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Desert grassland responses to climate and soil moisture suggest divergent vulnerabilities across the southwestern United States

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Abstract

Climate change predictions include warming and drying trends, which are expected to be particularly pronounced in the southwestern United States. In this region, grassland dynamics are tightly linked to available moisture, yet it has proven difficult to resolve what aspects of climate drive vegetation change. In part, this is because it is unclear how heterogeneity in soils affects plant responses to climate. Here, we combine climate and soil properties with a mechanistic soil water model to explain temporal fluctuations in perennial grass cover, quantify where and the degree to which incorporating soil water dynamics enhances our ability to understand temporal patterns, and explore the potential consequences of climate change by assessing future trajectories of important climate and soil water variables. Our analyses focused on long-term (20–56 years) perennial grass dynamics across the Colorado Plateau, Sonoran, and Chihuahuan Desert regions. Our results suggest that climate variability has negative effects on grass cover, and that precipitation subsidies that extend growing seasons are beneficial. Soil water metrics, including the number of dry days and availability of water from deeper (>30 cm) soil layers, explained additional grass cover variability. While individual climate variables were ranked as more important in explaining grass cover, collectively soil water accounted for 40–60% of the total explained variance. Soil water conditions were more useful for understanding the responses of C_3 than C_4 grass species. Projections of water balance variables under climate change indicate that conditions that currently support perennial grasses will be less common in the future, and these altered conditions will be more pronounced in the Chihuahuan Desert and Colorado Plateau. We conclude that incorporating multiple aspects of climate and accounting for soil variability can improve our ability to understand patterns, identify areas of vulnerability, and predict the future of desert grasslands.

Keywords: arid and semiarid, Chihuahuan Desert, climate change, climate variability, Colorado Plateau, drought, soil water dynamics, Sonoran Desert

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Introduction

Climate in the arid and semiarid regions of the southwestern United States is characterized by high temperatures, combined with low and variable precipitation (Noy-Meir, 1973; Davidowitz, 2002). The southwestern United States has already experienced significant warming and drying, and has been identified as a hotspot for increasing aridity as well as increasing variability in temperature and precipitation (Seager *et al.*, 2007; Archer & Predick, 2008; Diffenbaugh *et al.*, 2008). These changes have the potential to push southwestern ecosystems beyond tolerance thresholds, resulting in species loss, declining ecosystem services, and habitat alteration and degradation. Anticipating such consequences requires understanding what aspects of climate drive temporal patterns of vegetation change and how these changes will be manifested on the landscape. This challenge is especially pronounced in ecosystems that are particularly vulnerable to climate change such as desert grasslands. Grasslands are regionally important sources of biodiversity, net primary production, livestock forage, and wildlife habitat (Bahre, 1995; McClaran, 1995; Sala & Paruelo, 1997). Losses of perennial grasses in dryland regions can contribute to destabilization of soils, which in turn results in reduction of nutrient availability and water-holding capacity, and increases soil erosion and dust storm activity (Schwinning *et al.*, 2008; Munson *et al.*, 2011b; Belnap *et al.*, 2014). Therefore, loss of grass cover can trigger ecological state transitions and further vegetation losses in desert regions, which can feedback into further loss of ecosystem function. In addition, grasslands may be particularly at risk to climate change because they contain

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many shallow-rooted, shorter-lived species, highlighting the need to identify vulnerability or resilience to climate change (Peters *et al.*, 2012; Petrie *et al.*, 2014).

Productivity of grasslands of the southwestern United States is tightly linked to mean annual precipitation across spatial gradients, yet explaining temporal dynamics of productivity at individual sites in relation to climate has proven difficult (Lauenroth & Sala, 1992; Huxman *et al.*, 2004; Sala *et al.*, 2012; Reichmann *et al.*, 2013). For temporal patterns, variability in temperature and precipitation may be more influential than mean conditions (Knapp *et al.*, 2008; Thomey *et al.*, 2011). In arid and semiarid regions, the timing and extent of precipitation events can have stronger effects on plant performance than annual totals (Huxman *et al.*, 2004; Reynolds *et al.*, 2004; Schwinning & Sala, 2004). Temperature exerts strong influences, both because of its direct effect on plant physiological processes and indirect impacts through water balance (Berry & Bjorkman, 1980; Allen & Ort, 2001).

In arid regions, soil and landscape properties can mediate plant responses to climate, because they influence the timing, scale, and location of available water (Munson *et al.*, 2015). For example, surface textures affect infiltration and runoff of precipitation, with more water loss from fine relative to coarse textured soils (Noy-Meir, 1973). Such patterns can lead to greater plant vulnerability to drought at sites with high clay and silt in the surface horizons (Noy-Meir, 1973; Sala *et al.*, 1988). Ecosystem water balance modeling is one approach for integrating soil properties into understanding plant responses to climate. These models can incorporate the effects of climate, soil properties, and vegetation structure into estimates of soil water availability throughout the soil profile through time, providing dynamic measures of when and where water is available for plant uptake and use (Parton, 1978; Sala *et al.*, 1992; Bradford *et al.*, 2006; Lauenroth & Bradford, 2006).

Understanding how climate and soil water have influenced historical species abundance can provide a foundation for predicting plant community shifts under future climate change and provide an early warning sign of ecosystem changes. Many studies that investigate climate-plant abundance relationships use space for time substitutions, which neglects variation in edaphic properties and assumes that vegetation is in equilibrium with climate (Elmendorf *et al.*, 2015). To improve these efforts, the use of data at a high temporal resolution can identify how climate and soil water availability dynamically relate to plant abundance, which is crucial for predicting future patterns. In addition, long-term data can allow for incorporation of antecedent conditions and interactions with other plants, which are both likely to affect responses to climate (Brooker, 2006; Sala *et al.*, 2012). Furthermore, data from long-term monitoring can be used to identify environmental conditions that lead to shifts from increasing to decreasing plant abundance, providing early warning indicators for ecosystem change (Munson, 2013). Such analysis of historical vegetation change and associated environmental conditions can then be used to assess vulnerability to declines and losses under projected climate change.

Here, we utilize 20–56 years of vegetation monitoring across the southwestern United States to identify potential climate and soil water drivers of plant abundance, compare patterns across deserts in the region, and explore possible impacts of future climate change on plant dynamics. We focus on perennial grasses, because of their regional importance, but also because loss of this functional type can result in ecological state transitions and land degradation (Sala & Paruelo, 1997; Peters *et al.*, 2012; Petrie *et al.*, 2014). We examine sites in the Sonoran Desert, Chihuahuan Desert, and Colorado Plateau regions, which encompass a gradient of climate conditions and a range of plant functional types broadly representative of grasslands in the southwestern United States. Our research addresses the following questions: (i) What aspects of climate and soil water explain past patterns of perennial grass cover? (ii) Does incorporating soil water dynamics enhance our ability to understand grassland dynamics? and, (iii) How might climate change impact these grassland systems? To meet our objectives, we combined long-term measurements of plant abundance in grassland communities with climate, soil properties, and an ecosystem water balance model (SOILWAT).

