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SPECIAL TOPIC: COORDINATED APPROACHES TO GLOBAL CHANGE RESEARCH

C_3 and C_4 plant responses to increased temperatures and altered monsoonal precipitation in a cool desert on the Colorado Plateau, USA

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Abstract Dryland ecosystems represent >40 % of the terrestrial landscape and support over two billion people; consequently, it is vital to understand how drylands will respond to climatic change. However, while arid and semi-arid ecosystems commonly experience extremely hot and dry conditions, our understanding of how further temperature increases or altered precipitation will affect dryland plant communities remains poor. To address this question, we assessed plant physiology and growth at a long-term (7-year) climate experiment on the Colorado Plateau, USA, where the community is a mix of shallow-rooted C_3 and C_4 grasses and deep-rooted C_4 shrubs. The experiment maintained elevated-temperature treatments (+2 or +4 °C) in combination with altered summer monsoonal precipitation (+small frequent precipitation events or +large infrequent events). Increased temperature negatively affected photosynthesis and growth of the C_3 and C_4 grasses, but effects varied in their timing: +4 °C treatments negatively affected the C_3 grass early in the growing season of both years, while the negative effects of temperature on the C_4 grass were seen in the +2 and +4 °C treatments, but only during the late growing season of the drier year. Increased summer precipitation did not affect photosynthesis or biomass for any species, either in the year the precipitation was applied or the following year. Although previous research suggests dryland plants, and C_4 grasses in particular, may respond positively to elevated temperature, our findings from a cool desert show marked declines in C_3 and C_4 photosynthesis and growth, with temperature effects dependent on the degree of warming and growing-season precipitation.

Keywords *Achnatherum hymenoides* · *Atriplex confertifolia* · Altered precipitation · Climate change · Colorado Plateau · Cool desert · Elevated temperature · *Pleuraphis jamesii*

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Introduction

Hyper-arid, arid, semiarid, and dry-subhumid ecosystems, hereafter called drylands, make up over 40 % of the global terrestrial surface (Lioubimtseva and Adams 2004; Reynolds et al. 2007; Maestre et al. 2012) and 35 % of the United States (Oldfield 2004). These ecosystems range from deserts with little to no visible vascular plant cover to the productive Great Plains of the USA. Dominant dryland vegetation can include C_3 and C_4 grasses, shrubs, and trees (Tielborger and Salguero-Gomez 2014). Over 38 % of the human population lives in dryland ecosystems, with this number expected to increase due to population growth, demand for resources, and dryland expansion (Yang et al. 2005; Zeng and Yoon 2009). In particular, grass-dominated rangelands account for over 30 % of Earth's terrestrial surface and provide most of the forage for the world's domestic livestock (Asner et al. 2004; Suttie et al. 2005). Despite the importance of drylands, our understanding of

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how climate change—specifically, increases in temperature and alterations to precipitation regimes—will affect these extensive ecosystems remains notably poor. While several studies have investigated the effects of temperature and/or precipitation on dryland plants, dryland communities are diverse and support a host of shallow- and deep-rooted perennial C_3 and C_4 grasses and shrubs. Due in part to this functional diversity, an integrated understanding of how drylands will respond to altered climate remains elusive, as the organisms themselves vary so greatly. Accordingly, while it is possible that an increase in temperature or a decrease in precipitation would uniformly affect growth across the community, it may be more likely that climate change will affect function via a shift in community composition. Long-term monitoring data (25-year) support this supposition by suggesting that climate change has already altered the composition of vascular plant communities in some drylands (Munson et al. 2011). However, elucidating causal relationships between shifts in plant community and climatic change is difficult with observational data.

For the southwestern USA, a region with both cool and warm dryland grass and shrublands, mean air temperature is expected to increase by ~3–5.3 °C by 2100 (Garfin et al. 2014). For many ecosystems, it is commonly assumed that increased temperatures would benefit plant growth by moving the temperature closer to the optimum for photosynthesis (Way and Oren 2010). Yet, this pattern will not hold if individuals are already located near their thermal growth optimum. In addition, the effects of altered climate may vary depending on plant functional type. It is often suggested that C_4 plants will respond more positively to temperature increases relative to C_3 plants, as C_4 plants typically have a higher photosynthetic temperature optimum, and the C_4 photosynthetic pathway reduces the potential for photorespiration (Berry and Bjrkman 1980; Sage et al. 2012). Accordingly, an increase in temperature alone has the potential to differentially affect fundamental plant functions such as carbon assimilation and biomass accumulation, which can result in changes in ecosystem function not only via physiological effects on current plant communities but also through longer-term shifts in plant community composition (Zavaleta et al. 2003; Morgan et al. 2011; Wu et al. 2012).

Drylands are defined by their relative deficits in water, so the role of climate-induced changes to soil water availability is central to considerations of how drylands will respond to global change. Beyond direct effects, increases in temperature can indirectly affect dryland flora via increased soil drying resulting from increased evapotranspiration rates, which can ultimately drive a decrease in stomatal conductance (g_s) and photosynthesis (A_{net}) (Yahdjian and Sala 2006; Golluscio et al. 2009; Seneviratne et al. 2010; Sala et al. 2012). Changes to precipitation patterns can also strongly affect dryland productivity and community composition, and both the timing and amount of precipitation are important controls (Knapp and Smith 2001). Regardless of the driver (i.e., increased temperature or altered precipitation), reductions in soil moisture during the growing season will likely differentially affect different plant functional types; for example, plants using the C_4 photosynthetic pathway typically have a higher water use efficiency, which can reduce the demand for soil water and even extend a growing season (Morgan et al. 2011). In contrast, C_3 plants may more strongly respond to reductions in soil water, as they tend to have a lower water use efficiency (Taylor et al. 2014). Additionally, deep-rooted shrubs access moisture that has infiltrated deeper into the soil and represents a water source that is available for a longer time after the precipitation occurred, such as from snow melt (Bates et al. 2006). Taken together, physiological differences among functional groups suggest that, relative to C_3 plants, both shallow-rooted C_4 plants and deep-rooted shrubs may be less negatively affected by climate-induced reductions in soil moisture.

Despite previous studies investigating the impact of temperature and precipitation on dryland ecosystems, we still have a relatively poor understanding of how these communities will respond to changes in climate. In part, this poor understanding can be traced to four key sources: (1) the relatively small number of manipulative studies that have been conducted in arid and semiarid ecosystems (reviewed in Tielborger and Salguero-Gomez 2014); (2) the diverse plant functional types common in dryland communities, which may respond quite differently to climate change; (3) dryland plant communities could take many years to respond to a change in climate, and many studies may be too short to observe treatment effects; and (4) most climate experiments in dryland ecosystems only manipulate a single environmental parameter at a single level of change, although predictions are for variable modifications to both temperature and precipitation. In order to address these experimental obstacles, we investigated the effects of two levels of increasing growth temperature (ambient +2 °C for 4 years then +4 °C for 3 subsequent years or ambient +2 °C for 3 years) and altered summer precipitation (ambient precipitation +the addition of small frequent or +the addition of large infrequent watering events), applied singly and in combination, on a cool dryland ecosystem on the Colorado Plateau, USA. Measurements of in situ photosynthesis and biomass accumulation were made multiple times over the course of the growing season during a year of normal precipitation (2011) and a dry year (2012). Based on previous research (Morgan et al. 2011; Sala et al. 2012), we hypothesized that plant functional groups would respond differently to increased temperature—with C_4 plants responding positively and C_3 plants having no response—and that all plants

would benefit from the large infrequent monsoonal watering events. Owing to the relatively long study time and the use of mature native plants, our findings highlight notable possible changes in plant physiology and community composition for the Colorado Plateau.

Materials and methods

Site description

The study site and experimental design have been described in Reed et al. (2012) and Zelikova et al. (2012). Briefly, the site is located in a cool desert ecosystem on the Upper Colorado Plateau (36.675 N, −109.416 W, 1310 m.a.s.l.) near Castle Valley, UT, USA. The soils are classified as sandy loam, calcareous, Rizno series with a bulk density of 1.35 g/cm^3. The site's vegetation is dominated by the native C_3 perennial grass *Achnatherum hymenoides* (syn. *Stipa hymenoides*), the native C_4 perennial grass *Pleuraphis jamesii* (syn. *Hilaria jamesii*), the native C_4 perennial shrub *Atriplex confertifolia*, and the exotic invasive C_3 grass *Bromus tectorum*. There are numerous other annual and perennial plants within the site, but they were not abundant and not the subject of this study (all plant species present within the study plots are listed in Table S1 of the Electronic supplementary material, ESM). Biological soil crust communities at the site are dominated by the cyanobacterium *Microcoleus vaginatus*, the cyanolichens *Collema tenax* and *C. coccophorum*, and the moss *Syntrichia caninervis*. The site is located on a west-facing slope and has a history of limited to no anthropogenic activity prior to plot establishment.

Experimental design

In 2005, five blocks of four treatments each (hereafter, "B-plots") were established ($n = 20$ plots) and, in 2007, another five blocks of four treatments were established (hereafter, "C-plots;" $n = 20$). All 40 plots were 2 × 2.5 m and were oriented with the long side running east to west (parallel to the slope). For B-plots, the plots within each block were randomly assigned one of four treatments: ambient temperature and precipitation (B-T_A P_A); elevated temperature (+4 °C) and ambient precipitation (B-T_{+4} P_A); ambient temperature and elevated precipitation [small (1.2 mm) frequent summertime precipitation events] (B-T_A P_{SF}); or elevated temperature and altered precipitation (B-T_{+4} P_{SF}). B-plot temperature treatments began as +2 °C above ambient in 2005 and, in 2009, the B-plot treatment was increased to ambient +4 °C to account for modified climate predictions. For C-plots, the plots within each block were randomly assigned one of four treatments: ambient temperature and precipitation (C-T_A P_A); elevated temperature (+2 °C) and ambient precipitation (C-T_{+2} P_A); ambient temperature and altered precipitation (larger infrequent summertime precipitation events) (C-T_A P_{LI}); or elevated temperature and altered precipitation (C-T_{+2} P_{LI}).

