

Effects of monsoon precipitation variability on the physiological response of two dominant C₄ grasses across a semiarid ecotone

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Abstract For the southwestern United States, climate models project an increase in extreme precipitation events and prolonged dry periods. While most studies emphasize plant functional type response to precipitation variability, it is also important to understand the physiological characteristics of dominant plant species that define plant community composition and, in part, regulate ecosystem response to climate change. We utilized rainout shelters to alter the magnitude and frequency of rainfall and measured the physiological response of the dominant C₄ grasses, *Bouteloua eriopoda* and *Bouteloua gracilis*. We hypothesized that: (1) the more drought-adapted *B. eriopoda* would exhibit faster recovery and higher rates of leaf-level photosynthesis (A_{net}) than *B. gracilis*, (2) A_{net} would be greater under the higher average soil water content in plots receiving 30-mm rainfall events, (3) co-dominance of *B. eriopoda* and *B. gracilis* in the ecotone would lead to intra-specific differences from the performance of each species at the site where it was dominant. Throughout the study, soil moisture explained 40–70 % of the variation in A_{net} . Consequently, differences in rainfall treatments were not evident from intra-specific physiological function without sufficient divergence in soil moisture. Under low frequency, larger rainfall events *B. gracilis* exhibited improved water status and longer periods

of C gain than *B. eriopoda*. Results from this study indicate that less frequent and larger rainfall events could provide a competitive advantage to *B. gracilis* and influence species composition across this arid–semiarid grassland ecotone.

Keywords Leaf gas exchange · *Bouteloua eriopoda* · *Bouteloua gracilis* · Chihuahuan Desert · Rainfall

Introduction

For the southwestern United States, climate models project a 4–7 °C increase in mean surface temperature and persistent drying throughout the century with lower frequency, yet larger rainfall events or wet seasons (Seager and Vecchi 2010; IPCC 2013). Such a change in the magnitude and timing of precipitation will substantially impact arid–semiarid ecosystems because plant community composition is influenced by soil water availability (Muldavin et al. 2008; Báez et al. 2013). Recent studies in Chihuahuan Desert grassland (CDG) also suggest inter-specific differences in the physiology and morphology of C₄ perennial grasses in response to changes in water availability (Senock et al. 1994; Fernández and Reynolds 2000; Fernández et al. 2002).

While most arid–semiarid studies emphasize plant functional type responses to increased precipitation variability, physiological differences among dominant plant species of a given functional type can also influence ecosystem response to climate change (Langley and Megonigal 2010). Novel climate patterns have long been predicted to affect species abundances across ecotones (Gosz and Sharpe 1989; Neilson 1993). This sensitivity arises because: (1) temperature and water are the dominant controls on ecotone position (Neilson 1993) and plant function, and (2)

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ecotones may occur where species reach their physiological limits (Risser 1995). In central New Mexico, USA, CDG and shortgrass steppe (SGS) form a narrow ecotone (Peters et al. 2006a). The southern CDG ecosystem primarily occurs in Mexico but extends north into Arizona, New Mexico, and Texas (Allred 2005). The northern SGS ecosystem is located along the eastern side of the Rocky Mountains in Colorado extending south into New Mexico and Texas and east into Oklahoma (Lauenroth et al. 2008). *Bouteloua eriopoda* and *Bouteloua gracilis* are the dominant C_4 (same pathway variant) perennial bunchgrasses of CDG and SGS, respectively. In the ecotone, both species transition to small pure or mixed-species patches and are co-dominant (Gosz 1993). Previous studies show that soil depth, climate, and seedling recruitment influence species distribution and patterns of species dominance in the ecotone (Minnick and Coffin 1999; Peters 2002; Buxbaum and Vanderbilt 2007). Yet, the specific physiological traits that may also influence the pattern of species abundance between *B. eriopoda* and *B. gracilis* are largely unknown. In this study, we sought to understand how a shift to lower frequency, yet larger precipitation events may affect the physiological response of *B. eriopoda* and *B. gracilis* across the ecotone.

Several factors are likely to influence the physiology and productivity of *B. eriopoda* and *B. gracilis*. First, both species are highly responsive to changes in precipitation that alter soil moisture. Previous studies show higher leaf-level photosynthesis (A_{net}), water potential (Ψ) and above-ground net primary productivity (ANPP) when *B. eriopoda* and *B. gracilis* receive large infrequent (≥ 20 -mm) rainfall additions than when they receive equivalent rainfall delivered as small frequent (5-mm) events (Heisler-White et al. 2008; Thomey et al. 2011). Second, N and water can co-limit productivity in semiarid ecosystems (Hooper and Johnson 1999). In *B. gracilis*, ANPP, cover and abundance are significantly higher as water or as N and water become more available while ANPP, A_{net} and abundance are higher in *B. eriopoda* primarily in response to increased water availability (Senock et al. 1994; Milchunas and Lauenroth 1995; Ladwig et al. 2012). Third, changes in cover of *B. eriopoda* and *B. gracilis* differentially affect each species. For example, *B. eriopoda* cover increased when *B. gracilis* was removed while *B. gracilis* cover remained unaffected when *B. eriopoda* was removed in the ecotone, in part, due to differences in resource availability and utilization in the absence of each species (Peters and Yao 2012). Finally, *B. eriopoda* may be more drought tolerant than *B. gracilis* because extended drought (>40 days without rain) is significantly more prevalent in southern CDG ecosystem compared to northern SGS ecosystem where *B. gracilis* is the dominant species (Hochstrasser et al. 2002).

To test the effect of low frequency, larger precipitation events on the physiological performance of *B. eriopoda* and *B. gracilis*, we excluded ambient precipitation and applied two summer monsoon precipitation regimes to plots in CDG and SGS and in the ecotone between them at the Sevilleta National Wildlife Refuge (SNWR) in central New Mexico, USA. Our precipitation regimes consisted of equivalent amounts of water applied as either 10 mm of water every 10 days or 30 mm of water every 30 days. On average, these rainfall events are 9 and 5 % of the daily precipitation events that occur during the summer monsoon (1988–2008), where 70 % of ambient monsoon rainfall events are ≤ 5 mm and occur approximately every 5 days. We expected that A_{net} , stomatal conductance (g_s) and pre-dawn leaf Ψ (Ψ_{pd}) would generally increase with soil moisture, and sought to understand the responses of these closely related species from different climatic regions to our precipitation regimes. Specifically, we hypothesized that:

1. The more drought-adapted *B. eriopoda* would exhibit faster recovery and higher rates of gas exchange following watering compared to *B. gracilis*.
2. Leaf gas exchange would be greater under the higher average soil water availability expected in plots receiving 30-mm treatment compared to plots receiving 10-mm treatment.
3. Co-dominance of *B. eriopoda* and *B. gracilis* in the ecotone would lead to intra-specific differences from the performance of each species at the site where it was dominant.

