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Warming and Elevated CO_2 Interact to Alter Seasonality and Reduce Variability of Soil Water in a Semiarid Grassland

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ABSTRACT

Global changes that alter soil water availability may have profound effects on semiarid ecosystems. Although both elevated CO_2 (eCO_2) and warming can alter water availability, often in opposite ways, few studies have measured their combined influence on the amount, timing, and temporal variability of soil water. Here, we ask how free air CO_2 enrichment (to 600 ppmv) and infrared warming (+ 1.5 °C day, + 3 °C night) effects on soil water vary within years and across wet-dry periods in North American mixed-grass prairie. We found that eCO_2 and warming interacted to influence soil water and that those interactions varied by season. In the spring, negative effects of warming on soil water largely offset positive effects of eCO_2. As the growing season progressed, however, warming reduced soil water primarily (summer) or only (autumn) in plots treated with eCO_2. These interactions constrained the combined effect of eCO_2 and warming on soil water, which ranged from neutral in spring to positive in autumn. Within seasons, eCO_2 increased soil water under drier conditions, and warming decreased soil water under wetter conditions. By increasing soil water under dry conditions, eCO_2 also reduced temporal variability in soil water. These temporal patterns explain previously observed plant responses, including reduced leaf area with warming in summer, and delayed senescence with eCO_2 plus warming in autumn. They also suggest that eCO_2 and warming may favor plant species that grow in autumn, including winter annuals and C_3 graminoids, and species able to remain active under the dry conditions moderated by eCO_2.

Key words: elevated carbon dioxide; warming; climate change; free air CO_2 enrichment, evapotranspiration; soil moisture; seasonality; phenology; mixed-grass prairie; northern Great Plains.

INTRODUCTION

Seasonal variation in water availability is one of the defining features of semiarid systems (Noy-Meir 1973; Weltzin and others 2003; Austin and others 2004). For example, ecosystems with summer-dominated precipitation regimes tend to have a greater proportion of water and roots at shallow depths, and to be dominated by herbaceous perennial species, particularly C_4 grasses, while those with autumn- or winter-dominated precipitation regimes have deeper water and roots, and more shrubs, winter-annual grasses and forbs (Paruelo and Lauenroth 1996; Schenk and Jackson 2002). Less predictable variation in water availability also occurs within seasons, and across years. Such variation in water availability can lead to wide fluctuations in primary and secondary productivity and presents an array of challenges for organisms in semiarid ecosystems, including domestic livestock (Noy-Meir 1973; East 1984; Sala and others 1988; Knapp and Smith 2001; Austin and others 2004; Reeves and others 2014a).

Because the timing of water availability has profound effects on semiarid ecosystems, it is important to understand how global changes may alter that timing (Weltzin and others 2003; Polley and others 2013; Ponce-Campos and others 2013). Previous work has focused primarily on predicted changes in precipitation, and showed that changes in seasonality or variability can alter productivity, diversity, interspecific interactions, and biogeochemistry (Knapp and others 2002; Suttle and others 2007; Heisler-White and others 2009; Robertson and others 2010). Effects of other global changes on the timing of water availability have been much less studied. In particular, both elevated CO_2 (eCO_2) and warming can strongly influence soil water and therefore semiarid ecosystems (Norby and Luo 2004; Kirtman and others 2013). Elevated CO_2 often increases leaf-level water use efficiency, which can in turn reduce plant water use and soil water loss, increase plant productivity, or some combination of the two (Morgan and others 2004; Niklaus and Korner 2004; Ainsworth and Long 2005; Morgan and others 2011; Hovenden and others 2014). Conversely, most models and experiments indicate that warming will directly increase evapotranspiration and aridity, constraining potential increases in plant productivity, and in some regions increasing plant mortality (McDowell and others 2008; Kirtman and others 2013; Liu and others 2013; Hufkens and others 2016). To understand how semiarid ecosystems are likely to change in the future, we need to know how CO_2 and warming effects on soil water availability vary across seasons and environmental conditions.

Elevated CO_2 is likely to reduce plant water use and soil drying most when leaf area and transpiration are relatively high, but soils are dry enough to induce partial stomatal closure (Fredeen and others 1997; LeCain and others 2003; Morgan and others 2004; Niklaus and Korner 2004; Nowak and others 2004b; Hovenden and others 2008; Adair and others 2011). Within and among seasons, eCO_2 effects on soil water tend to be cumulative, becoming stronger during dry-down periods following rain events (Niklaus and others 1998; Nelson and others 2004; Hovenden and others 2008). Weaker CO_2 effects on soil water have been observed when transpiration is limited by low leaf area or very low soil water, under very wet conditions, or when eCO_2-driven increases in whole-plant production offset leaf-level reduction in transpiration (Fredeen and others 1997; Hui and others 2001; Morgan and others 2004; Nowak and others 2004a, b; Hovenden and others 2008; Adair and others 2011). In semiarid ecosystems, eCO_2 tends to have more positive effects on soil water in moderately dry years and sites (rainfall from 300 to 500 mm) (LeCain and others 2003; Morgan and others 2004; Nowak and others 2004a, b), but variation within and among seasons remains poorly understood.