Materials and methods

Study sites

Our study was conducted at three arid to semiarid sites in the southwestern United States: the Santa Rita Experimental Range, Jornada Long Term Ecological Research Site, and three national parks in southeastern Utah (Fig. 1). The Santa Rita Experimental Range (31°54′N, 110°53′W; *hereafter* Santa Rita) is located in the Sonoran Desert region, approximately 80 km south of Tucson, Arizona USA (McClaran, 2003). The Jornada Basin Long Term Ecological Research Site (32°37′N, 106°40′W; *hereafter* Jornada) occupies the northern extent of the Chihuahuan Desert 37 km north-east of Las Cruces, New Mexico USA (Huenneke *et al.*, 2001; Yao *et al.*, 2006). Canyonlands National Park (38°19′N, 109°51′W), Arches National Park (38°43′N, 109°36′W), and Natural Bridges National Monument (37°36′N, 110°1′W) are in southeastern Utah, USA and are referred to as Colorado Plateau sites here.

These three desert sites encompass a range of precipitation and temperature regimes observed across the southwestern

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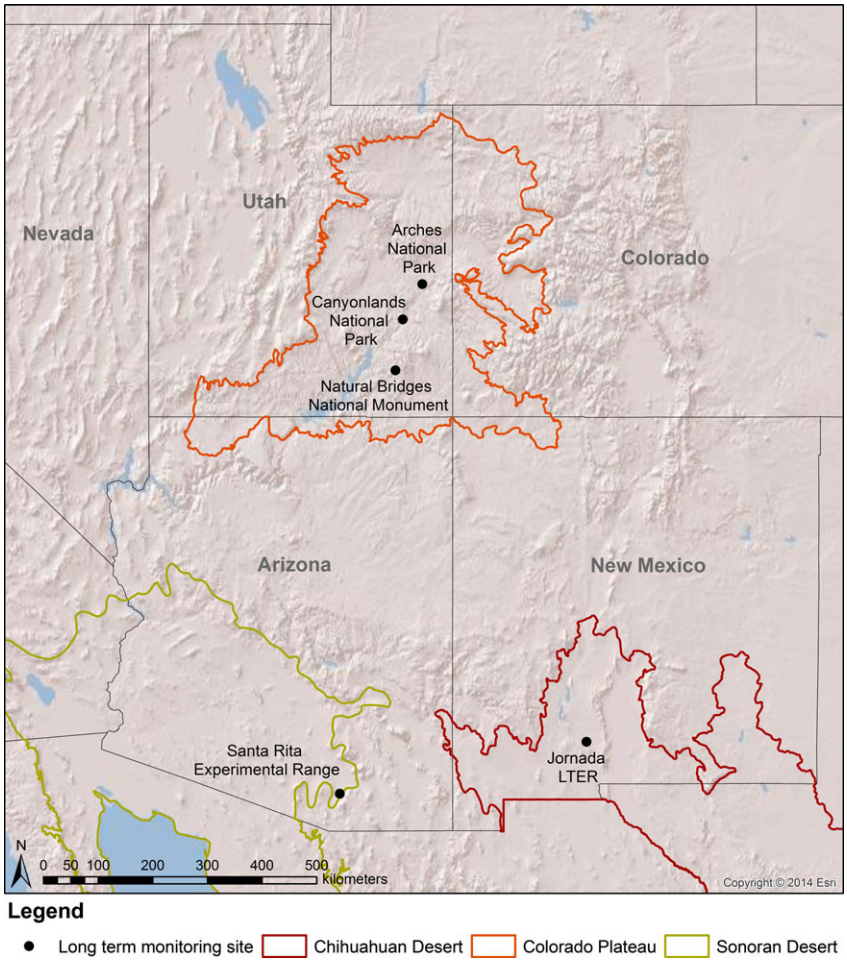

Fig. 1 Long-term vegetation monitoring sites in the Sonoran Desert (yellow outline), Chihuahuan Desert (red outline), and Colorado Plateau (orange outline).

United States. Precipitation at Santa Rita comes in distinct periods during the summer monsoon (July to September) and winter, with summer precipitation comprising more than half of mean annual precipitation (Fig 2a), which is 494 mm (1949–2010). Precipitation is unimodal at Jornada, with a mean annual precipitation of 250 mm that mostly comes during the summer monsoon (Fig 2b). The Colorado Plateau sites have a mean annual precipitation of 221 mm that falls evenly throughout the year (Fig 2c). In the summer (June to August), temperature regimes across the sites are fairly similar (Santa Rita mean high = 33.5 °C, Jornada = 34.1 °C, and Colorado Plateau = 32.7 °C). In the winter, the Colorado Plateau and Jornada sites have colder temperatures (Colorado Plateau mean low = −6.5 °C, Jornada = −5.1 °C), than at Santa Rita (mean = 1.7 °C).

Vegetation data

Vegetation measurements at Santa Rita were taken in 11 different areas, along ten 30 m transects in each area, through gently rolling slopes (0–5°) dominated by the shrub *Prosopis velutinus* (velvet mesquite) and C_4 perennial grasses dominated by *Eragrostis lehmanniana* (non-native), *Digitaria californica*, *Muhlenbergia porteri*, and *Bouteloua* spp. (McClaran, 2003; Munson, 2013). Santa Rita has experienced light to moderate grazing, but no other human disturbances in the last century (McClaran, 2003). At Santa Rita, the line-intercept transect method was used to measure plant species cover every year from 1953 to 1966 and then approximately every 3 years from 1970 to 2009 (with two larger gaps that spanned five and seven years) for a total of 26 measurements over 56 years. We removed transects that had fire or herbicide treatments for this analysis, leaving a total of 82 transects.

Forty-nine 1 m^2 quadrats spaced evenly apart within one large plot were established in each of three areas with black grama (*Bouteloua eriopoda*) dominated plant communities at Jornada in 1989 (Huenneke *et al.*, 2001). Areas were open to grazing prior to initiation of the Jornada study, but have been ungrazed since then. These plots are dominated by C_4 grass species, with *Bouteloua eriopoda*, *Muhlenbergia porteri*, *Sporobolus flexuousus*, and *Scleropogon brevifiolius* being among the most common species. As part of a study on net primary productivity,

