

## Effects of climate and water balance across grasslands of varying $C_3$ and $C_4$ grass cover

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**Abstract.** Climate change in grassland ecosystems may lead to divergent shifts in the abundance and distribution of  $C_3$  and  $C_4$  grasses. Many studies relate mean climate conditions over relatively long time periods to plant cover, but there is still much uncertainty about how the balance of  $C_3$  and  $C_4$  species will be affected by climate at a finer temporal scale than season (individual events to months). We monitored cover at five grassland sites with co-dominant  $C_3$  and  $C_4$  grass species or only dominant  $C_3$  grass species for 6 yr in national parks across the Colorado Plateau region to assess the influence of specific months of climate and water balance on changes in grass cover.  $C_4$  grass cover increased and decreased to a larger degree than  $C_3$  grass cover with extremely dry and wet consecutive years, but this response varied by ecological site. Climate and water balance explained 10–49% of the inter-annual variability of cover of  $C_3$  and  $C_4$  grasses at all sites. High precipitation in the spring and in previous year monsoon storms influenced changes in cover of  $C_4$  grasses, with measures of water balance in the same months explaining additional variability.  $C_3$  grasses in grasslands where they were dominant were influenced primarily by longer periods of climate, while  $C_3$  grasses in grasslands where they were co-dominant with  $C_4$  grasses were influenced little by climate anomalies at either short or long periods of time. Our results suggest that future changes in spring and summer climate and water balance are likely to affect cover of both  $C_3$  and  $C_4$  grasses, but cover of  $C_4$  grasses may be affected more strongly, and the degree of change will depend on soils and topography where they are growing and the timing of the growing season.

**Key words:**  $C_3$  grass;  $C_4$  grass; climate change and variability; Colorado Plateau; long-term monitoring; native perennial grass cover; semiarid grasslands; Special Feature: Science for Our National Parks' Second Century; water balance.

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### INTRODUCTION

Long-term vegetation monitoring results, including those generated by the National Park Service's (NPS) Inventory and Monitoring (I&M) Program, are essential to understand the effects of climate at both regional scales and smaller, management-relevant scales. The response of grasslands to climate is of particular concern for

many land managers because these ecosystems and the plants within are important sources of diversity, provide forage and habitat for both wildlife and livestock, and engender soil fertility and stability (McClaran 1995). Grasslands may be especially vulnerable to climate change because grasses are shallow-rooted, short-lived, and can have large response to changes in water availability (Knapp and Smith 2001, Gremer

et al. 2015), likely challenging the NPS in the continued fulfillment of their mission to “conserve resources unimpaired for future generations” (NPS Organic Act 1916). As natural resource managers in national parks (NP) with grasslands prepare for climate change, they would benefit from knowing how the abundance of different grass functional types may shift, as these changes could alter ecosystem functions (e.g., soil stability and water storage) and have implications for managing parks with current or historical grazing.

Grass functional types can be determined by life span (annual or perennial) and photosynthetic pathway ( $C_3$  or  $C_4$ ), which are traits that affect timing of grass growth and overall performance across climate gradients.  $C_3$  grasses are generally more productive in cool climates at higher elevations and latitudes, while  $C_4$  grasses are generally more productive in warm climates at lower elevations and latitudes (Sage et al. 1999). Because of their higher water-use efficiency,  $C_4$  grasses are generally superior competitors under low water availability as well (Raven et al. 1992). Therefore,  $C_4$  grasses are thought to be favored by a dry spring and hot, wet summer, while  $C_3$  grasses tend to be favored by a wet spring and dry summer (Monson et al. 1983) with moderate temperatures (von Fischer et al. 2008).

$C_3$  and  $C_4$  grasses co-occur on the northern Colorado Plateau and can overlap in their growing seasons for much of the year, making this region an ideal place to study drivers of changes in the cover of the two grass functional types. The Colorado Plateau lies at the northern distribution of the North American Monsoon, which brings moisture north from the Gulfs of California and Mexico, and therefore, precipitation during the monsoon season from July through September has high inter-annual variability (Schwinning et al. 2008). On the northern Colorado Plateau,  $C_3$  grasses grow primarily in spring and early summer and secondarily in fall (Comstock and Ehleringer 1992). Depending on the species and intra-annual precipitation (i.e., seasonality of precipitation within a year),  $C_4$  grasses may initiate growth only slightly later than  $C_3$  species or may stay dormant until May, and then primarily grow throughout late summer when moisture is available (Comstock and Ehleringer 1992). The balance of  $C_3$  and  $C_4$  grasses is important to land

managers on the Colorado Plateau because livestock tend to utilize nutritionally rich  $C_3$  grasses more heavily in grasslands with both functional types due to grazing rotations that coincide primarily with the timing of  $C_3$  grass growth.

Soil and landscape attributes in dryland ecosystems are important moderators of climate that translate precipitation into plant water availability (Munson et al. 2015). Slope, aspect, and elevation can all have significant effects on the redistribution of water across the landscape, and soil properties such as depth, texture, and available water storage can affect the retention or depletion of water (Noy-Meir 1973, Smith et al. 1995). The moderating effects of soil and landscape attributes can be evaluated by stratifying the landscape according to ecological sites and through soil water balance models that both account for these attributes (Stephenson 1998, Lutz et al. 2010). Ecological sites are classified based on distinctive land types with specific soil, climate, and landscape factors that have the potential to produce distinctive kinds and amounts of vegetation, and respond to disturbance in a predictable way (USDA/USDI 2013). Water balance models add this site-specific information to temperature (T) and precipitation (P) data to derive the amount of stored soil moisture (SM), water that is lost from the soil via evapotranspiration (AET), and water deficits (D) that are related to the magnitude and length of drought stress that plants experience (Stephenson 1998). These metrics may be more directly related to plant physiological response than precipitation alone because SM storage in water-limited environments helps maintain plant productivity through dry seasons and years (Bisigato et al. 2013, Campo-Bescós et al. 2013).

Seasonality of precipitation, and more specifically, the proportion of total precipitation in summer, is related to the productivity of  $C_4$  grasses (Paruelo and Lauenroth 1996, Winslow et al. 2003). The amount of cool-season precipitation has also been linked to changes in cover of  $C_3$  grasses on the Colorado Plateau (Munson 2013). However, there is still much uncertainty about how the balance of  $C_3$  and  $C_4$  species will be affected by climate at a finer temporal scale than season (individual events to months). Relationships between climate/water balance and vegetation production in grasslands at monthly

timescales have only recently been examined, and the importance of different climate and water balance metrics can vary by month and season (Thoma et al. 2016).

In addition, extreme climate events, such as longer, more intense droughts and large amounts of precipitation that fall over a relatively short period of time, are predicted to become more common (Schlesinger and Mitchell 1987, Mitchell 1990); but how these extremes will affect the balance of  $C_3$  and  $C_4$  grass species is not well understood. Overall, the southwest is projected to be hotter and drier (Ault et al. 2014, Garfin et al. 2014), and any potential increases in precipitation that may occur will not likely be enough to offset the drying effect caused by higher temperature (Seager et al. 2007). Temperature already exceeds its historic range of variability in parks of the southwest (Monahan and Fisichelli 2014), and warmer conditions potentially favor  $C_4$  grasses because they have a higher optimal temperature for photosynthesis and higher drought resistance (Sage et al. 1999). Fewer larger (extreme) rainfall events increased aboveground productivity relative to many small events at a semiarid short-grass prairie ( $C_4$ -dominated), but not at a northern mixed grass prairie ( $C_3$ -dominated; Wilcox et al. 2015), and thus, we might expect different responses from  $C_3$  and  $C_4$  grasses within grasslands co-dominated by both functional types or among different ecological sites.

We analyzed changes in cover at five grassland sites in the Colorado Plateau region with varying degrees of  $C_3$  and  $C_4$  species dominance, and related these changes to climate (T and P) and water balance (SM, AET, and D) anomalies from the long-term mean. To better understand climate at a finer temporal resolution, we examined how individual months of climate influenced grass cover and compared this with the additive effect of climate that spans longer than a month, which is likely to be an important influence on drought resistant, dryland species that can take longer than a month of water shortage or surplus to respond. Our analysis emphasized months when especially high or low values of a climate or water balance variable had a strong effect on grass cover.

In this study, we had two main objectives, which we assessed across communities with varying degrees of  $C_3$  and  $C_4$  grass species

dominance. First, we compared the inter-annual changes in  $C_3$  and  $C_4$  grass cover across semiarid grassland ecological sites and examined how they responded to extreme climate events and, more specifically, to a six-month drought followed by an extreme precipitation event ( $>90$  mm over 8 days). We hypothesized that inter-annual changes in cover would be related to cool-season moisture for  $C_3$  grasses and monsoon moisture for  $C_4$  grasses. We also hypothesized that the cool-season drought in our study would reduce cover of  $C_3$  grasses more than  $C_4$  grasses and that extremely high P in monsoon months would benefit  $C_4$  grasses more than  $C_3$  grasses. In addition, we expected that sites with the capacity to store a large amount of soil moisture would contain grasses less affected by drought and that strongly increased in abundance following extreme precipitation events.