Materials and methods

Study area

We experimentally controlled the magnitude and frequency of rainfall events at the Sevilleta Long-Term Ecological Research (LTER) site on the SNWR (34.324°–106.706° WGS84) located 97 km south of Albuquerque, New Mexico, USA (Online Resource 1). The SNWR lies at the transition between CDG and SGS. Grazing has been excluded from the SNWR since 1973. Climate at the SNWR is characterized as arid–semiarid with dry, cool winters and springs. Mean annual temperature is 13.1 °C with an average low of 1.6 °C in January and high of 25.1 °C in July. Precipitation is highly variable within and between years. The SNWR receives 250 mm year⁻¹ of precipitation of which 132 mm (53 %), on average, occurs during the summer monsoon season (Muldavin et al. 2008). In this study, each experimental plot received 120 mm of monsoon precipitation (June–September mean, 1988–2008); a 30-mm

pre-monsoon pulse in June 2010 and 90 mm delivered by the two treatments July–September 2010. For the 2010 monsoon season, each study site received 111, 127, and 102 mm of ambient rainfall at the CDG, SGS and ecotone sites, respectively.

Study sites

Prior to the 2010 monsoon season, three study sites were established along an 8-km transect spanning the arid–semi-arid grassland boundary (Online Resource 2). One site was located in CDG dominated by *B. eriopoda*, a second site was located in SGS dominated by *B. gracilis*, and a third site was located in the ecotone, where *B. eriopoda* and *B. gracilis* are co-dominant. Mean plant cover in plots at CDG was $0.52 \pm 0.03 \text{ m}^2$ and consisted of ~90 % *B. eriopoda* with *Muhlenbergia arenicola*, *Sporobolus* spp., *Sphaeralcea* spp., and *Gutierrezia sarothrae* as subdominant species. Mean plant cover in plots at SGS was $0.35 \pm 0.02 \text{ m}^2$ and consisted of ~76 % *B. gracilis* with *M. arenicola*, *Chamaesyce* spp., and *Hymenopappus filifolius* as subdominant species. Mean plant cover in plots at the ecotone was $0.55 \pm 0.02 \text{ m}^2$ and consisted of ~55 % *B. eriopoda* and ~38 % *B. gracilis*. Subdominant species included *Pleuraphis jamesii*, *Sporobolus* spp., and *Chaetopappa ericoides*. On average, mean ANPP (2008–2012) for *B. eriopoda* and *B. gracilis* at the ecotone site is 34.26 ± 4.54 and 16.02 g m^{-2} , respectively. Soil texture was also variable across the study sites. Soils at CDG and SGS had a significantly higher proportion of silt ($F = 0.01$, $P = 0.01$) and clay ($F = 19.50$, $P = 0.02$). The proportion of sand was 22 % higher at the ecotone than at CDG and SGS (Table 1).

Experimental design

In 2009, ten 2.13×2.44 -m complete rainout shelters were constructed in a 10×40 -m area at each site for a total of 30 rainout shelters. All sites were on level soil and in

Table 1 Elevation and soil texture in the top 30 cm of soil sampled from each site

	CDG	Ecotone	SGS
Elevation (m)	1,616	1,600	1,670
Sand (%)	57.5 ± 0.5	74.5 ± 0.5	59.5 ± 1.5
Silt (%)	18.5 ± 0.5 b	10.0 ± 1.0 a	17.5 ± 0.5 b
Clay (%)	24.0 ± 1.0 b	15.5 ± 0.5 a	23.5 ± 1.5 b

CDG Chihuahuan Desert grassland, SGS shortgrass steppe

^a Soil texture is reported as mean \pm SE ($n = 2$ for each site)

^b Across study sites, different letters indicate significant difference between means ($\alpha \leq 0.05$) based on Kruskal–Wallis test for model significance and all pairwise comparisons (% sand) or single-factor ANOVA with Tukey test for multiple comparisons (% silt, % sand)

homogeneous vegetation. Rainout shelters were assembled to obtain a maximum shelter height of 1.22 m angled to a minimum height of 0.91 m. Roofing consisted of clear polycarbonate panels (Suntuf Plus; Palram Americas, Kutztown, PA) that eliminated ultraviolet radiation but transmitted 90 % of visible light. Rain gutters were attached to each rainout shelter with a downspout extending 2–5 m in order to divert ambient rainfall away from the experimental plots. In addition, aluminum flashing was buried to 10 cm along the perimeter of each experimental plot to avoid run-on of ambient rainfall. Most of the root mass of *B. eriopoda* and *B. gracilis* occurs directly below the plant (20–30 cm), with few roots that radially extend beyond 30–40 cm from the plant center (Lee and Lauenroth 1994; Gibbens and Lenz 2001). Nevertheless, we limited our measurements to a 1-m^2 subplot located in the center of each rainout shelter leaving a 50-cm buffer along the perimeter. Control plots (no shelter but similar precipitation patterns) were not established, because total monsoon rainfall and rainfall treatments were based on a 20-year analysis of monsoon precipitation. Therefore, the magnitude and frequency of our rainfall treatments are consistent with historical patterns and were not tied to specific rainfall events during 2010. At each site, one unsheltered ambient plot served as a reference in order to monitor shelter effects.

Rainout shelters were installed on 1 June 2010, one month prior to rainfall treatments, to exclude ambient precipitation from all experimental plots and reach consistent soil moisture across all sites. This dry period was followed by a 30-mm pre-monsoon rainfall event that was applied to each experimental plot on 15 June 2010 in order to initiate the summer growing season (Ignace et al. 2007). Starting 1 July 2010, experimental plots were randomly assigned to one of two rainfall treatments ($n = 5$ per treatment); one 30-mm rainfall event applied once per month (every 30 days) or three 10-mm rainfall events applied three times per month (every 10 days). Each experimental plot was irrigated using a hand-held garden wand that delivered water in a 360° pattern with an average flow rate of 15.7 L min^{-1} . Water used for irrigation was obtained from a reverse-osmosis system located at the University of New Mexico and transported to storage tanks located at each site as described by Thomey et al. (2011).

Sensor measurements

Sensors were installed horizontally to measure soil water content (θ_{soil}) at 5- and 15-cm depth (ECH₂O EC-5; Decagon Devices, Pullman, WA) since perennial grass roots are primarily distributed within the top 20–30 cm (McCulley et al. 2004). For each treatment, integrated θ_{soil} was also calculated as the mean θ_{soil} at 5- and 15-cm depths. Soil temperature (T_{soil}) was measured at 2-cm depth using

copper constantan thermocouple wire (Omega Engineering, Stamford, CT) in all experimental and reference plots ($n = 10$ and $n = 1$, respectively). At each site, air temperature (T_{air} ; CS-107 and 41303-5A Radiation Shield; Campbell Scientific, Logan, UT) and relative humidity (RH; iButton DS1923-F5; Maxim Integrated Products, Sunnyvale, CA) were monitored in one 10-mm, one 30-mm rainfall-addition plot and in the reference plot. T_{air} sensors were installed 30 cm above the soil surface, and RH sensors were installed 20 cm above the soil surface. Photosynthetically active radiation (PAR) (LI-190SB; LI-COR, Lincoln, NE) was measured under one rainout shelter and compared with ambient (unsheltered) PAR located within 100 m of the research site. Shelter effects were determined by comparing daily mean T_{air} , T_{soil} , RH and the hourly mean for PAR between rainout shelter and reference plots.

