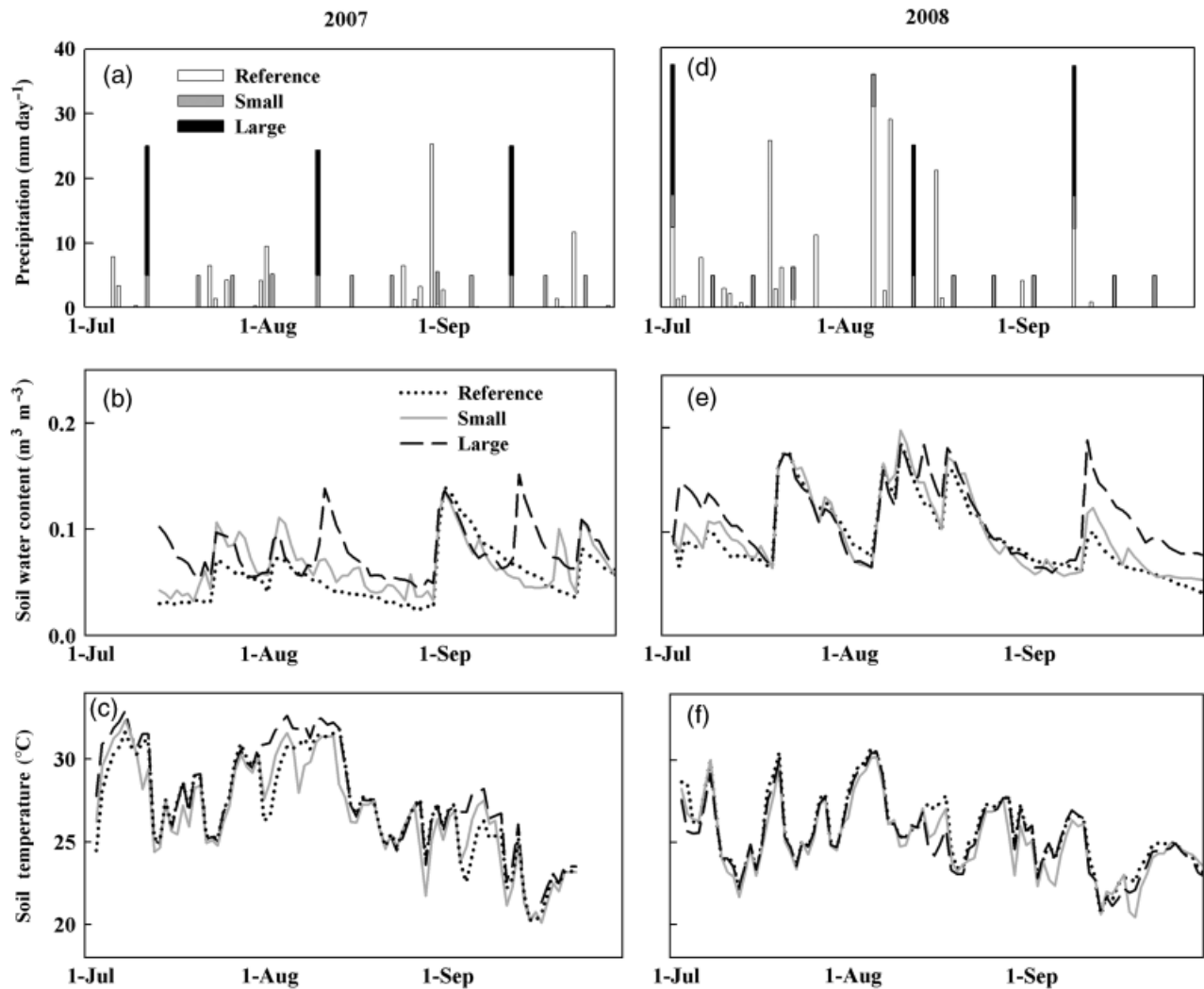
Fig. 1 Daily record of physical conditions across treatment and reference plots during the 2007 and 2008 monsoon season. (a, d) Rainfall additions include ambient rainfall plus four 5 mm events each month (small) and ambient rainfall plus one 20 mm event each month (large). Reference plots represent ambient precipitation. Bars corresponding with rainfall additions represent the total amount of water that each plot received. (b, e) Daily soil moisture content (θ). Error bars were removed for clarity. The average standard error measured 8.6%, 8.5%, and 8% of the mean (2007) and 7.3%, 9.8%, and 6.5% of the mean (2008) for reference, small and large rainfall additions, respectively. (c, f) Soil temperature integrated over 2–16 cm depth. Error bars were removed for clarity. The average standard error measured 1.0%, 0.94%, 0.64% of the mean (2007) and 1.17%, 0.93%, 0.94% of the mean (2008) for reference, small and large rainfall additions, respectively. Lines are the mean (unweighted) for each treatment ($n = 5$) integrated over 2–16 cm depth and reference ($n = 3$) plots. The mean soil θ (2007 monsoon season): 0.06, 0.11, and 0.10 $m^3 m^{-3}$ and mean soil θ (2008 monsoon season): 0.09, 0.12, and 0.13 $m^3 m^{-3}$ for reference, small, and large plots, respectively. The mean soil temperature (2007 monsoon season): 27.66, 26.73, and 27.00 °C and mean soil temperature (2008 monsoon season): 25.63, 25.11, and 25.30 °C for reference, small, and large plots, respectively.

