Received: 14 January 2017 | Revised: 21 May 2017 | Accepted: 6 June 2017
DOI: 10.1002/eco.1880

WILEY

**RESEARCH ARTICLE**

# Seasonally contrasting responses of evapotranspiration to warming and elevated $CO_2$ in a semiarid grassland

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**Funding information**
Biological and Environmental Research, Grant/Award Number: DE-SC0006973; Division of Environmental Biology, Grant/Award Number: 1021559; National Science Foundation, Grant/Award Number: DEB#1021559; Terrestrial Ecosystem Science program, Grant/Award Number: #DE-SC0006973

## Abstract

Global climate change is expected to alter seasonal patterns and rates of evapotranspiration in dry regions. Although climate change will involve elevated $CO_2$ and increased temperatures, independently, these factors may have different impacts on actual evapotranspiration (AET) due to their opposing effects on transpiration. We used canopy gas exchange chambers to quantify AET in a semiarid grassland experimentally altered by elevated $CO_2$ and warming over 3 years with contrasting ambient precipitation. Seasonal and interannual variations in AET due to background climate variability were larger than the effects of climate manipulation treatments. However, in a year with average precipitation, cumulative growing season AET was suppressed by warming by 23%. Across years, warming increased AET early in the growing season and suppressed it later in the growing season. By contrast, elevated $CO_2$ suppressed AET early in the growing season and enhanced it later, but only in years with average or above-average precipitation. Vegetation greenness (a proxy for photosynthetically active leaf area) was consistently the strongest predictor of AET, whereas soil moisture and vapor pressure deficit were secondary drivers. Our research demonstrates that effects of increased atmospheric $CO_2$ and temperature on AET will be mediated by plant phenological development and seasonal climatic conditions.

**KEYWORDS**

climate change, evapotranspiration, greenness, phenology, semiarid grasslands, soil moisture

## 1 | INTRODUCTION

Semiarid grasslands and rangelands cover more than 25% of the earth's terrestrial surface and provide important ecosystem services such as forage for livestock (Asner, Elmore, Olander, Martin, & Harris, 2004; Suttie, Reynold, & Batello, 2005). Models predict that climate change will be associated with more atmospheric evaporative demand and increase the frequency and severity of drought in semiarid ecosystems (Easterling et al., 2000; Woodhouse, Meko, MacDonald, Stahle, & Cooke, 2010). Episodic rain events and long periods of drought are characteristics of semiarid grassland, where productivity is primarily limited by water (Lauenroth & Bradford, 2009; Lauenroth & Sala, 1992). Consequently, increased evaporative demand associated with climate change may threaten the capacity of these grasslands to support domestic livestock and biological diversity (Asner et al., 2004; Volk, Niklaus, & Korner, 2000). However, grassland productivity could also increase with warming, despite increased aridity, as the phenology of growth shifts toward earlier spring greening (Hufkens et al., 2016).

Evapotranspiration (ET) integrates feedbacks between vegetation and climate, with broader impacts on overall ecosystem water cycling (Gerten et al., 2008; Law et al., 2002). ET is closely related to primary productivity (Field, Jackson, & Mooney, 1995; Law et al., 2002), soil respiration (Raich & Schlesinger, 1992), biogeochemical cycling (Pastor & Post, 1986; Pielke et al., 1998), and partitioning of precipitation between runoff and storage (Felzer et al., 2011). Although potential ET (PET) depends on meteorological factors such as radiation and vapor pressure deficit ($D_v$), actual ET (AET) is mediated through stomatal conductance, and transpiration becomes the dominant path of water loss as plant cover increases (Ferretti et al., 2003; Wang et al., 2010; Wythers, Lauenroth, & Paruelo, 1999).

The effects of climate change on AET are driven by feedbacks between meteorological and plant physiological factors. Two features of global climate change—elevated atmospheric $CO_2$ and increased temperatures—independently may have contrasting impacts on AET (Korner, 2000), but also may exhibit complex interactions. Although elevated $CO_2$ ($eCO_2$) and warming may independently lead to reduced transpiration, warming may also lead to increased evaporation when plant cover is low (Morgan, Hunt, Monz, & LeCain, 1994; Morgan et al., 2011; Morgan et al., 2004; Wullschleger, Tschaplinski, & Norby, 2002). Alternatively, when temperatures are favorable and water is not

https://doi.org/10.1002/eco.1880

limited, warming may instead lead to increased transpiration as $D_v$ increases (Berry & Bjorkman, 1980; Morison & Gifford, 1983). Thus, the magnitude and direction of these effects are likely to depend on plant cover and soil moisture, which vary throughout the growing season (Gray et al., 2016; Zelikova et al., 2015). This seasonal variation is particularly strong in the semiarid grasslands of southeastern Wyoming (Bachman et al., 2010; Lauenroth & Bradford, 2009), where soil moisture is the highest early in the growing season followed by progressive drying during summer and autumn (Blumenthal et al., in press; Kurc & Small, 2007).

Given the contrasting effects of $eCO_2$ and warming on plant cover, evaporation and transpiration, the response of the water cycle to climate change in grasslands is difficult to predict (Morgan et al., 2004; Wullschleger et al., 2002; Zavaleta et al., 2003). Therefore, we assessed the effects of $eCO_2$ and temperature on AET at the Prairie Heating and Elevated $CO_2$ Enrichment (PHACE) experiment in southeastern Wyoming, USA, where future climate conditions altered soil moisture and nutrient availability, increased productivity, and lengthened growing seasons (Morgan et al., 2011; Mueller et al., 2016; Reyes-Fox et al., 2014). A secondary objective was to understand the potential of soil moisture, canopy temperature, $D_v$, and canopy cover to predict AET. Because seasonal and interannual climate variation can have large impacts on AET, we considered treatment effects on AET both intra-seasonally and among 3 years with contrasting precipitation. We expected that effects of $eCO_2$ and warming on AET would vary during the growing season. Early in the growing season, when AET is energy limited, we expected warming to increase AET. Later in the growing season, when AET is increasingly moisture limited, we expected $eCO_2$ to mitigate reductions in plant activity, leading to enhanced AET relative to ambient conditions. Overall, we expected soil moisture to exert the strongest independent control on AET.

## 2 | METHODS

The PHACE experiment was located at the United States Department of Agriculture Agricultural Research Service High Plains Grassland Research Station located about 15 km west of Cheyenne, Wyoming (latitude 41°11′ N, longitude 104°54′ W). This ecosystem is a high-elevation (1,930 m) native northern mixed-grass prairie dominated by the $C_4$ grass *Bouteloua gracilis* and two $C_3$ grasses *Hesperostipa comata* and *Pascopyrum smithii*. Soils are in the Mollisol order (fine-loamy, mesic Aridic Argiustoll, mixed Ascalon, and Altvan series) with 62% sand, 23% silt, and 15% clay. The 30-year mean annual precipitation near the site in Cheyenne, WY, was 397 mm, and mean annual temperature was 8 °C (1984–2013; Mueller et al., 2016).