Leaf-level measurements

For each field campaign, leaf Ψ_{pd} was measured on two to three leaves of *B. gracilis* or *B. eriopoda* at SGS and CDG and from both species in the ecotone. Leaves were collected (pre-dawn) and put immediately into plastic bags, stored in a cooler and returned to the laboratory to be measured at 1400–1500 hours with a Scholander-type pressure chamber (PMS model 1000; PMS Instrument, Corvallis, OR).

Leaf-level gas exchange (A_{net}) was measured using a LI-6400 portable photosynthesis system (LI-COR) with a standard leaf chamber. Our field campaigns were limited to July and August 2010 and occurred at the beginning of each month 24 h prior (i.e., pre-pulse) to the initial 10- and 30-mm rainfall applications and at 1, 3, 5 and 9 days following each rainfall addition (i.e., post-pulse). Within each species and study site, mean post-pulse A_{net} (day 1, 3, 5, 9) was compared to mean pre-pulse A_{net} (day -1) in order to indicate pulse response and drought recovery. Additional field campaigns across all rainfall treatments occurred 24 h prior to and following each successive 10-mm rainfall event until the month's end. For each field campaign, all sites and experimental plots were sampled in random order. Measurements were recorded on one or two fully expanded leaves of *B. eriopoda* (CDG), *B. gracilis* (SGS), and from both species at ecotone. A_{net} and Ψ_{pd} were measured on multiple leaves within a plot and averaged. Irradiance (red/blue light-emitting diode light source) was set to saturating light conditions ($1,000 \mu\text{mol m}^{-2} \text{s}^{-1}$) that had been determined by light response curves for a subset of *B. eriopoda* and *B. gracilis* individuals. At each site, the CO_2 concentration ($400 \mu\text{mol mol}^{-1}$) and block temperature were set to ambient conditions prior to the first measurement and held constant across all experimental plots in order to maintain consistent chamber conditions throughout the measurement period (0800–1400 hours all sites). Leaf area was determined

by multiplying the measured width of each leaf by the length of the leaf chamber. Rates of A_{net} were corrected for leaf area using LI-6400 simulator software (OPEN V6).

Data analysis

All data were analyzed using SAS version 9.2 (SAS, Cary, NC). For each measured variable, data obtained from a single plot were averaged daily such that each plot represented an experimental unit ($n = 5$ for each rainfall treatment). Soil texture is reported as the mean % sand, % silt, and % clay per study site. In this study, the main effects were divided into two groups: pulse response of θ_{soil} and A_{net} , where the data were analyzed using the average July–August mean pre- (day -1) and post- (day 1, 3, 5, 9) rainfall-addition measurements; and seasonal response of A_{net} , g_s , Ψ_{pd} , θ_{soil} , T_{air} , T_{soil} , RH, where data were analyzed across the monsoon season (July–August). For each main effect, a single-factor ANOVA (PROC GLM) was used to test for differences between and within rainfall treatments (10 and 30 mm) and was followed by a Tukey test for multiple comparisons when the model was significant at $\alpha \leq 0.05$. Data that did not meet the assumptions of ANOVA were log or square root transformed. We used simple linear regression (PROC REG) to analyze the relationship between daily mean A_{net} and θ_{soil} as well as daily mean A_{net} and Ψ_{pd} . Since mean A_{net} lagged behind θ_{soil} , the 3–5 days post-pulse mean daily θ_{soil} was used in our regression analysis according to treatment and study site. Moreover, analysis of covariance (PROC GLM) was used to test for significant intra-specific difference between regression slopes within a study site. Last, data that failed to meet the assumptions of ANOVA despite transformation were analyzed using Kruskal–Wallis (PROC npar1way; Wilcoxon's) for treatment effects and multiple comparisons. For all analyses, α was set to ≤ 0.05 .

Results

Shelter effects

At each study site, there were no significant differences in mean T_{air} and RH among treatments and the reference plots (Table 2). At SGS, mean T_{soil} did not vary significantly among treatments and the reference, at CDG mean T_{soil} was significantly different between the treatments ($H = 10.66$, $P = 0.01$) but not different from the reference, and all rainfall treatments and reference were different at the ecotone ($H = 19.67$, $P = 0.01$; Table 2). The differences in T_{soil} were inconsistent between CDG and the ecotone. At CDG, mean T_{soil} in the 10-mm treatment ($28.81 \pm 0.27 \text{ }^\circ\text{C}$) was lower than the reference ($29.40 \pm 0.32 \text{ }^\circ\text{C}$) but higher in the 30-mm treatment ($30.12 \pm 0.26 \text{ }^\circ\text{C}$). In contrast, mean

Table 2 Shelter effects for each site

CDG	T_{air} (°C)	RH (%)	T_{soil} (°C)
Ambient	25.32 ± 0.28	46.95 ± 2.00	29.40 ± 0.32 ac
10-mm rainfall	25.33 ± 0.27	45.49 ± 1.89	28.81 ± 0.27 a
30-mm rainfall	25.37 ± 0.27	46.01 ± 1.89	30.12 ± 0.26 c
Ecotone			
Ambient	25.14 ± 0.28	47.88 ± 1.91	28.41 ± 0.27 a
10-mm rainfall	25.05 ± 0.27	46.45 ± 1.87	29.29 ± 0.29 b
30-mm rainfall	25.04 ± 0.27	46.47 ± 1.74	30.29 ± 0.33 c
SGS			
Ambient	25.31 ± 0.30	45.33 ± 2.27	29.77 ± 0.37
10-mm rainfall	25.27 ± 0.28	47.31 ± 2.30	29.40 ± 0.38
30-mm rainfall	25.25 ± 0.28	44.35 ± 1.85	29.59 ± 0.37

Each value represents the seasonal mean ± SE. For each variable, $n = 1$ ambient, $n = 1$ for 10-mm rainfall and 30-mm rainfall [air temperature (T_{air}) and relative humidity (RH)], $n = 5$ for 10-mm rainfall and 30-mm rainfall [soil temperature (T_{soil})]. Within each study site, different letters indicate means that are significantly different ($\alpha \leq 0.05$) based on Kruskal–Wallis test for model significance and all pairwise comparisons. For other abbreviations, see Table 1

T_{soil} at ecotone was 1–2 °C higher in both rainfall treatments (10 mm, 29.29 ± 0.29 °C; 30 mm, 30.29 ± 0.33 °C) than in the reference (28.41 ± 0.27 °C). Rainout shelters reduced average daily PAR by up to 34.12 ± 6.77 % (0300–1900 hours). However, the daily peak measure of PAR under the rainout shelters did not fall below saturating light conditions for A_{net} (1,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$) as determined by light-response curves for a subset of *B. eriopoda* and *B. gracilis* individuals (data not shown).