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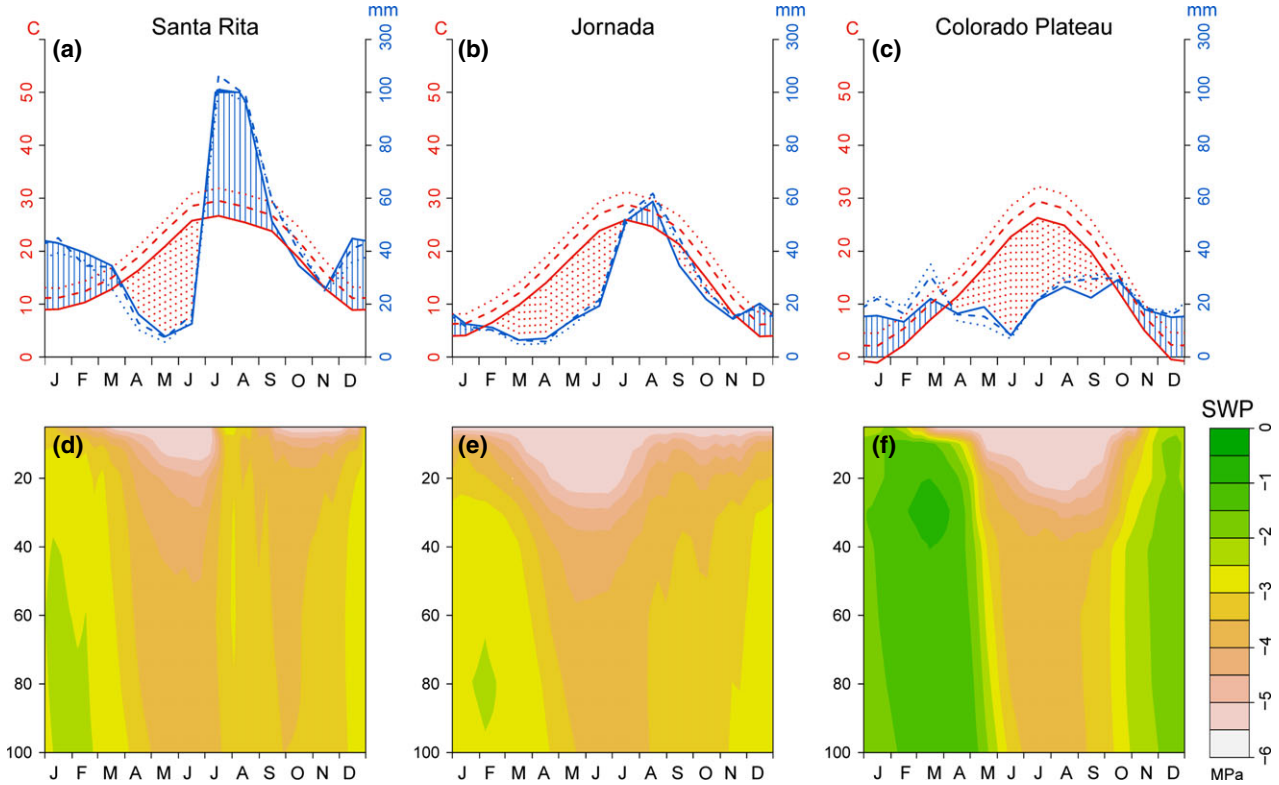

Fig. 2 Average climate and soil water throughout the year for each study site. Upper panels (a–c) show temperature (°C, red, left *y*-axis) and precipitation (mm, blue, right *y*-axis) throughout the year. Axes are scaled to indicate dry periods (red regions) and wet periods (blue regions; *sensu* Walter & Lieth, 1967). Solid lines indicate current conditions (mean of 1979–2010), dashed lines indicate median values under the RCP 4.5 emissions scenario, and dotted lines indicate median values under the RCP 8.5 emissions scenario (see Materials and methods for details). Lower panels (d–f) illustrate soil water potential (SWP) through the year at various soil depths under current climate. Warmer colors indicate drier soils (lower SWP) and green colors indicate wetter soils (higher SWP).

percent cover of individuals of each plant species was collected in each quadrat in every year of the study (Huenneke *et al.*, 2001). Percent cover was aggregated across individual plants of each species and averaged across quadrats in each plot between 1989–2009.

On the Colorado Plateau, vegetation monitoring was established in each park and national monument in 1989, when 100 permanently marked 0.5 × 0.5 m quadrats were established along two 100 m transects per location. Between 1989 and 2009, percent cover was recorded by species in each quadrat and mean cover of each species was calculated for every location in each year of the study. Because these plots encompass a range of plant communities across the Colorado Plateau, nonmetric multidimensional scaling (NMDS) and cluster analysis was used to designate communities that were dominated by perennial grass species (functions metaMDS and hclust in the VEGAN Package in R, Oksanen *et al.* 2015; Munson *et al.*, 2011a; see Appendix S1 for details). NMDS and cluster analysis were also conducted at Santa Rita and Jornada, and results were consistent with the consideration of all plots at Santa Rita as grasslands and including only the black grama plots at Jornada (as described above). In contrast with Santa Rita and Jornada that only had C_4 grasses, sites on the Colorado Plateau exhibited species with a mix of C_3 and C_4 photosynthetic pathways, including *Hesperostipa comata* (C_3), *Achnatherum hymenoides* (C_3), *Pleuraphis jamesii* (C_4), *Sporobolus airoides* (C_4), and *Bouteloua gracilis* (C_4). Plots that were dominated by C_3 species (n = 10 plots) were analyzed separately from those dominated by C_4 species (n = 11 plots; see Appendix S1 for details). Across the southwestern United States, shrub encroachment into grasslands has been documented (Van Auken, 2000; McClaran, 2003; Munson *et al.*, 2012), which has the potential to affect perennial grasses and can influence their responses to climate and soil water. However, we found that grasses were positively and weakly related to shrub cover (r = 0.09, P = 0.01), and this relationship did not change through time (shrub x time interaction: P > 0.60; see Appendix S2 for more details).

Climate data

For each site, we extracted daily maximum and minimum temperatures and precipitation from 1/8-degree grids for 1949 to 2010 (Maurer *et al.*, 2002) and calculated monthly averages, which we then used to calculate 'bioclimatic' variables as developed by WorldClim (function 'biovars' in DISMO package, Hijman *et al.*, 2013). These bioclimatic variables represent annual trends (such as mean annual precipitation and

Table 1 Climate and soil water variables included in analyses for each site

Site	Climate variables	Soil water variables
Santa Rita	Mean annual temperature (MAT)	Mean number of dry days (dry_{days})
	Mean monthly temperature range (T_{range})	Annual number of wet spells (wet_{spells})
	Temperature seasonality (T_{seas})	Prop. of wet days in winter ($prop_{winter}$)
	Precipitation of the driest quarter (P_{dry})	Prop. of transpiration from deeper layers ($trans_{depth}$)
	Precipitation of the coldest quarter (P_{cold})	Months of the longest wet/dry spell ($month_{wet}$ & $month_{dry}$)
Jornada	Mean annual temperature (MAT)	Mean number of dry days (dry_{days})
	Mean monthly temperature range (T_{range})	Annual number of wet spells (wet_{spells})
	Temperature seasonality (T_{seas})	Prop. of wet days in winter ($prop_{winter}$)
	Mean annual precipitation (MAP)	Prop. of transpiration from deeper layers ($trans_{depth}$)
	Precipitation of the driest quarter (P_{dry})	Months of the longest wet/dry spell ($month_{wet}$ & $month_{dry}$)
	Monsoon precipitation ($P_{monsoon}$)	Prop. of transpiration from shallow soil layers ($trans_{shallow}$)
Colorado Plateau	Mean monthly temperature range (T_{range})	Mean number of dry days (dry_{days})
	Temperature seasonality (T_{seas})	Annual number of wet spells (wet_{spells})
	Mean temp. of the wettest quarter (T_{wet})	Proportion of wet days in winter ($prop_{winter}$)
	Mean annual precipitation (MAP)	Proportion of transpiration from shallow layers in the summer (summer $trans_{shallow}$)
	Precipitation seasonality (P_{seas})	Months of the longest wet/dry spell ($month_{wet}$ & $month_{dry}$)

Climate variables: T_{seas} = standard deviation of temperature * 100; T_{range} = mean of monthly (maximum – minimum temperature); $P_{monsoon}$ = July to September precipitation; P_{seas} = coefficient of variation of monthly precipitation. Soil variables: 'Dry' = soil water potential (SWP) below −3.0 MPa; 'wet' = SWP above −1.5 MPa; spells = consecutive days that were wet or dry in any soil layer; surface soil layers are 0–5 cm deep, shallow layers are between 5–30 cm deep, and deep layers are below 30 cm in depth; 'Winter' = October to March, 'summer' = June to September. $Trans_{depth}$/ $Trans_{shallow}$ = the proportion of water available for transpiration at shallow vs. deeper (depth) layers annually; summer $trans_{shallow}$ = the proportion of transpiration that occurred in shallow layers during summer vs. the rest of the year; $prop_{winter}$ = proportion of wet days in winter versus the rest of the year.

temperature), extreme conditions (e.g., temperature of the coldest month), and seasonal weather (e.g., precipitation of the warmest quarter) that are expected to be biologically meaningful. Bioclimatic variables were calculated for each 'growing season year', defined as 12 subsequent months from the month after the sampling period (e.g., October through the following September, if sampling was usually in September). We also calculated summer monsoon (July–September) precipitation because it can affect grass abundance (Peters *et al.*, 2010; Munson, 2013).