The PHACE experimental infrastructure consists of 20, 3.4-m-diameter rings (experimental plots) that are subject to two atmospheric $CO_2$ concentrations (ambient and 600 ppm) and two temperature levels (ambient and 1.5/3.0 °C above ambient during day/night) in a factorial design with five replicates. Free-air $CO_2$ enrichment technology is used to elevate $CO_2$ concentration during the daylight hours of the growing season, whereas ceramic infrared heaters are used to raise canopy temperatures around the clock during the entire year (Kimball et al., 2008; Miglietta et al., 2001). The treatments are abbreviated as follows: ct (ambient $CO_2$ and ambient temperature), cT (ambient $CO_2$ and warmed temperature), Ct ($eCO_2$ and ambient temperature), and CT ($eCO_2$ and warmed temperature). Experimental plots were isolated from surrounding soil by plastic flanges buried to 60 cm. Volumetric soil moisture (Sentek Envirosmart sensors, Sentek Sensor Technologies, Stepney, SA, Australia) at soil depth of 5–15 cm and air temperature (20 cm height) were continuously recorded in the plots. Site climate parameters, including air temperature, precipitation, and photosynthetically active radiation, were recorded by a HOBO meteorological station located at the site. Detailed information about the experiment and treatment performance has been reported elsewhere (Bachman et al., 2010; Morgan et al., 2011).

Ecosystem gas exchange measurements of $H_2O$ and $CO_2$ were collected during most seasons of the 7-year PHACE experiment (Bachman et al., 2010; Pendall et al., 2013). AET measurements were obtained by placing a static gas exchange chamber onto a 0.2-m$^2$ square aluminum base for a period of 2 min in each plot. The chamber system contains a fast-response open-path infrared gas analyzer (LI-7500, LI-COR Inc., Lincoln, NE) mounted inside a clear acrylic chamber that enables measurement of $H_2O$ fluxes within less than 1 min of chamber closure. $H_2O$ concentrations were recorded at 1 Hz between 15 and 45 s after chamber closure. During chamber closure, air temperature inside the chamber was monitored and changed by less than 2 °C/min.

Data quality checks were performed to ensure that the slope of $H_2O$ concentrations over time was increasing linearly. AET (mmol $H_2O$ $m^{-2}\cdot s^{-1}$) was calculated by Equation 1 where $d[H_2O]/dt$ ($mmol\cdot m^{-2}\cdot s^{-1}$) is the changing $H_2O$ concentration during 30 s of measurement, $P$ is air pressure (kPa), $T$ is air temperature (°C), $V$ is chamber volume (m$^3$), $A$ is chamber area (m$^2$), and $W_i$ is initial $H_2O$ (mmol/mol) concentration. Vapor pressure deficit ($D_v$) values in the chamber were calculated by Equation 2.

$$\mathrm{AET} = \frac{\frac{d[\mathrm{H_2O}]}{dt} \times P \times V \times (1000 - Wi)}{8.314 \times A \times (T + 273)}. \tag{1}$$

$$Dv = 0.611^{\frac{17.27 \times T}{(T+273.3)-[\mathrm{H_2O}]}}. \tag{2}$$

During nine sampling campaigns in 2009 and 2010 and seven campaigns in 2012, AET measurements were conducted at midday (11:00 a.m.–2:00 p.m.) during the growing season, between May and October (day of year [DOY] 121–274), under sunny, stable weather conditions. Photosynthetic photon flux density was generally between 1,200 and 2,000 $\mu mol\cdot m^{-2}\cdot s^{-1}$, except on June 3, 2010, when photosynthetic photon flux density was 920 $\mu mol\cdot m^{-2}\cdot s^{-1}$. These midday measurements were coupled with diurnal campaigns on four dates during each growing season when AET was measured 3 times during the day: in the morning (7:00 a.m.–10:00 a.m.), midday, and evening (3:00 p.m.–6:00 p.m.). Cumulative AET over the daytime period (mm per daytime) was estimated by plotting AET values versus the three diurnal time points on each date and integrating the area under the curve using the *trapz* command for trapezoidal numerical integration (MATLAB 7.10.0, The MathWorks Inc., Natick, MA, 2010).

Percentage of green vegetation (greenness) in each plot was measured with time series repeat photography and quantification of