Warming of the plots was accomplished using two 800 W infrared (IR) radiant heaters (Kalglo Model MRM-2408) placed 1.3 m above the soil surface and oriented north to south. The plots not receiving warming have identical "control lamps" placed in the same configuration but generating no heat. While IR warming is a common method employed in climate change manipulative studies (Aronson and McNulty 2009), all methods for increasing ecosystem temperature have caveats and the IR approach is no exception. Infrared warming was selected for this research because it allows for a high degree of manipulative accuracy at all times of day and because it does not have the problems associated with chamber warming infrastructure—such as altered light conditions, dew formation, and restricted air flow—or the soil disturbance of warming cables (Kimball 2005; Aronson and McNulty 2009). However, a central issue is that the IR warming can also dry the soil in ways that complicate the partitioning of warming versus drying effects. In particular, because temperature is changed without a concurrent change in humidity, changes to vapor pressure deficit (VPD) can result in increased transpiration and a reduction in soil moisture (Amthor et al. 2010). We have addressed this caveat by assessing the effect of elevated temperature on soil moisture in the plots, and have interpreted all results within the context of treatment effects on both temperature and soil moisture.

Warming treatments increased both foliage and soil temperature (Fig. 2). Plot temperature treatments were regulated by controlling soil temperature at 5 cm depth. We used 5 cm soil depth as our temperature target for two key reasons. First, while we did assess foliar temperatures (Fig. 2e), they could not be used to control treatment temperatures due to highly heterogeneous plant composition and canopy cover across the plots. Second, surface soil temperature, as measured by IR sensors, could not be used due to spatial and temporal heterogeneity in surface albedo. We also inserted soil probes at surficial depths (2 cm), but because of the dynamic soil surface (i.e., significant biological soil crusts and frost heaving), these measurements proved too variable for monitoring and modifying temperature treatments. Thus, plot temperature control was best accomplished by regulating soil temperature at 5 cm depth. Measurements of soil temperature made at 5 cm in the control plots correlated strongly with air temperature (Fig. S1 of the ESM; $P < 0.001$; $T_{soil} - 2.71 + T_{air} \times 1.02259$, $r_2 = 0.903$). Relationships between surface soil and deeper soil temperatures with treatment were assessed prior to the start of this research (data not shown) to create the 5 cm soil depth temperature targets necessary to achieve the

desired surface warming: +4 °C surface warming (B-plots) was achieved by warming to 3.47 °C at 5 cm depth, and the +2 °C surface warming (C-plots) was established by warming to 1.58 °C at 5 cm depth.

Measurements of soil temperature and soil moisture were made at 5 cm depth using in-house-constructed, three-tipped thermopiles and volumetric soil probes (CS616 water content reflectometer, Campbell Scientific, Logan, UT, USA and EC-5 soil moisture probes, Decagon Devices, Pullman, WA, USA). Probes were placed on the southeast side of each plot at 30, 60, and 90 cm from the center of the plot. The voltage supplied to each elevated temperature IR lamp was adjusted weekly to meet the target soil temperatures. Air temperature, incoming photosynthetically active radiation (PAR), atmospheric relative humidity (RH), and precipitation were measured at the center of the site every minute and hourly averages were recorded. Foliar temperature was measured with infrared radiometer sensors (SI-121; Apogee Instruments, Inc., Logan, UT, USA) every minute with the hourly averaged recorded. The IR sensors were mounted 15–80 cm above the canopy, depending upon the canopy size. For the B-plots, sensors were placed above a single *P. jamesii* plant in randomly selected B-$T_A P_A$, B-T_{+4} P_A, B-T_A P_{SF}, and B-T_{+4} P_{SF} plots and, for C-plots, sensors were placed above a single plant for each species in randomly selected C-$T_A P_A$, C-T_{+2} P_A, C-T_A P_{LI}, and C-T_{+2} P_{LI} plots. Due to the lack of an observed precipitation treatment effect on foliar temperatures (data not shown), foliar IR sensors were assigned to the control and elevated temperature treatments to increase analytical power.

The small frequent (SF) monsoonal precipitation treatments were designed to mimic an increase in the frequency of short-duration precipitation inputs. The large infrequent (LI) precipitation treatments were applied to provide monsoonal inputs at the 30-year average and, for the years of this study, this was a significant increase in water compared with plots receiving no precipitation treatment. The watering treatments were applied from approximately June 15 through September 15 (Table S2 of the ESM). For the B-plot precipitation treatments, small (1.2 mm) precipitation events were applied 5 times every 2 weeks. For the C-plot precipitation treatments, a single large precipitation event was applied every 2 weeks to meet long-term precipitation averages. All watering treatments were applied by hand using a pump sprayer.

Measurements

While the three target species were dominant in the plant community, they were not universally present in the B-plots. This is because the B-plots were originally established in 2005 to focus on biological soil crust communities, not plant communities. When present in the plot, three target species were tagged for repeated measurements of aboveground biomass. All species were present in each C-plot. In June of 2010, 2011, and 2012, the biomasses of *A. hymenoides*, *P. jamesii*, and *A. confertifolia* were estimated by measuring tagged individuals: the total aboveground biomass was estimated using allometric relationships established for each species each year. Briefly, measurements of canopy volume, surface area of live canopy cover, percent green, and number of green culms were made for multiple individuals of each species outside of the treatment plots. Plants were then harvested, dried, and weighed, and the measurement(s) that most accurately captured the actual biomass were used to estimate the biomass within the plots. For *A. hymenoides*, biomass was related to the volume of the live plant material. For *P. jamesii*, biomass was related to number of green culms. For *A. confertifolia*, biomass was related to the surface area of canopy cover of green plant material.

Net photosynthesis (A_{net}) measurements were conducted on the three target species using a portable photosynthesis system (Li-6400, LiCor Biosciences, Lincoln, NE, USA). A fluorescence leaf chamber (LI-6400-40 LiCor Bioscience) was used to measure *A. hymenoides* and *P. jamesii*, while an opaque conifer chamber with an RGB light source (LI-6400-20L, LiCor Bioscience) was used to measure *A. confertifolia*. The conditions within the leaf cuvette were set to mimic the light, temperature, and CO_2 conditions to which the plants are normally exposed (Table S3 of the ESM). Measurements were conducted at 9:00, 12:00, 15:00, and 18:00 h in April, May, and June in 2011 and March, April, and May in 2012. Differences in measurement dates among years were related to the phenologic timing of green up and growth in each year: dates for both years capture early-season, mid-season, and late-season time points. Dark-acclimated foliar fluorescence was measured at 05:00 h either the day prior to or the day after gas exchange measurements to estimate the maximum quantum yield of photosystem II (F_v/F_m) (mini-PAM, Walz, Effeltrich, Germany).

Data analysis

All photosynthesis data were transformed to pass a Shapiro–Wilk's test for normality. There was no significant treatment × measurement hour interaction, so net photosynthesis averaged across the day was used for statistical comparisons among treatments and measurement dates. Significant differences in A_{net}, g_s, and F_v/F_m were determined using repeated-measures ANOVAs. The fixed effects were species (3 levels), treatment (4 levels), year (2 levels), and measurement date (3 levels per year); block × plot was the random factor and individual plant was the repeated effect. Significant differences in biomass production were determined using

repeated-measures ANOVAs with species, plot, treatment, and year as the fixed effects, block × plot as the random effect, and individual plant as the repeated effect. Correlations between biomass, temperature, and precipitation were tested using linear regression analyses. Significance was determined at $\alpha < 0.1$, and all analyses were performed using SAS (v. 9.1, SAS Institute Inc., Cary, NC, USA) software.

Results

Climate and treatment effects on soil temperature and soil moisture

In general, the air temperature from January 2010 through June 2012 was higher than the historical average; however, the mean air temperature never exceeded the historic maximum temperature during the study (Fig. 1). Annual precipitation during 2010 and 2011 was 190 and 199 mm, respectively, which was 27 and 24 % less than the 30-year annual precipitation average of 241 mm. The total precipitation from January through June 2012 was 44 mm, approximately 60 % less than this time period's 30-year average of 118 mm (Fig. 1). The total precipitation from February through May, which is the main growing season in this community, was 12.1 cm in 2010, 7.8 cm in 2011, and 3.47 cm in 2012, while the 30-year average is 7.5 cm.