Warming may reduce soil water most when both evaporation and transpiration are high: warm, moist periods of the growing season (Dunne and Leopold 1978; Harte and others 1995). Evapotranspiration increases with temperature, but only until it becomes limited by soil water availability (Dunne and Leopold 1978). Consequently, the timing of warming effects on soil water in semiarid environments may depend on ambient soil water availability. The timing of warming effects may also be mediated by plant phenology. Earlier spring growth with warming can accelerate transpiration and therefore soil drying (Fischer and others 2007), whereas earlier senescence with warming has been found to increase late-season water availability (Zavaleta and others 2003). The few experimental studies to date in semiarid ecosystems, including Mediterranean shrublands and temperate grasslands and shrub steppes, suggest that warming most often reduces soil water (Llorens and others 2004; Lellei-Kovacs and others 2008; Niu and others 2008; Collins and others 2010; Morgan and others 2011; Mueller and others 2016). Little is known, however, about how and why warming effects vary over time.

Warming and eCO_2 might also interact to influence soil water. For example, higher vapor pressure deficit due to warming could act on greater leaf area with eCO_2 to increase transpiration and offset CO_2-induced reductions in transpiration at the leaf level (Dieleman and others 2012). Furthermore, such interactions could themselves vary seasonally with changes in drivers such as leaf area and ambient soil water. Evidence for interactive effects of eCO_2 and warming on soil water is mixed. In a Tasmanian perennial grassland, warming decreased soil water most strongly in combination with eCO_2 (Hovenden and others 2008). In contrast, decreases in soil water with warming in a southeastern US old field were offset by positive trends in soil water with eCO_2, but CO_2 and warming did not interact (Dermody and others 2007). CO_2 and warming effects on soil water were also additive in a California annual grassland, but with positive effects of both warming (due to earlier plant senescence) and eCO_2 (Zavaleta and others 2003). A better understanding of whether, how, and when eCO_2 and warming interact to influence soil water is needed to predict grassland responses to these global changes.

Previously, we have reported that eCO_2 increased soil water in mixed-grass prairie, while warming had the opposite effect (Morgan and others 2011). Interactive effects of eCO_2 and warming on soil water were rare: in the final 2 years of the study, warming reduced soil water most in plots treated with eCO_2 (Mueller and others 2016). These changes in soil water contributed to CO_2 and warming effects on plants and soils: eCO_2 and warming together increased plant productivity, growing season length, ecosystem respiration and plant invasion, and altered the abundance of soil nitrogen and phosphorus (Morgan and others 2011; Dijkstra and others 2012; Blumenthal and others 2013; Pendall and others 2013; Reyes-Fox and others 2014; Ryan and others 2015; Mueller and others 2016). Previous reports from the PHACE experiment, however, have focused on soil water averaged across short time periods (for example, the time of most rapid plant growth: DOY 100-200), with no effort to understand variability in CO_2 and warming effects within the growing season.

Here, we describe how free air CO_2 enrichment (FACE) and infrared warming effects on soil water vary among seasons and wet-dry periods. We predicted that (1) warming would reduce soil moisture most in the spring when it hastens green-up (Reyes-Fox and others 2014; Zelikova and others 2015) and when ambient soil moisture is high, and

least in the autumn, when both soil moisture and transpiration are relatively low, and (2) eCO_2 would increase soil moisture most in the summer, when there is ample leaf area and therefore high transpiration under ambient conditions.

METHODS

Study Site

We studied temporal variation in soil water within the Prairie Heating and CO_2 Enrichment (PHACE) experiment, 15 km west of Cheyenne, Wyoming, USA (latitude 41°11'N, longitude 104°54'W, elevation 1930 m). The experiment was located on undisturbed native mixed-grass prairie. Mean monthly temperatures at this site range from $-2.5°$ C in winter (January) to $17.5°$ C in summer (July). Mean annual precipitation is 397 ± 76 mm (mean $\pm$ SD, recorded from 1984 to 2013 at Cheyenne Airport; GHCND: USW00024018). About 80% of the annual precipitation occurs during the March-September growing season. Vegetation is composed of C_3 graminoids, including *Pascopyrum smithii* (Rydb.) A. Love, *Hesperostipa comata* Trin and Rupr, and *Carex eleocharis* L. Bailey, C_4 grasses, primarily *Bouteloua gracilis* (H.B.K) Lag., and a variety of forbs and subshrubs, notably *Sphaeralcea coccinea* (Nutt.) Rydb., and *Artemisia frigida* Willd. Many ecosystem processes at this site are strongly limited by water, including plant growth, and cycling of carbon, nitrogen and phosphorus (Derner and Hart 2007; Dijkstra and others 2012; Pendall and others 2013).