Soil water dynamics

Ambient rainfall was effectively excluded from rainout shelter plots except for two ambient rainfall events that were blown in during periods of high winds in July at SGS (Fig. 1a–d). Across the study sites, daily mean θ_{soil} was highest at SGS, intermediate at CDG and lowest at the ecotone. Daily mean θ_{soil} across all study sites was significantly higher on each date corresponding with a 30-mm rainfall addition and for at least 8 consecutive days thereafter compared to plots that received 10-mm rainfall additions (Fig. 1a–d). Over the season, 30-mm rainfall additions significantly increased mean θ_{soil} at SGS ($H = 10.55$, $P = 0.001$) and CDG ($H = 13.20$, $P = 0.001$), but there was no significant treatment effect on seasonal mean θ_{soil} at the ecotone (Online Resource 3).

Pulse response: pre- vs. post-rainfall events

Throughout the study period, post-pulse mean daily θ_{soil} at 5- and 15-cm depths generally tracked the 10- and 30-mm

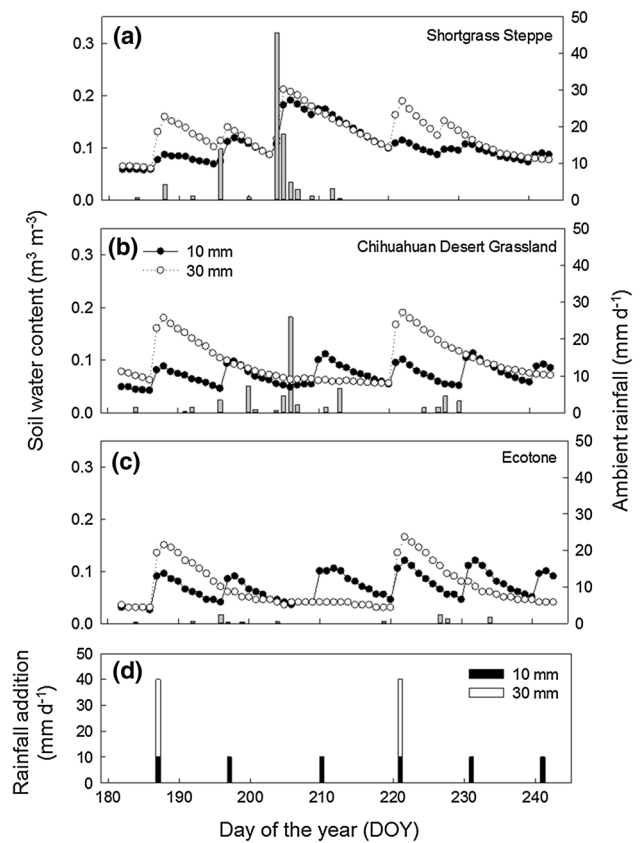


Fig. 1 Daily mean soil water content (θ_{soil}) integrated over 5- to 15-cm depths at the shortgrass steppe (SGS), Chihuahuan Desert grassland (CDG), and ecotone sites (a–c). Rainfall additions include three 10-mm events each month and one 30-mm rainfall event each month. SE was omitted for clarity. For each site the mean daily SE was: 10 % (10 mm) and 17 % (30 mm) of the mean at SGS; 14 % (10 mm) and 10 % (30 mm) of the mean at CDG; and 14 % (10 mm) and 28 % (30 mm) of the mean at the ecotone. For each study site, bars represent ambient precipitation (a–c) and the total precipitation added by treatment (d)

rainfall additions (Fig. 2a–f). At CDG and the ecotone, 10-mm rainfall additions significantly increased post-pulse mean θ_{soil} at 5 cm (Fig. 2a, c) and at 15 cm at the ecotone where there was also a significant seasonal difference in mean θ_{soil} by depth ($H = 5.99$, $P = 0.01$; Fig. 2c, inset). Across all sites, 30-mm rainfall events significantly increased post-pulse mean θ_{soil} at both depths within 24 h and there was a significant seasonal difference in mean θ_{soil} by depth (Fig. 2b, d, f, insets).

Irrespective of treatment, the highest mean post-pulse A_{net} in both species consistently lagged behind peak θ_{soil} (Figs. 2, 3). However, there was an inter-specific difference in drought recovery as indicated by the up-regulation of A_{net} following extended dry periods. At SGS and the ecotone, significantly higher mean A_{net} in *B. gracilis* occurred 1 day following a 10- or 30-mm rainfall addition (Fig. 3c–f), while significantly higher daily mean A_{net} in *B. eriopoda* at CDG