Soil temperature measured at a depth of 5 cm was higher in the elevated temperature treatments (Fig. 2). On average,

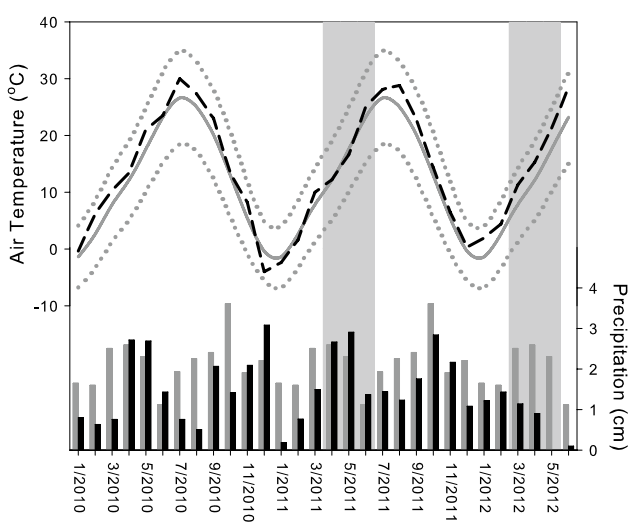

Fig. 1 *Upper* line graph depicts the historic monthly average temperature (*gray solid line*), historic mean maximum and minimum air temperature (*dotted gray line*), and the ambient air temperature over the course of this study (*dashed black line*). The *lower* bar graph depicts the historic monthly average precipitation (mm) (*gray bars*) and the ambient monthly precipitation over the course of this study (*black bars*)

soils in the B-T_{+4} plots (B-plots, +4 °C) were 2.93 °C warmer than those in the B-T_A plots (B-plots, ambient temperature) ($P = 0.08$), which is close to the target temperature of 3.47 °C. The C-T_{+2} plots (C-plots, +2 °C) were 1.65 °C warmer than the C-T_A (C-plots, ambient temperature) plots at a depth of 5 cm, which is close to the target temperature of 1.58 °C, but this difference was not statistically significant due to high variability across the year ($P = 0.32$) (Table 1). Neither the B-P_{SF} (B-plot, small frequent monsoon precipitation additions) nor the C-P_{LI} (C-plot, large infrequent monsoon precipitation additions) treatments significantly affected soil temperature (Fig. 2). The plots of the combined elevated temperature and precipitation treatments (B-T_{+4} P_{SF} and C-T_{+2} P_{LI}) had similar temperatures to the single-factorial temperature treatments (B-T_{+4} and C-T_{+2}; Fig. 2). Foliar temperatures averaged 5 °C higher in the B-T_{+4} treatment plots than in the B-T_A plots, and the difference in foliar temperature of *P. jamesii* between the B-T_A and the B-T_{+4} treatments tended to increase throughout the experiment (Fig. 2e), although no such trend was observed in soil temperature. Plants in the C-T_{+2} plots were on average 1.6 °C warmer than plants in the control plots (Fig. 2e), with temperatures similar in 2011 and 2012.

In general, soil moisture decreased from 2010 through 2012 (Fig. 2), likely driven by the above-average temperatures and low precipitation amounts experienced from 2011 through June 2012 (Fig. 1). Soil volumetric water content (VWC; V/V %) measured during the growing season significantly declined from 2010 through 2012 (2010: 9.2 %; 2011: 6.8 %; 2012: 4.1 %; $P < 0.001$ for all inter-year comparisons). Soil VWC was significantly reduced by both the B-T_{+4} and C-T_{+2} temperature treatments compared to the respective control plots ($P < 0.001$ for each) (Fig. 2). The small frequent precipitation treatment applied to the B-plots from mid-June through September resulted in an addition of 31.2 mm of precipitation in 2010 and 39.6 mm of precipitation in 2011 (Table S2 of the ESM). Averaged across the entire year, the B-P_{SF} treatment did not affect soil moisture ($P > 0.2$); however, during the time the treatments were applied (June through September), VWC was significantly increased compared to the B-P_A plots (2010: $P = 0.096$; 2011: $P = 0.055$). In the C-plots, the C-P_{LI} had 32.9 and 27.9 mm applied in 2010 and 2011, respectively, which did not affect annual averages of soil VWC ($P > 0.2$) nor VWC during the months the treatment was applied compared to the C-P_A plots (2010: $P = 0.22$; 2011: $P = 0.18$). This lack of effect is likely due to the relatively low frequency of events.

Seasonal and inter-annual climate effects on leaf-level measurements

To test the effects of natural variation in precipitation and temperature on leaf-level gas exchange and physiology,

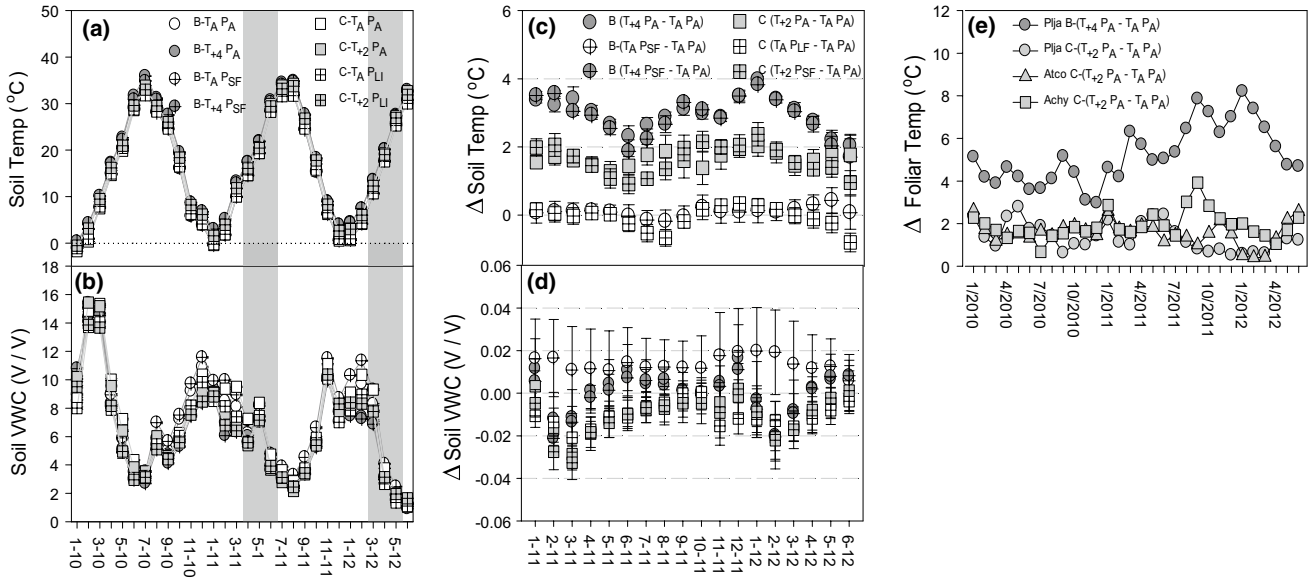

Fig. 2 **a** Monthly soil temperature (°C) and **b** monthly soil volumetric water content (% V/V) measured at 5 cm soil depth from January 2010 through June 2012. *Vertical gray shading* represents the months when foliar physiological measurements were conducted. Effects of climate manipulation treatments on **c** monthly soil temperature (Δ °C) and **d** monthly soil VWC (ΔVWC) measured at 5 cm soil depth from January 2011 through June 2012. *Error bars* represent 1 SEM. **e** Treatment effects on monthly foliar temperature (Δ °C) from January 2010 through April 2012. For panels **a** and **b**, the treatments are B-plots: ambient temperature and ambient precipitation (B-T_A P_A; *white circles*), elevated temperature (+4 °C), and ambient precipitation (B-T_{+4} P_A; *dark gray circles*), ambient temperature and elevated precipitation (+small frequent summer events) (B-$T_A P_{SF}$; *white circles with crosses*), and elevated temperature (+4 °C) and elevated precipitation (+small frequent summer events) (B-T_{+4} P_{SF}; *dark gray circles with crosses*); C-plots: ambient temperature and ambient precipitation (C-T_A P_A; *white squares*), elevated temperature (+2 °C) and ambient precipitation (C-T_{+2} P_A; *light gray squares*), ambient temperature and elevated precipitation (+large infrequent summer events) (C-T_A P_{LI}; *white squares with crosses*), and elevated temperature (+2 °C) and elevated precipitation (+large infrequent summer events) (C-T_{+2} P_{LI}; *light gray squares with crosses*). For panels **c** and **d**, the differences between treatments are B-plots: $T_{+4}P_A$—T_AP_A (*gray circles*), T_A P_{SF}—T_AP_A (*white circles with crosses*), T_{+4} P_{SF}—T_AP_A (*gray circles with crosses*); C-plots: $T_{+2}P_A$—T_AP_A (*gray squares*), T_A P_{LI}—T_AP_A (*white squares with crosses*), T_{+2} P_{LI}—T_AP_A (*gray squares with crosses*). For panel **e**, data show the difference in foliar temperature (Δ °C) between the B-T_A and B-T_{+4} treatments for *P. jamesii* (*dark gray circles*), C-T_A and C-T_{+2} treatments for *P. jamesii* (*light gray circles*), C-T_A and C-T_{+2} treatments for *A. confertifolia* (*light gray triangles*), and C-T_A and C-T_{+2} treatments for *A. hymenoides* (*light gray squares*)

Table 1 Monthly percent changes (and corresponding *P* values) in net photosynthesis (A_{net}) and stomatal conductance (g_s) measured on the target species in the control plots (B-T_A P_A and C-T_A P_A). For the C_3 and C_4 grasses *A. hymenoides* and *P. jamesii*, respectively, measurements were averaged across the B and C control plots, while measurements for the C_4 shrub *A. confertifolia* were averaged over the C control plots. Measurements were made in April, May, and June in 2011 and March, April, and May 2012. Percent change was calculated between months within a year and between the mean values of A_{net} and g_s between years

Species		2011				2012				2011–2012	
		April–May		May–June		March–April		April–May			
		% change	*P* value	% change	*P* value	% change	*P* value	% change	*P* value	% change	*P* value
A. confertifolia	A_{net}	−3.0	0.955	−40.5	0.107	**51.2**	**0.100**	**−57.6**	**0.013**	**56.1**	**0.065**
	g_s	**−52.1**	**0.023**	**−41.3**	**0.048**	**72.5**	**0.039**	**−71.9**	**<0.0001**	51.5	0.213
A. hymenoides	A_{net}	−10.1	0.270	**−63.9**	**<0.0001**	**−39.0**	**0.002**	2.7	0.836	**−56.9**	**<0.0001**
	g_s	−12.1	0.364	**−70.3**	**<0.0001**	**−24.5**	**0.004**	**−44.4**	**0.002**	**−64.3**	**<0.0001**
P. jamesii	A_{net}	10.2	0.367	**−58.4**	**<0.0001**	–	–	−8.1	0.927	**−70.6**	**<0.0001**
	g_s	−12.2	0.247	**−51.9**	**<0.0001**	–	–	**−23.4**	**0.005**	**−75.0**	**<0.0001**