Because several of the bioclimatic variables were highly correlated, we used principal components analysis to narrow the pool of candidate variables (principal function in the 'PSYCH' package, Revelle, 2014). We chose the variable with the highest loading to include in analysis when variables were correlated or loaded on the same component axis. This reduction resulted in five to six orthogonal climate variables for each site (Table 1), which varied slightly due to differences in correlations among the three sites in climatic regimes.

SOILWAT modeling and variables

We used a soil water model, SOILWAT, to translate variability in climate into estimates of soil water conditions that may drive plant responses. SOILWAT is a daily time step, multiple soil layer, process-based, simulation model of ecosystem water balance (Parton, 1978; Bradford *et al.*, 2006, 2014; Lauenroth & Bradford, 2006). Inputs to SOILWAT include weather, vegetation, and soil properties (Bradford *et al.*, 2014). Climate data for SOILWAT simulations were the same as described above (see Climate data) with mean monthly values of cloud cover, humidity, and wind speed from Climate Maps of the United States (https://www.ncdc.noaa.gov/cgi-bin/climaps/climaps.pl; Bradford *et al.*, 2014). Soil texture (sand, silt, and clay proportions for each layer) and depth at each site were derived from the NRCS State Soil (STATSGO) Geographic Database set gridded to 1 km^2 (Miller & White, 1998). Although more accurate soils data was available for some sites/plots, we used broad-scale STATSGO soils data to limit how varying resolution in soils data would affect results. The model output includes daily estimates of water interception by litter and vegetation, evaporation, infiltration and percolation, bare-soil evaporation, and transpiration from each soil layer (Parton, 1978; Bradford *et al.*, 2006, 2014). SOILWAT has been previously implemented to describe soil water balance for dry grasslands in the US (Lauenroth & Sala, 1992; Peters *et al.*, 2010).

Output from SOILWAT was used to calculate several metrics of soil water availability as potential drivers of grassland dynamics. As with the climate variables above, we used principal components analysis to select orthogonal variables for further analysis, which resulted in six to seven variables per site (see Table 1 for variables). Soils were considered 'dry' if soil water potential (SWP) was below −3.0 MPa and 'wet' if SWP was above −1.5 MPa; spells were defined as consecutive days that were dry or wet in any soil layer. Soil layers were grouped into surface (0–5 cm deep), shallow (up to 30 cm deep), and deep (below 30 cm) layers. 'Winter' and 'summer' variables refer to the winter growing season from October to

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March and the summer growing season from June to September, respectively.

Past perennial grass dynamics in relation to soil water and climate

To determine what aspects of climate and soil water explained variation in perennial grass cover, we used linear mixed-effects models. Perennial grass cover was analyzed together as a functional group and was arcsine- square root transformed prior to analyses, which normalizes proportional data (i.e, bounded by 0 and 1). In mixed models, each climate or soil water variable was included as a main effect. We used climate, soil water, and bioclimatic variables spanning the entire vegetation sampling interval, which was one year for most sites and dates. We found that using variables spanning longer than a year at Santa Rita (1970–2009) did not strongly affect inferences. In addition, we included transformed cover in the previous time step as a covariate to account for possible effects of previous history or density, as well as the interaction between the soil or climate variable and previous cover. An autoregressive covariance structure (AR1) with plot as a random factor was used to account for repeated measures, chosen from several error structures using corrected Akaike Information Criteria (AICc's; function lme in R, Pinheiro *et al.*, 2013). Observations with standardized residuals outside of the 95% quantile of the standard distribution (≤6% of data points) were removed as outliers from each analysis. Analyses were conducted for each desert region separately, though we expect that inferences would be similar with different sampling schemes (Munson *et al.*, 2011c).

Relative importance of climate and soil water variables

To understand the relative contribution of climate and soil water variables in explaining perennial grass cover, we used hierarchical partitioning (HP) analysis. This method provides a better estimate of the relative importance of each variable while accounting for multicollinearity (Murray & Conner, 2009). To account for correlated error structures that arise from repeated measures, as well as the effect of perennial grass cover in the previous time step in our HP analyses, we constructed mixed models with transformed cover as the response variable, transformed cover in the previous time step as a main effect, and plot as a random effect and related the residuals from these mixed models (*hereafter* cover residuals) to climate and soil water variables using HP. In these HP analyses, only climate and soil water variables that were significantly or marginally significantly related to perennial grass cover on their own were included (i.e. $P < 0.12$, see Results). To compare the relative importance of climate vs. soil water variables together, we then summed the independent effects of each category of variables on cover.

Future scenarios for climate and soil water variables

To understand how future conditions may impact perennial grass abundance, we compared the current distribution of variables that relate to contemporary grass cover dynamics with distributions projected by climate change models. Contemporary distributions for the most important climate and soil water variables for each site (Table 1) were constructed from annual data from 1979 to 2010. We examined 16 general circulation models [GCMs; selected to represent variability in model structure based on Knutti *et al.* (2013)] within each of two representative concentration pathways (RCPs): families 4.5 (relatively low emissions) and 8.5 (relatively high emissions; Moss *et al.*, 2010). For the years 2070–2099, we combined historic daily data with monthly GCM predictions using a hybrid-delta downscaling approach to obtain future daily forcing (Hamlet *et al.*, 2010; Dickerson-Lange & Mitchell, 2014), which were used by SOILWAT to simulate future soil water variables. For each variable, we ranked GCMs according to the average value for the variable, discarded the highest and lowest models as extremes, and present the high, median, and low models from the remaining 14 GCMs.

We estimated critical values of climate and soil water variables that corresponded to changes from increasing to decreasing cover. Because cover in the previous year was significantly related to perennial grass cover in all models (see Results), we estimated the point at which the relationship between cover residuals and each climate or soil water variable equaled zero (x-intercept). These 'neutral points' of climate or soil water represent conditions at which cover from the previous time-step can be maintained, and climate or soil water conditions do not cause an increase or decrease in cover. We then compared the location of these neutral points across current (1979–2010) and future (2070–2099) distributions, and determined the percentile for each neutral point within the distribution of values for each time period. This allowed us to estimate the proportion of years that are likely to have positive or negative effects on perennial grass cover under current vs. future conditions. For ease of interpretation, we present residuals from back-transformed predicted values, which provide estimates of the actual (not transformed) difference in expected cover that is due to climate or soil water.