rainfall addition plots. However, seasonal soil θ measured at 16 cm in large rainfall addition plots was significantly higher when compared with reference ($H = 27.81$, $P = <0.001$) and small rainfall addition plots ($H = 7.23$, $P = <0.001$; Fig. S2).

Total seasonal R_s was higher in large monthly rainfall addition plots compared with small weekly rainfall additions and reference plots (990, 760, and 620 g C m^{-2}; Fig. 3b) despite the lack of difference in mean seasonal soil θ in small and reference plots. Average diel patterns of R_s were always higher in large monthly rainfall addition plots compared with small

weekly rainfall addition and reference plots (Fig. 3f–h) and are consistent with the seasonal R_s results (Fig. 2e). Similar to 2007, precipitation treatments had no significant effect on seasonal soil temperature (2008: $F = 2.70$, $P = 0.26$; mean seasonal soil temperature: 25.63 ± 0.23, 25.11 ± 0.22, 25.30 ± 0.22 °C reference, small, and large, respectively; Fig. 1f).

For both years of the study, ANPP for all species (by functional type) was dominated by graminoids with *B. eriopoda* contributing the majority to production (Fig. 4a and b). Although mean ANPP for all species increased with the
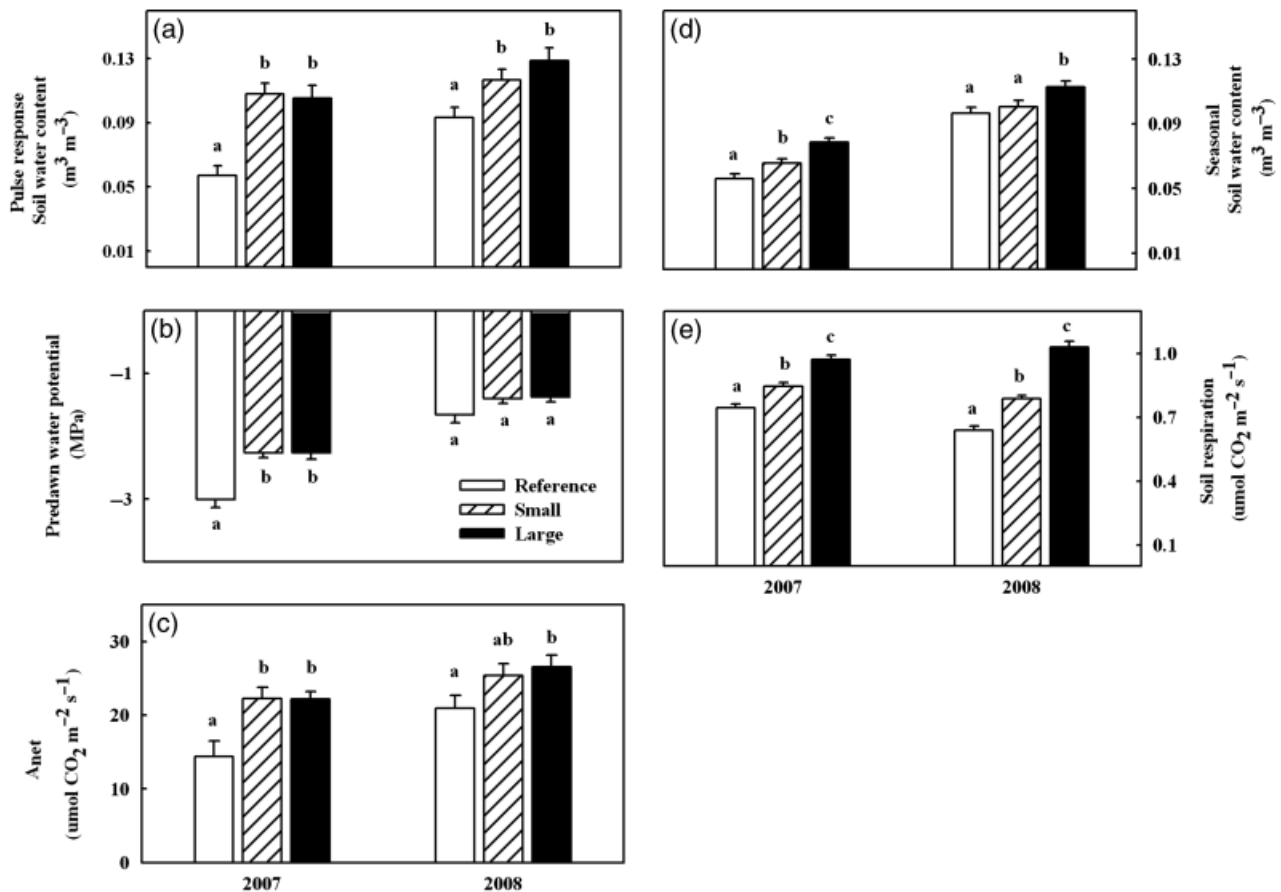