P values in bold represent significant differences ($\alpha < 0.1$)

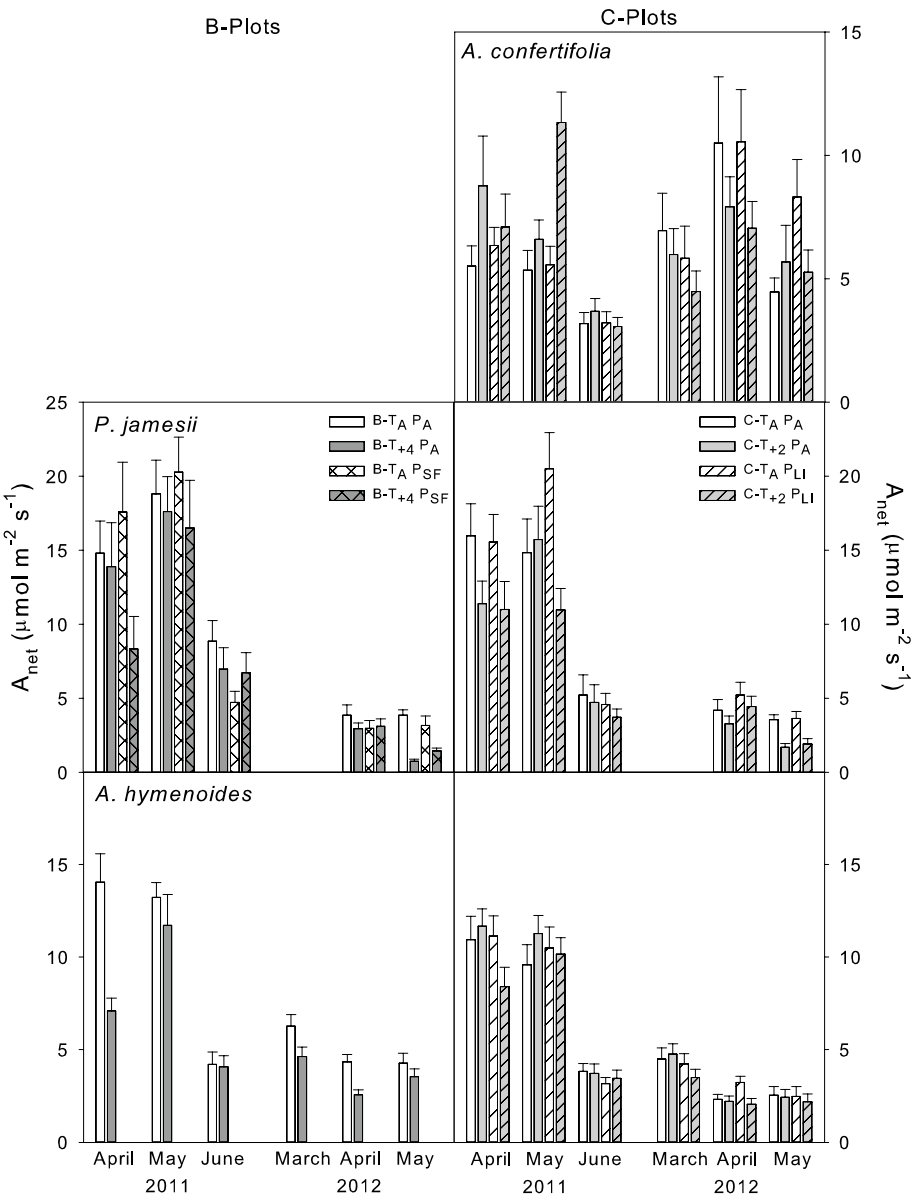

Fig. 3 Net photosynthesis (A_{net}, µmol CO_2 m^{-2} s^{-1}) of the three target species (*A. confertifolia*, *P. jamesii*, and *A. hymenoides*). Measurements were made three times during the growing season in 2011 and 2012. Significant differences between treatments are displayed in Table S5 of the ESM. The treatments are B-plots: ambient temperature and ambient precipitation (B-T_A P_A; *white*), elevated temperature (+4 °C) and ambient precipitation (B-T_{+4} P_A; *dark gray*), ambient temperature and elevated precipitation (+small frequent summer events) (B-T_A P_{SF}; *white with diagonal hashes*), and elevated temperature (+4 °C) and elevated precipitation (+small frequent summer events) (B-T_{+4} P_{SF}; *dark gray with diagonal hashes*); C-plots: ambient temperature and ambient precipitation (C-T_A P_A; *white*), elevated temperature (+2 °C) and ambient precipitation (C-T_{+2} P_A; *light gray*), ambient temperature and elevated precipitation (+large infrequent summer events) (C-T_A P_{LI}; *white with diagonal lines*), and elevated temperature (+2 °C) and elevated precipitation (+large infrequent summer events) (C-T_{+2} P_{LI}; *light gray with diagonal lines*)

we assessed measurements made on plants growing in the B and C control plots. Net photosynthesis (A_{net}) measurements in the control plots significantly varied over the course of each growing season, as well as between the 2011 and 2012 growing seasons, though the relationship differed among the three species. The deeply rooted C_4 shrub *A. confertifolia* was the least sensitive to seasonal temperature variation and inter-annual variation in precipitation (Fig. 3; Table 1). In both 2011 and 2012, A_{net} for this shrub significantly decreased from mid- to late-season measurements. Surprisingly, given the dry conditions in 2012, average A_{net} was actually 56 % higher in 2012 compared to 2011 ($P = 0.065$; Table 1). Stomatal conductance (g_s) of *A. confertifolia* followed a similar trend among measurement dates, but average g_s did not significantly vary from 2011 to 2012 (0.041 vs. 0.057 mol m^{-2} s^{-1}, $P = 0.213$) (Fig. 4; Table 1). Dark-acclimated foliar fluorescence (F_v/F_m) was significantly lower in 2012 compared to 2011 (0.82 vs. 0.76, $P = 0.001$; Table S4 of the ESM).

The C_3 grass *A. hymenoides* responded much more dramatically than *A. confertifolia* to within-season and inter-annual changes in climate, with A_{net} in the control plots consistently declining from the early season measurement to the late season measurement. Additionally, A_{net} was significantly lower in 2012, the drier year, compared to 2011, when growing season precipitation was close to historical values (3.9 vs. 9.1 µmol m^{-2} s^{-1} in 2010 and 2011, respectively, $P < 0.001$; Fig. 3; Table 1). In general, g_s of *A. hymenoides* responded similarly to A_{net}, with g_s declining with the same pattern and by similar amounts in both 2011 and

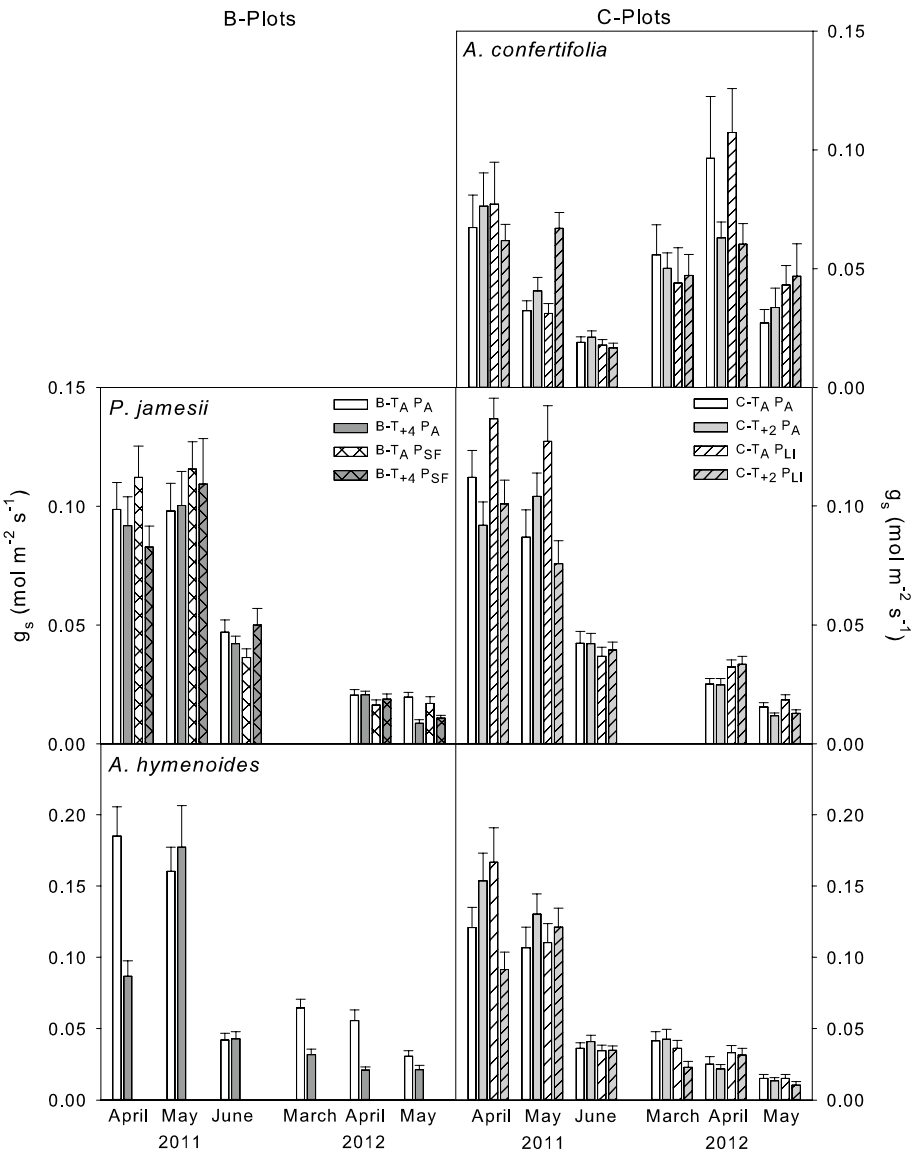

Fig. 4 Stomatal conductance (g_s, mol H_2O m^{-2} s^{-1}) of the three target species (*A. confertifolia*, *P. jamesii*, and *A. hymenoides*). Measurements were made three times during the growing season in 2011 and 2012. Significant differences between treatments are displayed in Table S5 of the ESM. The *treatment symbols* are defined in the legend for Fig. 3

2012 (Fig. 4; Table 1). Similar to *A. confertifolia*, dark-acclimated foliar fluorescence (F_v/F_m) was lower in 2012 compared to 2011 (0.81 vs. 0.84, $P = 0.086$; Table S4 of the ESM).