Experimental Design

The PHACE experiment contained four treatments: (1) control (ambient CO_2 and temperature), (2) free air CO_2 enrichment (FACE) to 600 ppmv, (3) infrared warming to increase canopy temperature 1.5 °C in the day and 3 °C at night, and (4) CO_2 enrichment plus warming. The target CO_2 and temperature levels were based on late 21st century projections for this region, which indicate that atmospheric CO_2 concentration could rise to 500–800 ppmv and mean annual temperature could increase 2.5–4 °C, under low and high emissions scenarios, respectively (Kunkel and others 2013). Actual treatment levels were 600.5 ± 50.4 ppmv CO_2 (mean $\pm$ SD, measured at 1 min intervals), and $+1.6 \pm 0.3$ °C (mean $\pm$ SD, measured at 1 h intervals) during the day and $+3.0 \pm 0.3$ °C at night (see Morgan and others 2011 for additional system performance details).

The CO_2 enrichment and warming treatments were applied to 7 m^2 circular plots beginning in 2006 and 2007, respectively. Five replications of each treatment were randomly assigned to 20 plots within two blocks, each occupying a different soil type: two replications within Ascalon Variant Loam (fine-loamy, mixed-mesic), and three replications within Altvan Loam (fine-loamy over sandy, mixed-mesic). The warming treatment was imposed year-round, and sometimes accelerated snowmelt during winter periods with measurable snow accumulation (D. LeCain, personal observation). Enrichment of CO_2 was limited to daylight hours when green plants were present and the site was not covered with snow. To control for potential infrastructure effects, we installed dummy FACE tubing and heaters at untreated plots. To minimize dilution of treatment effects through lateral water flow, we buried a 60-cm-deep plastic barrier around each plot prior to the start of the experiment.

Measurements

We measured soil volumetric water content (VWC) continuously with Sentek Envirosmart soil water sensors (Sentek Sensor Technologies, Stepney, SA, Australia) placed 10 and 20 cm below the soil surface. Sensors used frequency domain reflectometry to measure VWC. VWC records were logged hourly and then averaged daily. The soil volume measured by each sensor extends outward approximately 5 cm in all directions from its center; thus, the 10-cm sensor measured soil VWC between 5 and 15 cm, and the 20-cm sensor measured VWC between 15 and 25 cm. These measurements were averaged to estimate VWC at 5–25 cm depth. The 5–25-cm-depth increment contains most (> 75%) of the root biomass at this site (Schuman and others 1999), and facilitates comparison with previously reported soil VWC data from the site (Morgan and others 2011; Reyes-Fox and others 2014; Mueller and others 2016). Earlier reports show that this method of measuring VWC is accurate in soils with a range of textures (Campbell Scientific 2009; Maroufpoor and others 2009). Pre-experiment soil sampling adjacent to each PHACE plot revealed that soils at 0–30 cm depth were 60% sand (SD 5.0%, range 51–67%), 20% silt (SD 1.8%, range 17–24%), and 20% clay (SD 4.0%, range 14–29%). To accurately convert probe output to volumetric water content, the Envirosmart probes were initially normalized to the extremes of pure water and pure air (Sentek Sensor Technologies, Stepney, SA, Australia). The factory default calibration equation was then improved using three field calibrations, one in the center of each soil-type block, and one in an intermediate location. Soil cores were taken near the off-plot probes at each sensor depth over a typical range of soil water contents. Gravimetric soil core water content was converted to volumetric soil water content using soil bulk density. A linear correction was used to convert Sentek sensor readings to site-specific soil VWC measurements.

We recorded daily precipitation using a HOBO weather station (Onset Computer Corporation, Bourne, MA, USA) equipped with a tipping-bucket rain gauge (Onset S-RGB-M002). Missing data due to occasional sensor failure were replaced with data from a comparable weather station that was located approximately 1 km away from the PHACE experiment. The rain gauges at both weather stations did not adequately measure precipitation from snow events, so for months with substantial snowfall (October through May) we used average daily precipitation values derived from 5 weather stations in the National Climatic Data Center network (http://www.ncdc.noaa.gov/) that were within 10 km of the PHACE experiment.

We measured vegetation greenness from digital images of permanently marked 1 m^2 areas near the center of each plot. Images were taken from 2 m above ground (Booth and others 2004) between the end of March and the end of October at bi-weekly (in 2007, 2009, 2010 and 2011) or monthly (in 2008 and 2012) intervals. Greenness was calculated from each image using MATLAB R2011a to measure the hue, saturation, and value of each pixel within the image (The Math-Works, Natick, MA), as described in detail in Zelikova and others (2015). The resulting greenness values correlated well with plant cover measured using point count methods on the same images ($R^2 = 0.75$) (Zelikova and others 2015).

Data Analysis

We analyzed soil water patterns for the six full years of the study that included both eCO_2 and warming (2007–2012). As our primary interest was to understand interactions between global changes, soil water, and vegetation, we limited our analyses to the growing season, defined as the average date on which green plants were first observed (DOY 73) to the average date on which the last plants senesced (DOY 326) (Reyes-Fox and others 2014). We then divided the growing season into three equal sections that captured differences in plant cover and ambient soil water availability, two fac-

tors likely to influence CO_2 and warming effects (Figure 1). Hereafter, we refer to these three periods as spring, summer, and autumn (Figure 1; Appendix S1: Figure S1, Table S1). Spring (DOY 73-157, Mar 14–Jun 6) was relatively wet, with low green plant cover. Summer (DOY 158-242, Jun 7–Aug 30) encompassed both the dry-down period and the period of maximum green plant cover. Autumn (DOY 243-326, Aug 31–Nov 22) was relatively dry with low green plant cover.