Fig. 2 Components of carbon cycling and soil water dynamics for the 2007 and 2008 monsoon season. (a) Mean pulse-response soil θ integrated over 2–16 cm depth (unweighted), (b) Mean predawn leaf water potential (Ψ_{pd}) and (c) Mean leaf-level photosynthesis (A_{net}) for the dominant C$_4$ grass *Bouteloua eriopoda* (d) Mean seasonal soil θ integrated over 2–16 cm depth (unweighted) and (e) Mean soil respiration (R_s). For all plots, different letters are significantly different ($\alpha = 0.05$) based on single factor analysis of variance (ANOVA) (2008 A_{net}, 2007 and 2008 Ψ_{pd}, 2007 and 2008 ANPP, 2007 R_s] or Kruskal–Wallis test for model significance and all pair wise comparisons [2007 A_{net}, 2007 & 2008 Soil θ (pulse-response & seasonal), 2008 R_s]. ANPP, aboveground net primary productivity.

magnitude of the treatment, we did not detect significant treatment differences in either year of the study. In 2007, ANPP for all species reached maximum values in plots that received large monthly rainfall additions (306.1 g m^{-2}), followed by small weekly rainfall additions (230.9 g m^{-2}) and reference plots (142.5 g m^{-2}). This trend was repeated in 2008 with values reaching 278.7, 226.3, and 137.4 g m^{-2} for large, small, and reference plots, respectively. In 2007 and 2008, ANPP of *B. eriopoda* was significantly higher in large monthly rainfall addition plots compared with small weekly rainfall additions (2007: 227.0 g m^{-2} vs. 162.4 g m^{-2}; 2008: 176.6 g m^{-2} vs. 105.5 g m^{-2}). From 2007 to 2008 ANPP of *B. eriopoda* decreased whereas biomass production of other grasses increased in 2008 (Fig. 4a and b).