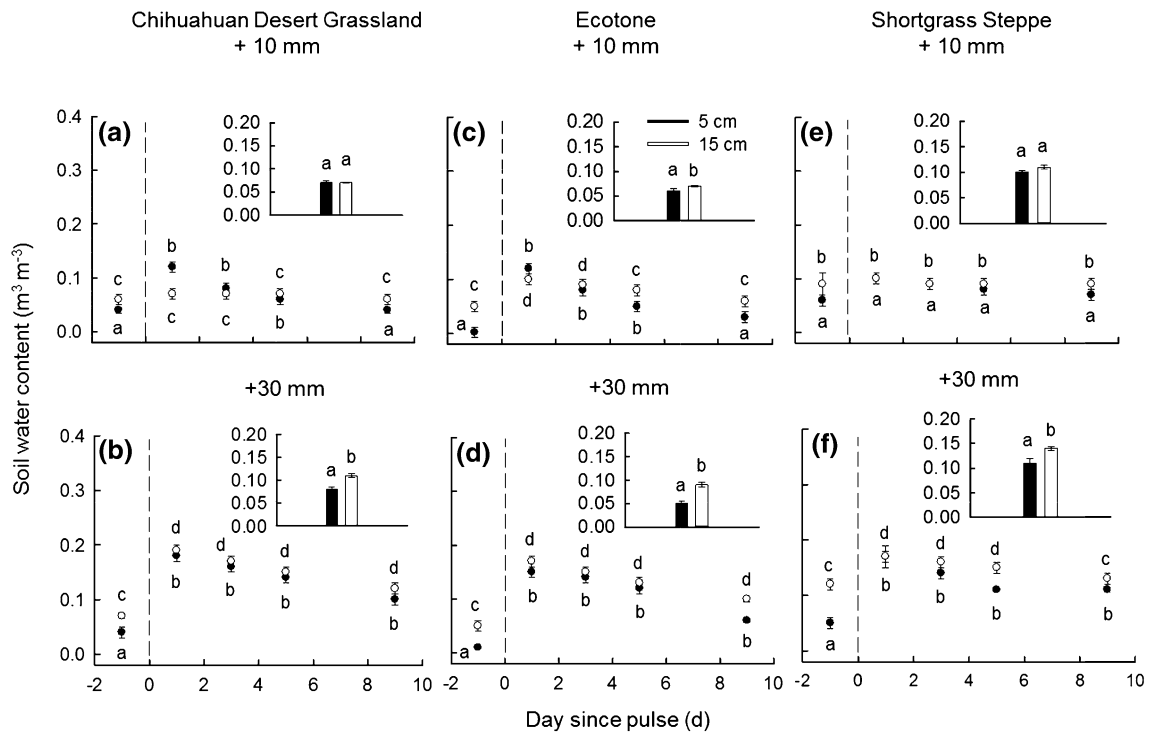


Fig. 2 Pre- (day -1) and post-pulse (days 1, 3, 5, 9) mean (\pm SE) θ_{soil} at 5- and 15-cm depths (*insets* are mean seasonal θ_{soil} at 5 and 15 cm) July–August across study sites; **a, b** CDG, **c, d** ecotone, **e, f** SGS. **a–f** Dashed line indicates rainfall additions. Different letters

indicate significant difference ($\alpha \leq 0.05$) between means [pre- vs. post-pulse or seasonal (*insets*)] based on Kruskal–Wallis analyses. For abbreviations, see Fig. 1

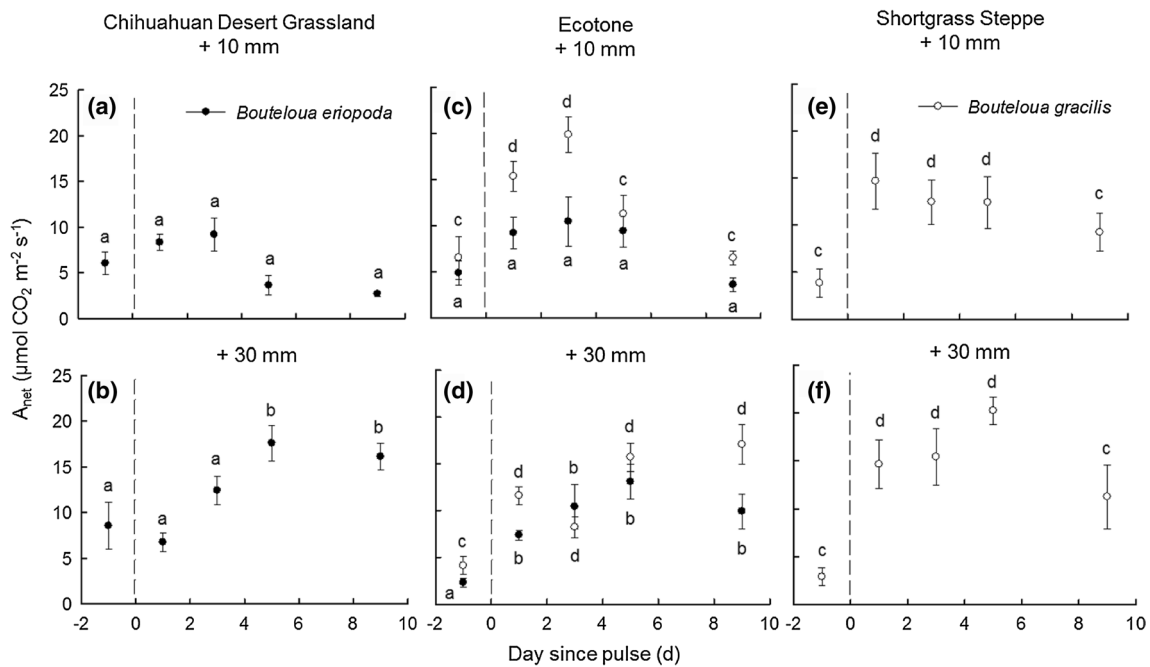


Fig. 3 Pre- (day -1) and post-pulse (days 1, 3, 5, 9) mean (\pm SE) leaf gas exchange (A_{net}) for each species in 10-mm and 30-mm irrigation plots (July–August) across study sites; **a, b** CDG, **c, d** ecotone, **e, f** SGS. **a–f** Dashed line indicates rainfall additions. Different letters

indicate significant difference ($\alpha \leq 0.05$) between means (pre- vs. post-pulse) within a species based on single-factor ANOVA and Tukey test for multiple comparisons between means. For other abbreviations, see Fig. 1

and the ecotone only occurred in 30-mm rainfall-addition plots 1–5 days following a rainfall application (Fig. 3a–d).

Seasonal responses

At all study sites, there was a significant and positive relationship between daily mean A_{net} and θ_{soil} and Ψ_{pd} in both species except for *B. eriopoda* at the ecotone (Fig. 4a–h). While there was no difference between the slopes of A_{net} and Ψ_{pd} , the slope of A_{net} and θ_{soil} in *B. gracilis* was significantly greater in 10-mm treatment plots than in 30-mm treatment plots at the ecotone ($F = 5.49$, $P = 0.03$) with a similar trend occurring at SGS (Fig. 4a, b). Within each rainfall treatment (10 and 30 mm) and between end-members (i.e., SGS and CDG) there were no significant differences in the slopes for A_{net} and θ_{soil} or Ψ_{pd} between *B. eriopoda* and *B. gracilis* (Fig. 4a, d, e, h).

The leaf-level intra-specific seasonal response to less frequent 10- and 30-mm precipitation events varied by study site. At CDG, significantly higher mean θ_{soil} in the 30-mm rainfall-addition plots (Online Resource 3) translated into significantly higher mean A_{net} ($H = 6.13$, $P = 0.01$), g_s ($H = 7.25$, $P = 0.01$), and Ψ_{pd} (i.e., less negative; $H = 4.45$, $P = 0.03$) in *B. eriopoda* compared to *B. eriopoda* in 10-mm rainfall-addition plots (Fig. 5a–c). Similarly, at SGS 30-mm rainfall events significantly increased mean θ_{soil} (Online Resource 3; $H = 10.55$, $P = 0.01$) and this corresponded with significantly higher g_s ($H = 4.67$, $P = 0.03$) and a trend towards higher A_{net} and Ψ_{pd} in *B. gracilis* (Fig. 5j–l). There was a slight reduction in the physiological performance of the co-dominant species from the end states (i.e., CDG and SGS) to the ecotone, but there was no treatment effect on seasonal mean θ_{soil} or on intra-specific A_{net} , Ψ_{pd} , and g_s at the ecotone (but see g_s in *B. eriopoda*) (Fig. 5d–i; Online Resource 3). Yet, there was a noticeable and significant inter-specific difference in mean seasonal A_{net} , g_s , and Ψ_{pd} within each rainfall treatment in the ecotone (Fig. 5d–i). On average, A_{net} was 20 % higher in *B. gracilis* than in *B. eriopoda* in the 10-mm treatment ($H = 3.93$, $P = 0.05$) and 30 % higher in the 30-mm treatment ($F = 13.05$, $P = 0.01$; Fig. 5d, g). In addition, *B. gracilis* was significantly less water stressed than *B. eriopoda* in 10-mm ($H = 6.87$, $P = 0.01$) and 30-mm ($H = 11.15$, $P = 0.001$) treatment plots in ecotone (Fig. 5f, i).