The phenological and physiological development of the C_4 grass *P. jamesii* was delayed by ~3 weeks compared to the C_3 grass *A. hymenoides* (data not shown). The delay in growth and A_{net} was especially clear in 2012, when *P. jamesii* was not physiologically mature enough to measure in March, likely attributable to the dry conditions, while the highest rates of A_{net} in *A. hymenoides* were observed during this period (Fig. 3; Table 1). The dry conditions of 2012 affected A_{net} of *P. jamesii* more than *A. hymenoides* (2011: 12.9 µmol m^{-2} s^{-1}; 2012: 3.8 µmol m^{-2} s^{-1}, $P < 0.001$). Like A_{net}, g_s of *P. jamesii* plants declined from the mid- to the late-season measurement dates in both years, though g_s declined more than A_{net} in the dry year of 2012 (Fig. 4; Table 1). Additionally, g_s was significantly lower in 2012 than 2011 (0.080 vs. 0.020 mol m^{-2} s^{-1}, $P < 0.001$). Similar to the other two species measured, measurements of F_v/F_m were significantly lower in 2012 compared to 2011 (0.73 vs 0.77, $P = 0.031$; Table S4 of the ESM).

Temperature treatment effects on leaf physiology

B-plots: soil surface temperature elevated by 4 °C

Only *A. hymenoides* and *P. jamesii* were present in enough numbers in plots receiving the highest temperature treatment to assess for physiological differences. The increase in growth temperature negatively affected A_{net} of both species, although the C_3 grass was affected to a greater extent than the C_4 grass (Fig. 3; Table S5 of the ESM). Averaged across all three measurement dates, A_{net} of *A. hymenoides*

was significantly lower in the elevated temperature plots in 2011 (10.4 vs 7.6 μmol m^{-2} s^{-1}, $P = 0.025$) and in 2012 (5.0 vs. 3.6 μmol m^{-2} s^{-1}, $P = 0.001$; Table S5 of the ESM). In 2011, this difference was driven by a 50 % reduction in A_{net} during the early-season measurements (14.0 vs. 7.1 μmol m^{-2} s^{-1}, $P < 0.001$). In 2012, A_{net} was lower in the elevated temperature plots for both early- and mid-season measurements (−26 %, $P = 0.07$; 49 %, $P < 0.001$, respectively). Stomatal conductance responded in very much the same pattern as A_{net}, with rates lower in the B-T_{+4} treatment in early-season measurements in 2011 and in all of 2012 compared to the B-T_A plots (Fig. 4; Table S5 of the ESM). Averaged across all measurement dates, g_s was significantly lower in 2012 (dry year) in the B-T_{+4} treatment compared to the B-T_A treatment (51 %, $P < 0.001$), but this was not the case in 2011, when spring precipitation totals were near normal. In 2011 and 2012, the B-T_{+4} treatment did not significantly affect F_v/F_m (0.89 and 0.79, respectively; Table S4 of the ESM).

In the C_4 grass *P. jamesii*, A_{net} was negatively affected by a +4 °C increase in temperature, although the effects were limited to 2012, when conditions were severely dry (Fig. 3; Table S5 of the ESM). In 2012, A_{net} measured during the later portion of the growing season was dramatically lower in the elevated temperature treatment (May: −80 %, $P < 0.001$) compared to the B-T_A treatment. Similarly, g_s was not affected by the elevated temperature treatment in 2011 or during the mid-season measurement date in 2012, but showed a large reduction in the elevated temperature plots during the late-season measurement date in 2012 (May: −56 %, $P < 0.001$) (Fig. 4; Table S5 of the ESM). There was no significant treatment effect on F_v/F_m in 2011 or 2012 ($P = 0.89$ and 0.79, respectively; Table S4 of the ESM).

C-plots: soil surface temperature elevated by 2 °C

All three species were present in the C-plots, which received a relatively moderate (+2 °C) increase in growth temperature. In line with the seasonal and inter-annual patterns discussed above, *A. confertifolia* was the species least sensitive to increased temperature. Neither A_{net} nor g_s were affected by the C-T_{+2} treatment at any measurement date (Figs. 3, 4; Table S5 of the ESM). There was also no significant treatment effect on *A. confertifolia* F_v/F_m at any single measurement date or when measurements were averaged across all dates in either 2011 or 2012 ($P > 0.5$ for all; Table S4 of the ESM).

While *A. hymenoides* A_{net} was significantly affected by a +4 °C increase in temperature, a +2 °C increase in growth temperature had no significant effect (Fig. 3; Table S5 of the ESM). In both the normal-precipitation year and the dry year, A_{net} values averaged across all measurement dates were similar between the control and elevated temperature plots (2011: 8.1 vs. 8.9 μmol m^{-2} s^{-1}, $P = 0.62$; 2012: 3.1 vs. 3.1 μmol m^{-2} s^{-1}, $P = 0.99$). Additionally, g_s of *A. hymenoides* was not affected by the elevated-temperature treatment at any measurement date in either 2011 or 2012 ($P > 0.17$ for all measurement date comparisons, Fig. 4; Table S5 of the ESM). There was no significant treatment effect on *A. hymenoides* F_v/F_m at any measurement date or when averaged across all measurement dates within a year ($P > 0.27$ for all comparisons; Table S4 of the ESM).

Finally, A_{net} of *P. jamesii* was affected by a +2 °C increase in temperature at one measurement time, the late-season measurement in 2012. On this date, the elevated temperature treatment reduced A_{net} of *P. jamesii* by 52 % (May, $P < 0.001$) (Table S5 of the ESM, Fig. 3). When A_{net} was averaged across all measurement dates, there was no difference between *P. jamesii* in elevated-temperature and control plots under the wet conditions of 2011 (−9 %, $P = 0.54$). However, under the dry conditions of 2012, A_{net} was lower in the elevated-temperature treatment compared to the control treatment (−52 %, $P = 0.02$). The elevated temperature treatment did not affect g_s on any measurement date at any time (Fig. 4; Table S5 of the ESM). There was no significant treatment effect on F_v/F_m at any measurement date or when measurements were averaged across all measurement dates within the year (Table S4 of the ESM).

Precipitation treatment effects on leaf physiology

B-plots: precipitation elevated by small frequent events

The precipitation manipulation in the B-plots was designed to simulate an increase in small summer rainfall events by applying a small amount of precipitation (1.2 mm) four times as frequently as the long-term average. Only *P. jamesii* was present in the B-plot precipitation (B-P_{SF}) plots in sufficient abundance to measure. In general, an increase in smaller, more frequent precipitation events had very little effect on *P. jamesii*. Averaged across all measurement dates, spring A_{net} was similar in the B-P_{SF} treatment compared to the control in 2011 (+0.4 %, $P = 0.61$). Averaged across all measurement dates, the g_s of *P. jamesii* did not differ between the B-P_{SF} plots and the control plots in 2011, but was significantly lower in the B-P_{SF} plots than in the B-P_A plots in the drier year of 2012 (2011: +10 %, $P = 0.81$; 2012: −17 %, $P = 0.08$) (Fig. 4; Table S5 in the ESM). The increased frequency of precipitation treatment did not have any effect on F_v/F_m on any measurement date or when averaged across all measurement dates within the year.

C-plots: precipitation elevated by large infrequent events

The precipitation treatment in the C-plots was applied to mimic an increase in infrequent but large summer monsoon

events. Compared to the control, the C-P_{LI} treatment had no consistent or significant effect on A_{net}, g_s, or F_v/F_m of *A. confertifolia* at any measurement date or when averaged across dates within a year (Fig. 3; Table S5 of the ESM). Similarly, this treatment had no significant effects on A_{net}, g_s, or F_v/F_m of *A. hymenoides* or *P. jamesii* on any measurement date or when averaged across dates within a year (Figs. 3, 4; Table S5 of the ESM), with one exception for each species. For *A. hymenoides*, A_{net} was 39 % and g_s was 31 % greater ($P = 0.04$ and 0.01, respectively) in the C-P_{LI} treatment compared to the control at the 2012 mid-season measurement time. For *P. jamesii*, A_{net} in the C-P_{LI} treatment was 38 % greater than in the control ($P = 0.07$) at the end of season in 2011, but at no other time. When g_s was averaged across all measurement dates, it tended to be higher in the watered treatment compared to the control in both 2011 (+27 %, $P = 0.12$) and 2012 (23 %, $P = 0.15$). *P. jamesii* F_v/F_m was not affected by the precipitation treatment.