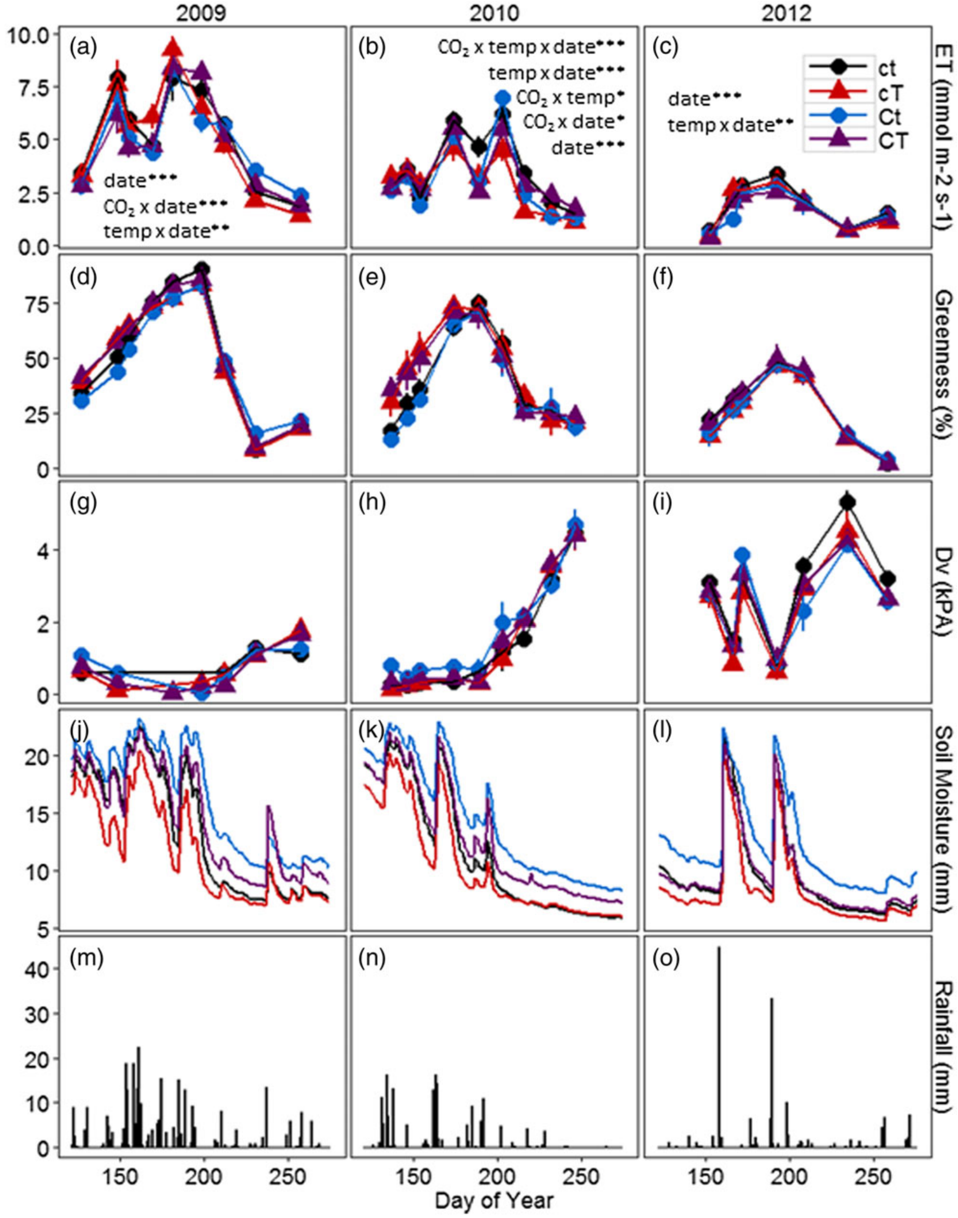

**FIGURE 1** (a–c) Average midday actual evapotranspiration (ET; mmol·m$^{-2}$·s$^{-1}$) for each treatment on each date actual evapotranspiration (AET) was measured during the growing season. Significant effects of CO$_2$, temperature, and date, as well as their interactions, are based on repeated measures analysis of variance (ANOVA), designated by symbols *** for $p < .001$, ** for $p < .01$, and * for $p < .05$ (Table 2). Because we found significant date by climate treatment interactions, we applied two-way ANOVA and Tukey's honestly significant difference test (α = .05) to indicate treatment effects at each date (for full ANOVA results, see Table 2, and for means separations, see Table S1). Treatment abbreviations are as follows: ct (ambient CO$_2$ + ambient temperature), cT (ambient CO$_2$ + warming), Ct (elevated CO$_2$ + ambient temperature), and CT (elevated CO$_2$ + warming). Error bars are ±1 *SE*. (d–f) Estimated average greenness (%) for each treatment on dates that AET was measured. Greenness was estimated by linear interpolation of greenness data measured from repeated digital photographs to correspond with dates that AET was measured. Error bars are ±1 *SE*. (g–i) Average midday treatment level vapor pressure deficit ($D_v$; kPa), calculated based on plot-level canopy temperature. (j–l) Average daily treatment level soil moisture (mm) at 5–15 cm below the surface for each treatment during the growing season. (m–o) Daily growing season precipitation during the 3 years (2009, 2010, and 2012) analyzed in this experiment

greenness in digital photographs (Zelikova et al., 2015). We included this greenness measurement as a proxy of phenological activity, which is directly linked to plant canopy gas exchange (Kurc & Benton, 2010). To measure greenness, pixel values were converted to a hue, saturation, and value scale, where boundaries were selected to define a range of hue, saturation, and value vales for "green" (Zelikova et al., 2015). Repeat photographs were taken during each growing season since 2006 on seven to 13 dates. To estimate greenness on the dates that AET was measured (which did not always correspond to the dates that photographs were taken), we used the *interp1* command for linear interpolation between 2 points (MATLAB 7.10.0, The MathWorks Inc., Natick, MA, 2010).

## 2.1 | Analyses

A simple linear regression analysis revealed a strong relationship between diurnal and midday AET measurements ($r^2$ = .97, $p < .001$). This allowed estimation of cumulative growing season AET (mm) over each growing season, between DOY 152 and 234, by integrating the curve of daily AET versus DOY each year. AET was integrated only over the subset of the growing season when measurement dates could be compared among all 3 years (DOY 152–234).

Growing season PET was estimated using the Penman–Monteith equation (Allen, Pereira, Raes, & Smith, 1998; Monteith, 1965; Penman, 1948; Zotarelli, Dukes, Romero, Migliaccio, & Morgan, 2013) based on daily air temperature, wind speed, atmospheric pressure, relative humidity, and net radiation site measurements over DOY 152–234. We calculated the ratio of PET to precipitation, known as the aridity index (AI; Arora, 2002) as well as the ratio of AET to precipitation for comparison of climatic conditions between years.

We tested the effects of $CO_2$, temperature, date, and their interactions on midday AET, using the *ezanova* command in the *ez* package to perform a repeated measures analysis of variance (ANOVA). We tested each year separately due to their strong hydrological differences. Post-hoc tests were performed on dates with significant treatment effects using the *aov* command for two-way ANOVA, with $CO_2$ and warming as the two factors, and Tukey's HSD command for Tukey's honestly significant difference (HSD) test (R Core Team, 2012). Two-way ANOVA and post hoc tests were also performed to assess intra-seasonal differences in $CO_2$ and warming effects on plot soil moisture and plot canopy temperature (R Core Team, 2012).

We evaluated climate change treatment effects ($CO_2$ and warming) on the relationships between midday AET and abiotic (soil moisture and vapor pressure deficit) and biotic (greenness) environmental variables using single-factor regressions, fitting both linear and quadratic models. Treatment effects on the slopes were considered significant when their confidence intervals did not overlap. We evaluated $CO_2$ and warming effects on covariation among soil moisture, vapor pressure deficit, and greenness using a similar approach. All variability is reported as standard error and significance is considered at $p < .05$ unless otherwise noted. All analyses were performed using R (R Core Team, 2012) and graphed with the *ggplot* command in the ggplot2 package.

## 3 | RESULTS

### 3.1 | Meteorological conditions and vegetation

In the semiarid mixed grass prairie, spring is generally cool and moist (May–mid-June), whereas summer (mid-June–August) and autumn (September–October) are warmer and drier. Annual precipitation was 468 mm in 2009, 357 mm in 2010, and 241 mm in 2012, compared to the 30-year mean of 397 mm. The seasonal distribution of precipitation varied between years (Figure 1m–o), leading to a wetter growing season in 2009 than 2010 or 2012 (Table 1). Average growing season daytime temperature was 20.1 (±0.5) °C in 2009, 21.2 (±0.5) °C in 2010, and 23.8 (±0.5) °C in 2012 (Table 1). Maximum growing season daytime temperatures were similar in 2009 (32.0 °C) and 2010 (31.4 °C) but warmer in 2012 (33.4 °C). PET during the growing season increased with temperature, and the AI (Arora, 2002) demonstrated that 2009 was least arid and 2012 was the most arid of the seasons we studied (Table 1). The ratio of AET to precipitation on ambient plots ranged from 51% in the driest year (2012) to 98% in the wettest year (2009; Table 1), demonstrating that the ability of vegetation to utilize rainfall inputs varied between growing seasons (e.g., Sala, Lauenroth, & Parton, 1992).