We used the mean absolute difference in mean daily soil moisture θ content to quantify the variability between treatment and reference plots. In 2007 (dry year) and 2008 (wet year), experimental rainfall additions significantly increased the variability in seasonal soil θ when compared with reference

plots (2007: $F = 5.38$, $P = 0.03$; 2008: $F = 4.99$, $P = 0.04$; Supporting Information, Fig. S3). Although soil water variability increased in 2008, the within-year variability between rainfall treatments and ambient plots was dampened in the wet year (Fig. S3). When compared with reference plots, large monthly rainfall applications increased soil water variability (Fig. S3) and this corresponded with a significant increase in pulse-response soil θ that was maintained for 6 consecutive days thereafter.

Discussion

Our results supported the hypothesis that increased within-season precipitation variability would increase ANPP of *B. eriopoda* and R_s (Knapp et al., 2008) but the magnitude of the response differed between years. These results highlight the importance of not only predicting relative changes within years, but also patterns of responses between years. Both
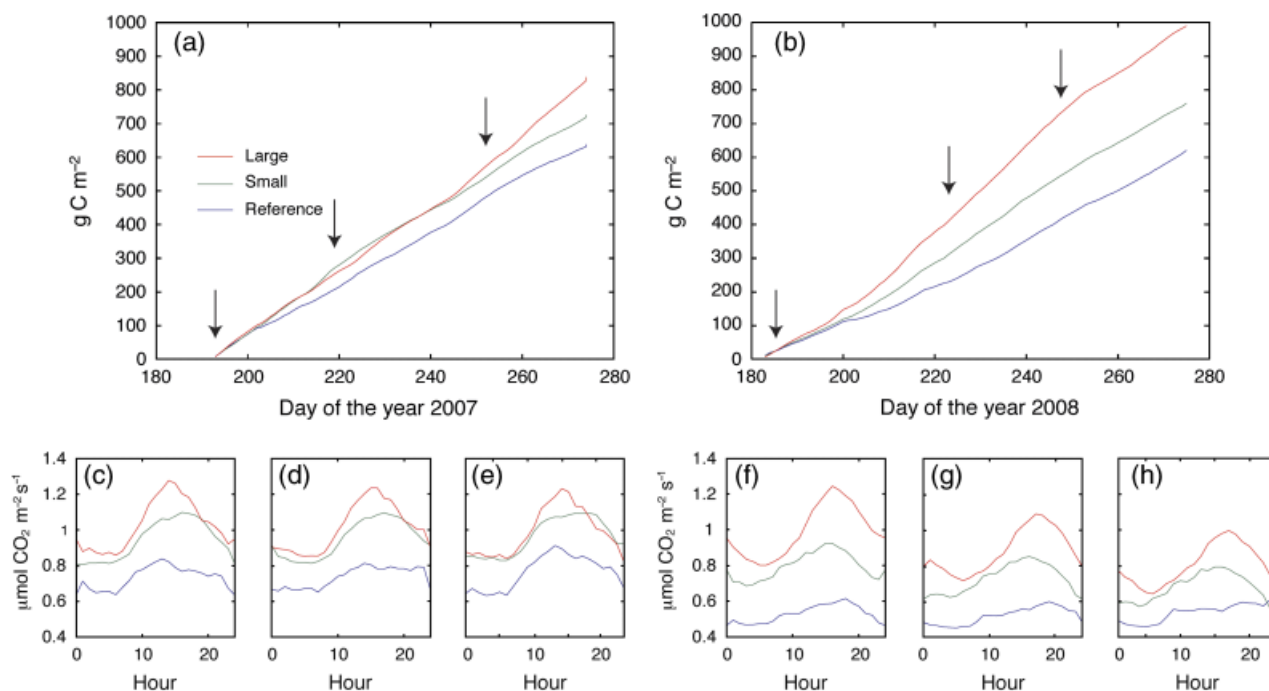
Fig. 3 Cumulative seasonal carbon release from soil respiration ($gC m^{-2}$) during the monsoon season of 2007 (a) and 2008 (b). Arrows indicate the approximate dates when the large rainfall additions were performed. Average diel patterns of soil respiration ($\mu mol CO_2 m^{-2} s^{-1}$) between large rainfall additions in treatment and reference plots during 2007 (c–e) and 2008 (f–h). For example, Fig. 3c represents the average diel patterns between day of the year (DOY) 191 and 212 and Fig. 3d the average diel patterns between DOY 255 and 273.
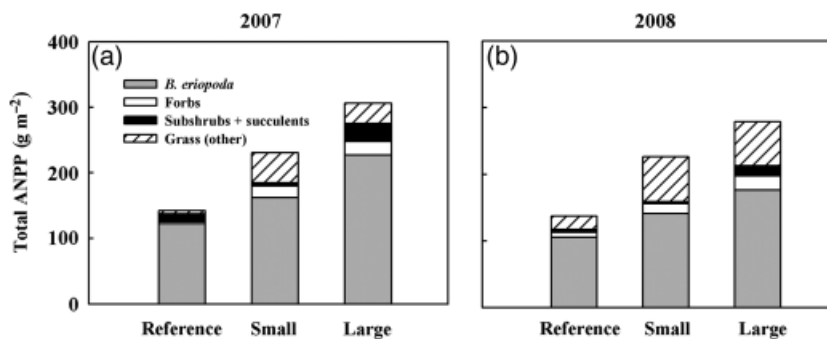
Fig. 4 Aboveground net primary productivity (ANPP) for each plant functional type in the (a) 2007 and (b) 2008 monsoon season. Bars represent mean ANPP for reference ($n = 3$), small rainfall (5 mm per week), and large (20 mm per month) rainfall treatment plots ($n = 5$).