Second, we evaluated which climate and water balance drivers, and which periods of time associated with these drivers, were most important for explaining changes in cover of  $C_3$  and  $C_4$  grasses. Overall, we expected grass cover to have positive correlations with P, AET, and SM, negative correlations with D, and positive correlations with T in the late winter and early spring months when growth could be accelerated, and negative correlations with T in the summer months because of increased evaporative losses from soil. We also expected water balance variables to be more closely related to grass cover than precipitation for both functional types. More specifically, we hypothesized that winter SM would be related to  $C_3$  grass cover, summer D would be related to  $C_4$  grass cover, and AET during the growing season would be related to cover of both functional types. Climate or water balance in other shorter periods of time could also be important, such as higher-than-average T in early spring or late fall months that could extend the growing season for  $C_3$  grasses.

## METHODS

### Sites

Grasslands were sampled in five NPs that spanned the northern Colorado Plateau, Uinta Basin, and Gunnison Basin (Fig. 1). Mean January low temperatures range from  $-16.6^{\circ}\text{C}$  in Curecanti National Recreation Area (NRA) to  $-7.2^{\circ}\text{C}$  in

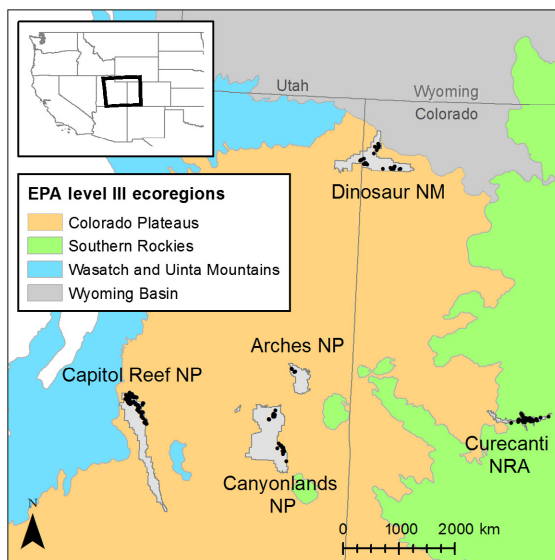


Fig. 1. Grasslands monitored in five national park units in and around the Colorado Plateau ecoregion. Dots represent locations of permanent vegetation plots.  $C_3/C_4$ -co-dominant grasslands are located in Arches, Canyonlands, and Capitol Reef national parks (NP).  $C_3$ -dominant grasslands are located in Curecanti National Recreation Area (NRA) and Dinosaur National Monument (NM). Ecoregions were defined using U.S. Environmental Protection Agency (EPA) Level III Ecoregions.

Canyonlands NP. Mean July high temperatures range from 27.2°C in Curecanti NRA to 34.7°C in Arches NP. All of the park grasslands are semi-arid with mean annual precipitation ranging from 231 to 350 mm. Precipitation tends to be evenly distributed throughout the year, with the exception that June is consistently the driest month and spring and late summer can be wetter. Precipitation in July–September is attributable to the North American Monsoon (hereafter, “monsoon”), but this source of precipitation has high inter-annual variability because the Colorado Plateau is situated at the monsoon’s northern-most distribution (Schwinning et al. 2008). All grasslands were historically grazed by livestock, and some parts of Capitol Reef NP, Curecanti NRA, and Dinosaur National Monument (NM) continue to have active livestock grazing allotments.

Based on our objectives above, we divided grasslands into two groups: (1) grasslands co-dominated by  $C_3$  and  $C_4$  grasses (i.e., at least

25% mean grass cover from each photosynthetic pathway, hereafter “ $C_3/C_4$  co-dominant”) and (2) grasslands dominated by  $C_3$  grasses with little or no cover of  $C_4$  grasses (hereafter “ $C_3$  dominant”). There were not enough grasslands dominated by  $C_4$  grasses to be considered further.

Grasslands were assigned ecological sites using ecological site descriptions (USDA/USDI 2013), Natural Resources Conservation Service (NRCS) soil surveys (USDA 1975, 2007, 2010a, b, USDA/USDI 2014), and field observations of landform, vegetation, and soil properties. We combined ecological sites with similar vegetation, soils, geomorphology, and response to disturbances into ecological site groups (ESGs), which reduces redundancy and can be used to effectively assess broad-scale drivers, including climate (Bestelmeyer 2015).

The  $C_3/C_4$ -co-dominant grassland consisted of three ESGs, Semidesert Sand, Saline-Alkaline, and Rocky, that spanned three NP units (see Table 1 for additional details). All of these ESGs have deep soils and occur at lower elevations (1200–2000 m), but vary in soil texture, salinity, and rock content, as the ESG names imply (e.g., Semidesert Sand has sandy soils, Saline-Alkaline has saline and/or alkaline soils, and Rocky has up to 60% cover of rocks). All ESGs have dominant native perennial grasses (see Table 1 for dominant species at each ESG). In the Saline-Alkaline and Rocky ESGs, cover of  $C_4$  grasses is higher than that of  $C_3$  grasses, while cover of  $C_3$  grasses is higher than that of  $C_4$  grasses in the Semidesert Sand ESG (Table 1).

The  $C_3$ -dominant grassland consisted of two ESGs, Mountain Loam and Sagebrush, which span two NP units (see Table 1). These ESGs occur at higher elevations (1800–2600 m) and have higher annual precipitation (333–350 mm) than  $C_3/C_4$ -co-dominant grasslands (231–257 mm). Cover of perennial grasses in  $C_3$ -dominant grasslands is more than two times higher than in  $C_3/C_4$ -co-dominant grasslands (Table 1). The growing season of  $C_3$  grasses in these grasslands starts a month or so later than in the  $C_3/C_4$ -co-dominant grassland (around April), and continues through approximately September (D. L. Witwicky, *personal observation*). Ecological site descriptions were not available for the Sagebrush ESG at Curecanti NRA so we used range sites from the soil survey (USDA 1975) to define this

Table 1. Description of long-term vegetation monitoring sites at C<sub>3</sub>/C<sub>4</sub>-co-dominant and C<sub>3</sub>-dominant grasslands in the northern Colorado Plateau ecoregion, including elevation, precipitation, total number of plots sampled, park units, ecological sites, soils, landforms, and dominant grass species and cover from 2009 to 2014.

| Site(s)                                    | Elevation (m) | Mean annual precipitation (mm) | Total number of plots | Park unit(s)     | Ecological sites†      | Soils and landforms                                                                                             | Dominant grass species (photosynthetic pathway)                                                                        | Mean perennial grass cover from 2009 to 2014 (SE) |                    |
|--------------------------------------------|---------------|--------------------------------|-----------------------|------------------|------------------------|-----------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------|--------------------|
|                                            |               |                                |                       |                  |                        |                                                                                                                 |                                                                                                                        | C <sub>3</sub> (%)                                | C <sub>4</sub> (%) |
| C <sub>3</sub> /C <sub>4</sub> co-dominant |               |                                |                       |                  |                        |                                                                                                                 |                                                                                                                        |                                                   |                    |
| Semidesert Sand                            | 1200–1900     | 255                            | 46                    | ARCH, CANY, CARE | DS, DSL, SDS, SDSL     | Deep sands and sandy loams on valley bottoms, cuestas, and structural benches                                   | ACHY (C <sub>3</sub> ), BOGR (C <sub>4</sub> ), HECO (C <sub>3</sub> ), PLJA (C <sub>4</sub> ), SPCR (C <sub>4</sub> ) | 4.4 (0.4)                                         | 3.2 (0.4)          |
| Saline-Alkaline                            | 1550–2000     | 244                            | 43                    | CARE             | AF, AB, DASL, DL, DStL | Deep fine sandy loams, silt loams, and loams with slight to strong salinity and/or alkalinity on valley bottoms | ACHY (C <sub>3</sub> ), BOGR (C <sub>4</sub> ), PLJA (C <sub>4</sub> ), SPAI (C <sub>4</sub> )                         | 2.6 (0.3)                                         | 5.5 (0.5)          |
| Rocky                                      | 1550–2000     | 231                            | 26                    | CARE             | SDStL                  | Deep stony sandy loams on benches and slopes                                                                    | ACHY (C <sub>3</sub> ), PLJA (C <sub>4</sub> )                                                                         | 2.4 (0.3)                                         | 3.8 (0.3)          |
| C <sub>3</sub> dominant                    |               |                                |                       |                  |                        |                                                                                                                 |                                                                                                                        |                                                   |                    |
| Mountain Loam                              | 1800–2450     | 350                            | 27                    | DINO             | ML, RL                 | Deep loams on benches and slopes                                                                                | HECO (C <sub>3</sub> ), PASM (C <sub>3</sub> ), POFE (C <sub>3</sub> )                                                 | 18.2 (1.6)                                        | 0.0 (na)           |
| Sagebrush                                  | 2300–2600     | 333                            | 29                    | CURE             | DML, ML                | Deep loams to shallower rocky soils on valley bottoms and slopes                                                | ACLE (C <sub>3</sub> ), HECO (C <sub>3</sub> ), POFE (C <sub>3</sub> )                                                 | 13.0 (0.9)                                        | 0.5 (0.1)          |