$eCO_2$ did not change daytime plot air temperature in any year, and warming significantly increased daytime plot air temperature only in 2010. However, the combination of $eCO_2$ and warming increased growing season daytime air temperature by 0.4 °C in 2009, 1.1 °C in

**TABLE 1** Ambient climatic conditions at the site during the growing season (DOY 121–234), including Pptn, PET, AET, the ratio of PET/Pptn (also known as the AI), and the ratio of AET/Pptn in ambient plots (top), and PHACE treatment effects on soil moisture, air temperature and AET(bottom)

| Ambient conditions | Year | Pptn (mm) | PET (mm) | PET/Pptn | AET/Pptn |
|---|---|---|---|---|---|
| | 2009 | 177 | 369 | 2.1 | 0.98 |
| | 2010 | 158 | 474 | 3.0 | 0.87 |
| | 2012 | 155 | 536 | 3.5 | 0.51 |
| PHACE treatment | | ct | cT | Ct | CT |
| Soil moisture (mm) | 2009 | 13.1(0.2)$^b$ | 11.6(0.1)$^a$ | 16.2(0.2)$^d$ | 14.5(0.2)$^c$ |
| | 2010 | 11.4(0.2)$^b$ | 10.4(0.2)$^a$ | 14.3(0.2)$^d$ | 12.6(0.2)$^c$ |
| | 2012 | 9.3(0.1)$^b$ | 8.3(0.1)$^a$ | 11.7(0.1)$^c$ | 9.4(0.1)$^b$ |
| Air temperature (°C) | 2009 | 23.8(0.2)$^a$ | 24.1(0.2)$^a$ | 23.6(0.2)$^a$ | 25.2(0.3)$^b$ |
| | 2010 | 25.0(0.3)$^a$ | 25.7(0.3)$^b$ | 24.7(0.2)$^a$ | 26.1(0.3)$^b$ |
| | 2012 | 26.9 (0.2)$^a$ | 26.9(0.2)$^a$ | 26.8(0.2)$^a$ | 27.3(0.2)$^a$ |
| AET (mm) | 2009 | 174(12)$^a$ | 175(9)$^a$ | 167(6)$^a$ | 175(3)$^a$ |
| | 2010 | 137(8)$^b$ | 105(8)$^a$ | 119(5)$^{ab}$ | 120(6)$^{ab}$ |
| | 2012 | 79(2)$^a$ | 76(1)$^a$ | 70(9)$^a$ | 69(4)$^a$ |
| Treatment effects on AET relative to ct | 2009 | | 1.0 | 0.95 | 1.0 |
| | 2010 | | 0.77 | 0.87 | 0.88 |
| | 2012 | | 0.96 | 0.89 | 0.87 |

*Note*. Climate change effects on average (±1 *SE*) plot soil moisture (5- to 15-cm depth; mm), canopy temperature, and AET are shown for the treatments: ct (ambient $CO_2$ + ambient canopy temperature), cT (ambient $CO_2$ + warming), Ct (elevated $CO_2$ + ambient canopy temperature), and CT (elevated $CO_2$ + warming). Differing superscript letters refer to significantly different soil moisture, canopy temperature, or AET assessed using two-way factorial ANOVA, by year, with $CO_2$ and warming as the two factors, and Tukey's HSD test ($\alpha = .05$). Treatment effects are also shown as ratios relative to the ct plots. AET = actual evapotranspiration; AI = aridity index; ANOVA = analysis of variance; DOY = day of year; HSD = honestly significant difference; PET = potential evapotranspiration; PHACE = Prairie Heating and Elevated $CO_2$ Enrichment; Pptn = precipitation.

2010, and had no effect in 2012, relative to the ambient treatment. Air temperatures were not increased as much as canopy temperatures, which were the target of the infrared heating (LeCain et al., 2015).

During the growing seasons, $eCO_2$ increased soil moisture at 5- to 15-cm depth by 24% in 2009, 35% in 2010, and 26% in 2012, relative to the ambient plots (Table 1; Figure 1j–l). The warming treatment decreased soil moisture on average by 11% in 2009, 9% in 2010, and 11% in 2012, compared to the ambient plots (Table 1).

Vegetation greenness tracked interannual variations in soil moisture and was highest in 2009, intermediate in 2010, and lowest in 2012 (Figure 1g–i). We focus on the relationship of greenness to AET by treatment in the current analysis (below), rather than treatment effects on greenness, which were described in Zelikova et al. (2015). We note that across the 3 years of study, greenness was strongly correlated with soil moisture ($p = 2.5 \times 10^{-12}$; $r^2 = .11$), and vapor pressure deficit was negatively correlated with greenness ($p = 2.2 \times 10^{-16}$; $r^2 = .23$) and soil moisture ($p = 2.2 \times 10^{-16}$; $r^2 = .31$), but climate change treatments did not alter any of these relationships (Table S2).

## 3.2 | Climate change effects on actual evapotranspiration

Cumulative AET did not differ among the PHACE treatments in 2009 or 2012 (Table 1). In 2010, warming decreased cumulative AET by 23% (Table 1). Average cumulative AET across all treatments was 30% lower in 2010 (an average precipitation year) and 57% lower in 2012 (a dry year) than in 2009 (a wet year; Table 1). Although the effect of PHACE treatments on cumulative AET was only significant in 2010, significant treatment effects on midday AET were observed on 15 out of 25 individual measurement dates (Table 2; Figure 1a–c; Table S1). In all 3 years, warming interacted with date, whereas $eCO_2$ interacted with date in 2009 and 2010, and a three-way interaction was noted in 2010 (Table 2).

The significant interactions between treatment effects and date led to seasonally contrasting patterns of AET responses (Figure 1; Table S1). Warming significantly enhanced AET early in the growing season of 2010 and marginally significantly during early 2009 (Figure 1). Warming suppressed AET later in the growing seasons of 2009 and 2012. $eCO_2$ suppressed AET in the middle of 2010 and enhanced AET later in the growing seasons of 2009 and 2010 (Figure 1; Table S1).

## 3.3 | Environmental controls of actual evapotranspiration

In all years and for all treatments, AET was significantly linearly related to vegetation greenness ($p < .0003$), with correlation coefficients ranging from .20 to .66 (Table 3; Figure 2b, 2e, and 2h). In 2009, significant treatment effects on the AET versus Greenness relationship were found: The slope was higher in the warming treatment than in $eCO_2$ and ambient treatments (Figure 2b; Table 3). In 2010 and 2012, no

**TABLE 2** Repeated measures ANOVA testing three-way interactive effects of elevated $CO_2$ ($eCO_2$) and warming on AET with date as the withinsubject (independent) variable