primary productivity and R_s increased in response to small and large rainfall events; however, large rainfall events resulted in significantly higher pulse-response soil θ in the top 16 cm of soil and extended the water pulse duration for up to 6 days longer when compared with small rainfall event plots (Figs 1b and e and S2). Thus, while A_{net} and Ψ_{pd} measurements of *B. eriopoda* did not reflect a difference in pulse magnitude (small vs. large), mean total seasonal R_s and ANPP of *B. eriopoda* were significantly higher in large rainfall event plots (Figs 3 and 4). Likely, *B. eriopoda* maintained high A_{net}, beyond our 1-day pulse-response sampling period, leading to

higher ANPP when compared with small event plots where soil θ was ephemeral (Figs 1b and e and S1). This interpretation is supported by: (a) diel patterns of R_s were consistently higher in the large rainfall event plots compared with small event plots and ambient plots (Fig. 3c–h); and (b) total seasonal R_s was related to ANPP via photosynthesis (Vargas *et al.*, 2010).

Warm desert perennial grasses, such as *B. eriopoda*, are adapted to efficiently utilize episodic summer rain events by having shallow root systems and the ability to rapidly respond with high rates of photosynthesis following rainfall (Nobel, 1980; Smith *et al.*, 1997). At our study site, perennial grass roots

are primarily distributed within the top 20–30 cm (McCulley et al., 2004; Kurc & Small, 2007) but *B. eriopoda* roots have also been found as deep as 45 cm (Gibbens & Lenz, 2001). The 5 mm rainfall additions reached shallow depths compared with the 20 mm rainfall additions and this is reflected in the integrated daily mean soil θ reported in Fig. 1. As a result, mean pulse-response soil θ in small and large rainfall addition plots was significantly higher and this corresponded with a significant increase in A_{net} and Ψ_{pd} (less negative) when compared with reference plots (Fig. 2a–c). Similar to *B. gracilis* in the short-grass steppe (Sala & Lauenroth, 1982), *B. eriopoda* also has the capacity to respond to rain events as small as 5 mm. We found that rainfall additions within the rooting zone of *B. eriopoda* initially elicited similar physiological responses independent of pulse size (Fig. 2c). Gross primary production in Mongolian semiarid grasslands responded similarly irrespective of pulse size (Chen et al., 2009) indicating that grassland species can utilize both shallow ($\sim$20 cm below the soil surface) and deeper (20–60 cm below the soil surface) water sources (Zhao et al., 2009a,b). In arid–semiarid ecosystems, rooting depth influences the ability of plants to up-regulate photosynthesis in response to the 'pulsed' precipitation regimes characteristic of this region (Williams et al., 1999; Schenk & Jackson, 2002; Ogle & Reynolds, 2004). Although we did not eliminate ambient precipitation, our results suggest that *B. eriopoda* responds to $\geq$ 5 mm summer rain events to maximize carbon gain during favorable periods (Smith et al., 1997; Schwinning et al., 2003).