Gaps in soil water content data due to the failure of sensors to record or transmit data occurred in
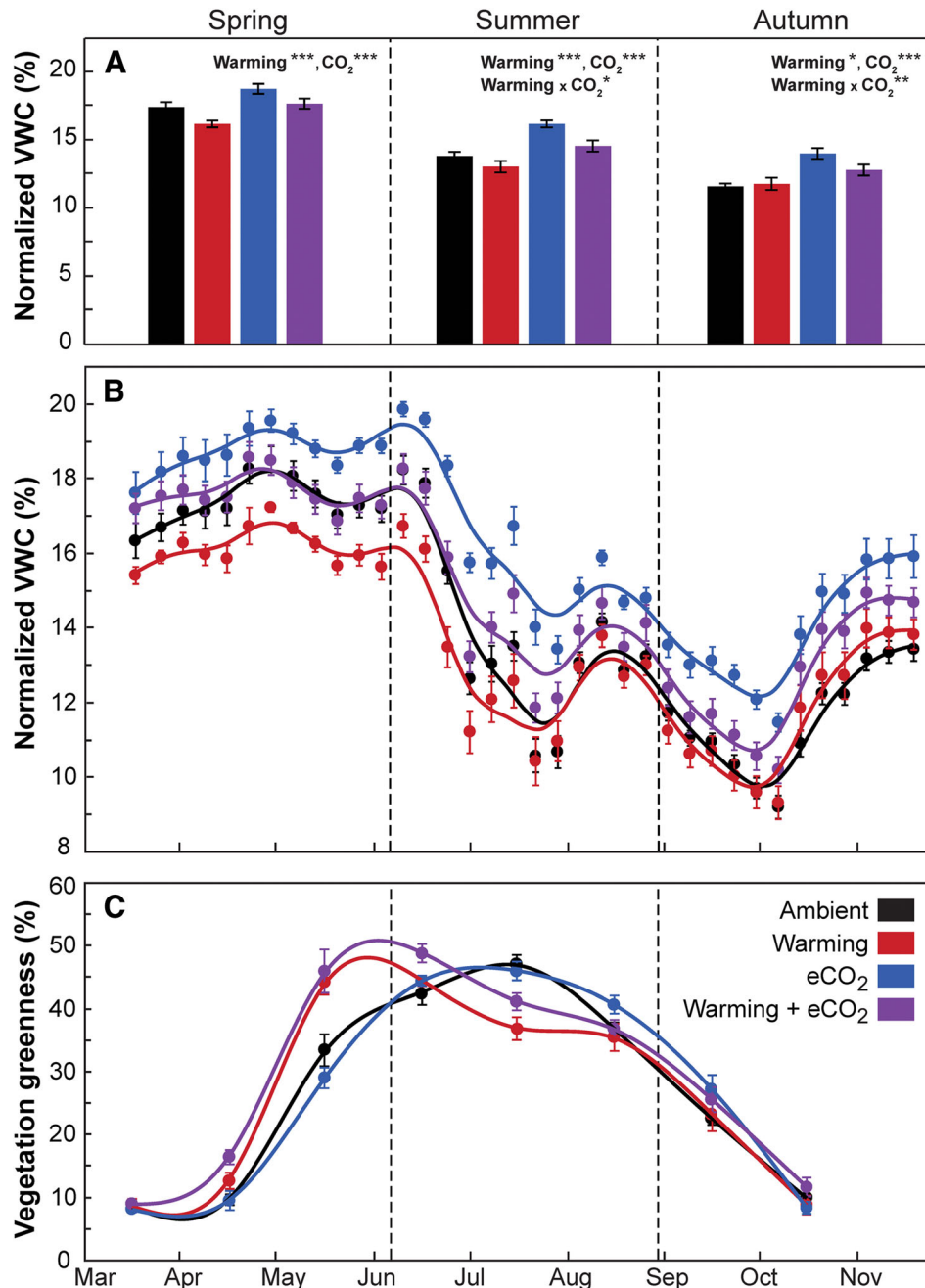
Figure 1. Seasonal patterns of normalized soil volumetric water content (VWC_{norm}) at 5–25 cm depth and greenness in spring (Mar 14–Jun 6), summer (Jun 7–Aug 30), and autumn (Aug 31–Nov 22). **A** Seasonal VWC_{norm} averaged across years and replicates, **B** weekly VWC_{norm} averaged across years and replicates with spline fit (lambda = 0.5); note that Y-axis starts at 8% VWC, **C** monthly greenness averaged across years and replicates, calculated from digital images, with spline fit (lambda = 0.5). In all panels, error bars represent variation among replicates ($\pm$ 1 SE); *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

only 2.9% of 30,480 observations. We filled these gaps using a regression approach. For each plot, we first determined which other plot had the most closely correlated VWC data. We then calculated predicted values for the plot containing the gap using a regression with the following predictor variables: VWC of closely correlated plot, month in experiment, and VWC × month (to account for variation in relationships between plots over time). In all cases, R^2 was greater than 0.98. Gaps were then filled with predicted values for the same days. For gaps that were also present in the most closely correlated plot, this process was repeated with the next most closely correlated plot until all gaps were filled.