Results

Differences in soil water dynamics across sites

Differences in climate interact with soil properties at each site, resulting in contrasting soil water regimes. Data from STATSGO suggested that, as general descriptions, soils are deepest at Santa Rita (mean 150 ± 2 cm standard error; range = 35–152 cm), intermediate at Jornada (113 cm ± 27, range = 35–152 cm), and shallowest on the Colorado Plateau (mean = 46 ± 7 cm, range = 6–119). Surface textures also vary across desert sites, with Santa Rita having the highest proportion of sand (62%, SE = 0.11), and the Colorado Plateau having the highest clay content (18%, SE = 0.005), though textures vary by plot and throughout soil profiles. These differences in soil properties interact with differences in temperature and

precipitation patterns to determine soil water dynamics at each site. Soils at Santa Rita have two distinct wet periods that correspond with the monsoon, with intervening dry periods in the spring and fall (Fig. 2d). In contrast, both the Jornada and Colorado Plateau sites are characterized by a single dominant dry period beginning in the spring (Jornada) or early summer (Colorado Plateau; Fig. 2e, f). Although the Jornada climate is also strongly affected by the summer monsoon, surface soils at Jornada stay quite dry throughout the year and, unlike the Santa Rita site, average summer precipitation is not sufficient to wet the entire soil profile. Winter precipitation at the Colorado Plateau study sites provides deep soil recharge, wetting the entire profile and maintaining moisture well into the spring.

Past perennial grass dynamics in relation to climate

Perennial grass cover was explained by the magnitude and timing of weather events, both in terms of precipitation and temperature (Table 2, Fig. 3). At Santa Rita, precipitation of the driest quarter (P_{dry}) was positively related to grass cover (Fig. 3a), while temperature seasonality (T_{seas}) and temperature range (T_{range}) were negatively related. Perennial grass cover was negatively related to T_{seas} at Jornada (Fig. 3b), while cover was higher in years with more monsoon precipitation ($P_{monsoon}$). Plots dominated by C_3 and C_4 grasses responded differently to temperature and precipitation on the Colorado Plateau, with cover negatively related to T_{range} in plots dominated by C_3 grasses (Fig. 3c), while plots dominated by C_4 grasses negatively responded to precipitation seasonality (P_{seas}) and mean annual precipitation (MAP; Fig. 3d, h). However, MAP has a positive interaction with cover in the previous time step, which creates a pattern such that the relationship is negative at low amounts of $cover_{t\text{-}1}$, but positive at higher values. Since approximately 70% of the observed previous cover values are above the threshold at which the relationship becomes negative, the relationship between perennial grass cover and MAP is generally positive (Fig. 3h). For all sites, cover in the previous year was significantly related to perennial grass cover and the effect was usually positive ($P < 0.001$ for all models, Appendix S3).

Past perennial grass dynamics in relation to soil water

Soil water variables that described the location of available water in the soil profile, the timing of wet conditions, and number of dry days were important in explaining variation in perennial grass cover (Table 2, Fig. 3). At Santa Rita, the proportion of water available for transpiration from layers deeper than 30 cm ($trans_{depth}$) and annual number of wet spells (wet_{spells}) were negatively related to perennial grass cover (Fig. 3e). Conversely, at Jornada, $trans_{depth}$ was positively related to cover (Fig. 3f), but the proportion of wet days that occurred in winter ($prop_{winter}$) had a negative effect (Table 2). Plots dominated by C_3 grasses on the Colorado Plateau had higher cover in years with fewer dry_{days} (Fig. 3g), and dry spells that occurred later in the year ($month_{dry}$; Table 2). C_4 grasses on the Colorado Plateau did not respond strongly to soil water variables, though the timing of wet and dry spells ($month_{wet}$ and $month_{dry}$) had opposite effects, since cover was lower when wet spells did not occur until later in the year, but higher when dry spells were confined to later in the year (Table 2).

Relative importance of climate and soil water variables in explaining grassland dynamics

Climate variables typically had the highest rankings in hierarchical partitioning analyses, but for many sites, soil water metrics were the second most important explanatory variable (Table 3). The exception to this pattern is for plots dominated by C_4 grasses on the Colorado Plateau, where soil water variables were all ranked lower than climate variables. When taken together, climate variables accounted for 58% of the explained variation in perennial grass cover at Santa Rita, while soil water variables accounted for the remaining 42%. Patterns at Jornada were similar, with climate accounting for slightly over half of the explained variation (57%). Soil water variables had the highest contribution for Colorado Plateau C_3 plots, accounting for 68% of the explained variation, and the lowest for Colorado Plateau C_4 plots at only 6%.

Future trends for climate and soil water

Projections of these important climate and soil moisture variables from climate change scenarios indicate that future conditions may shift away from values that support perennial grass cover, particularly for C_4 grass plots at Jornada and on the Colorado Plateau (Fig. 3). At Santa Rita, climate projections indicate uncertainty in future directions for precipitation of the driest quarter (P_{dry}) and the proportion of water used for transpiration at deeper layers ($trans_{depth}$; Fig. 3a, e). However, most scenarios for both variables have higher frequencies of conditions that are related to perennial grass increases. For perennial grasses at Jornada, climate scenarios consistently project an increase in temperature seasonality (T_{seas}) and strong decreases in $trans_{depth}$ (Fig. 3b, f). Under current scenarios (1979–2010), conditions for T_{seas} and $trans_{depth}$ (respectively) favor

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Table 2 Results of mixed models for perennial grass cover in relation to climate and soil water variables. Full models included the climate or soil water variable of interest, cover in the previous time step, and the interaction of the two, as well as plot as a random factor (see Materials and methods for more details)

Variable	Type	Sign	*F* statistic	Degrees of freedom	*P* value	Marginal R^2	Conditional R^2
Santa Rita							
P_{dry}	Climate	+	180.36	1663	<0.001	0.56	0.57
$Trans_{depth}$	Soil water	–	58.32	1640	<0.001	0.56	0.57
T_{seas}	Climate	–	44.15	1658	<0.001	0.53	0.53
Wet_{spells}	Soil water	–	51.69	1654	<0.001	0.56	0.57
Dry_{days}	Soil water	–	162.24	1659	<0.001	0.53	0.54
P_{cold}	Climate	+	130.80	1659	<0.001	0.52	0.53
$Month_{dry}$	Soil water	+	41.41	10 638	<0.001	0.62	0.64
T_{range}	Climate	+	5.88	1658	0.02	0.54	0.54
MAT	Climate	–	160.43	1658	<0.001	0.54	0.54
$Month_{wet}$	Soil water	+	68.69	6644	<0.001	0.62	0.62
Jornada							
T_{seas}	Climate	–	8.06	1,51	0.01	0.60	0.66
$Trans_{depth}$	Soil water	+	8.50	1,34	0.01	0.40	0.74
$P_{monsoon}$	Climate	+	7.41	1,52	0.01	0.46	0.61
$Prop_{winter}$	Soil water	+	3.63	1,50	0.06	0.52	0.65
MAT	Climate	–	9.24	1,52	0.00	0.37	0.58
Wet_{spells}	Soil water	+	5.08	1,52	0.03	0.33	0.57
$Month_{dry}$	Soil water	+	7.93	7,39	<0.001	0.43	0.75
$Month_{wet}$	Soil water	+	7.65	6,41	<0.001	0.71	0.71
$Trans_{shallow}$	Soil water	–	2.97	1,53	0.09	0.32	0.51
Colorado Plateau, C_4 grasses							
P_{seas}	Climate	–	6.80	1121	0.01	0.43	0.70
MAP	Climate	–	4.03	1120	0.05	0.41	0.66
T_{range}	Climate	+	11.71	1120	<0.001	0.54	0.64
$Month_{wet}$	Soil water	–	3.38	1121	0.07	0.35	0.67
$Month_{dry}$	Soil water	+	5.70	5118	<0.001	0.42	0.73
T_{seas}	Climate	+	3.74	10 102	<0.001	0.44	0.72
Colorado Plateau, C_3 grasses							
T_{range}	Climate	–	98.74	1130	<0.001	0.76	0.79
Dry_{days}	Soil water	–	4.59	1134	0.03	0.59	0.68
$Month_{dry}$	Soil water	+	3.63	9119	<0.001	0.59	0.71
Wet_{spells}	Soil water	–	68.13	1131	<0.001	0.74	0.74
$Prop_{winter}$	Soil water	+	4.67	1134	0.03	0.61	0.68
Summer $trans_{shallow}$	Soil water	+	10.14	1118	0.00	0.62	0.68
$Month_{wet}$	Soil water	+	5.02	5128	<0.001	0.60	0.68
T_{wet}	Climate	–	4.56	1135	0.03	0.61	0.68