Temperature and precipitation treatment effects on leaf physiology

B-plots: soil surface temperature elevated by 4 °C and precipitation elevated by small frequent events

Averaged across all measurement dates, A_{net} of *P. jamesii* was substantially lower in the combined elevated-temperature and large infrequent precipitation treatment (B-T_{+4} P_{SF}) compared to the controls in 2011 (−25 %, $P = 0.034$) and 2012 (−41 %, $P = 0.003$) (Fig. 3; Table S5 of the ESM). Despite the reduction in A_{net}, the g_s of *P. jamesii* did not significantly differ in the B-T_{+4} P_{SF} plots compared to the controls, with one exception: during the late-season measurement under the dry conditions of 2012, g_s was significantly lower in the treatment than the control plots (May, −45 %, $P = 0.04$) (Fig. 4; Table S5 of the ESM). The B-T_{+4} P_{SF} did not affect F_v/F_m, though there were two exceptions: during the early-season measurement in 2011, F_v/F_m tended to be higher in the B-T_{+4} P_{SF} compared to the control (+3 %, $P = 0.10$), and at the late-season measurement date in 2012, F_v/F_m was significantly lower in the treated plots (−9 %, $P = 0.019$). Averaged across all measurement dates, F_v/F_m was not significantly different between the B-T_{+4} P_{SF} treatment and the control in 2011 or 2012 (Table S4 of the ESM).

C-plots: soil surface temperature elevated by 2 °C and precipitation elevated by large infrequent events

The C-T_{+2} P_{LI} treatment did not have a consistent effect on A_{net} of *A. confertifolia* (Fig. 3; Table S5 of the ESM). During the mid-season measurement in 2011, A_{net} of *A. confertifolia* was more than doubled in the C-T_{+2} P_{LI} treatment compared to the control (May: 111 %, $P = 0.002$); however, in the proceeding and subsequent measurement dates, A_{net} was not significantly different (April: $P = 0.70$ and June: $P = 0.80$, respectively). Averaged across all measurement dates, A_{net} of *A. confertifolia* was significantly higher in the C-T_{+2} P_{LI} treatment compared to the control in 2011 (+55 %, $P = 0.02$) but not 2012 (−23 %, $P = 0.20$). Averaged across all measurement dates, g_s of *A. confertifolia* was not affected by the C-T_{+2} P_{LI} treatment in 2011 ($P = 0.44$) or 2012 ($P = 0.95$) (Fig. 4; Table S5 of the ESM). The C-T_{+2} P_{LI} treatment had a variable effect on F_v/F_m, with F_v/F_m of *A. confertifolia* tending to be lower in early-season measurements in 2011 (−5.4 %, $P = 0.13$) and 2012 (−4.7 %, $P = 0.12$), but higher at the mid-season measurement date in 2011 (+6.3 %, $P = 0.08$). When averaged over all measurement dates, F_v/F_m was marginally affected only in 2012 (−4.3 %, $P = 0.08$).

The C-T_{+2} P_{LI} treatment did not affect A_{net} of *A. hymenoides*, with one exception: A_{net} was 23 % lower in the 2011 early-season measurements (April: $P = 0.06$). Despite having a limited effect on A_{net}, the C-T_{+2} P_{LI} treatment reduced g_s of *A. hymenoides* in early- and late-season 2012 measurements (March: −45 %, $P = 0.007$; May: −30 %, $P = 0.12$) (Fig. 4; Table S5 of the ESM). At no measurement date was F_v/F_m affected by the C-T_{+2} P_{LI} treatment. While the C-T_{+2} P_A treatment had only a minor impact on A_{net} of *P. jamesii*, the C-T_{+2} P_{LI} treatment had a more of a negative effect (Fig. 3; Table S5 of the ESM). In 2011, A_{net} of *P. jamesii* was lower during the early-season measurement (April 2011: −31 %, $P = 0.056$). In 2012, A_{net} of *P. jamesii* was lower at the late-season measurement (−45 %, $P = 0.003$), but not the mid-season measurement (+5 %, $P = 0.67$). g_s of *P. jamesii* was not affected by the C-T_{+2} P_{LI} treatment (2011: −10 %, $P = 0.46$; 2012: +12 %, $P = 0.94$), and there was no significant treatment effect on F_v/F_m at any measurement date.

Biomass

For all species tracked in this study, total biomass decreased from 2010 through 2012 (Fig. 5). For the grass species (*A. hymenoides* and *P. jamesii*), this decline occurred because the plants are winter deciduous and less biomass was added in the springtime. For the woody shrub (*A. confertifolia*), a decrease in biomass was achieved through localized necrotic events within individual plants. For all three species, biomass was not correlated with total annual precipitation from the previous year, nor with average monthly precipitation from the preceding winter (September through January; Fig. 6). Rather, biomass was correlated with current year growing-season precipitation (averaged from March through June; Fig. 6). Biomass accumulation

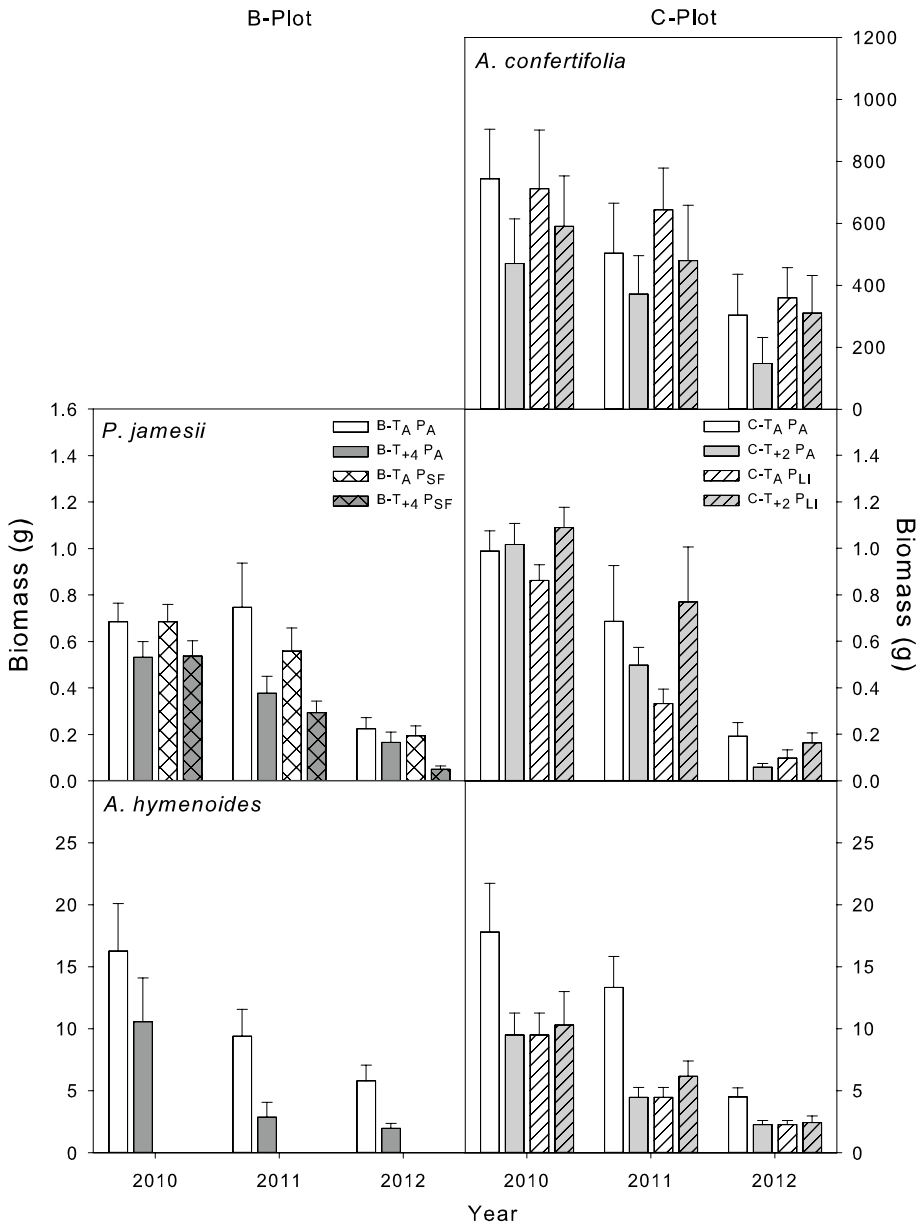

Fig. 5 Aboveground plant biomass (g) of the three target species (*A. confertifolia*, *P. jamesii*, and *A. hymenoides*). Measurements were made at the end of the growing season in 2010, 2011, and 2012. The *treatment symbols* are defined in the legend for Fig. 3

was not correlated with mean temperature for the previous year, the previous winter, or the growing season (data not shown).

In *A. confertifolia*, there was no significant treatment effect on biomass in either year (Fig. 5). Total biomass averaged across all treatments did not significantly change from 2010 to 2011 (−21 %, $P = 0.29$), but did significantly decrease from 2011 to 2012 (−43 %, $P < 0.001$). For *A. hymenoides*, plants in the B-T_{+4} plots tended to be smaller than plants in the B-T_A plots, though the difference was not significant ($P = 0.16$). In contrast, plants grown in the C-T_{+2} P_A, C-T_A P_{LI}, and C-T_{+2} P_{LI} treatments were significantly smaller than the control in 2010 (−49 %, $P = 0.003$; −43 %, $P = 0.004$; and −45 %, $P = 0.003$; respectively) and 2011 (−68 %, $P < 0.001$; −53 %, $P = 0.002$; and −50 %, $P = 0.005$; respectively). In 2012, because plants in the C-T_A P_A were smaller (likely due to continuing drought conditions), this effect diminished (−49 %, $P = 0.10$; −46 %, $P = 0.021$; and −52 %, $P = 0.068$; respectively). There was no significant difference in biomass among the three treatments (C-T_{+2} P_A vs. C-T_A P_{LI} vs. C-T_{+2} P_{LI}) in any year ($P > 0.3$ for all comparisons). Biomass of *A. hymenoides* averaged across all treatments declined by 38 % from 2010 to 2011 and by 60 % from 2011 to 2012 ($P < 0.001$ for both comparisons) (Fig. 5).