Notes: Park unit abbreviations are as follows: ARCH, Arches National Park; CANY, Canyonlands National Park; CARE, Capitol Reef National Park; DINO, Dinosaur National Monument; CURE, Curecanti National Recreation Area. Ecological site abbreviations are as follows: AB, Alkali Bottom (greasewood); AF, Alkali Flat (greasewood); DASL, Desert Alkali Sandy Loam (alkali sacaton); DL, Desert Loam (shadscale); DML, Dry Mountain Loam; DS, Desert Sand (fourwing saltbush); DSL, Desert Sandy Loam (fourwing saltbush); DStL, Desert Stony Loam (shadscale-budsage); ML, Mountain Loam (mountain big sagebrush); RL, Rolling Loam; SDS, Semidesert Sand (fourwing saltbush); SDSL, Semidesert Sandy Loam (fourwing saltbush); SDStL, Semidesert Stony Loam (shadscale). Species abbreviations are as follows: ACHY, *Achnatherum hymenoides*; ACLE, *Achnatherum lettermanii*; BOGR, *Bouteloua gracilis*; HECO, *Hesperostipa comata*; PASM, *Pascopyrum smithii*; PLJA, *Pleuraphis jamesii*; POFE, *Poa fendleriana*; SPAI, *Sporobolus airoides*; SPCR, *Sporobolus cryptandrus*. SE, standard error.

† Ecological sites are part of the following Major Land Resource Areas (MLRAs): MLRA 35 for ARCH, CANY, and CARE; MLRA 34 and 47 for DINO; MLRA 48 for CURE.

ESG, which included a wider range of soils than the other ESGs.

#### Data and sampling design

**Vegetation.**—All sites are part of the northern Colorado Plateau long-term inventory and

monitoring program for upland vegetation (Witwicki et al., *in press*), which utilizes complex survey and revisit designs to provide robust estimates of status and trend of resources (Urquhart and Kincaid 1999, Stevens and Olsen 2004). Within each park, grasslands were mapped by ESG, and

spatially balanced random points (Stevens and Olsen 2004, Kincaid and Olsen 2006, Theobald et al. 2007) within those areas designated the center of each monitoring plot. Due to the complex schedule of plot visits (i.e., no plot was visited every year and the number of plots visited in each ESG varies by year), we only included plots with two or more visits between 2009 and 2014 in our analysis (see Table 1 for the total number of plots by ESG). The plots in each ESG were monitored within the same 4 weeks each year, timed to approximately coincide with the peak of growth. In the  $C_3/C_4$ -co-dominant grasslands, we sampled plots in April, May, or June, and in the  $C_3$ -dominant grasslands, we sampled plots in June, July, August, or September. Any plots sampled outside of these seasonal time frames were excluded from the analysis.

Plots consisted of three parallel 50-m transects that were spaced 25 m apart and marked with permanent monuments. Along transects, we sampled live cover of plant species at 300 points using a line-point intercept method derived from Herrick et al. (2005) and described in detail in Witwicki et al. (*in press*). We summarized the cover of native perennial grasses by photosynthetic pathway ( $C_3/C_4$ ; Osborne et al. 2014) for each plot by year by dividing the total number of intercepted points for each functional type by 300 and multiplying by 100. To account for different lengths of time between revisits, we calculated change in cover at each plot between each sampling date following Munson (2013) as

$$\text{Change in cover} = \frac{\ln(\text{cover}_{t2}/\text{cover}_{t1})}{t2 - t1} \times 10 \quad (1)$$

where  $\text{cover}_{t2}$  is plant cover in year  $t2$  and  $\text{cover}_{t1}$  is plant cover in the previous sampling year,  $t1$ . We then calculated the mean change in cover across all plots in an ESG by year (indicated by  $t2$ ).

*Climate and water balance.*—We obtained climate data from Daymet (Thornton et al. 2014) for the 1-km pixel that coincided with the center of each plot. Mean monthly temperature, mean monthly precipitation, and soil water holding capacity (WHC) were summarized and entered into a Thornthwaite-type monthly water balance model that estimates water input to the soil, soil moisture storage, and loss of water via evapotranspiration (Dingman 2002). The monthly water balance

equations were identical to Lutz et al. (2010), except that we calculated the water balance for each year separately and carried December soil moisture and snow pack over to the following January as recommended by Bisigato et al. (2013). Soil WHC was derived from the entire soil profile of the corresponding soil components in NRCS soil map units (USDA 1975, 2007, 2010a, b, USDA/USDI 2014) and was an average weighted by the percentage of each soil component within a map unit.

Based on previous studies of plant growth in semiarid regions (Huber et al. 2011, Campo-Bescós et al. 2013), we chose the following set of climate and water balance variables: (1) temperature (T), (2) precipitation (P), (3) soil moisture (SM), (4) actual evapotranspiration (AET), and (5) water deficit (D). Soil moisture is the quantity of water stored in the soil at the end of each month (mm). Actual evapotranspiration is the monthly upward loss of water from soil via transpiration and evaporation, which is limited by soil moisture availability. The model also includes potential evapotranspiration (PET), which is the amount of water that could be evaporated and transpired with available energy if water availability was unlimited to a short grass. Deficit, a measure of drought stress, is the amount of additional water vegetation would use if it was available, calculated as the difference between monthly PET and AET (Stephenson 1998). For data summarized over multiple months, P, AET, and D were summed over the months of interest while T and SM were averaged.

Climate and water balance data were relativized as the difference from the long-term mean (1980–2014) for each plot. To evaluate the P received during the years of our study, we plotted percentiles of the historic P distribution (1980–2014) for annual (i.e., water year = October of preceding year through September) and seasonal measures of P and delineated the following categories similar to Knapp et al. (2015): extremely dry (<10th percentile) and extremely wet (>90th percentile). For the summer monsoon, we summed P in July through September, and for the cool season, we summed P in October through April.

## Analyses

*Inter-annual changes in  $C_3$  and  $C_4$  grass cover and responses to extreme climate events.*—We summarized grass cover by ESG and year to show absolute cover over the years of our study; however, all hypothesis

tests were performed on the change in cover data. We used linear models and repeated-measures linear mixed-effects models to test for significant changes in grass cover by year for  $C_3$  and  $C_4$  functional types in each ESG. We used change in cover as our response variable and associated this value with the later year used in the calculation (i.e., by  $t_2$  in Eq. 1). Observations more than three standard deviations from the mean were removed as outliers (<2% of data), and the minimum sample size was four. We analyzed mixed-effects models in R 3.1.1 (R Core Team 2014) with the lme4 package (Bates et al. 2015) and used the multcomp package for linear contrasts (Hothorn et al. 2008). We adjusted  $P$ -values with the false discovery rate (FDR; Benjamini and Hochberg 1995), which controls the proportion of type I errors (i.e., false discoveries) without the unwanted side effect of high type II errors (i.e., not recognizing significant findings) that occurs with a familywise error rate (Verhoeven et al. 2005, Pike 2011). Due to the complex schedule of plot visits (i.e., all plots were not visited every year), we were not able to test changes in cover for the Saline-Alkaline, Rocky, and Mountain Loam ESGs in 2010, the Sagebrush ESG in 2011, or the Mountain Loam ESG in 2012.

*Correlations of  $C_3$  and  $C_4$  grasses with climate and water balance.*—We assessed how climate and water balance variables related to change in grass cover up to 12 months prior to each sampling date using zero-order correlations. In the  $C_3/C_4$ -co-dominant grasslands, we evaluated cover of  $C_3$  and  $C_4$  grasses separately, and in the  $C_3$ -dominant grasslands, we evaluated only the cover of  $C_3$  grasses. For all three groups, we correlated change in cover with the relativized difference of each monthly or multi-month climate and water balance variable (T, P, D, AET, SM) using Pearson's product-moment correlation coefficient. For each correlation, observations more than three standard deviations from the mean were removed as outliers ( $\leq 6\%$  of data).

Monthly climate and water balance variables were related to changes in cover and were used to help isolate important events, such as the beginning of the growing season and the monsoon. Monthly anomalies were calculated as

$$\text{Anomaly}_m = c_m - \frac{\sum_{y=1981}^{y=2014} c_m}{n} \quad (2)$$

where  $c_m$  is the sum (P, D, AET) or mean (T, SM) of each climate or water balance term at the end of a single month,  $y$  is year, and  $n$  is total number of months in the long-term record.