Discussion

We sought to understand how changes in precipitation might affect the physiological response of *B. eriopoda* and *B. gracilis* in the end states and in the ecotone of this transition. Throughout the study period, θ_{soil} and Ψ_{pd} explained 40–70 % of the variation in A_{net} for both species (Fig. 4). As

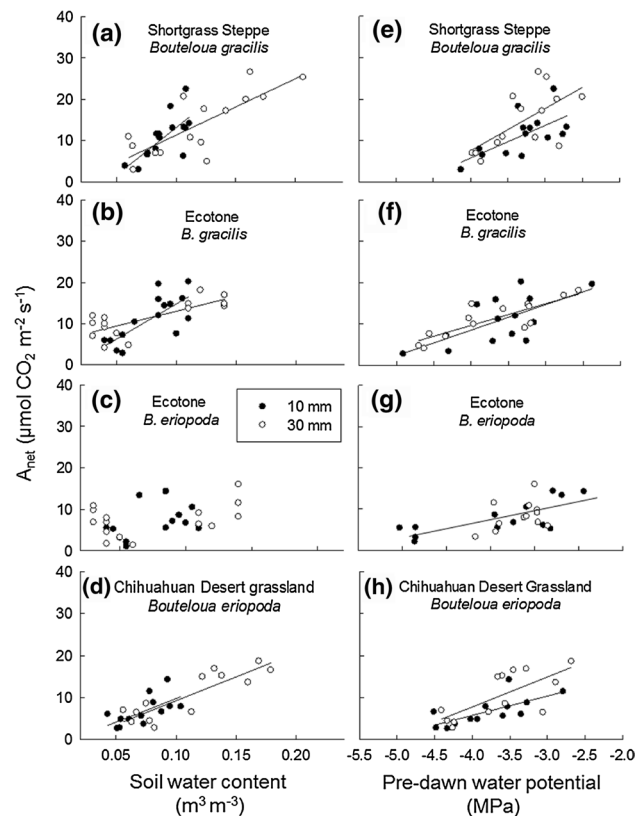


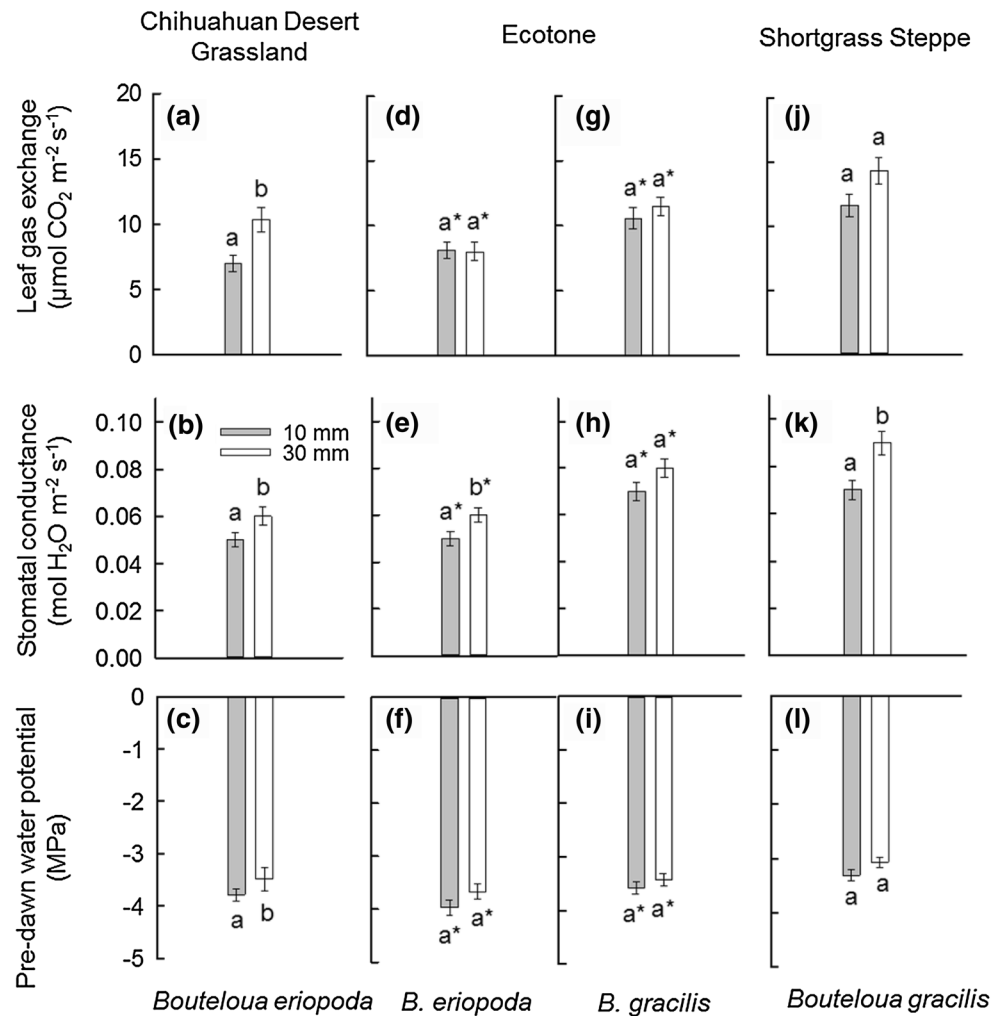
Fig. 4 Simple linear regression of daily mean A_{net} and integrated θ_{soil} (a–d) and pre-dawn water potential (Ψ_{pd}) (e–h) within each rainfall treatment and across study sites. Regression equations at $\alpha \leq 0.05$: **a** *B. gracilis*—SGS 10 mm, $A_{\text{net}} = -9.92 + 230\text{SWC}$, $r^2 = 0.51$; 30 mm, $A_{\text{net}} = -2.33 + 137\text{SWC}$, $r^2 = 0.62$, **b** *B. gracilis*—ecotone 10 mm, $A_{\text{net}} = -2.21 + 170\text{SWC}$, $r^2 = 0.55$; 30 mm, $A_{\text{net}} = 5.86 + 71.8\text{SWC}$, $r^2 = 0.59$, **d** *B. eriopoda*—CDG 10 mm, $A_{\text{net}} = -1.49 + 113\text{SWC}$, $r^2 = 0.41$; 30 mm, $A_{\text{net}} = -2.09 + 113\text{SWC}$, $r^2 = 0.75$, **e** *B. gracilis*—SGS 10 mm, $A_{\text{net}} = 37.3 + 7.87\Psi_{\text{pd}}$, $r^2 = 0.43$; 30 mm, $A_{\text{net}} = 48.3 + 10.2\Psi_{\text{pd}}$, $r^2 = 0.41$, **f** *B. gracilis*—ecotone 10 mm, $A_{\text{net}} = 33.3 + 6.19\Psi_{\text{pd}}$, $r^2 = 0.44$; 30 mm, $A_{\text{net}} = 30.7 + 5.25\Psi_{\text{pd}}$, $r^2 = 0.69$, **g** *B. eriopoda*—ecotone 10 mm, $A_{\text{net}} = 24.1 + 4.18\Psi_{\text{pd}}$, $r^2 = 0.56$, **h** *B. eriopoda*—CDG 10 mm, $A_{\text{net}} = 24.2 + 4.61\Psi_{\text{pd}}$, $r^2 = 0.50$; 30 mm, $A_{\text{net}} = 36.4 + 7.15\Psi_{\text{pd}}$, $r^2 = 0.51$. For other abbreviations, see Figs. 1 and 3