Across the 20 plots in this experiment, there was a range of water holding capacity, which confounded the treatments and thus biased treatment effects. To account for this plot-level variation in VWC, we normalized the data relative to the maximum soil water content observed for each plot during the experiment (ranging from 20 to 28%). Shortly after periods of high rainfall, soils in all treatments were saturated, and this maximum soil water content was therefore not influenced by the experimental treatments. To create normalized VWC values, we first calculated the proportion of the daily VWC relative to each plots' maximum water content ($VWC_{daily}/MaxVWC_{plot}$). To return the response to VWC units, we then multiplied the daily proportion by the average of $MaxVWC_{plot}$ (24.5%). Using the normalized response values, mean values for each week (7 days) were calculated, with 12 weeks in each season.

Overall, VWC varied from 6.2 to 28% with a mean of 14.8% and standard deviation of 4.9%. For analyses of seasonal variation in CO_2 and warming effects, we accounted for large VWC fluctuations due to ambient climatic conditions (precipitation events of different duration and intensity) by calculating the deviations of the daily plot VWC value from the daily mean of all plots. These deviations were further consolidated into weekly averages and then used as response variables in repeated measures mixed model analyses. Mixed model analyses of VWC were conducted in SAS 9.4 with CO_2 and warming treatments, Season and their interactions as fixed effects. Because we accounted for spatial variation due to water holding capacity and temporal trends in VWC, blocking locations and year were not significant in explaining random variation. However, there was year to year variation explained by the plot by year random effect. Additionally, the treatments within a given year across all weeks were a significant

source of variation. These random effects were included in the mixed model (G-side); additionally, the repeated measures of weekly means for each plot within season were included (R-side) using an AR(1) covariance structure with sequential correlation dropping from $r = 0.87$ for week 1–2, to $r = 0.22$ for week 1–12 for an example plot.

To learn how treatment effects on soil water varied with ambient soil water, we regressed weekly means for each treatment (averaged across both days and replicates) against weekly means in control plots in JMP 12. To determine how global change treatments influenced daily variability in soil VWC, we calculated the daily coefficient of variation across the entire experiment for each plot. We then analyzed the response of the coefficient of variation to global change treatments with a 2-way CO_2 by warming mixed model in JMP 12, with block as a random effect. Greenness values were averaged by month and fitted with splines by treatment in JMP 12. Statistical analyses of greenness data have previously been reported by Zelikova and others (2015), and we refer to that work rather than re-analyzing greenness here.

RESULTS

Annual precipitation during the 2007–2012 study period ranged from 56 to 125% of the 30-year average (in 2007–2012, precipitation totaled 435, 410, 496, 378, 426, and 224 mm, respectively). Most growing season precipitation occurred during the spring and summer, whereas autumn precipitation was relatively low (Appendix S1: Figure S1, Table S1; see modified season definitions based on plant phenology in Materials and Methods). In general, spring and summer precipitation totals were similar, with the exception of 2010, when spring precipitation was higher than summer, and 2012, when summer precipitation was higher than spring.

Across 6 years, the response of normalized volumetric soil water content (VWC_{norm}) to eCO_2 was consistently positive, while responses to warming varied with both season and CO_2 level (Figure 1A, B; Table 1). In the spring, warming strongly reduced VWC_{norm} both on its own and in combination with eCO_2. As the season progressed, however, warming by CO_2 interactions indicated that the warming effect weakened in the absence of eCO_2. In the summer, warming reduced VWC_{norm} more in plots treated with eCO_2 than in plots with ambient CO_2. In the autumn, negative warming effects were observed only in eCO_2 plots. As reported previously by Zelikova and others (2015),

Table 1. Mixed Model Results for Effects of Warming and eCO_2 on Soil Volumetric Water Content Among and Within Seasons

Variable	Full growing season		Spring		Summer		Autumn	
	F_{df}	P	F_{df}	P	F_{df}	P	F_{df}	P
Warming	$67_{1,411}$	**<0.0001**	$37_{1,119}$	**<0.0001**	$44_{1,144}$	**<0.0001**	$6.2_{1,125}$	**0.014**
CO_2	$242_{1,410}$	**<0.0001**	$71_{1,118}$	**<0.0001**	$118_{1,143}$	**<0.0001**	$49_{1,125}$	**<0.0001**
Warming $\times$ CO_2	$8.9_{1,410}$	**0.003**	$0.15_{1,118}$	0.7	$4.7_{1,143}$	**0.032**	$7.4_{1,125}$	**0.0074**
Season	$0_{2,401}$	1						
Season $\times$ Warming	$3.2_{2,401}$	**0.043**						
Season $\times$ CO_2	$0.24_{2,401}$	0.78						
Season $\times$ Warming $\times$ CO_2	$4.1_{2,401}$	**0.018**						

Bold values indicate significant effects (P < 0.05).

warming hastened plant development and therefore increased greenness in the spring and decreased greenness later in the growing season (Figure 1C).