| Year | Effect | DFn | DFd | SSn | SSd | F | p |
|---|---|---|---|---|---|---|---|
| 2009 | | | | | | | |
| | (Intercept) | 1 | 16 | 4.08E+02 | 1.90307 | 3.43E+03 | **4.27E-20** |
| | eCO2 | 1 | 16 | 8.19E-03 | 1.90307 | 6.88E-02 | 7.96E-01 |
| | warming | 1 | 16 | 1.06E-01 | 1.90307 | 8.89E-01 | 3.60E-01 |
| | date | 8 | 128 | 4.04E+01 | 5.415126 | 1.19E+02 | **1.38E-55** |
| | eCO2:warming | 1 | 16 | 3.66E-03 | 1.90307 | 3.08E-02 | 8.63E-01 |
| | eCO2:date | 8 | 128 | 1.44E+00 | 5.415126 | 4.27E+00 | **1.44E-04** |
| | warming:date | 8 | 128 | 9.74E-01 | 5.415126 | 2.88E+00 | **5.61E-03** |
| | eCO2:warming:date | 8 | 128 | 3.73E-01 | 5.415126 | 1.10E+00 | 3.66E-01 |
| 2010 | | | | | | | |
| | (Intercept) | 1 | 16 | 1.92E+02 | 2.813355 | 1089.32 | **3.81E-16** |
| | eCO2 | 1 | 16 | 6.96E-03 | 2.813355 | 0.039563 | 8.45E-01 |
| | warming | 1 | 16 | 6.07E-02 | 2.813355 | 0.345277 | 5.65E-01 |
| | date | 8 | 128 | 3.46E+01 | 7.410249 | 74.73028 | **1.58E-44** |
| | eCO2:warming | 1 | 16 | 1.34E+00 | 2.813355 | 7.629404 | **1.39E-02** |
| | eCO2:date | 8 | 128 | 1.03E+00 | 7.410249 | 2.21898 | **3.00E-02** |
| | warming:date | 8 | 128 | 1.94E+00 | 7.410249 | 4.18119 | **1.80E-04** |
| | eCO2:warming:date | 8 | 128 | 1.71E+00 | 7.410249 | 3.690667 | **6.59E-04** |
| 2012 | | | | | | | |
| | (Intercept) | 1 | 8 | 255.9034 | 3.087675 | 663.0319 | **5.55E-09** |
| | eCO2 | 1 | 8 | 1.144582 | 3.087675 | 2.965551 | 1.23E-01 |
| | warming | 1 | 8 | 0.082686 | 3.087675 | 0.214234 | 6.56E-01 |
| | date[a] | 6 | 48 | 58.70987 | 5.15531 | 91.10586 | **3.16E-12** |
| | eCO2:warming | 1 | 8 | 0.066173 | 3.087675 | 0.17145 | 6.90E-01 |
| | eCO2:date[a] | 6 | 48 | 1.42802 | 5.15531 | 2.215998 | 1.20E-01 |
| | warming:date[a] | 6 | 48 | 2.073176 | 5.15531 | 3.21715 | **4.65E-02** |
| | eCO2:warming:date[a] | 6 | 48 | 0.072885 | 5.15531 | 0.113103 | 9.40E-01 |

*Note*. We show degrees of freedom (*df*s) and sum of squares (SS) for numerator (n) and denominator (d), *F*-statistic (*F*), and probability of significance (*p*) for each factor. Bold *p*-values indicate $p < .05$, and italics indicate $p < .01$. AET = actual evapotranspiration.

[a] Mauchly's test for sphericity was nonsignificant in 2009 and 2010 and corrected using the Greenhouse–Geisser correction in 2012.

significant differences in the slope of AET versus Greenness were found. These results indicate that warming increased the rate of AET per unit of green leaf area, whereas eCO$_2$ tended to decrease it, but only in the year with highest precipitation.

Linear and nonlinear regressions were performed to assess the relationship between soil moisture and AET (Figure 2). In 2009, there were significant quadratic relationships between soil moisture and AET (Table 4; Figure 2c, 2f, and 2i) with correlation coefficients ranging from .22 to .37, and the relationship varied among treatments. For all treatments, soil moisture had a positive effect on AET up to a maximum where AET began to decrease with increasing soil moisture (Figure 2c and 2f). This optimum water content for maximum AET differed among treatments, ranging from 13% in the warmed treatment to 17% under eCO$_2$, with intermediate values in the ambient and eCO$_2$ + warming treatments.

In 2010, significant quadratic relationships between AET and soil moisture occurred in the ambient, warmed, and eCO$_2$ treatments (Table 3; Figure 2c). However, the relationships were variable, and results should be interpreted with caution given low correlation coefficients in the ambient ($r^2 = .09$) and eCO$_2$ ($r^2 = .14$) treatments. Under the warmed treatment, the optimal soil moisture for maximum AET was 14%.

In 2012, which had a dry spring, soil moisture and AET were linearly correlated ($p < .003$), with correlation coefficients ranging from .35 to .68 across treatments (Table 4; Figure 2i). The slope of the relationship between AET and soil moisture was significantly higher in the warming treatment (.163 ± .0244) than under eCO$_2$ (.106 ± .0310). This suggests that warming increased AET per unit of soil moisture, whereas eCO$_2$ decreased it.

Significant negative correlations were found between AET and $D_v$ in the three study years (Table 5; Figure 2a, 2d, and 2g), but the slope of this relationship was not significantly different among treatments. The negative correlation can be explained by the negative relationship between $D_v$ and greenness (Table S2). There was no relationship between temperature and AET in any year.

## 4 | DISCUSSION

In semiarid ecosystems that are characterized by intermittent precipitation, AET varies greatly through time as water availability changes (Kurc & Small, 2007; Lauenroth & Bradford, 2009; Sala et al., 1992; Vivoni et al., 2008). In the 3 years examined here, seasonal and interannual variations in AET were much larger than the effects of warming and eCO$_2$ treatments. AET rates were strongly influenced by seasonal soil moisture availability (Noy-Meir, 1973; Sala et al., 1992) and were related to vegetation greenness, as estimated from digital photographs (Zelikova et al., 2015). Across all years, warming enhanced AET in spring when soils were moist but suppressed it later in the season as moisture limitations set in. By contrast, eCO$_2$ suppressed AET early in the growing season and enhanced it later, but not in a dry year. Thus, the seasonally contrasting effects of warming and eCO$_2$ on AET

**TABLE 3** Model $p$-values, $r^2$ values, intercept, and slope coefficients (±1 *SE*) for the linear relationship between midday evapotranspiration (AET; mmol·m$^{-2}$·s$^{-1}$) and GR (%)

| | ct | cT | Ct | CT | All |
|---|---|---|---|---|---|
| 2009 | | | | | |
| | $p < 0.0001$ | $p < 0.0001$ | $p < 0.0001$ | $p < 0.0001$ | $p < 0.0001$ |
| | $r^2 = 0.45$ | $r^2 = 0.62$ | $r^2 = 0.30$ | $r^2 = 0.59$ | $r^2 = 0.50$ |
| | DF = 43 | DF = 43 | DF = 43 | DF = 43 | DF = 178 |
| Int. | 2.145 (0.5853)$^c$ | 0.9 (0.5629) | 2.497 (0.6172)$^c$ | 1.239 (0.5178)$^a$ | 1.693 (0.2857)$^c$ |
| slope | 0.059 (0.0099)$^c$ | 0.083 (0.0097)$^c$ | 0.05 (0.0112)$^c$ | 0.07 (0.0087)$^c$ | 0.066 (0.0049)$^c$ |
| 2010 | | | | | |
| | $p < 0.0001$ | $p < 0.0001$ | $p = 0.001$ | $p = 0.001$ | $p < 0.0001$ |
| | $r^2 = 0.45$ | $r^2 = 0.40$ | $r^2 = 0.20$ | $r^2 = 0.20$ | $r^2 = 0.26$ |
| | DF = 43 | DF = 43 | DF = 43 | DF = 43 | DF = 178 |
| Int. | 1.366 (0.4134)$^b$ | 1.301 (0.4160)$^b$ | 1.716 (0.4778)$^c$ | 1.893 (0.4449)$^c$ | 1.619 (0.2242)$^c$ |
| slope | 0.056 (0.0092)$^c$ | 0.036 (0.0082)$^c$ | 0.038 (0.0112)$^b$ | 0.031 (0.0091)$^b$ | 0.039 (0.0048)$^c$ |
| 2012 | | | | | |
| | $p = 0.0003$ | $p = 0.0002$ | $p = 0.0002$ | $p = 0.0002$ | $p < 0.0001$ |
| | $r^2 = 0.48$ | $r^2 = 0.50$ | $r^2 = 0.49$ | $r^2 = 0.49$ | $r^2 = 0.49$ |
| | DF = 19 | DF = 19 | DF = 19 | DF = 19 | DF = 82 |
| Int. | 0.745 (0.3067)$^a$ | 0.598 (0.3067)$^‡$ | 0.514 (0.2849)$^‡$ | 0.673 (0.2459) | 0.644 (0.1416)$^c$ |
| slope | 0.042 (0.0095)$^c$ | 0.048 (0.0105)$^c$ | 0.043 (0.0094)$^c$ | 0.034 (0.0075)$^c$ | 0.041 (0.0004)$^c$ |