a consequence, changes in the magnitude and frequency of rainfall events were not evident from intra-specific physiological function until there was sufficient divergence in θ_{soil} between rainfall treatments. The improved water status and consistently higher photosynthesis observed in *B. gracilis* at SGS (high θ_{soil}) and the ecotone (low θ_{soil}) compared to *B. eriopoda* under the rainfall treatments suggest that these species respond differently to event size and frequency.

Soil water dynamics

Throughout the study period, mean seasonal θ_{soil} was not equal across the sites, particularly at SGS where

Fig. 5 Seasonal A_{net} , stomatal conductance, and Ψ_{pd} for each species across study sites, **a–c** CDG, **d–i** ecotone, **j–l** SGS. **a–l** Bars represent seasonal (July–August) means (\pm SE) for 10- and 30-mm rainfall additions. Different letters indicate a significant intra-specific difference between means and each rainfall treatment. Asterisks indicate significant inter-specific difference between means within a rainfall treatment. Analysis were performed using single-factor ANOVA and Tukey test for multiple comparisons between means or Kruskal–Wallis ($\alpha \leq 0.05$). For abbreviations, see Figs. 1, 3 and 4



ambient rainfall resulted in higher seasonal mean θ_{soil} (Online Resource 3). Along with the characteristic “pulsed” arid–semiarid rainfall regime (Noy-Meir 1973; Reynolds et al. 2004), available soil moisture in these ecosystems is also influenced by soil texture, canopy interception, run off, and evaporation (Loik et al. 2004). For example, infiltration is usually highest on coarse-textured soils (sand) and lowest on fine-textured soils (silt/clay) where porosity is limited and surface water is quickly evaporated [i.e., inverse-texture hypothesis (Noy-Meir 1973; Sala et al. 1988)]. We found some evidence of deeper infiltration where 10-mm rainfall additions significantly increased post-pulse and seasonal mean θ_{soil} at 15 cm on coarse-textured soils in the ecotone but not at CDG and SGS (Fig. 2a, c, e, insets). In contrast, daily mean θ_{soil} on fine-textured soils was either more variable at the surface in 10-mm treatment plots at CDG or similar throughout the soil profile at SGS where higher θ_{soil} may have minimized soil texture effects (Sala et al. 1988; English et al. 2005; Online Resource 4). While ambient rainfall influenced θ_{soil} at SGS, plant cover was also lower at SGS (wettest site) and higher at the ecotone

(driest site). In other semiarid grasslands, lower canopy cover has resulted in higher θ_{soil} (Dodd et al. 1998; Hamerlynck et al. 2010, 2011). In addition to soil texture and plant cover patterns, significantly higher mean T_{soil} under rainout shelters at the ecotone (Table 2) may have increased evaporation, contributing to lower mean θ_{soil} and lack of treatment effect despite the initial divergence in θ_{soil} following each rainfall application (Fig. 1c). Regardless of treatment type, multiple factors likely contributed to the difference in θ_{soil} that we observed across our study sites.

Pulse response: pre- vs. post-rainfall events

Because periods of extended drought are significantly more prevalent in the CDG ecosystem, we hypothesized *B. eriopoda* would recover from extended dry periods (10 vs. 30 days) in less time and with higher A_{net} following 10-mm and 30-mm rainfall additions than *B. gracilis*. Contrary to our hypothesis, *B. gracilis* rapidly (i.e., within 24 h) recovered from prolonged inter-pulse periods in both treatments with significantly higher A_{net} that mirrored the

increase in post-pulse θ_{soil} in SGS and the ecotone (Fig. 2, 3). These results were consistent at the wettest site (SGS) and at the driest site (ecotone) where ambient rainfall did not influence θ_{soil} . In *B. eriopoda* significantly higher A_{net} only occurred in 30-mm rainfall plots where significantly higher post-pulse θ_{soil} was sustained (Figs. 2, 3). One explanation for this unexpected result could be differences in plant allocation strategies. *B. eriopoda* responds to drought by allocating more biomass to roots and less to shoots, which corresponds with reduced leaf area and adjustments in leaf morphology (Fernández et al. 2002). This reduction in aboveground biomass not only reduces water loss but also limits leaf area for photosynthetic C gain and may initially delay up-regulation of photosynthesis (Fernández and Reynolds 2000; Hamerlynck et al. 2011). Ignace et al. (2007) also note a delay in photosynthetic up-regulation in the C_4 bunchgrass *Heteropogon contortus* due to leaf-area development. In contrast, *B. gracilis* responds to drought with tightly curled green leaves that quickly expand under favorable conditions (Ares 1976). Moreover, deeper suberized roots are discarded preserving shallow newly differentiated roots that account for the majority of soil water uptake (Lauenroth et al. 1987). Following a rainfall event ≥ 5 mm, *B. gracilis* exhibits improved leaf Ψ by using available root mass and then initiates new root growth within 48 h to sustain plant water status (Sala and Lauenroth 1982). Regardless of higher water stress, *B. eriopoda* eventually reached similar rates of A_{net} as *B. gracilis* in plots that received one 30-mm rainfall event every 30 days (Fig. 3b, d). In this way, *B. eriopoda* exhibits drought tolerance but not by the mechanism (i.e., rapid up-regulation of A_{net}) that we anticipated. It is also possible that our 30-day inter-pulse may not have been long enough to measure the point at which *B. eriopoda* recovers from drought better than *B. gracilis*.