On a weekly time-scale, eCO_2 and warming effects also varied with ambient soil water content (Figure 2). Warming effects were most negative under moderately wet conditions (> 15% ambient VWC_{norm}) and changed to neutral or even positive as soils dried out (Figure 2A). The effects of eCO_2 were more positive for weeks with low to moderate ambient soil moisture (approximately 10–17% ambient VWC_{norm}), and less positive under very wet conditions (ambient VWC_{norm} > 20%) (Figure 2B). In combination, warming and eCO_2 tended to increase VWC_{norm} in dry weeks and have little effect on VWC_{norm} in weeks with high ambient soil moisture (Figure 2C). Strong positive effects of both warming and eCO_2 during weeks with intermediate ambient VWC_{norm} in 2011 followed an October snow storm and may be related to warming effects on snow. By ameliorating dry conditions, eCO_2 also led to a reduction in the daily coefficient of variation (CV) of VWC_{norm} from 32 to 28% ($F_{1,15} = 8.3$, $P = 0.01$) (Figure 3). Although the effect of eCO_2 on the CV appeared to be larger under ambient than elevated temperature conditions, the CO_2 by warming interaction was not significant ($F_{1,15} = 2.3$, $P = 0.15$).

DISCUSSION

Water availability, which mediates most plant ecological and biogeochemical processes in semiarid ecosystems, is likely to change with increasing atmospheric CO_2 concentrations and temperatures (Noy-Meir 1973; Norby and Luo 2004; Nowak and others 2004b; Mueller and others 2016). Here, we found that contrasting and interactive effects of eCO_2 and warming on soil water (Morgan and others 2011; Mueller and others 2016) vary over time, leading to net increases in soil water with eCO_2 and warming under dry conditions in the late summer and autumn, and reduced temporal variability in soil water.

Seasonal Effects of Warming and Elevated CO_2

Seasonal changes in both warming effects and warming by CO_2 interactions were pronounced (Table 1; Figure 1A, B). In ambient CO_2 plots, warming effects became progressively less negative as the growing season progressed. In contrast, warming effects in eCO_2 plots were consistently negative. We speculate that this CO_2 by warming by season interaction was caused by a combination of more persistent warming effects under the wetter soil conditions induced by eCO_2, and increased plant biomass (and likely transpiration) with the combination of warming and eCO_2 (Mueller and others 2016). Similar warming by CO_2 interactions have been observed at yearly time steps both in a Tasmanian grassland (Hovenden and others 2008) and in the final 2 years of the PHACE study (Mueller and others 2016). Earlier inter-annual analyses from the PHACE experiment in which the interaction was not observed included a subset of years and did not correct for plot-level variation in soil water (Morgan and others 2011; Reyes-Fox and others 2014). Stronger warming effects with eCO_2 in the summer and autumn may allow warming to counteract positive effects of eCO_2 on soil water during most of the growing season, and