In 2010, biomass of *P. jamesii* was not significantly different among the four B-plot treatments ($P > 0.3$ for all comparisons). However, in 2011, the biomasses of the plants growing in the B-T_{+4} P_A and B-T_{+4} P_{SF} treatments were significantly smaller than that of the plants grown

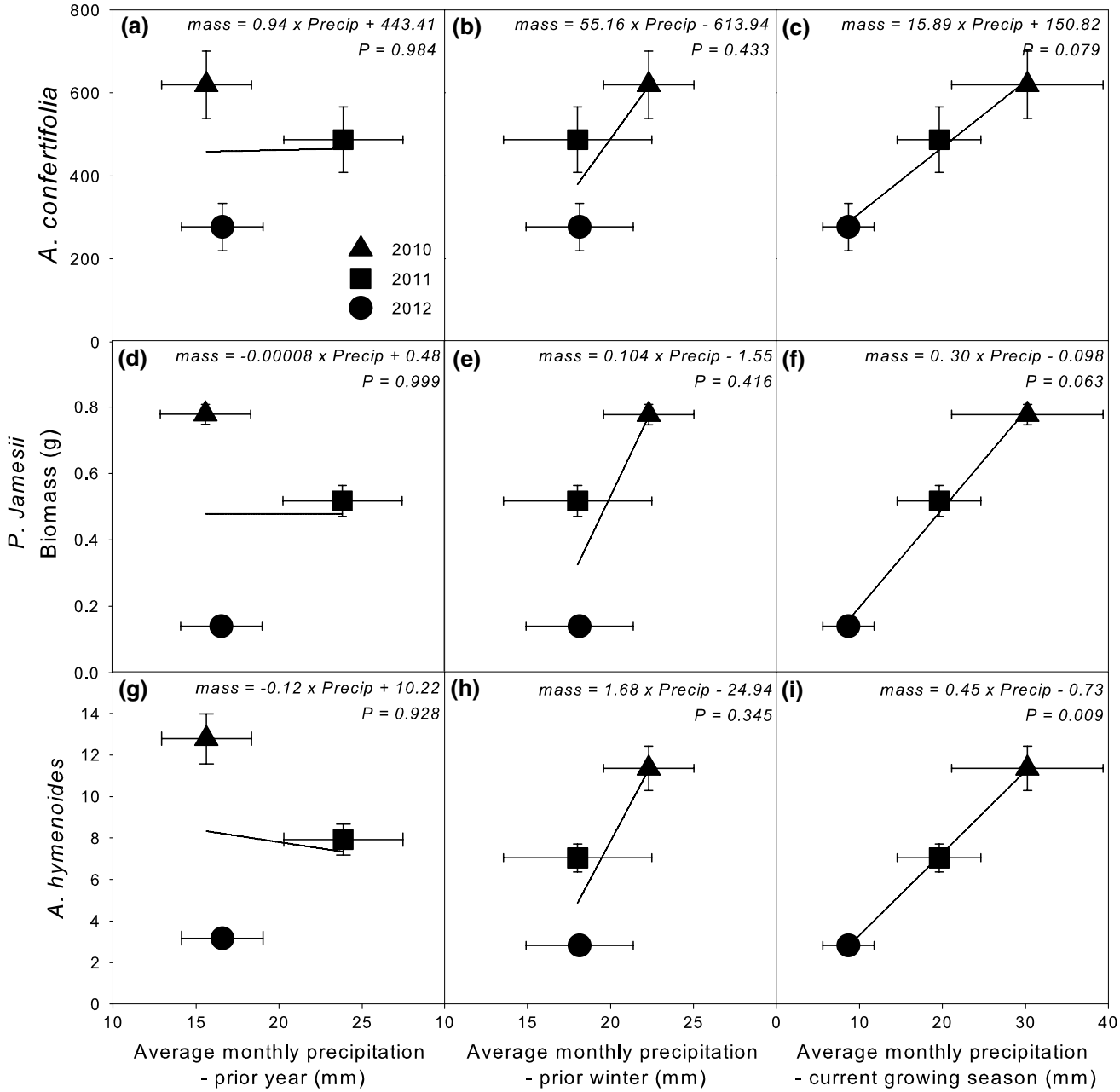

Fig. 6 Relationship between biomass of **a–c** *A. confertifolia*, **d–f** *P. jamesii*, or **g–i** *A. hymenoides* and the prior year's average monthly precipitation, the prior winter's average monthly precipitation (September–January), and the average monthly precipitation of the measurement year's growing season (March through June). 2010 data are shown as *triangles*, 2011 data as *squares*, and 2012 as *circles*. *Error bars* represent 1 SEM

in the B-T_A P_A treatment (−48 %, $P = 0.013$; −60 %, $P < 0.001$; respectively). In 2012, the biomass of *P. jamesii* was still significantly smaller in plants from the B-T_{+4} P_{SF} (−78 %, $P = 0.007$) but not the B-T_{+4} P_A (−26 %, $P = 0.28$) treatment as compared to the B-T_A P_A treatment. The B-T_A P_{SF} treatment did not affect biomass relative to the B-T_A P_A treatment in any year. In 2010, there was no difference in biomass between the four treatments in the C-plots ($P > 0.22$). In 2011, the biomass of plants in the C-T_{+2} P_{LI} treatment was lower than the biomass of plants growing in the C-T_A P_A treatment (−51 %, $P = 0.091$). In 2012, the biomasses in the C-T_{+2} P_A and C-T_{+2} P_{LI} treatments were significantly smaller than the biomass in the C-T_A P_A treatment (−69 %, $P = 0.042$ and −49 %, $P = 0.075$, respectively). Biomass averaged across all B-plot and C-plot treatments declined by 33 % from 2010

to 2011 and by 73 % from 2011 to 2012 ($P < 0.001$ for both comparisons).

Discussion

Plant responses to inter-annual variation in temperature and precipitation

Plant production in this dryland community was more strongly regulated by inter-annual fluctuations in precipitation than by any of the experimental climate manipulations imposed in the study. In particular, aboveground biomass accumulation for our three target species—which included a shallow-rooted C_3 perennial bunch grass, a shallow-rooted C_4 perennial rhizomatic grass, and a deep-rooted C_4 evergreen shrub—was strongly correlated with the amount of precipitation occurring during that year's active growing season (March through May), and not with total annual precipitation, precipitation in the preceding winter, or precipitation in the previous year (Fig. 6). This is in contrast to results from some other dryland ecosystems, where winter precipitation is considered a central driver of biomass production (e.g., Beatley 1974; Muldavin et al. 2008) or where legacies from the previous year's precipitation play a large role in regulating plant growth (e.g., Wu et al. 2012; Sala et al. 2012). During the measurement period at our study site, annual precipitation was lower than all but one of the sites utilized by the Sala et al. (2012), and our data add to the meta-analysis results by suggesting that the correlation between biomass production and previous year's precipitation may be completely absent in more arid ecosystems (Fig. 6). Indeed, while drylands are all considered moisture limited, there is some debate regarding the effects of precipitation timing (Fay et al. 2003; Guo et al. 2012) and frequency (Heisler-White et al. 2008; Thomey et al. 2011) on net primary production. Our findings reinforce the supposition that, as annual precipitation totals decline, the timing of precipitation becomes more important.

It was somewhat surprising that all three target species showed such similar relationships between precipitation and aboveground biomass accumulation both within and among years, as the plants have notably distinct functional traits related to water use. Indeed, even within the C_3 functional group, data from a manipulative study in an inner Mongolian grassland (MAT: 0.92 °C, MAP: 337 mm) suggested significant variability between rhizomatic and bunch grasses in their biomass accumulation responses to varied precipitation patterns (Liu et al. 2012). Yet we observed that neither the increased WUE of the C_4 photosynthetic pathway nor the differences in rooting depth mitigated plant-growth reductions in response to the natural precipitation declines that occurred between 2010 and 2012 (C_4 grass *P. jamesii*: 75 % reduction; C_4 shrub *A. confertifolia*: 59 % reduction; C_3 grass *A. hymenoides*: 67 % reduction). The growth of all three species dramatically declined in concert among years (Figs. 5, 6).

A point of interest was the decoupling of A_{net} and aboveground biomass accumulation observed in the C_4 shrub *A. confertifolia*. For both grass species in this study (*A. hymenoides* and *P. jamesii*), patterns between A_{net} and biomass appeared closely coupled, as reported for other grass species (e.g., Pearcy et al. 1981; Fernández and Reynolds 2000). Like the grasses, biomass accumulation patterns in *A. confertifolia* showed reduced growth in the drier years, but A_{net} of *A. confertifolia* did not respond in the same way to variation in precipitation and actually increased from 2011 to 2012, despite strong declines in growing season precipitation. It is likely that this deep-rooted shrub can access water unavailable to the shallower-rooted grasses, and thus a lack of response in A_{net} is not unexpected. However, the increase in A_{net} did not translate into increases in aboveground biomass accumulation for the shrub. Photosynthesis is more sensitive to short-term environmental fluctuations than biomass accumulation, and it is possible that measurements of A_{net} for *A. confertifolia* were conducted on days where rates were higher due to unusually favorable conditions, which were not frequent and/or long enough to stimulate additional growth. If so, these conditions were not equally favorable for the shallower-rooted grasses, as A_{net} was measured concurrently for all three species and on representative days. High shrub CO_2 losses via night-time respiration and/or selective branch mortality (allowing for the maintenance of higher A_{net} in the remaining foliage) could also explain the pattern and, taken as a whole, the data propose several interesting lines of inquiry that should be further explored. Regardless of the cause, the decoupling between photosynthesis and growth is a pattern observed in multiple ecosystems (e.g., Luo et al. 1997), and different trajectories of photosynthesis and growth have significant implications for model predictions of ecosystem carbon balance, plant survival, and community composition.