Another explanation for the lag in response of A_{net} in *B. eriopoda* could be that these species respond differently when small (<10-mm) rainfall events are eliminated as *B. eriopoda* is mainly distributed in the southwestern US whereas *B. gracilis* is widely distributed throughout North America. Although small rainfall events only wet the surface layers, they occur more frequently in the southwestern US and are more dependable sources of water for shallow-rooted species (Sala et al. 1992). Moreover, small rainfall events may also function to maintain canopy or root systems needed for drought recovery following an extended dry inter-pulse period (Lauenroth and Sala 1992). Compared to the response of *B. eriopoda* measured in this study (–small rainfall events), under ambient rainfall (+small rainfall events) Pockman and Small (2010) and Thomey et al. (2011) both reported more rapid improvements in photosynthesis and substantially higher rates of A_{net} following irrigation or rainfall events that were similar in size

to ours. Likewise, in CDG Robertson et al. (2009) found that high annual net primary productivity in *Bouteloua curtipendula* was correlated with small (<5-mm) frequent (<10-day) rainfall events. Certainly large rainfall events are important in water-limited ecosystems, but in the absence of the most abundant small rainfall events *B. eriopoda* and other desert grassland species may initially lack the canopy or root system needed to utilize additional water resources.

Seasonal responses

Consistent with previous observations of higher A_{net} and productivity in treatments with larger (≥ 20 -mm) rainfall events, we hypothesized that A_{net} , g_s and Ψ_{pd} would be greater in *B. eriopoda* and *B. gracilis* under the higher average soil water availability expected in 30-mm rainfall-addition plots. In general, we found that θ_{soil} and Ψ_{pd} explained 40–70 % of the variation in daily mean A_{net} in both species, but there was no difference between treatment slopes except for *B. gracilis* in ecotone where A_{net} is more sensitive to changes in θ_{soil} in plots receiving 10-mm rainfall additions (Fig. 4). The seasonal data did not support our hypothesis across all sites. Over the study period, our treatments at the ecotone did not result in a significant difference in mean θ_{soil} or intra-specific A_{net} , g_s , Ψ_{pd} (but see g_s for *B. eriopoda*; Fig. 5d–i). In contrast, mean θ_{soil} was significantly higher in 30-mm plots than in 10-mm plots at SGS and CDG (Online Resource 3). However, the difference in seasonal mean θ_{soil} between treatments was greatest at CDG (~40 % difference) where ambient rainfall did not influence θ_{soil} . Consequently, A_{net} , g_s , and Ψ_{pd} were significantly higher for *B. eriopoda* in 30-mm treatment plots at CDG (Fig. 5a–c). At SGS, we also compared the physiological characteristics in *B. gracilis* in 10-mm rainfall treatment plots with and without periods of ambient blow-in (i.e., excluding two periods in July) and did not find a significant difference in A_{net} ($H = 0.10$, $P = 0.79$), g_s ($H = 0.10$, $P = 0.80$), or Ψ_{pd} ($H = 0.10$, $P = 0.79$). Previous studies in desert grasslands have also shown a lack of response to water additions during periods of high soil moisture because plants are already operating at physiological capacity (Ignace et al. 2007; Patrick et al. 2009). In our study, it is also possible that we may not have sampled enough during the blow-in period to detect a difference in performance.

As the cover of *B. eriopoda* and *B. gracilis* is differentially affected when each species is removed (Peters and Yao 2012), we hypothesized that co-dominance of *B. eriopoda* and *B. gracilis* in the ecotone would lead to intra-specific differences from the performance of each species at the site where it was dominant. While there was an intra-specific decrease in the performance of *B. eriopoda* and *B. gracilis* from CDG and SGS to the ecotone (Fig. 5),

these results were confounded as the reduction in leaf-level physiology from each vegetation end state (CDG and SGS) to ecotone may reflect the average decrease in mean θ_{soil} (~34 %). Instead, similar to up-regulation of A_{net} , there was a notable inter-specific difference in physiological performance in the ecotone. Even though mean θ_{soil} was equal across rainfall treatments at the ecotone, *B. gracilis* maintained significantly higher seasonal mean A_{net} , g_s and Ψ_{pd} than *B. eriopoda* (Fig. 5d–i). Because both species have similar rooting depths, it is conceivable that competition for water could occur (Casper and Jackson 1997; Goldberg and Novoplansky 1997). Previous studies indicate that *B. gracilis* pre-empts water resources from seedlings and shrubs within its rooting depth (Augilera and Lauenroth 1993; Lee and Lauenroth 1994). The ability of *B. gracilis* to exploit water resources and maintain longer periods of higher C gain than *B. eriopoda* may be due to negative interference [i.e., one species having an indirect negative impact on another species (Fowler 1986)]. This could partially explain why a significant linear relationship between A_{net} and mean θ_{soil} existed in *B. gracilis* but not in *B. eriopoda* at ecotone (Fig. 4). Furthermore, the difference in physiological performance may also provide a novel mechanism for the increase in *B. eriopoda* cover in response to *B. gracilis* removal at the ecotone (Peters and Yao 2012). Additional long-term studies are needed to further elucidate how future changes in precipitation regime as well as the differential response in physiology actually translate into differences in productivity (ANPP) or into changes in cover type (Neilson 1986), because leaf-level patterns do not necessarily translate to whole-plant response (Huxman et al. 2004). Moreover, soil depth and soil texture can control vegetation patterns (Bestelmeyer et al. 2006; Monger and Bestelmeyer 2005) along this ecotone. For example, *B. gracilis* is mostly constrained to deeper cumulic soils with thicker B horizons while *B. eriopoda* occurs on shallow soils (i.e., stationary transitions; Peters et al. 2006a). On the other hand, a local shift in dominance between *B. gracilis* and *B. eriopoda* can occur if abiotic factors such as lower frequency, yet larger rainfall events, favor one end member (SGS and CDG, respectively) over another in the ecotone [i.e., shifting transitions (Peters et al. 2006a)]. Empirical studies that characterize the relationship between soil texture and plant morphology and physiology (i.e., Hamerlynck et al. 2002) across these study sites would also be useful. However, the ability of *B. gracilis* to be less water stressed and rapidly initiate and maintain higher A_{net} on fine- and coarse-textured soils, in response to lower frequency, yet larger precipitation events, as we observed in this study, could provide a competitive advantage.

In summary, *B. eriopoda* and *B. gracilis* account for the majority of aboveground primary productivity in arid–semiarid grasslands in the study region. Previous studies show

that *B. gracilis* is more tolerant of grazing and fire and is less susceptible to woody shrub encroachment than *B. eriopoda* (Peters et al. 2006b; Parmenter 2008; Yanoff and Muldavin 2008; Augustine et al. 2010). We also found that when small (<10-mm) frequent rainfall events are replaced with larger (≥ 10 -mm) infrequent rainfall events, *B. gracilis*, the dominant species of SGS, consistently exhibited rapid improvements in water status and C gain compared to *B. eriopoda*, the dominant species of CDG. Monsoon precipitation across the CDG–SGS ecotone is presently dominated by rainfall events ≤ 5 mm and the abundance of *B. eriopoda* is increasing at a greater rate than that of *B. gracilis* (Collins and Xia 2015). Our results suggest that a change to less frequent, yet larger rainfall events could shift the competitive advantage in this ecotone in favor of *B. gracilis*, the dominant species of the northern SGS ecosystem.

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