Effect describes whether the relationship between cover (arcsine-square root transformed) and the variable is positive (+) or negative (–). Marginal R^2 refers to variance explained by fixed factors, conditional R^2 quantifies the variance explained by both fixed and random factors.

increases in perennial grass abundance in 61% and 47% of years, but favorable conditions are less frequent under both emissions scenarios (T_{seas}: RCP 4.5 range 10–58%, RCP 8.5 range 3–55%; $trans_{depth}$: RCP 4.5 range 6–16%, RCP 8.5 range 6–19%), with conditions being far worse under extreme models. On the Colorado Plateau, projections for temperature range (T_{range}), and mean number of soil dry days (dry_{days}) for C_3 grass sites are quite variable (Fig. 3c, g). The proportion of years with T_{range} conditions that favor perennial grasses are fairly similar among all scenarios (current = 59%, RCP 4.5 = 51–65%, RCP 8.5 = 42–65%). Similar patterns are observed for dry_{days}, with only the most extreme model (high model for RCP 8.5) suggesting strong reductions in favorable conditions (Fig. 3g). For C_4 grass sites, precipitation seasonality (P_{seas}) projections show consistent increases, which will increase the proportion of years with P_{seas} conditions that are associated with declines in perennial grass cover (current: 22%, RCP 4.5: 33–51%, RCP 8.5: 41–69%; Fig. 3d). While there is high variability in projections for annual precipitation (MAP) on the Colorado Plateau, with both increases

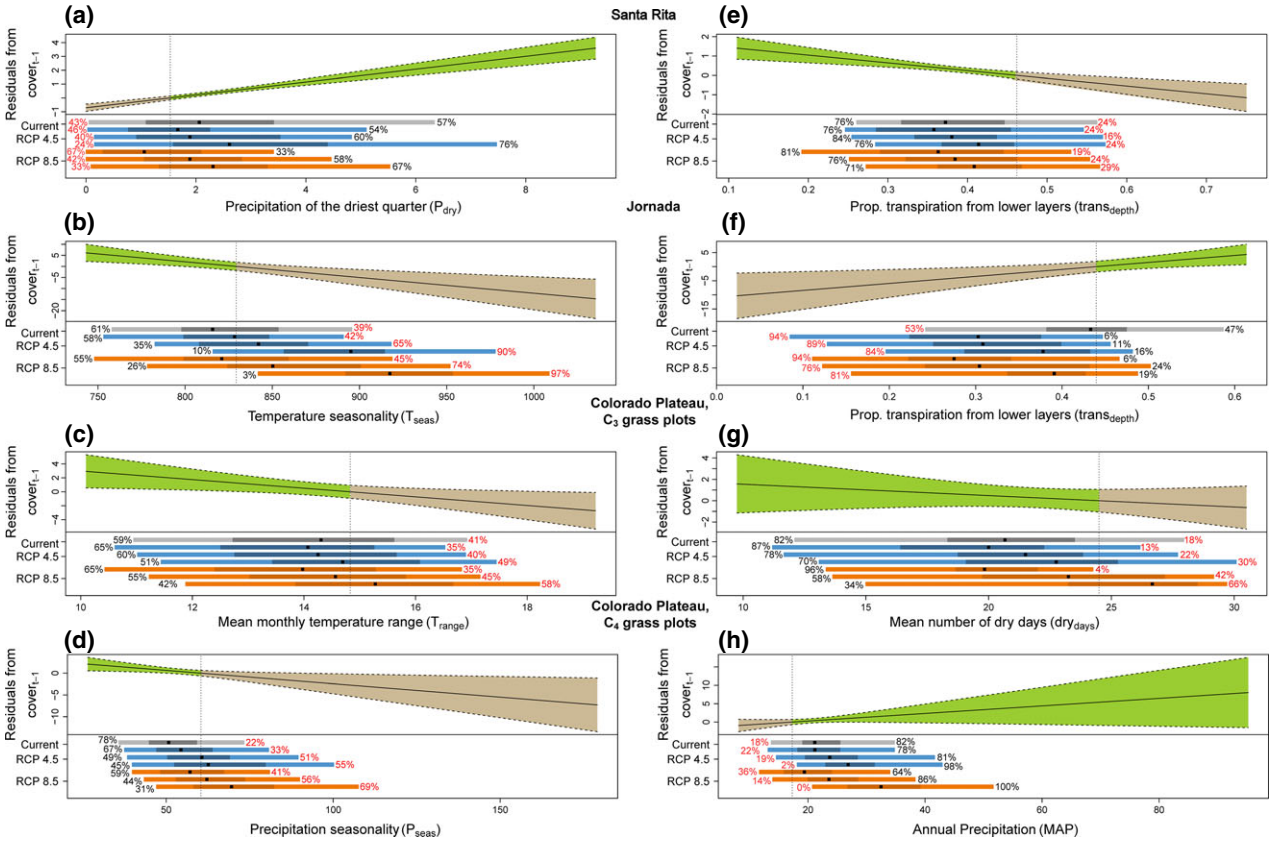

Fig. 3 Perennial grass cover in relation to the two most important climate and soil water variables for each site. The *y*-axis represents the residuals from the relationship of perennial grass cover with cover in the previous year and accounts for repeated measures (see *Methods* for details). Dashed lines indicate 95% confidence intervals. Vertical dotted lines indicate neutral points, where residuals cross zero. Shading above and below neutral points indicate values with positive (green) or negative (brown) associations with cover. Colored bars below relationships represent distributions for variables under current (1979–2010; gray bars), RCP 4.5 (low, median, and high projections; blue bars), and RCP 8.5 emissions scenarios (low, median, and high projections; orange bars; see Materials and methods for details). Lighter colored bars represent 90% percentiles, darker bars are the interquartile range (25–75%), and black points represent median values. Percentages in red are the proportion of the distribution that is in the negative effect region, black percentages represent proportion of the distribution associated with positive effects on cover.

and slight decreases forecasted, most scenarios have high frequencies of conditions that support increases in perennial cover for C_4 sites on the Colorado Plateau (Fig. 3h).