Manipulative treatments

Elevated temperature

We hypothesized that an increase in growth temperature would increase photosynthesis during the cooler portion of the growing season, when soil moisture is less limiting, and would have no effect on photosynthesis during the warmer portion of the growing season, when low soil moisture likely already limits growth. Overall, we predicted that increasing temperatures would result in a net increase in photosynthesis and plant growth in this cool desert, as has

been observed in drylands elsewhere (e.g., Morgan et al. 2011). In contrast to our hypothesis, the elevated temperature treatments reduced photosynthesis and aboveground biomass for both the C_3 and C_4 grasses, and the negative response to increased temperature depended on the magnitude of the warming (2 vs. 4 °C), the soil moisture content during the growing season (which varied strongly across years), and plant functional type. An increase in temperature can directly negatively affect plant physiology, for example by increasing photorespiration relative to photosynthesis or through damage to enzymes and membranes in the photosynthetic pathway. Increased temperature can also have indirect effects via increased VPD and soil drying, and the IR methods of warming used in this study can exacerbate such indirect effects (De Boeck et al. 2012). For example, an elevated temperature and [CO_2] manipulation experiment in a Wyoming dryland saw significant soil drying with IR warming treatments; however, even with the associated drying, the increased temperature treatments resulted in increased growth of C_4 grasses and no effect on C_3 grasses (Morgan et al. 2011). While our C_3 and C_4 grasses responded negatively to increased temperature, because the IR warming treatments not only warmed plants and soils but also dried soils (Fig. 2), partitioning the direct effect of increased temperature from the indirect effect of drying is a complex task. However, because we measured photosynthesis multiple times throughout the growing season, within-growing season patterns in photosynthetic response lend insight into the controls.

The response of photosynthesis to an increase in temperature varied among the three species measured. For the deep-rooted C_4 shrub, there was no effect of increased temperature on photosynthesis or growth, which may be due to the fact that either photosynthesis was insensitive to high temperatures or access to deep soil moisture aided in alleviating moisture stress. In contrast, the ambient +4 °C increased-temperature treatment negatively affected the photosynthesis of *A. hymenoides* (the C_3 grass) early in the growing season (Fig. 3), when temperatures were relatively low and immediately following the time when the soil-drying effect of increased temperature was relatively pronounced (Fig. 2). These reductions in A_{net} are likely driven by the observed reduction in g_s (Fig. 4), resulting in a decrease in photosynthesis and an increase in photorespiration. Thus, the data suggest the potential for warming-induced soil drying to help explain the reduction in photosynthesis. That said, soil moisture did not vary significantly between the ambient and elevated-temperature plots in April 2011, March 2012, or April 2012 measurement times (Fig. 2d), and the reduction in g_s may also be attributed to an increase in VPD and/or increased foliar temperature negatively affecting leaf water potential. We did not observe similar trends in *A. hymenoides* of the +2 °C elevated-temperature plots or in the other species exposed to +4 °C elevated temperature in this time period. The spring reduction in A_{net} with an increase in temperature contrasts with our hypothesis and suggests that even when temperatures are relatively low, an increase in temperature in this community may negatively affect photosynthesis. While we cannot quantitatively partition the direct role of temperature from the indirect role of drying, the data suggest that even early in the growing season, the increased temperatures and soil drying (both of which are expected for the Southwestern USA; Garfin et al. 2014) could negatively affect the photosynthesis of this C_3 grass.

In contrast to the temporal patterns observed for *A. hymenoides*, temperature increases of both +2 and +4 °C negatively affected photosynthetic rates of the C_4 grass *P. jamesii* only at the end of the growing season during a very dry year (Figs. 2, 3). At that time, high air temperatures coincided with the lowest soil moisture values observed (Fig. 2), resulting in very low g_s values and very high foliar temperatures (likely due to the limited potential for evaporative cooling; Figs. 2, 4). Indeed, *P. jamesii* foliar temperatures during June 2012 reached 58.5 °C (compared to 51.4 °C in control plots), and dramatic reductions in C_4 photosynthesis when temperatures become supra-optimum have been well documented (e.g., Yamori et al. 2014). Further, we did not observe significantly lower g_s values in the elevated-temperature plots relative to control plots; nor was soil moisture significantly different between the elevated and ambient temperature plots for either May or June 2012. Thus, while the low soil moisture values likely contributed to the high foliar temperatures, the data suggest strong direct treatment effects of temperature on C_4 photosynthesis at this measurement time.

Increasing warming and drying are predicted to occur simultaneously in the Southwestern USA, and the plant and soil temperatures and soil moistures achieved in this experiment are within the range predicted for the Colorado Plateau by 2100 (Garfin et al. 2014). Our data suggest that some grasses in these ecosystems will respond negatively to predicted changes in climate. Indeed, although patterns in treatment effects varied among the species investigated in this study, we never saw any sign of warming-induced increases to photosynthesis or growth for any species. A long-term monitoring study in the same region showed that increased air temperatures for the previous 25 years (with an ~2 °C increase in temperature) were significantly correlated with reductions in C_3 perennial grass cover (dominated by *Achnatherum* spp.) (Schlenker and Roberts 2009; Muller et al. 2011; Munson et al. 2011). The data shown here provide a physiological mechanism for the observed decline and, taken together, the observational and experimental studies suggest that consistent reductions in A_{net} and aboveground growth for a common C_3 grass are causing,

and will continue to cause, a decline in C_3 abundance on the Colorado Plateau. Although less consistent, we also observed reductions in photosynthesis and biomass growth for the C_4 grass *P. jamesii*, suggesting that expected higher photosynthetic temperature thresholds and WUE were not enough to counter the effects of manipulated climate in all years, and in no years did they result in a benefit to the plants.

These are the first data of which we are aware outside of the tropics that suggest significant reductions in plant photosynthesis and growth with a manipulative increase in temperature. As discussed above, our findings are in contrast to the dryland warming study conducted in Wyoming, where increased temperature resulted in increased growth of the C_4 grasses and no effect on C_3 grasses (Morgan et al. 2011). A multifactorial study conducted in a dryland plant community in central California, USA showed a 1 °C increase in temperature to have no effect on grass biomass accumulation (Zavaleta et al. 2003), and a dryland grass community in northern Arizona, USA showed that increases in growth temperature (+2 to +6 °C, achieved by transporting microcosms along an elevation gradient) increased grass biomass production (Wu et al. 2012). Taken together, the results seen here are worrisome, as C_3 grasses (including *A. hymenoides*) are a keystone functional group in Colorado Plateau ecosystems and represent a significant food source for a host of native species, as well as for domestic livestock. The effect of increasing temperature on plant productivity and community composition could have serious implications for the region, implications that span ecological, economic, and social realms.

Elevated precipitation

Based on the important role that soil moisture plays in regulating dryland function, the universal lack of precipitation treatment effects on vascular plants was surprising, and likely resulted from the timing and the size of the precipitation manipulations and from the low monsoon precipitation totals in our measurement years. In conjunction with summer monsoon seasons that were relatively mild, we may not have applied enough water during each event to significantly affect plant performance. Plants on the Colorado Plateau and in some other dryland ecosystems often have a bimodal growth pattern: while a growth period always occurs with spring rains, a second period can occur if late summer (mid-July through September) monsoon rains are of a sufficient quantity (Schwinning et al. 2005). Late summer green up has been observed in all perennial grass species found on the Colorado Plateau, including *A. hymenoides* and *P. jamesii* at our study site, and has been well documented in *Stipa tenacissima* in Spain (Pugnaire et al. 1996). During 2011 and 2012, however, no second monsoon season growth period occurred, likely due to below-average summer precipitation and above-average temperatures during late summer. Had a second growth period occurred, it is possible that the additional water provided by our elevated precipitation treatments would have increased late season A_{net} and resulted in a positive change in aboveground biomass. In addition, we found that the larger, infrequent precipitation events (which were applied during the day) infiltrated less than 10 cm into the soil (data not shown); thus, much of the added water may have been lost to evaporation prior to plant access. The soil water-holding capacity at this site is also extremely low, reflected by the low soil VWCs (Fig. 2), and this reduces the amount of water that could be stored between events and thus the overall effect of an event. Accordingly, while our results suggest that the increases in monsoonal precipitation we applied have no effect on aboveground biomass growth, effects would need to be assessed in years where monsoonal green up and growth occur in order to garner a true understanding of the precipitation control.

Conclusions

The patterns observed here suggest that, in this relatively arid dryland, growing-season precipitation dominates control over patterns in plant growth for the three species studied, each representing a different plant functional type: the C_3 grass *A. hymenoides*, the C_4 grass *P. jamesii*, and the C_4 shrub *A. confertifolia*. In addition, we observed that increased temperature treatments negatively affected the net photosynthesis and biomass growth of *A. hymenoides* and, when precipitation was substantially lower than historical values, *P. jamesii*. These are among the first data of which we are aware that show significant reductions in plant photosynthesis and growth with an increase in temperature in any ecosystem. They are also some of the first to show that, although a common assumption is that C_4 grasses as a group will respond positively to a warming climate, the C_4 grass studied in this cool desert responded negatively to increased temperature. The multi-faceted interactions between the direct effects of increased growth temperature and the indirect effects of soil drying remain unresolved, but these data point to a detailed assessment of climate effects in the growing season as an important focus. While only a single species from each functional type was investigated at a single site, our findings suggest that population versus community responses to climate change will depend on the type of change and will not be universal.

Author contribution statement JB designed the manipulation experiment; JB, SCR, and TMW designed the research questions; TMW performed the measurements,

analyzed the data, and wrote the first draft of the manuscript; and all authors contributed significantly to data interpretation and final revisions of the manuscript.

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