Multi-month climate and water balance variables considered the additive effect of climate beginning the month before we sampled a plot and continuing back in time through the month we were evaluating. The multi-month approach helps to account for the additive effect of climate or water balance that spans longer than a month, including important seasons like summer monsoon and cool-season precipitation. Multi-month anomalies were calculated as

$$\text{Anomaly}_1 = \sum_{m=i}^{m=j} \text{Anomaly}_m \quad \text{for variables P, AET, and D} \quad (3)$$

and

$$\text{Anomaly}_1 = \frac{\sum_{m=i}^{m=j} c_m}{q} - \frac{\sum_{y=1981}^{y=2014} \frac{\sum_{m=i}^{m=j} c_m}{q}}{n} \quad \text{for variables T and SM} \quad (4)$$

where  $m$  is month,  $i$  is the month immediately prior to when a plot was sampled,  $j$  is a month one to 12 months before a plot was sampled, and  $q$  is the total number of months from  $i$  to  $j$ .

We were interested in the influence of monthly climate and water balance variables, but grass cover was sampled over a range of months that varied by park and ESG. Therefore, we selected a month in the center of the sampling window for each grassland type as the first month to examine correlations (i.e., May for  $C_3/C_4$ -co-dominant and July for  $C_3$ -dominant grasslands). We then isolated the climate and water balance effects of months just prior to the cover sampling window in our analysis. FDR (Benjamini and Hochberg 1995) was used to adjust  $P$ -values for determining multiple monthly and multi-month anomaly correlations for each climate and water balance variable. We assessed overall goodness of fit ( $R^2$ ) of multiple regression models with repeated measures using the MuMIn package (Barton 2016) in R. In each model, we included all climate and water balance variables that were correlated with change in cover as fixed effects and year as a random effect to account for temporal autocorrelation.

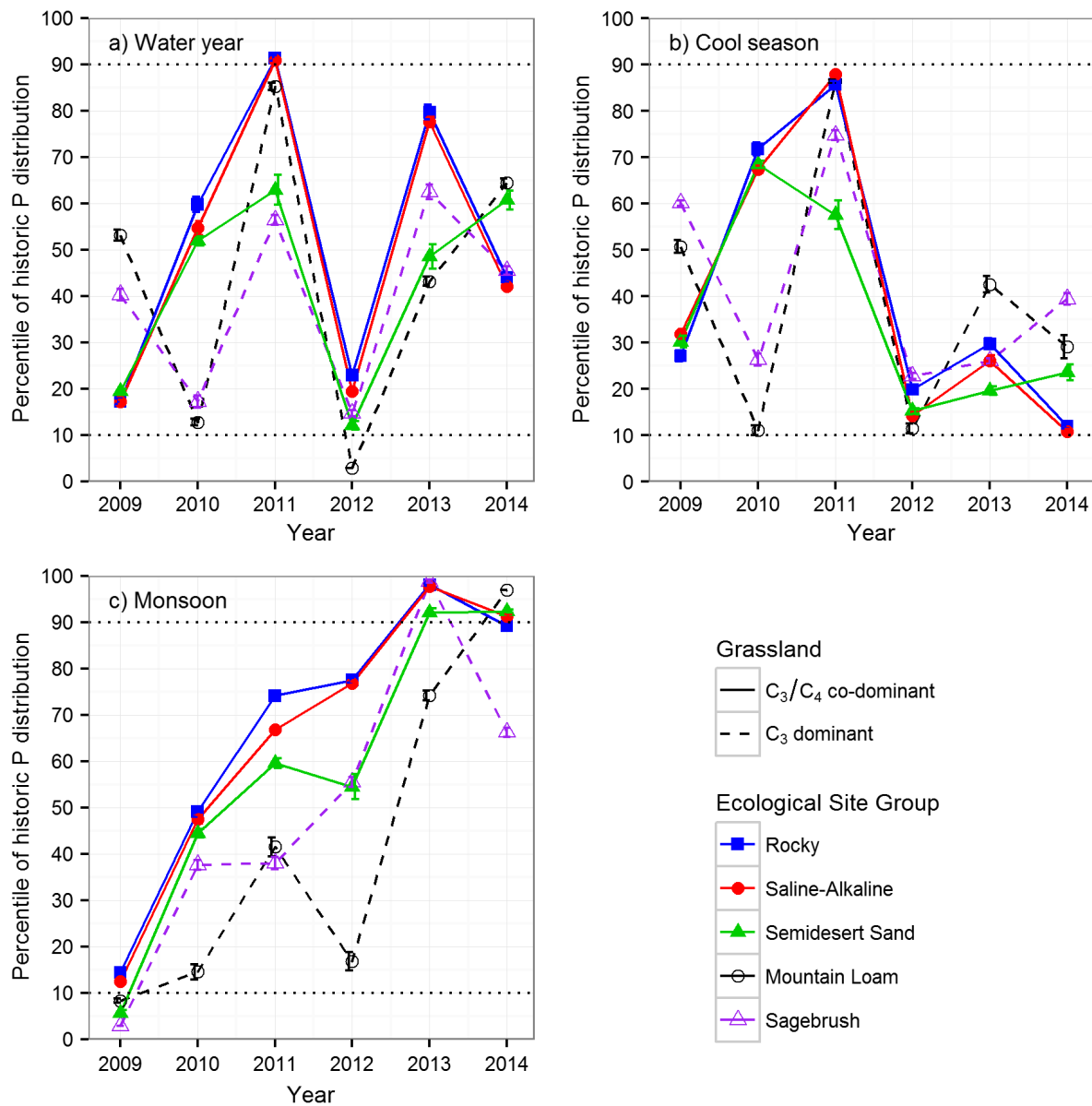


Fig. 2. Annual and seasonal precipitation summaries by ecological site group for 2009–2014. Values are percentiles of historic precipitation (P) distribution (1980–2014) for (a) water year (October of preceding year through September), (b) cool season (October through April), and (c) monsoon (July, August, and September). Error bars are standard errors. Values >90th percentile are considered extremely wet, and values <10th percentile are considered extremely dry.

## RESULTS

### *Inter-annual changes in C<sub>3</sub> and C<sub>4</sub> grass cover and responses to extreme climate events by ecological site group*

Cool-season, monsoon, and water year precipitation varied widely over the years of our study

(Fig. 2), yet there were few changes in C<sub>3</sub> grass cover in ESGs of either grassland type (Fig. 3a; Appendix S1: Fig. S1a). In C<sub>3</sub>-dominant grasslands, there were no changes in C<sub>3</sub> grass cover from 2009 to 2014 except a marginally significant decrease in cover at the Sagebrush ESG in 2010 ( $z = -2.3$ ,  $P_{\text{adj}} = 0.08$ ). The only significant

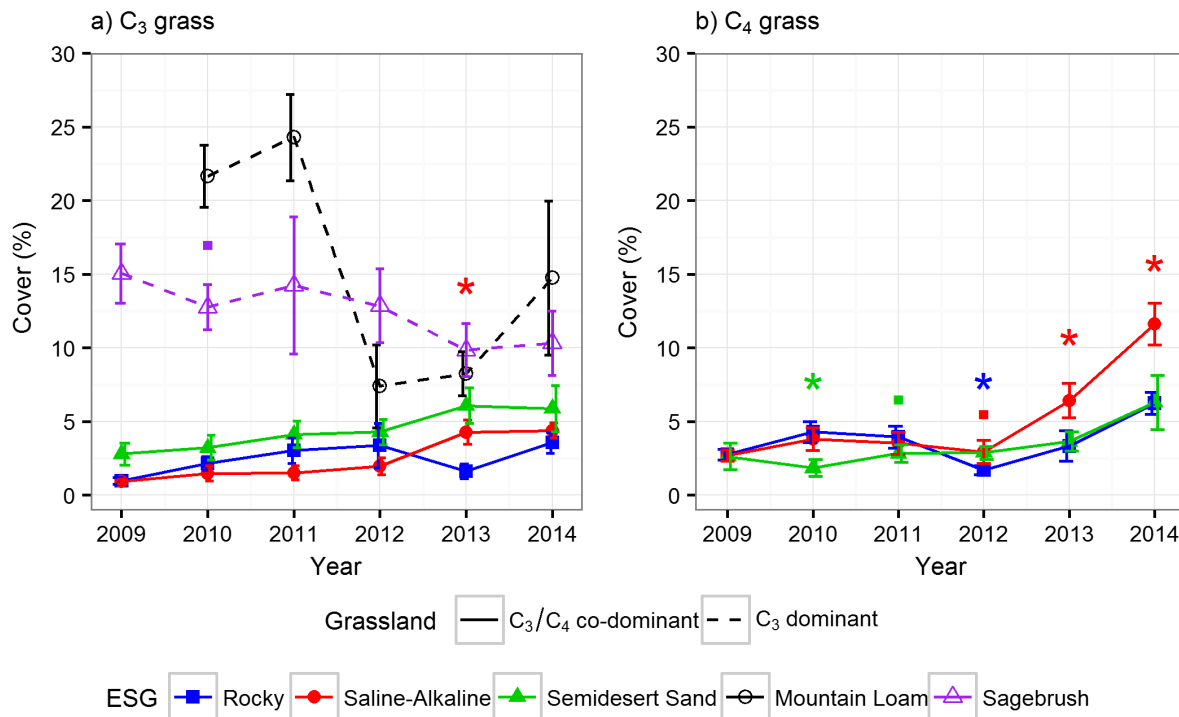


Fig. 3. Native perennial (a) C<sub>3</sub> and (b) C<sub>4</sub> grass cover by ecological site group (ESG) and year. Error bars are standard errors. Asterisks indicate significant ( $P_{adj} < 0.05$ ) increases or decreases in grass cover by year and are color-coded by ESG. Dots indicate marginal significance ( $P_{adj} < 0.1$ ). The decrease in C<sub>3</sub> grass cover at the Mountain Loam ESG in 2012 could not be tested due to a low sample size.