*Note*. Results are reported for each individual treatment and across all treatments for each year. Treatment abbreviations are as follows: ct (ambient CO$_2$ + ambient temperature), cT (ambient CO$_2$ + warming), Ct (elevated CO$_2$ + ambient temperature), and CT (elevated CO$_2$ + warming). AET = actual evapotranspiration; GR = greenness.

[a] $p < .05$.

[b] $p < .01$.

[c] $p < .001$.

[‡] $p < .10$ (nearly significant values).

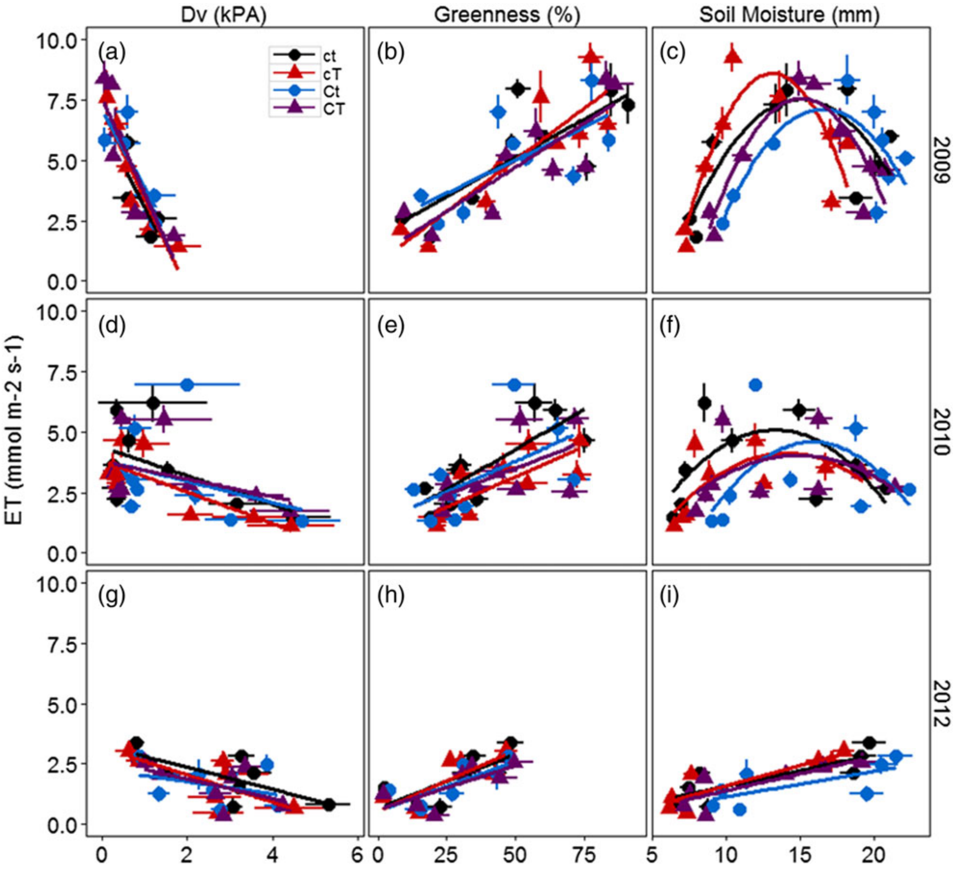

**FIGURE 2** (a, d, and g) Relationship between average midday evapotranspiration (actual evapotranspiration [AET]; mmol·m$^{-2}$·s$^{-1}$) versus average chamber vapor pressure deficit ($D_v$; kPa) for each treatment on each date, separated by year. (b, e, and h) Simple linear relationships between average midday evapotranspiration (AET; mmol·m$^{-2}$·s$^{-1}$) and average greenness (%), for each treatment on each date, separated by year. (c, f, and i) Quadratic relationships (2009 and 2010) and simple linear relationships (2012) between average midday evapotranspiration (AET; mmol·m$^{-2}$·s$^{-1}$) and average soil moisture (mm). Refer to Tables 3--5 for *p*-values and correlation coefficients for each treatment by year combination. Error bars show ±1 *SE*. Treatment abbreviations are as follows: ct (ambient CO$_2$ + ambient temperature), cT (ambient CO$_2$ + warming), Ct (elevated CO$_2$ + ambient temperature), and CT (elevated CO$_2$ + warming)

worked in opposition, leading to small (or no) effects on cumulative growing-season water fluxes. Our results indicate that future climate conditions may affect AET in semiarid grasslands most strongly via changes in vegetation phenology and soil moisture, but may not extend the growing season, in contrast to Hufkens et al. (2016). Separate measurements of evaporation and transpiration (e.g., Niu et al., 2011) would improve understanding of the processes underlying climate change impacts on ecosystem water fluxes.

In this semiarid grassland, AET was strongly controlled by variation in precipitation. Generally, semiarid grasslands have high precipitation variability both within growing seasons and between years (Bachman et al., 2010; Lauenroth & Bradford, 2009). However, seasonal distribution and timing of rainfall may be more important than the total amount of growing season precipitation for plant growth (Bachman et al., 2010; Knapp, Briggs, & Koelliker, 2001; Sala et al., 1992; Williams, Scott, Huxman, Goodrich, & Lin, 2006) and therefore the relative contributions of transpiration and evaporation to total ET (Jasechko et al., 2013). The ratio of AET to precipitation was lowest in 2012, the year with the lowest AET and highest AI, because most precipitation fell in two large events that year, both after the critical late-spring period that vegetation depends on in this region (Derner & Hart, 2007; Figure 1; Table 1). A more even seasonal distribution of precipitation in 2009 sustained higher soil moisture in early summer compared to 2010 or 2012, leading to 30–40% higher AET rates with only 12% greater precipitation (Figure 1; Table 1). The interaction of precipitation seasonality with biotic factors, such as genetic constraints on physiological responses (Chaves, Maroco, & Pereira, 2003; Patrick, Ogle, Bell, Zak, & Tissue, 2009) and plant community composition (Knapp et al., 2002), complicates our ability to predict the influence of precipitation variability on AET (Potts et al., 2006; Sala et al., 1992). Understanding moisture effects on ecosystem phenology will improve with greater availability of repeat photography or PhenoCam imagery in grasslands (e.g., Hufkens et al., 2016; Zelikova et al., 2015), and this will in turn improve predictions of carbon and water fluxes.