Although we did not detect a significant difference in measures of A_{net} and Ψ_{pd} between 5 and 20 mm rainfall treatments (Fig. 2b and c), ANPP of *B. eriopoda* was significantly higher in plots that received large monthly (more extreme) precipitation events when compared with small weekly and ambient plots (Fig. 4). We attribute the increase in ANPP of *B. eriopoda* to sustained levels of A_{net} that likely extended beyond our 1-day sampling period due to prolonged soil water availability in the large rainfall treatments (Fig. 1b and e). As discussed, this result is supported by higher average diel R_s patterns (Fig. 3) and because seasonal R_s has been shown to be related to photosynthetic rates in several ecosystems (Vargas et al., 2010). When compared with small and ambient reference plots, we found that large (20 mm) rainfall events maintained significantly higher soil θ for up to 6 consecutive days following an experimental addition (Fig. 1b and e). Thus, over the duration of the study, small weekly (5 mm) events were likely depleted rapidly through evapotranspiration whereas large monthly (20 mm) events were more effective in promoting production due to deeper soil water recharge (Schwinning & Sala, 2004). Indeed, at the deepest measured depth (16 cm) we found that large rainfall additions significantly increased seasonal soil θ when compared with reference and small rainfall addition plots (Fig. S2). These findings support a soil moisture threshold for growth in *B. eriopoda* (Muldavin et al., 2008) in which a 5 mm rainfall event stimulates a transient physiological response that translates into a pulse of ANPP, and that larger rainfall events initiate a sustainable physiological response that results in larger increments of ANPP. Small and large rainfall events stimulate similar responses to R_s as well as those observed for ANPP.

Overall, ANPP of all plant functional types responded to the treatments, but large rainfall treatments significantly increased ANPP of the dominant C_4 grass *B. eriopoda* which contributes the majority of primary production (Fig. 4a and b) However, the magnitude of response in ANPP of *B. eriopoda* decreased from 2007 (dry year) to 2008 (wet year) across all treatments (Fig. 4a and b). Previous studies have also reported a decrease in plant response from dry to wet years. Ignace et al. (2007) found that grasses in the Sonoran desert did not increase A_{net} or Ψ_{pd} in response to experimental water addition during a wet year, because favorable soil water content was already facilitating high plant performance. Using an ecosystem model, Gerten et al. (2008) demonstrated that NPP was most responsive during water-limited periods and least pronounced or absent in non-water-limited periods. Patrick et al. (2009) found that photosynthesis of *B. curtipendula* in a sotol grassland decreased during a wet year due to lower leaf nitrogen concentrations. In our study, we found that leaf nitrogen concentrations increased from 2007 (reference: 1.04%, small rainfall addition: 1.11%, large rainfall addition: 0.99% N dry mass) to 2008 (reference: 1.45%, small rainfall addition: 1.36%, large rainfall addition: 1.27% N dry mass). The increase in A_{net} despite the trend towards lower leaf nitrogen concentrations in water addition plots suggests that *B. eriopoda* is primarily limited by water rather than nitrogen availability (Stephens & Whitford, 1993; Báez et al., 2007). The decrease in ANPP of *B. eriopoda* in 2008 (Fig. 4a and b) may also have been a function of low productivity before the onset of the monsoon season, because winter/early spring conditions could modify ANPP in arid–semiarid grassland ecosystems (Heisler-White et al., 2008; Muldavin et al., 2008). Another factor may be the observed increase in ANPP among subdominant grass species (Fig. 4a and b). Jankju (2008) noted an increase in competition among perennial plant species in plots that received large infrequent rainfall events (20 mm/bi-monthly) in an arid rangeland. At local scales, other studies attribute a weak correlation between ANPP and precipitation to a potential lag in the response of ANPP to precipitation and productivity from the previous year (Osterheld et al., 2001; Yahdjian & Sala, 2006). In our study, ANPP of *B. eriopoda* was highest in a dry monsoon season (2007) that was preceded by record breaking wet season (2006) where monsoon precipitation measured 30% above the long-term mean, and lowest in a wet year (2008) that was preceded by a dry year (2007) where monsoon precipitation measured 36% below the long-term mean. In this study, we did not collect annual root biomass data, however, the carbon gained from higher A_{net} in 2008 may have been allocated belowground rather than to aboveground biomass (ANPP) as a result of below average rainfall that occurred in the previous year (2007).