inter-annual change in C<sub>3</sub> grass cover for the C<sub>3</sub>/C<sub>4</sub>-co-dominant grasslands was an increase in cover at the Saline-Alkaline ESG in 2013 ( $z = 3.9$ ,  $P_{adj} < 0.001$ ), which corresponded with increases in *Achnatherum hymenoides* cover ( $z = 5.3$ ,  $P < 0.001$ ; Appendix S1: Fig. S2a).

Changes in C<sub>4</sub> grass cover occurred in all ESGs in the C<sub>3</sub>/C<sub>4</sub>-co-dominant grasslands, but varied by ESG and year (Fig. 3b; Appendix S1: Fig. S1b). In the Semidesert Sand ESG, C<sub>4</sub> grass cover decreased in 2010 ( $t = -2.9$ ,  $P_{adj} = 0.03$ ) and increased marginally in 2011 ( $t = 2.1$ ,  $P_{adj} = 0.096$ ). Increases in C<sub>4</sub> grass cover occurred at the Saline-Alkaline ESG in 2013 ( $z = 2.4$ ,  $P_{adj} = 0.03$ ) and corresponded with increases in *Bouteloua gracilis* cover ( $z = 2.6$ ,  $P_{adj} = 0.02$ ; Appendix S1: Fig. S2b). All other changes in C<sub>4</sub> grass cover were associated with extreme climate conditions that occurred during our study.

There was a very warm (+1.7°C relative to long-term mean across all plots) and dry (6th–29th percentile of cool-season P across all

plots) period during the first half of 2012 (Fig. 2a, b). In these drought conditions, C<sub>4</sub> grass cover declined marginally at the Saline-Alkaline ESG ( $z = -2.0$ ,  $P_{adj} = 0.07$ ; Fig. 3b; Appendix S1: Fig. S1b) and declined significantly at the Rocky ESG ( $z = -3.1$ ,  $P_{adj} = 0.008$ ; Fig. 3b; Appendix S1: Fig. S1b) corresponding with decreases in *Pleuraphis jamesii* cover at this ESG (Appendix S1: Fig. S2c). There were no significant declines in C<sub>3</sub> grass cover in either C<sub>3</sub>/C<sub>4</sub>-co-dominant or C<sub>3</sub>-dominant grasslands (Fig. 3a; Appendix S1: Fig. S1a). Our summary of grass cover by ESG and year suggests that there may have been a decrease in C<sub>3</sub> grass cover in the Mountain Loam ESG in 2012 (Fig. 3a), but we were unable to test this, due to a low sample size that year. Cover of *Hesperostipa comata*, the dominant grass species in the ESG, increased significantly in 2013, the summer following the drought ( $z = 2.1$ ,  $P_{adj} = 0.03$ ), as well as in 2011 and 2014 ( $z = 2.5$ ,  $P_{adj} = 0.02$  for both years; Appendix S1: Fig. S2d).

The 2013 and 2014 monsoon months were exceptionally wet (i.e., >90th percentile) for some ESGs (Fig. 2c), and July through September of 2013 was one of the wettest monsoons on record for the Rocky and Saline-Alkaline ESGs (97th–100th percentile across all plots), which included an 8-day period in September when 93 mm of rain fell. Following the extremely wet 2013 monsoon, cover of  $C_4$  but not  $C_3$  grass, increased, but this response varied by ESG (Fig. 3b; Appendix S1: Fig. S1b). In 2014, the increase in cover of  $C_4$  grasses was pronounced in the Saline-Alkaline ESG ( $z = 2.6$ ,  $P_{\text{adj}} = 0.03$ ), and although the Rocky and Semidesert Sand ESGs followed this pattern as well, the increase in cover at these two ESGs was not significant. Cover of *B. gracilis* and *P. jamesii* followed similar patterns as cover of  $C_4$  grasses overall in 2014, but the increase was only significant for *B. gracilis* in the Saline-Alkaline ESG ( $z = 3.1$ ,  $P_{\text{adj}} = 0.007$ ; Appendix S1: Fig. S2).

#### Correlations of $C_3$ and $C_4$ grass cover with climate and water balance

In the overall goodness-of-fit analysis, multi-month anomalies of climate and water balance explained more variability than monthly anomalies of climate and water balance for  $C_3$  grass cover in the  $C_3$ -dominant grasslands (44% and 10%, respectively) and  $C_4$  grass cover in the  $C_3/C_4$ -co-dominant grasslands (47% and 16%, respectively). Monthly anomalies of climate and water balance explained more variability than multi-month anomalies of climate and water balance for  $C_3$  grass cover in the  $C_3/C_4$ -co-dominant grasslands (49% and 31%, respectively).

In the  $C_3$ -dominant grasslands, the direction of the  $C_3$  grass correlations tended to follow expected patterns (positive correlations for precipitation [P], actual evapotranspiration [AET], and soil moisture [SM] and negative correlations for water deficit [D]) for multi-month relationships (Fig. 4) and for many months of the monthly relationships, although many of these relationships were not significant (data not shown). The correlations were significant for multi-month AET for April, May, and June prior to cover measurements, back through the previous November. February and March SM were also significantly correlated with changes in  $C_3$  grass cover in the multi-month relationships.

In the  $C_3/C_4$ -co-dominant grasslands, there were no significant relationships between change in  $C_3$  grass cover and monthly or multi-month anomalies of climate or water balance. The multi-month correlations were especially weak, with most between  $-0.1$  and  $0.1$  (Fig. 5).

In the  $C_3/C_4$ -co-dominant grasslands, the direction of the  $C_4$  grass correlations tended to follow expected patterns (positive correlations with P and ET and negative correlations with D) for the early growing season (April, May) and many of the monsoon months (July, August, September), but any positive correlations with SM were weak. The correlations were significant for multi-month P for April and May and multi-month AET for July and August of the previous growing season (Fig. 5), as well as monthly P and AET in August (Fig. 6). Other significant monthly correlations with changes in  $C_4$  grass cover included T in April and June, P in December and February, D in June, and SM in June, July, and August.

## DISCUSSION

#### *The role of ecological site group in grass functional type abundance and mediating response to extreme climate events*

Our results demonstrate that grassland ESGs on the Colorado Plateau support different amounts of  $C_3$  and  $C_4$  grass cover. Decreasing  $C_3$  and increasing  $C_4$  grass cover with decreasing elevation of ESGs was consistent with a shift in optimal grass photosynthetic pathway from sites with cool to warm temperatures (Sage et al. 1999). Relatively high  $C_4$  grass cover in sites with high salinity (Saline-Alkaline ESG) and low WHC (Rocky ESG) was likely due to the high water-use efficiency of this functional type (Monson et al. 1983).