Discussion

Predicting how plants in arid and semiarid regions will respond to climate change requires identifying what aspects of climate drive shifts in abundance and how these relationships are mediated by soil properties. Predictions are particularly challenging in arid regions of the southwestern United States, where both climate and soil properties are highly variable (Davidowitz, 2002; Huenneke & Schlesinger, 2006; Cable *et al.*, 2008) and precipitation is difficult to predict (Peters *et al.*, 2010; IPCC, 2014). Here, we examined how temporal dynamics of perennial grasses across drylands of the southwestern United States are driven by key climate and soil water availability indicators. We found that different aspects of climate were important at each desert, consistent with strong differences in the dominant precipitation regime among sites. Despite differences in the particular component of variability that is important for grass cover across sites, our results indicate that seasonal timing of precipitation, as well as variability in temperature and precipitation, are important for controlling temporal dynamics of perennial grass abundance across the region. Although climate variables were ranked most important as univariate predictors of grass cover, attributes of the soil water regime collectively contributed 40–60% of explained variance depending on location and grass photosynthetic pathway. Our results suggest that accounting for

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Table 3 Results of hierarchical partitioning analysis for all sites. Percent of R^2 is the amount of explained variance that can be attributed to each individual variable, while accounting for multicollinearity (see Materials and methods for more details)

Variable	Type	Percent of R^2
Santa Rita, C_4 grasses		
P_{dry}	Climate	33.58
$Trans_{depth}$	Soil water	17.48
T_{seas}	Climate	14.41
Dry_{days}	Soil water	9.56
P_{cold}	Climate	4.92
$Month_{dry}$	Soil water	3.70
MAT	Climate	3.52
T_{range}	Climate	1.85
$Month_{wet}$	Soil water	1.21
Climate total		***58.28***
Soil water total		***41.72***
Jornada, C_4 grasses		
T_{seas}	Climate	36.20
$Trans_{depth}$	Soil water	30.66
$P_{monsoon}$	Climate	16.42
$Prop_{winter}$	Soil water	4.87
MAT	Climate	3.95
Wet_{spells}	Soil water	2.97
$Month_{dry}$	Soil water	2.91
$Month_{wet}$	Soil water	1.34
$Trans_{depth}$	Soil water	0.67
Climate total		***56.58***
Soil water total		***43.42***
Colorado Plateau, C_4 grasses		
P_{seas}	Climate	63.29
MAP	Climate	15.59
T_{range}	Climate	8.50
T_{seas}	Climate	6.45
$Month_{wet}$	Soil water	4.59
$Month_{dry}$	Soil water	1.57
Climate total		***93.83***
Soil water total		***6.17***
Colorado Plateau, C_3 grasses		
T_{range}	Climate	37.10
Dry_{days}	Soil water	24.32
$Month_{dry}$	Soil water	16.48
Wet_{spells}	Soil water	12.84
$Prop_{winter}$	Soil water	4.11
Summer $trans_{shallow}$	Soil water	3.17
$Month_{wet}$	Soil water	1.49
T_{wet}	Climate	0.50
Climate total		***37.59***
Soil water total		***62.41***

Sums for climate variables and soil water variables for each site are in bold italic fonts.

ways in which soil properties mediate impacts of climate on plant communities will enhance our ability to forecast the future of these grassland communities.

Perennial grass dynamics in relation to climate and soil water

Our results corroborate studies that suggest that the timing, not just total amount, of precipitation is critical to the condition of perennial grasses (Huxman *et al.*, 2004; Schwinning & Sala, 2004; Heisler-White *et al.*, 2008; Weltzin *et al.*, 2008; Petrie *et al.*, In press). While plants in arid- and semiarid ecosystems usually respond more strongly to larger storm events or a series of events, small pulses of rain, even as small as 5 mm, may alleviate stress that accumulates during dry periods and maintain physiological processes (Sala & Lauenroth, 1982; Huxman *et al.*, 2004). At Santa Rita, we found that precipitation of the driest quarter (P_{dry}) is important for grass abundance, which suggests that small precipitation events occurring before or after the summer monsoon season can help repair accumulated damage or trigger photosynthetic activity. On the other hand, higher P_{dry} may simply represent an extension of the growing season. Temporal distribution of precipitation was also important for perennial grass dynamics on the Colorado Plateau, where abundance in C_4-dominated plots was more strongly linked to precipitation seasonality (P_{seas}; coefficient of variation of monthly precipitation), than annual precipitation (MAP). Lower values of P_{seas} indicate that precipitation was more evenly delivered throughout the year and likely represent consistency of available water for C_4 growth, particularly in warmer months when temperatures are more conducive for C_4 species. Higher values for P_{seas} can indicate larger storm events that are less evenly distributed, which may be beneficial in other systems. At a dry shortgrass steppe site in the US Central Plains, experimental watering treatments involving fewer, but larger, precipitation events resulted in increases in soil water availability, plant water status, and productivity relative to treatments with the same amount of water delivered in frequent, but smaller rainfall events (Heisler-White *et al.*, 2008). However, these responses may depend on climate regime, since patterns were reversed at a more mesic tall grass site, where longer dry intervals reduced water availability and decreased productivity (Heisler-White *et al.*, 2009). Together these patterns suggest that timing and extent of precipitation is important for grassland responses, but it is critical to understand how that variability drives changes in soil moisture availability.

While research often focuses on precipitation in dryland systems, temperature can exert strong influences either directly, by affecting physiological processes and growth, or indirectly, by influencing water availability and movement (Noy-Meir, 1973; Berry & Bjorkman, 1980; Comstock & Ehleringer, 1992). Moreover, recent

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analyses suggest that contemporary drought in the southwestern United States is increasingly driven by temperature (Gutzler & Robbins, 2011). Our analyses revealed that temperature seasonality (T_{seas}) and mean monthly temperature range (T_{range}) were negatively related to perennial grass cover. Both of these variables can indicate exposure to extreme high and low temperatures. Low temperatures in the winter could affect abundance by reducing viable meristems and axillary buds, which are critical for productivity of these grasses (Reichmann *et al.*, 2013). Conversely, high temperatures in the summer will negatively affect soil water availability and plant water relations by increasing atmospheric water demand, as well as reduce primary productivity by increasing respiration and decreasing photosynthetic efficiency (Amthor, 2000; Bernacchi *et al.*, 2002). Interestingly, T_{seas} and T_{range} were more important than variables representing minimum and maximum temperatures, suggesting that the overall temperature regime is important in perennial grass dynamics, which is consistent with work suggesting that physiological responses to temperature depend on temperature regime (Berry & Bjorkman, 1980; Hikosaka *et al.*, 2006; Medek *et al.*, 2011).