North American grasslands are predicted to become warmer and more arid in the coming century (Hufkens et al., 2016), leading to reductions in soil water availability (Seneviratne et al., 2010) and increased evaporative demand. In our experiment, warming reduced cumulative AET in 2010, a year with average precipitation, probably because of reduced transpiration via stomatal limitation (Friend & Cox, 1995; Niklaus, Spinnler, & Korner, 1998), especially in the

**TABLE 4** Model *p*-values, $r^2$ values, and coefficients (± standard errors) for the relationships between midday evapotranspiration (AET; $\mathrm{mmol \cdot m^{-2} \cdot s^{-1}}$) and SM (mm)

| | ct | cT | Ct | CT | All |
|---|---|---|---|---|---|
| 2009 | | | | | |
| | $p < 0.0001$ | $p < 0.0001$ | $p = 0.0018$ | $p < 0.0001$ | $p < 0.0001$ |
| | $r^2 = 0.33$ | $r^2 = 0.36$ | $r^2 = 0.22$ | $r^2 = 0.37$ | $r^2 = 0.24$ |
| | DF = 42 | DF = 42 | DF = 42 | DF = 42 | DF = 177 |
| Int. | -7.062 (2.6334)[a] | -13.19 (3.6206)[c] | -9.42 (4.0799)[a] | -12.67 (3.3859)[c] | -6.083 (1.4977) |
| SM | 1.788 (0.4048)[c] | 3.103 (0.6244)[c] | 1.789 (0.5434)[b] | 2.438 (0.4791)[c] | 1.589 (0.2223) |
| $SM^2$ | -0.057 (0.0140)[c] | -0.1161 (0.0243)[c] | -0.051 (0.0168)[b] | -0.076 (0.0157)[c] | -0.0503 (0.0075) |
| 2010 | | | | | |
| | $p = 0.05$ | $p < 0.001$ | $p = 0.02$ | $p = 0.26$ | $p < 0.0001$ |
| | $r^2 = 0.09$ | $r^2 = 0.26$ | $r_2 = 0.14$ | $r^2 = 0.02$ | $r^2 = 0.10$ |
| | DF = 42 | DF = 42 | DF = 42 | DF = 42 | DF = 177 |
| Int. | -1.083 (1.8623) | -3.584 (1.6767)[a] | -7.053 (3.4128[a] | ns | -1.213 (0.9537) |
| SM | 0.08 (0.3137)[a] | 1.082 (0.2960)[c] | 1.394 (0.4748)[b] | ns | 0.679 (0.1506)[c] |
| $SM^2$ | -0.028 (0.0114)[a] | -0.038 (0.0115)[b] | -0.043 (0.0151)[b] | ns | -0.022 (0.0052)[c] |
| 2012 | | | | | |
| | $p < 0.0001$ | $p = 0.0001$ | $p = 0.003$ | $p < 0.0001$ | $p < 0.0001$ |
| | $r^2 = 0.62$ | $r^2 = 0.68$ | $r^2 = 0.35$ | $r^2 = 0.64$ | $r^2 = 0.52$ |
| | DF = 19 | DF = 19 | DF = 19 | DF = 19 | DF = 82 |
| Int. | 0.292 (0.3104) | -0.029 (0.3031) | 0.072 (0.4826) | -0.021 (0.2932) | 0.185 (0.178) |
| SM slope | 0.129 (0.0223)[c] | 0.163 (0.0244)[c] | 0.106 (0.0310)[b] | 0.121 (0.0234)[c] | 0.124 (0.0134)[c] |

*Note*. Quadratic models were fit in 2009 and 2010 and a linear model in 2012. Treatment abbreviations are as follows: ct (ambient $CO_2$ + ambient temperature), cT (ambient $CO_2$ + warming), Ct (elevated $CO_2$ + ambient temperature), and CT (elevated $CO_2$ + warming). Nonsignificant coefficients are designated by ns. AET = actual evapotranspiration; SM = soil moisture.

[a] $p < .05$.

[b] $p < .01$.

[c] $p < .001$.

middle and end of the growing season (Figure 1). in tandem with plant senescense (Reyes-Fox et al., 2014). Warming enhanced AET per unit of green leaf area in 2009, an unusually wet year, especially in spring when soils were moist (Figure 2). but this did not lead to cumulative enhancement, possibly because of reductions in stomatal conductance later in the season (Niu et al., 2011). In a similar study, experimental warming did not significantly affect AET in semiarid Chinese grassland, despite reducing soil moisture content, potentially because of feedbacks between leaf-level stomatal conductance and aerodynamic effects at the ecosystem level (Niu et al., 2011). Our results provide evidence that impacts of future warming on atmospheric demand ($D_v$) on vegetation—climate interactions are challenging to distinguish from soil moisture effects (Novick et al., 2016).

Warming-induced drying will combine with other climate change factors, particularly $eCO_2$, to impact ecosystem structure and function (Hufkens et al., 2016; Mueller et al., 2016). $eCO_2$ suppressed AET and increased soil moisture in a scrub oak ecosystem, as expected from leaf-level conductance responses (Hungate et al., 2002). However, in our mixed $C_3$/$C_4$ grassland with a significant forb component, contrasting responses of individual plant species to climate change factors may have had compensating effects (Blumenthal et al., 2013). Over seven growing seasons at PHACE, $eCO_2$ and temperature combined to enhance late-season soil moisture availability, while reducing its overall variability (Blumenthal et al., in review). These treatment effects on soil moisture likely interacted with individual species phenology (Reyes-Fox et al., 2014) to play a role in regulating AET during our study.

Vegetation greenness, a proxy for photosynthetically active leaf area, was a strong predictor of AET in all 3 years, emphasizing the importance of canopy controls on ecosystem water fluxes and suggesting that transpiration was the dominant component of AET. In our experiment and in others (Hungate et al., 2002), ecosystem scale reduction in AET under $eCO_2$ was usually offset by increased soil moisture and greenness (Cleland, Chiariello, Loarie, Mooney, & Field, 2006). For instance, $eCO_2$ enhanced AET after mid-July in the 2009 growing season as it increased soil water and greenness (Zelikova et al., 2015) and extended the growing season (Reyes-Fox et al., 2014). The importance of vegetation greenness in modulating the relationship between AET and soil moisture has been emphasized in grasslands of the U.S. Southwest (Vivoni et al., 2008). Our results indicate that incorporating vegetation feedbacks will improve quantitative predictions of climate change impacts on ecosystem fluxes (DeKauwe et al., 2017).