Over the six years of our study, there was an exceptionally warm and dry period during the first half of 2012 and some exceptionally wet periods during the monsoon months in 2013 and 2014. Some of the largest decreases in cover occurred in 2012 and increases occurred in 2013, suggesting the important role extreme events play in influencing grass cover. These climate extremes are similar to climate projections that include more severe and frequent droughts due to warming temperatures in the region (Seager et al. 2007, Garfin et al. 2014, Cook et al. 2015),

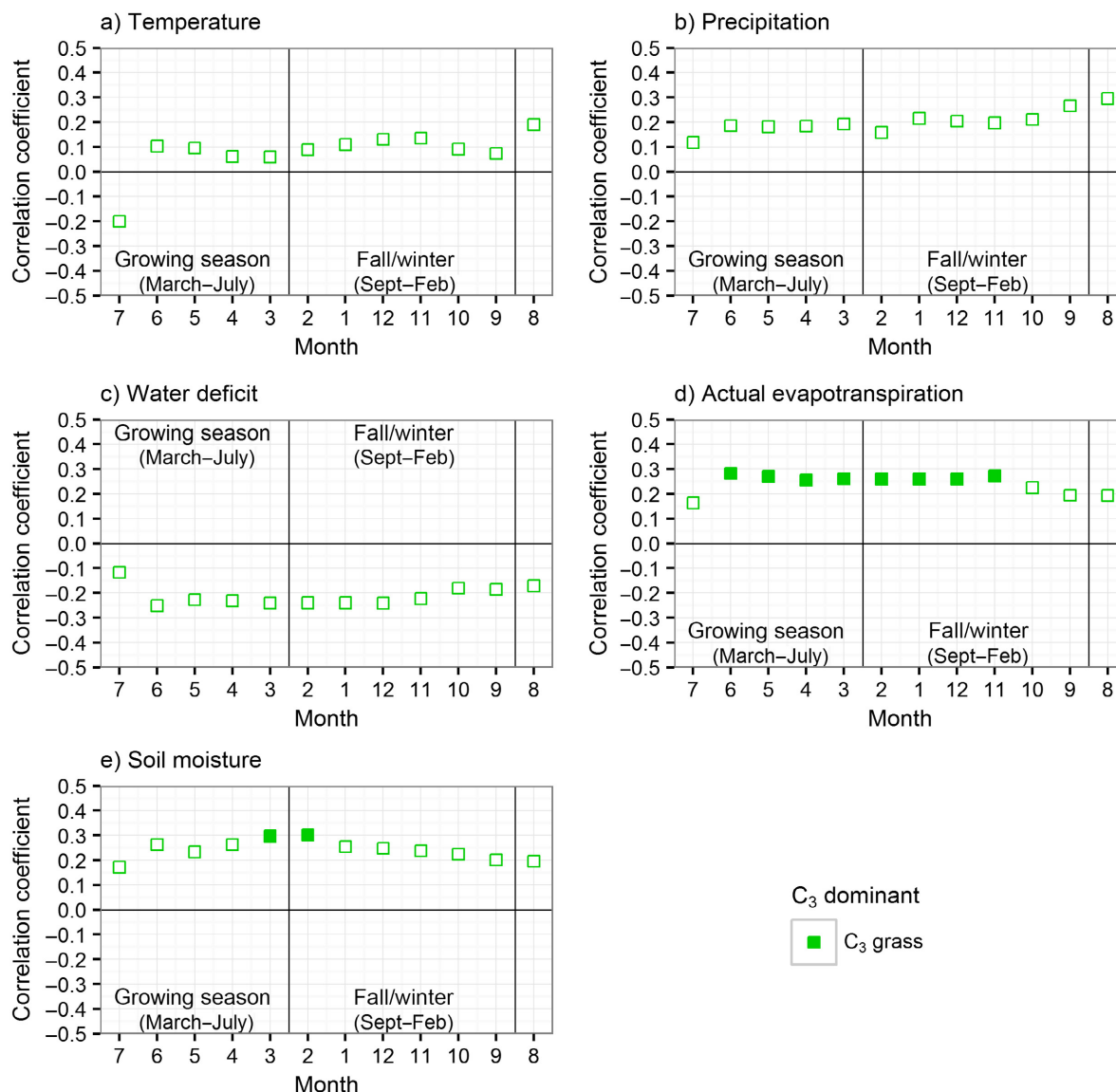


Fig. 4. Relationships between multi-month anomalies of (a) temperature, (b) precipitation, (c) water deficit, (d) actual evapotranspiration, and (e) soil moisture and change in cover of native perennial  $C_3$  grasses (green) in  $C_3$ -dominant grasslands for 12 months preceding sampling. On the  $x$ -axis, 1 = Jan, 2 = Feb, 3 = March, 4 = Apr, 5 = May, 6 = June, 7 = July, 8 = Aug, 9 = Sept, 10 = Oct, 11 = Nov, and 12 = Dec. Closed symbols are significant at  $P_{adj} < 0.05$ .

declines in winter precipitation, and more intense monsoon precipitation events (Prein et al. 2016). The response of  $C_3$  and  $C_4$  grasses to extreme events is of particular interest to land managers, as it can ultimately influence plant community composition and phenology, with important feedbacks to primary production, wildlife habitat, and ecosystem properties.

Within each grassland type ( $C_3/C_4$  co-dominant or  $C_3$  dominant), ESGs had similar assemblages of dominant perennial grass species and experienced similar climate extremes and average conditions over the six years of our study, yet changes in  $C_3$  and  $C_4$  grass cover were noticeably different. In the drought conditions of 2012, only the ESG with low WHC (range of 69–135 mm at

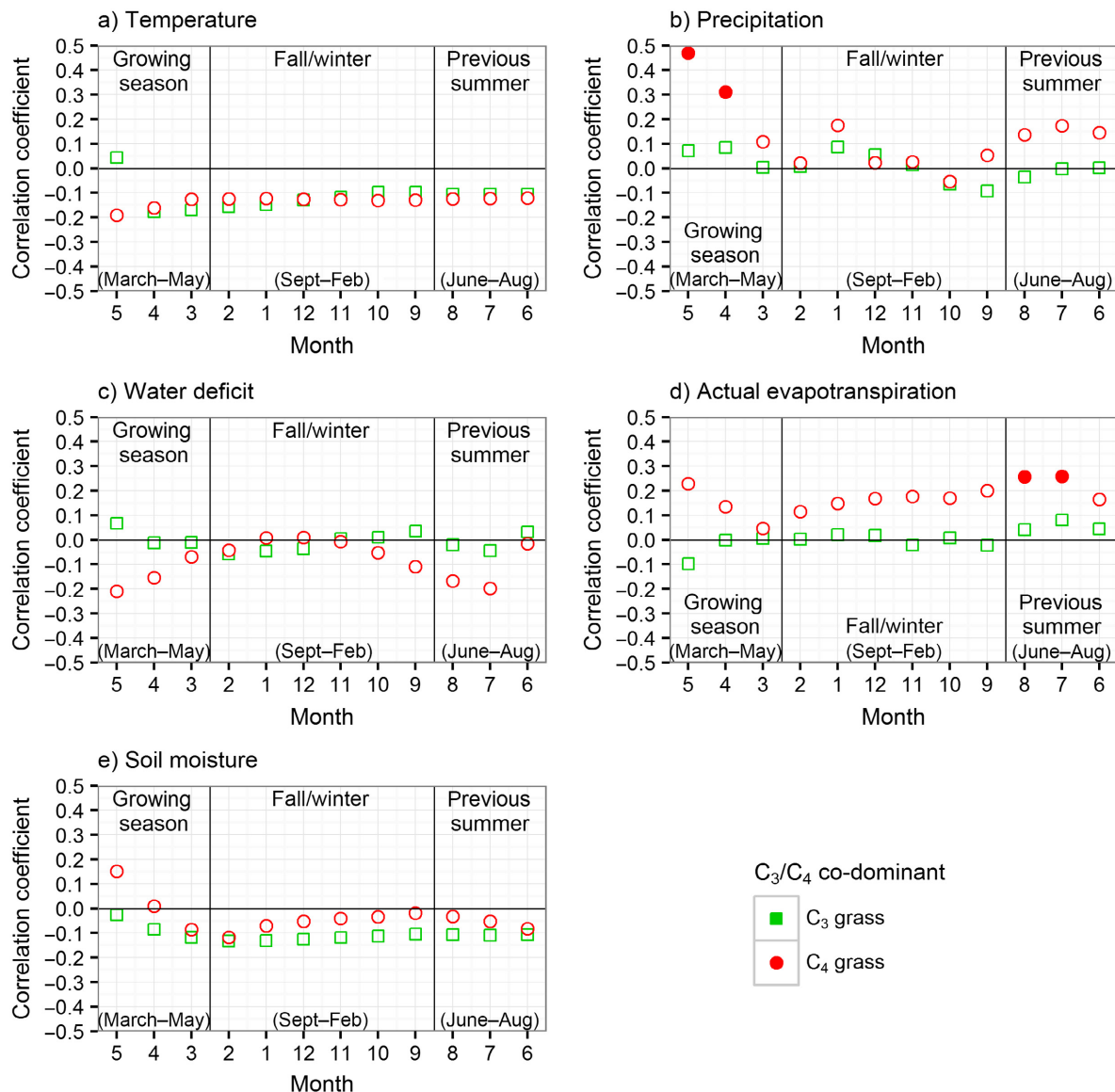


Fig. 5. Relationships between multi-month anomalies of (a) temperature, (b) precipitation, (c) water deficit, (d) actual evapotranspiration, and (e) soil moisture and change in cover of native perennial  $C_3$  (green) and  $C_4$  (red) grasses in  $C_3/C_4$ -co-dominant grasslands for 12 months preceding sampling. On the x-axis, 1 = Jan, 2 = Feb, 3 = March, 4 = Apr, 5 = May, 6 = June, 7 = July, 8 = Aug, 9 = Sept, 10 = Oct, 11 = Nov, and 12 = Dec. Closed symbols are significant at  $P_{adj} < 0.05$ .