Throughout the study period, we found that significant differences in seasonal R_s reflected ANPP of *B. eriopoda*. It is widely accepted that soil respiration is largely dependent on soil temperature and moisture (Raich & Tufekcioglu, 2000), but R_s is also influenced by photosynthesis and substrate supply (Craine et al., 1999; Wan & Luo, 2003; Sponseller, 2007; Vargas

et al., 2010). We did not detect a significant difference in mean daily soil temperature between treatment and reference plots (Fig. 1c and f). However, when compared with reference plots, seasonal soil θ and ANPP of *B. eriopoda* were significantly higher in large plots and this corresponded with a significant increase in seasonal R_s (Fig. 2e). Furthermore, mean diel patterns of R_s in large rainfall additions were consistently higher than in reference and small rainfall treatment plots (Fig. 3c–h) throughout the monsoon season. Overall, our data suggest that increased R_s is related to higher soil moisture that likely increased substrate availability for R_s by: (a) dissolution of substrate in soil organic matter and (b) substrate supplied by an increase in photosynthetic rates associated with large rainfall events (R. Vargas *et al.*, unpublished results). Moreover, these results support previous observations where soil moisture availability is more important than soil temperature in regulating R_s in semiarid grasslands (Liu *et al.*, 2009; Zhao *et al.*, 2009a, b; Vargas *et al.*, 2010).

Grassland species are sensitive to precipitation variability due to their shallow rooting depths (<50 cm) which limits water availability to atmospheric precipitation rather than groundwater (Shen *et al.*, 2009). The bucket model (Knapp *et al.*, 2008) predicts that extreme precipitation events accompanied by longer dry intervals will increase soil water availability in arid but not mesic ecosystems. As a result, arid ecosystems could experience an increase in the number of nonstressed days leading to higher primary productivity and soil respiration. We found that soil water variability was highest in large rainfall addition plots where rainfall applications significantly increased seasonal soil θ (Fig. S3). In contrast to studies from mesic grasslands (e.g. Knapp *et al.*, 2002), A_{net}, ANPP, and R_s were highest in large (20 mm) rainfall addition plots where higher pulse-response and seasonal soil θ and soil water variability, associated with larger pulses, increased the amount of time this system was in a nonstressed

state. Similar results were also found by Heisler-White *et al.* (2009) in semiarid steppe where a small number of large events increased soil θ leading to increased ANPP and midday water potential (less negative) in *B. gracilis*.

The sensitivity of this desert grassland to precipitation variability differed between years and was contingent on the amount and pattern of ambient precipitation. The bucket model (Knapp *et al.*, 2008), as presented, is a static within-season model in which variance changes but the mean remains constant (Fig. 5). The bucket model does not account for year-to-year changes in precipitation that would alter the degree to which within season variability affects ecosystem response. In effect, as seasonal precipitation varies from year-to-year, then less variability is needed to cross the stress threshold during a wet year and larger extreme events are needed in a dry year (Fig. 5). For example, during our study ambient precipitation measured 36% below (2007) and 30% above (2008) the long-term mean. Although the increase in precipitation increased soil θ and A_{net} across all plots, the magnitude of the responses between treatment and reference plots was highest in the dry year (2007) and dampened in the wet year (2008) (Fig. 2). Other studies also report an increase in the magnitude of the response of soil respiration and A_{net} when precipitation events are preceded by a dry period (Cable *et al.*, 2008; Xu *et al.*, 2009). By definition, variability in mean annual precipitation characterizes aridland ecosystems (Noy-Meir, 1973) and thus we propose a more dynamic bucket model (Fig. 5) that takes into account interannual variability which pushes arid ecosystems towards or away from the nonstressed state from 1 year to the next.