The relationship between AET and soil moisture appeared to be quadratic rather than linear in 2009 and 2010, because the highest soil moisture occurred in spring (Kurc & Small, 2007; Niklaus et al., 1998), when plant cover is minimal and air temperature limits AET. This interaction between soil moisture and air (or canopy) temperature is likely responsible for the shape of the observed quadratic relationship (Krishnan, Meyers, Scott, Kennedy, & Heuer, 2012; Seneviratne et al., 2010). In the middle of the growing season, high vegetation cover is

**TABLE 5** Model *p*-values, $r^2$ values, intercept, and slope coefficients (± standard errors) for the relationship between midday evapotranspiration (AET; mmol·m$^{-2}$·s$^{-1}$) and vapor pressure deficit ($D_v$; kPa)

| | ct | cT | Ct | CT | All |
|---|---|---|---|---|---|
| 2009 | | | | | |
| | p = 0.04 | p = 0.0002 | p = 0.003 | p = 0.0005 | p < 0.0001 |
| | $r^2$ = 0.19 | $r^2$ = 0.47 | $r^2$ = 0.37 | $r^2$ = 0.47 | $r^2$ = 0.40 |
| | DF = 17 | DF = 20 | DF = 18 | DF = 18 | DF = 79 |
| Int. | 4.6591 (0.6894)[c] | 6.1147 (0.6642)[c] | 6.3671 (0.7103)[c] | 5.4383 (0.5488)[c] | 5.7098 (0.3236)[c] |
| slope | -1.5431 (0.6789)[a] | -2.6628 (0.5981)[c] | -2.3642 (0.6747)[b] | -2.1291 (0.5026)[c] | -2.244 (0.3025)[c] |
| 2010 | | | | | |
| | p = 0.003 | p < 0.0001 | p = 0.07 | p = 0.02 | p < 0.0001 |
| | $r^2$ = 0.20 | $r^2$ = 0.46 | r2 = 0.05 | $r^2$ = 0.12 | $r^2$ = 0.18 |
| | DF = 35 | DF = 33 | DF = 41 | DF = 39 | DF = 154 |
| Int. | 4.2795 (0.3748)[c] | 3.8528 (0.2788)[c] | ns | 3.6755 (0.2845)[c] | 3.88802 (0.17636)[c] |
| slope | -0.5349 (0.1686)[b] | -0.6316 (0.1164)[c] | ns | -0.3119 (0.1255)[a] | -0.45986 (0.07697)[c] |
| 2012 | | | | | |
| | p = 0.001 | p = 0.005 | p = 0.3496 | p = 0.0139 | p < 0.0001 |
| | $r^2$ = 0.40 | $r^2$ = 0.32 | $r^2$ = -0.004 | $r^2$ = 0.24 | $r^2$ = 0.23 |
| | DF = 19 | DF = 18 | DF = 19 | DF = 19 | DF = 81 |
| Int. | 3.244 (0.3844)[c] | 2.919 (0.4148)[c] | ns | 2.669 (0.4159)[c] | 2.693 (0.2119)[c] |
| slope | -0.4465 (0.1177)[b] | -0.4622 (0.1457)[b] | ns | -0.3956 (0.1461)[a] | -0.3599 (0.0719)[c] |

*Note*. Results are reported for each individual treatment and across all treatments for each year. Treatment abbreviations are as follows: ct (ambient $CO_2$ + ambient temperature), cT (ambient $CO_2$ + warming), Ct (elevated $CO_2$ + ambient temperature), and CT (elevated $CO_2$ + warming). Nonsignificant coefficients are designated by ns. AET = actual evapotranspiration.

[a] $p < .05$.

[b] $p < .01$.

[c] $p < .001$.

expected to increase the demand for soil moisture (Niu et al., 2011) and the contribution of transpiration to AET (Wang et al., 2010; Wythers et al., 1999). However, desiccating conditions at the height of the growing season may cause a water-saving stomatal response, resulting in an AET soil moisture threshold where AET ceases to increase with soil moisture (Figure 2).

The chamber method for measuring ET has been used in multiple contexts (McLeod, Daniel, Faulkner, & Murison, 2004; Raz-Yaseef, Rotenberg, & Yakir, 2010), including investigations of $eCO_2$ on ecosystem water dynamics (Bunce, 2001; Hungate et al., 2002; Niu et al., 2011). However, this method is not without caveats. Traditionally, static chambers are not advisable for AET measurements because boundary layer conductance and incoming radiation are altered once the chamber is implemented (Denmead, 1984; Dugas, Reicosky, & Kiniry, 1997). However, due to relatively low leaf area, chamber design, and experimental infrastructure at the PHACE site, we were able to estimate climate change treatment effects on AET. The dry site conditions and small fans within the chamber allowed us to maintain a relatively stable temperature under the chamber without a buildup of moisture on chamber walls (Bachman et al., 2010). Further, the use of a fast-response LI-7500 infrared gas analyzer within the chamber enabled AET measurements within 45 s of chamber closure (LI-7500, LI-COR Inc., Lincoln, NE). The midday rates reported here are equivalent to rates of 0.5 to 3.0 mm/day, consistent with estimates of AET from a similar grassland (Lauenroth & Bradford, 2006). However, because we did not make measurements on rainy days, when water losses would be minimal, our cumulative estimates of AET may be 10–20% too high, especially in the rainy 2009 growing season.

The PHACE experiment in native, semiarid grassland is a unique climate manipulation that allowed us to assess the effect of $eCO_2$ and warming on AET in 3 years with contrasting precipitation. Warming and $eCO_2$ tended to have opposing effects on AET, and the magnitude and direction of treatment effects across the growing season were variable and contingent upon concurrent changes in plant cover and greenness as well as soil water availability. These feedbacks between environmental drivers, plant activity, and ecosystem fluxes can be used to test models and potentially improve predictions of grassland functional responses to climate change. Terrestrial biosphere models perform poorly at reproducing vegetation phenology and its response to soil moisture stress in semiarid grasslands (DeKauwe et al., 2017), and experiments such as this are useful as benchmarks to test model performance and predictions.

## ACKNOWLEDGEMENTS

We thank Shannon Albeke, Amanda Brennan, Samantha Ewers, Jana Heisler-White, Sierra Jech, Dan LeCain, and David Smith for their assistance in the experimental design and maintenance, and collection and analysis of data. We thank Jack Morgan for PHACE project leadership. This material is based upon the work supported by the U.S. Department of Energy Office of Science (BER), through the Terrestrial Ecosystem Science program (#DE-SC0006973) and the Western Regional Center of the National Institute for Climatic Change Research, and by the National Science Foundation (DEB#1021559). Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation. The authors declare no potential conflict of interest related to this publication.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

**How to cite this article:** Sorokin Y, Zelikova TJ, Blumenthal D, Williams DG, Pendall E. Seasonally contrasting responses of evapotranspiration to warming and elevated $CO_2$ in a semiarid grassland. *Ecohydrology*. 2017;10:e1880. https://doi.org/10.1002/eco.1880