the Rocky ESG compared with >200 mm WHC at many of the other ESGs) had significant declines in grass cover and only in the  $C_4$  grass functional type. The steep slopes at this ESG (up to 40%) can increase water runoff, decreasing the amount of water infiltrating the soil, while low WHC and high rock content can limit the amount of water that is available for growth. We expected

$C_3$  grass cover to decrease in drought conditions as well, because  $C_4$  grasses are generally known to be more drought tolerant. However, high annual precipitation in the 2011 water year (see Fig. 2a) and the availability of SM from winter recharge (Lauenroth et al. 2014) may have helped to moderate the effects of drought on  $C_3$  grasses, which grow earlier in the season than  $C_4$  grasses

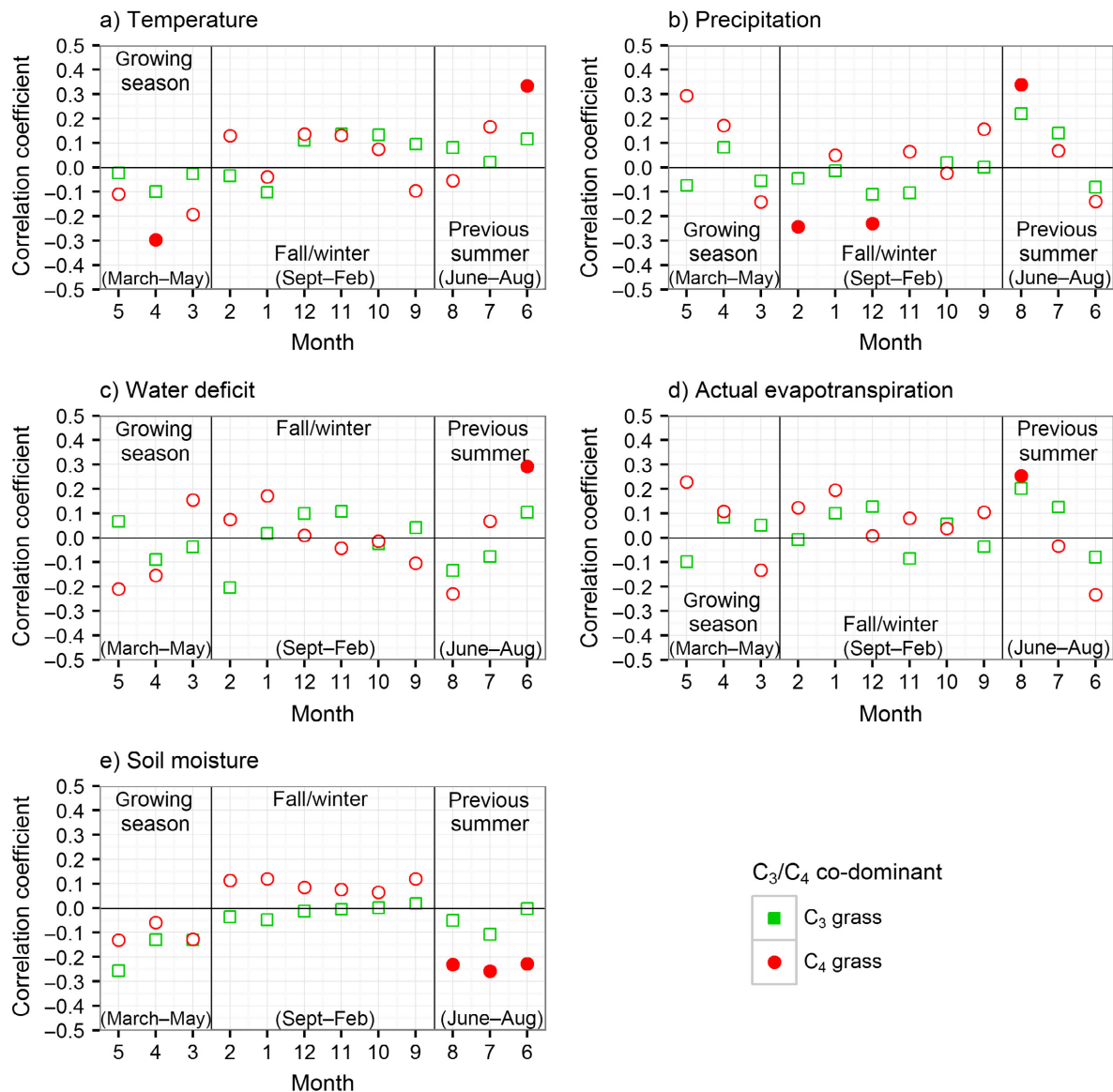


Fig. 6. Relationships between monthly anomalies of (a) temperature, (b) precipitation, (c) water deficit, (d) actual evapotranspiration, and (e) soil moisture and change in cover of native perennial  $C_3$  (green) and  $C_4$  (red) grasses in  $C_3/C_4$ -co-dominant grasslands for 12 months preceding sampling. On the x-axis, 1 = Jan, 2 = Feb, 3 = March, 4 = Apr, 5 = May, 6 = June, 7 = July, 8 = Aug, 9 = Sept, 10 = Oct, 11 = Nov, and 12 = Dec. Closed symbols are significant at  $P_{adj} < 0.05$ .

(Comstock and Ehleringer 1992) when the effects of the drought were likely less severe.  $C_3$  grasses were more negatively impacted by drought than  $C_4$  grasses in an experimental study, despite many of the same  $C_3$  and  $C_4$  grass species occurring in both studies (Hoover et al. 2015). However, the soils in the Hoover et al.'s (2015) study were generally much shallower (<50 cm compared with

100–180 cm in our study), and the sandy soils at our sites probably allowed water to translocate to deeper layers, minimizing evaporative losses, which reinforces the importance of soils and landscape in moderating plant responses to climate (Munson et al. 2015). High annual precipitation in the 2011 water year (see Fig. 2a) may also have helped to moderate the effects

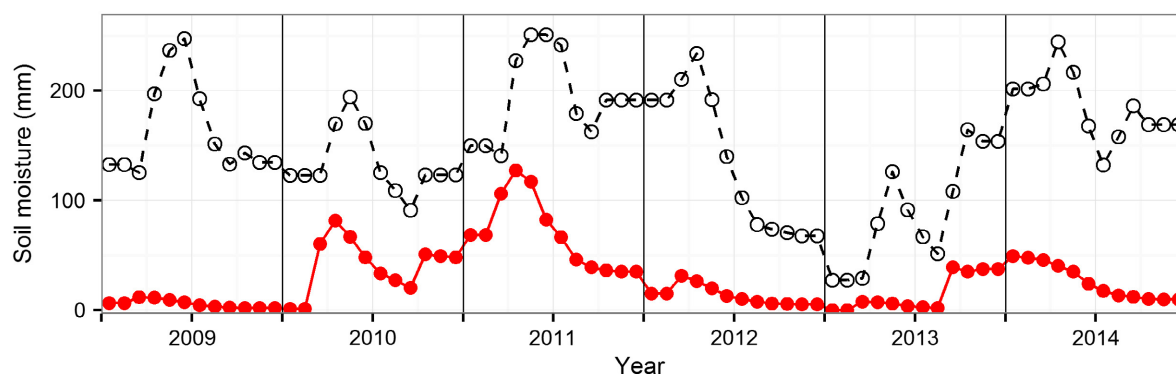


Fig. 7. Monthly soil moisture in 2009–2014 for a  $C_3/C_4$ -co-dominant plot in the Saline-Alkaline ecological site group (ESG; red closed circles) and a  $C_3$ -dominant plot in the Mountain Loam ESG (black open circles) with similar soil water holding capacity (257 mm and 251 mm, respectively). Dots represent soil moisture in millimeters of water at the end of each month. Because these two locations were >270 km apart, differences in annual and seasonal precipitation should also be considered when interpreting differences in soil moisture at each of these ESGs (see Table 1 and Fig. 2).

of the 2012 drought in the Saline-Alkaline and Semidesert Sand ESGs, because plants gain more leaves and roots during a wet period that allows for a more exhaustive exploitation of resources the following year (Sala et al. 2012), and these ESGs had higher soil WHCs than the Rocky ESG.

Cover of  $C_4$  grass increased in the spring of 2014 following an extremely wet monsoon, which was consistent with our expectations and similar to Concilio et al. (2015), but the increase was only significant in the Saline-Alkaline ESG. The Saline-Alkaline ESG, with deep soils that tended to be sandy loams on the surface and finer textured below (loams, silty loam, and silty clays; USDA/USDI 2014), was likely able to allow infiltration and water retention at rooting depth from this extreme event (Noy-Meir 1973), which could be utilized for plant growth at the end of the 2013 growing season. Indeed, our water balance model corroborated this, with SM at the Saline-Alkaline ESG increasing substantially from August to September (from 1 to 37 mm) and remaining high for many months (see Fig. 7). In addition, *Bouteloua gracilis*, the species largely responsible for increases in  $C_4$  grass cover in the Saline-Alkaline ESG (Appendix S1: Fig. S2b), can rapidly respond to summer precipitation (Sala and Lauenroth 1982). Experimental summer wet and winter dry conditions increased native  $C_4$  grass cover in a mixed grass prairie (Prevéy and Seastedt 2014), and the conditions in our study

followed a similar pattern, with the extremely wet monsoon in 2013 followed by a dry cool season at the beginning of the 2014 water year (see Fig. 2).