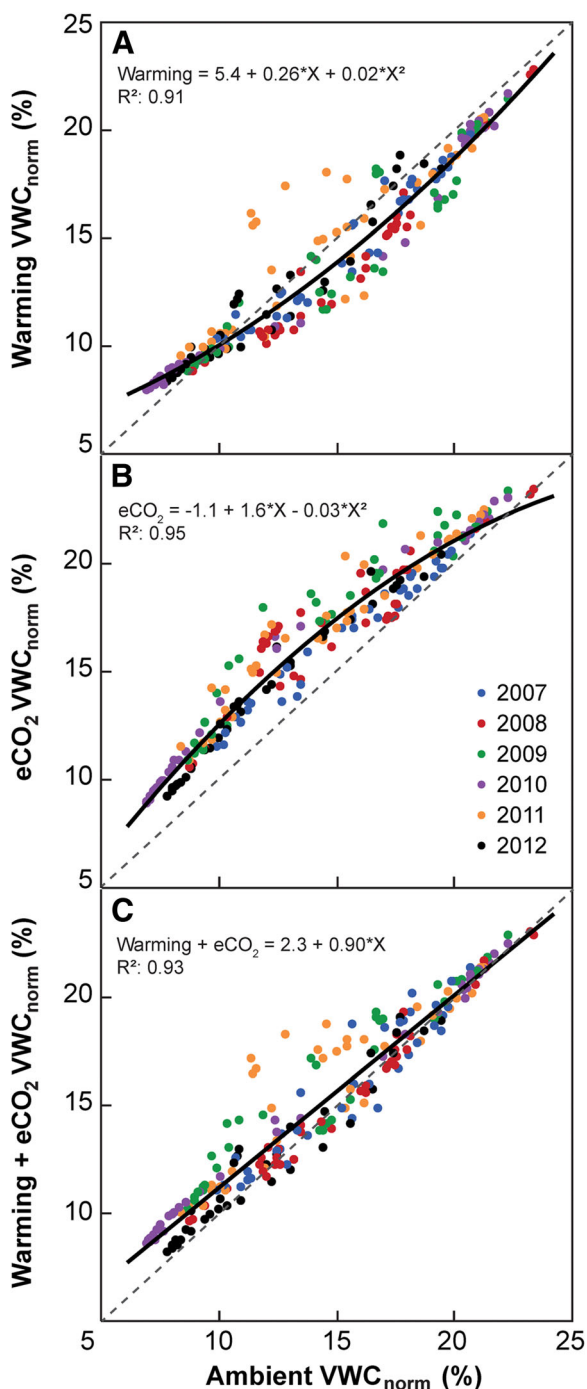Figure 2. Weekly normalized volumetric soil moisture content (VWC$_{norm}$) in each treatment relative to the control (5–25 cm depth). Each point depicts the treatment average across all replications and days within a given week. Points above and below dashed 1:1 lines depict positive and negative treatment effects, respectively. Second-degree polynomials were used when they resulted in lower AICc values, indicating more parsimonious models.
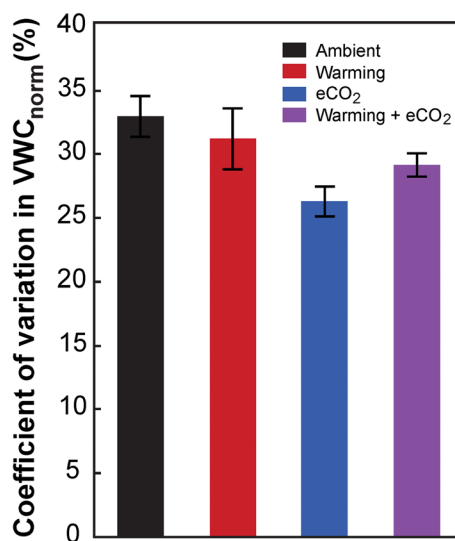

Figure 3. Effects of warming and eCO$_2$ on variability in normalized soil VWC (VWC$_{norm}$) at 5–25 cm depth. Coefficient of variation (CV) was calculated from normalized daily values of soil water content. Error bars are ± 1 SE.

limit net positive effects of these global changes on soil water availability. The presence of interactive effects on soil moisture also underscores the need for multi-factor studies to accurately capture and subsequently model global change effects in semi-arid ecosystems (Dieleman and others 2012).

Several processes may have caused the influence of warming alone to decline as the growing season progressed. First, as soils become drier in the late spring and early summer (Figure 1B), low soil water can limit both evapotranspiration and the absolute effect of temperature on evapotranspiration. Accordingly, evapotranspiration measured at PHACE in 2009–2012 decreased strongly late in the growing season, and only responded positively to temperature early in the growing season (Sorokin and others 2017). Both plant stomatal conductance and warming effects on soil water declined when soil VWC dropped below about 12% (Appendix S1: Figure S1) (Blumenthal and others 2013), further suggesting that warming had limited potential to influence transpiration, and therefore soil water, at such low VWC. Second, warming increased early-season leaf area, as measured by greenness (Figure 1C) (Zelikova and others 2015), which may have increased transpiration. Higher leaf area with experimental warming can also decrease evaporative water loss from soils (Harte and others 1995). However, the importance of transpiration in the hydrologic cycle of this region during the early growing season (Lauenroth and Bradford 2006)

suggests that higher leaf area with warming most likely increased early-season evapotranspiration (Sorokin and others 2017) and contributed to soil drying.

The sensitivity of warming effects to ambient water availability and leaf area (and therefore also to CO_2 effects on soil water and leaf area) seems likely to be common in water limited ecosystems. For example, in studies of Tasmanian grassland and Spanish Mediterranean shrubland, warming effects were often apparent under wet conditions early in the growing season and disappeared when soils became sufficiently dry (Llorens and others 2004; Hovenden and others 2008). These patterns, together with the results of the present study, suggest that in ecosystems with wide seasonal fluctuations in ambient water availability, warming may speed the onset of drought and then have smaller effects on soil water once conditions are very dry.

Where warming hastens vegetation senescence, it can actually increase soil water, as observed in a California annual grassland with predominantly winter precipitation (Zavaleta and others 2003). In our study, positive effects of warming on soil water were rare, but did occur under very dry conditions (Figure 2A), potentially due to earlier plant senescence with warming (Reyes-Fox and others 2014). The largest positive effects of warming were observed following an autumn snow storm in 2011 (Figure 2, orange points; Appendix S1: Figure S1), suggesting that warming sped snowmelt and thus either reduced sublimation, which can be substantial in this region (Schlaepfer and others 2014), or kept snow from blowing off of plots. Thus, another way in which warming may sometimes increase soil water is by increasing the proportion of winter precipitation that enters the soil.