Climate models consistently indicate a future with altered precipitation patterns and an increase in extreme precipitation events (IPCC, 2007). Southwestern North America may also experience increasing aridity (Cook *et al.*, 2004; Seager *et al.*, 2007). Understanding how the spatial and temporal patterns in
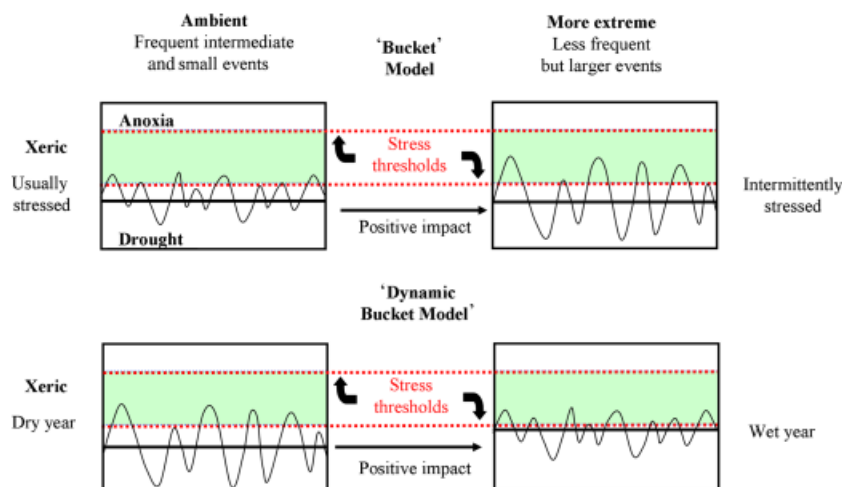
Fig. 5 A revised bucket model (Knapp *et al.*, 2008) based on interannual variation in mean rainfall. In each figure, the solid black line represents mean soil water content and the undulating line is the variability in soil water content. Xeric ecosystems are in a 'nonstressed' state when soil water content falls within the grey area, and are in a 'stressed' state when values of soil water content extend beyond the stress-threshold (outside of the grey shaded area). If annual precipitation increases, less variability is needed to reduce stress whereas if annual precipitation decreases, more extreme events are needed to reduce water stress.

precipitation will affect ecosystem processes and carbon dynamics is important because soil water availability drives ecosystem carbon exchange in aridland ecosystems (Huxman *et al.*, 2004a, b). Moreover, models predict that arid and semiarid ecosystems are likely to be highly responsive to future climate variability (Diffenbaugh *et al.*, 2008). Although production and C fluxes from aridland ecosystems are relatively small compared with mesic systems, arid and semiarid ecosystems cover 45% of the terrestrial surface (Schimel 2010) and therefore collectively contribute significantly to the global carbon budget. Therefore, it is essential that we understand how arid and semiarid ecosystems will respond to increased precipitation variability as a consequence of global environmental change.

Acknowledgements

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Supporting Information

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

Figure S1. Temporal patterns in A_{net} and predawn leaf water potential for the 2007 and 2008 monsoon seasons. Error bars indicate $\pm$ SE of the mean.

Figure S2. Mean daily soil water content at 16 cm for the 2007 and 2008 monsoon seasons. Lines are the mean for each treatment ($n = 5$) and reference ($n = 3$) plots. The mean soil θ at 16 cm (2007): 0.05, 0.06, and 0.08 $m^3 m^{-3}$ and mean soil θ (2008): 0.11, 0.13, and 0.15 $m^3 m^{-3}$ for reference, small, and large plots, respectively. The average standard error measured 6.47%, 6.56%, 4.69% of the mean (2007) and 4.86%, 3.86%, 3.54% of the mean (2008) for reference, small and large rainfall additions, respectively.

Figure S3. Seasonal mean absolute difference in mean daily soil θ used as a measure of soil water variability across all plots (the seasonal mean (unweighted) is integrated over 2–16 cm depth). Different letters are statistically significant ($\alpha = 0.05$) based on single-factor Kruskal-Wallis test for model significance and all pair wise comparisons.

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