#### Climate, water balance, and influential periods of time

While many studies relate mean climate conditions over relatively long time periods to plant cover, we assessed the influence of specific months of climate and water balance on grass cover and compared this with the influence of climate and water balance over longer periods of months. A recent study that examined monthly relationships between climate/water balance and the Normalized Difference Vegetation Index (NDVI) in grasslands, including overlapping areas of our Saline-Alkaline and Semidesert Sand ESGs in Capitol Reef NP, found strong relationships with long-term average soil moisture (SM) in cool-season months, switching to strong relationships of short-term indicators of drought, water input, or water use in the warm season months (D, P, AET; Thoma et al. 2016). Our study complemented these results by providing understanding of these climate- and water balance-induced changes at the functional type and species levels.

Our results suggest that grasses are responsive to both monthly and multi-month anomalies of climate and water balance and that the relative

importance of each varies by grassland ( $C_3/C_4$  co-dominant or  $C_3$  dominant) and grass functional type ( $C_3$  or  $C_4$ ). Individual monthly correlations helped to isolate the effects of climate events that occurred in certain months (e.g., higher-than-average temperature [T] in June was related to higher  $C_4$  grass cover in the  $C_3/C_4$ -co-dominant grasslands), while the multi-month correlations showed the effect of longer periods of climate and helped identify important seasonal patterns (e.g., higher soil moisture [SM] in early spring through summer was related to higher grass cover in the  $C_3$ -dominant grasslands). Overall, most dryland grass species responded to multi-month periods of water availability. In some cases, multiple climate or water balance variables in the same month were related to grass cover, emphasizing that multiple aspects of climate have the potential to influence grass cover and that some periods of time were especially influential in our study (e.g., multi-month AET and monthly P and AET in August were all related to higher cover of  $C_4$  grasses). Similar overlapping relationships were found between multi-month windows of climate or water balance variables and productivity in semiarid grasslands using monthly time steps and multi-model averaging techniques (Thoma et al. 2016).

The lack of relationships with climate or water balance variables, especially multi-month anomalies, for  $C_3$  grasses in the  $C_3/C_4$ -co-dominant grasslands was striking, particularly because  $C_3$  grass cover on the Colorado Plateau has previously been related to cool-season precipitation (Munson et al. 2011). In both wet and dry years, the cover of  $C_3$  grasses fluctuated less than the cover of  $C_4$  grasses in  $C_3/C_4$ -co-dominant grasslands and less than  $C_3$  grasses in the  $C_3$ -dominant grasslands.  $C_3$  grasses in the  $C_3/C_4$ -co-dominant grassland grow primarily in spring (compared with summer for  $C_3$  grasses in the  $C_3$ -dominant grasslands), when water from winter recharge is a reliable source of SM (Munson et al. 2011, Lauenroth et al. 2014). Although increases in spring SM were very small in some years (see Fig. 7), the timing of this increase in SM consistently coincided with the beginning of the  $C_3$  grass-growing season (in March and April each year) and seemed to buffer the influence of extreme climate conditions on grass cover.

The shift from low to high monsoon precipitation over the period of our study appears to have played a large role in influencing grass cover. Summer precipitation was important for  $C_4$  grasses and was among the highest monthly correlations for  $C_3$  grasses in both grasslands, which is consistent with other studies that have found seasonal precipitation to be a better predictor of annual net primary productivity than annual precipitation (McClaran 1995, Robinson et al. 2013). This has been noted for  $C_4$  grasses because they generally grow later in the growing season than  $C_3$  grasses, but  $C_3$  grasses are also capable of regrowth in the fall months when conditions are favorable (Comstock and Ehleringer 1992). Monsoon precipitation likely stimulated growth of grasses during the end of the previous growing season, which increased the meristem density and potential for grasses to respond the following year when cover was measured (Reichmann et al. 2013, Peters et al. 2014). Monsoon rains may also allow grasses to store carbon belowground, which can be put toward growth early in the following growing season, and there is evidence that the  $C_4$  grass, *B. gracilis*, can rapidly add roots and store carbon after even small wetting events (Lauenroth et al. 1987). The middle of the typical monsoon season in August appears to have been a critical period for grass productivity throughout the region (Schwinning et al. 2008), when after several months of high summer temperatures, water availability has been depleted, and  $C_4$  grass growth has been linked to the consistency of water available for growth in warmer months (Gremer et al. 2015). Furthermore, when considering multi-month anomalies of precipitation, spring precipitation was also important in influencing  $C_4$  grass cover.

In addition to precipitation, water balance variables were influential in both grasslands, especially multi-month anomalies of AET. Other studies have demonstrated benefits of using a water balance approach in arid and semiarid systems (Notaro et al. 2010, Feng et al. 2012, Lauenroth et al. 2014, Thoma et al. 2016). The multi-month relationship of AET with  $C_3$  grass cover in the  $C_3$ -dominant grasslands demonstrated that water use during the growing season, especially in April, May, and June, was related to  $C_3$  grass cover later in the season. Although multi-month AET remained significant for the

five months preceding that (October through March), there was little to no additional accumulation over those months, and correlations with these months are likely not meaningful. Similarly, multi-month relationships with AET were important for  $C_4$  grasses through the previous monsoon season. In both cases, relationships with AET were stronger than relationships with P over the same time period, which is not surprising because AET simultaneously accounts for water and energy, and favorable conditions of both are needed for plant growth (Stephenson 1998).

In the  $C_3/C_4$ -co-dominant grasslands, we expected that live  $C_4$  grass cover would decrease following high D in summer months, similar to the influence that D had on NDVI in a similar study (Thoma et al. 2016). Although this pattern was evident, none of the correlations were significant, which may be attributable to drought resistance of  $C_4$  grasses (Sage et al. 1999). Monthly T and D in June were both positively correlated with  $C_4$  grass cover, highlighting that high temperatures in this month were more beneficial to  $C_4$  grasses than additional water because some SM remained in June in most years (see Fig. 7). This supports that semiarid grassland soils are acting as capacitors (Bisigato et al. 2013), accumulating water during the cool season and releasing it even as late as June. Additionally, we expected  $C_3$  grass cover in the  $C_3/C_4$ -co-dominant grasslands would increase following higher T in early spring, thereby increasing growing season length and biomass (Hufkens et al. 2016), but we did not see evidence of this. Alternatively, water deficits that occurred around the beginning of spring growth (February D; not significant, but one of the strongest monthly correlations), even though they were small, had disproportionately negative effects on  $C_3$  grass cover compared with other times of the year.

Our study only included six years of data, and there is still much variance that our models did not explain. Additional years of monitoring with more extreme inter-annual changes in cover and more extreme climate conditions would help refine our understanding of how climate and water balance influence grass cover at a finer temporal resolution. Our initial analyses demonstrate that water balance variables and finer timescales are worth investigating further and

that understanding future climate change effects will require understanding the effects of extreme climate conditions at multiple temporal scales, especially for  $C_4$  grasses.

## CONCLUSIONS

Our results suggest that  $C_4$  grasses respond to both short and long climatic windows of time, while the influential times for  $C_3$  grasses vary by grassland ( $C_3/C_4$  co-dominant or  $C_3$  dominant).  $C_3$  grasses in  $C_3$ -dominant grasslands were influenced primarily by longer periods of climate, while  $C_3$  grasses in  $C_3/C_4$ -co-dominant grasslands were influenced little by climate anomalies at either short or long periods of time. Climate conditions that occurred around the beginning of spring growth and during the previous year's monsoon influenced  $C_4$  grasses most strongly, and spring climate conditions influenced  $C_3$  grasses in the  $C_3$ -dominant grasslands most strongly as well. Water balance metrics that integrated climate and site-specific information provided a deeper understanding of water availability to grasses than climate alone. Our results emphasized that (1) carryover of soil moisture in spring months helps to buffer against climate extremes, especially in  $C_3$  grasses in the  $C_3/C_4$ -co-dominant grasslands, and (2) actual evapotranspiration, which includes water utilized for plant growth, in late spring and summer is often more strongly related to grass cover than precipitation. While both  $C_3$  and  $C_4$  grasses are likely to be affected by future changes in spring and summer water balance, cover of  $C_4$  grasses may be more sensitive as they can adjust growth more quickly to drought or wet conditions. The interaction between landscape properties and climate across broad areas results in complex spatial and temporal grassland response. In this study, we demonstrate important features of response linked to the timing and magnitude of water input, drought, and soil properties that can be used by land managers to identify areas that may be more or less susceptible to land use and climate change impacts.

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## SUPPORTING INFORMATION

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