Elevated CO_2 increased soil water across seasons, as indicated by the lack of a significant CO_2 by season interaction. Trends toward stronger eCO_2 effects in the summer and autumn, however, contributed to net increases in soil water with eCO_2 and warming together (Figure 1). These results are generally in accord with previous grassland studies showing eCO_2 to retard soil water loss either throughout the growing season or primarily later in the growing season (Fredeen and others 1997; Niklaus and others 1998; Dermody and others 2007).

Variation in CO_2 and Warming Effects with Ambient Soil Moisture

Warming and CO_2 effects had very different relationships with ambient soil moisture: eCO_2 made

the soil wetter when it was dry, and warming dried the soil when it was wet. Similarly, previous studies in European calcareous grassland and North American shortgrass steppe found eCO_2 to increase soil water most during drying cycles and least when soils were either saturated or dry enough that evapotranspiration was universally low (Niklaus and others 1998; LeCain and others 2003; Nelson and others 2004). Stronger effects of warming under wet conditions may be due to increased temperature sensitivity of evapotranspiration in the absence of water limitation. Because wet soil conditions were most common in the spring, earlier leaf development and water loss through transpiration may also have contributed to more negative warming effects on soil water. As with CO_2 effects, however, warming effects disappeared under very wet conditions, presumably because precipitation brought soils in all plots close to field capacity (Niklaus and others 1998). Combined effects of warming and eCO_2 on soil water ranged from neutral under wet soil conditions to positive under dry soil conditions.

By making the soil wetter during dry periods (Figure 2), eCO_2 also reduced temporal variation in soil water (Figure 3). Temporal variation in precipitation in mixed-grass prairie is expected to increase, with larger precipitation events and longer intervals between precipitation events, which may increase percolation, reduce evaporation, and increase productivity (Heisler-White and others 2009; Kunkel and others 2013; Sala and others 2015). Among years, both wetter- and drier-than-average seasons are also likely to become more common (Swain and Hayhoe 2015). Although eCO_2 may reduce within-season variability in soil water by slowing plant drawdown of soil water during dry periods between precipitation events (Figure 2), it may be less likely to ameliorate long-term droughts, because its influence on soil water declines during extended dry periods (Appendix S1: Figure S1) (Niklaus and others 1998; Nelson and others 2004).

Implications for Semiarid Grasslands

Both models and experiments suggest that water can mediate productivity responses to eCO_2 and warming (Rustad and others 2001; Morgan and others 2004; Nowak and others 2004a; Fatichi and others 2016; Hufkens and others 2016). Predictions for North American grasslands suggest that increases in productivity with longer growing seasons will be only partially offset by drier conditions, even without accounting for CO_2 effects (Hufkens

and others 2016). Here, increases in soil water with eCO_2 were often larger than decreases in soil water with warming, particularly under dry conditions when water is most limiting to plant growth (Figure 2), and therefore probably contributed to greater plant biomass with eCO_2 and warming together (Mueller and others 2016). These results suggest that in some semiarid grasslands, eCO_2 and warming will combine to yield modest increases in both soil water and plant productivity. They are also in accord with suggestions that models that do not incorporate eCO_2 may underestimate future grassland productivity (Reeves and others 2014b; Hufkens and others 2016).

Soil water can both influence and be influenced by plant phenology (Zavaleta and others 2003; Fischer and others 2007; Moore and others 2015). In the PHACE experiment, warming often hastened the development of plant canopies in the spring and sometimes reduced canopy greenness in mid-summer, while eCO_2 sometimes delayed senescence in the autumn (Reyes-Fox and others 2014; Zelikova and others 2015). Our finding that warming reduced soil water most in spring and summer (Figure 1) helps to explain why it reduced greenness in summer (Zelikova and others 2015), but rarely hastened full senescence in autumn (Reyes-Fox and others 2014). Furthermore, net positive effects of eCO_2 and warming on autumn soil water availability help to explain why eCO_2 delayed senescence not only on its own (Reyes-Fox and others 2014), but also in combination with warming. Together with direct effects of warming on early-season growth (Reyes-Fox and others 2014; Zelikova and others 2015; Hufkens and others 2016), these patterns suggest that the seasonal distribution of plant activity in semiarid grasslands may begin, peak, and decline earlier in the season but extend further into dry periods in the summer and autumn.

The timing of water-mediated CO_2 and warming effects can also influence plant communities. For example, in a Tasmanian grassland, reductions in winter and spring water availability with warming inhibited seedling survivorship of perennials (Hovenden and others 2008). The increases in soil water later in the growing season observed at PHACE could favor species which remain active during dry and cool conditions or autumn-germinating winter-annual species (Blumenthal and others 2016). While cool-season graminoids, many of which remain green during both dry and cool periods, did increase in relative abundance with eCO_2 plus warming (likely due in part to increased N availability), other late-season species, such as the subshrub *Artemisia frigida*, had the opposite response (Mueller and others 2016).

In sum, shifts toward greater late-season water availability with eCO_2 and warming may lead to longer growing seasons, modest increases in plant productivity, and increased abundance of plant species that can use mid- to late-season soil water. Such changes may be common in semiarid ecosystems, where variation in ambient moisture can alter the relative and interactive strength of CO_2 and warming effects on soil water.

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