Temperature and precipitation interact with soil properties to determine the amount, timing, and location of water available to plants. Here, we used a process-based soil water model (SOILWAT) to translate variation in climate and soil properties into measures of water availability for plants. Our analyses revealed that the location of available water in the soil profile ($trans_{depth}$) and number of dry days per month (dry_{days}) were important in driving perennial grass dynamics in this arid region. In particular, soil water variables were collectively most important for explaining grass dynamics in C_3 plots on the Colorado Plateau. C_3 species have an early phenology, and often must rely on storage of soil water from winter and spring rains for growth (Craine *et al.*, 2011; Munson *et al.*, 2011a). This suggests that soil profile attributes that mediate plant water availability (e.g. water holding capacity) may be more valuable for understanding plant responses to climate in systems and functional groups that are more dependent on storage of non-growing season precipitation (Lauenroth *et al.*, 2014). In our study, climate variables were ranked most important for all sites and soil water variables ranked second at most sites (Table 3). However, our ability to accurately represent soil-moisture impacts on plant dynamics may have been limited by both soils and vegetation data. To ensure consistency among sites, we utilized soils information from STATSGO, a national-scale soil mapping effort that may have insufficiently captured spatial variability at the plot-level. In addition, while soil water is highly dynamic throughout the year, vegetation sampling at these sites was conducted at annual or multiyear intervals. Therefore, soil water metrics were often averaged over longer time frames than those at which plants may be responding to soil conditions. It is likely that using plot-level soil information and more intensive vegetation sampling within years would increase the importance of soil water variables in our analysis. Ideally, studies would use plot-level information on soil properties and temporal soil water dynamics, but such measurements can be time and cost intensive, which is not feasible for many studies. Here, we asked whether incorporating readily available data on climate and soil properties enhances our ability to understand drivers of grassland dynamics, and our results suggest that even relatively coarse metrics improve relationships.

Many studies use space-for-time substitutions to determine climate responses, which have been shown to overestimate the magnitude of effects, particularly over shorter time scales (decadal or shorter; Elmendorf *et al.*, 2015). Here we used long-term monitoring data with relatively fine-scale temporal resolution, which allowed us to incorporate antecedent conditions that can mediate grass responses to climate (Peters *et al.*, 2012, 2014). In Chihuahuan Desert grasslands, Reichmann *et al.* (2013) observed lower above-ground net primary production (NPP) when the previous year was relatively dry and higher NPP following wet years, due to differences in stolon density driven by precipitation in the previous year (Yahdjian & Sala, 2006; Peters & Yao, 2012; Peters *et al.*, 2014; Reichmann & Sala, 2014). Likewise, our analysis revealed an interaction between MAP and cover in the previous year for C_4 plots on the Colorado Plateau, suggesting that the responses of these grasses to climate are contingent on previous conditions. In addition, competition and facilitation can mediate responses. Our data were not well suited to evaluate such interactions individually, yet we found patterns that may be consistent with competition. The effect of transpiration from deeper soils ($trans_{depth}$) differed among sites, with a negative relationship at Santa Rita and a positive relationship at Jornada. The grassland plots at Jornada, examined here, have relatively few shrubs, while shrubs are fairly abundant at the Santa Rita plots, so differences in species interactions may explain these contrasting responses. However, strong evidence for competition between shrubs and grasses at Santa Rita is lacking (Appendix S2; McClaran & Angell, 2006). On the other hand, differences in rooting distributions of dominant grass species and soil water dynamics at depth may be driving these divergent responses, since the dominant species at Santa Rita (*Eragrostis lehmanniana*) is more shallowly rooted than

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the dominant at Jornada (*Bouteloua eriopoda*; Gibbens & Lenz, 2001; Huenneke *et al.*, 2001; McClaran, 2003; Huenneke & Schlesinger, 2006). Further research is needed to disentangle the effects of competition, rooting distributions of grasses and shrubs, and soil water dynamics in producing the observed patterns. If antecedent conditions and competition mediate grassland responses to climate (Reichmann *et al.*, 2013; Peters *et al.*, 2014), then reductions in soil water availability over multiple years can accumulate, feeding back to produce increasingly unfavorable conditions for grass persistence and recovery.

Climate change impacts

Our results indicate that perennial grasslands in the southwestern United States will experience substantial shifts in climate and soil moisture conditions that are important to grass dynamics, though the magnitude of expected changes varies among global circulation models (GCMs) and emission scenarios. Several projections suggest increased variability in temperature and climate (Fig. 3b–d) across the region. Although most GCMs project increases in annual precipitation (MAP) for the Colorado Plateau (Fig. 3h), these precipitation increases are concurrent with increasing P_{seas} and increasing mean dry days (dry_{days}, Fig. 3d, g). These patterns are consistent with predictions that while annual precipitation may increase, regions may still experience decreases in wet days and elevated overall water limitation, due to the temporal distribution of precipitation and effects of increased temperature (IPCC, 2014; Fig. 2). Indeed, climate change models forecast larger precipitation events, with longer intervals between events (Knapp *et al.*, 2008, 2015). This potential for contradictory, simultaneous climate-driven impacts on perennial grasses highlights the need to consider the timing of precipitation pulses, even small ones, and their net effects on soil moisture.

To better understand the potential impacts of climate change on perennial grass abundance, we estimated 'neutral points' above and below which we expect decreases and increases in perennial grass cover. Our results indicate that the magnitude of climate change impacts are modest at Santa Rita and for C_3 grasses on the Colorado Plateau, but that projected changes at Jornada imply negative consequences for perennial grasses. At Jornada, the majority of global circulation models (GCMs) under both emissions scenarios (RCP 4.5 and RCP 8.5) show increased frequency of conditions that are unfavorable for grass abundance in the future. Likewise, forecasted climate conditions for the Colorado Plateau suggest an increasing proportion of years with conditions that are related to declining C_4 grass cover, due to increased P_{seas}, which was ranked as most important in our analyses. Our approach also allows us to incorporate uncertainty associated with different GCMs. Perhaps not surprisingly, the extreme models for most variables (high models under the RCP 8.5 scenario) forecast large increases in unfavorable conditions for perennial grasses across the region. Admittedly, our analyses assume that abundance relationships based on past and current climate will hold under future conditions. While historical models can reliably predict responses to climate and temperature alterations, accuracy strongly depends on the quality of historical data, the strength of relationships, and the effect of nonstationarity in patterns (Adler *et al.*, 2013; Wolkovich *et al.*, 2014). Future studies that include experimental manipulations of temperature, precipitation, and soil water availability in conjunction with long-term data would increase understanding of these relationships and the mechanisms driving them (Elmendorf *et al.*, 2015). Our results underscore the need for such studies, considering that loss of perennial grasses in drylands can result in land degradation, exotic species invasions, and declining ecosystem services, which can feedback to increase vulnerability to further climate change and disturbance (Schwinning *et al.*, 2008; Munson *et al.*, 2011b; Peters & Yao, 2012; Munson, 2013; Petrie *et al.*, 2014).

Significance

Understanding temporal plant dynamics in response to climate change is challenging, due to complex interactions between climate and edaphic properties. Climate change will have effects at landscape and regional scales, while factors such as soil properties and plant community composition exhibit high variation at local scales. Such patterns can create no-analogue conditions, complicating predictions of future plant distributions and communities. We integrated long-term monitoring data with widely available soil property information, an ecosystem water balance model, and global circulation models to address these complexities for sites in three southwestern deserts. Our results underscore that climate change impacts may differ substantially among the three deserts of the southwestern United States, and suggest that grasslands at Jornada may be more vulnerable than those on the Colorado Plateau, and that Santa Rita may be surprisingly resilient to changing climate. Ideally, results from our study would be compared across multiple sites within each desert, to test for generalities within and among deserts. Such comparisons are currently difficult, given the scarcity of long-term datasets for desert grasslands across the region. Nonetheless, our work illustrates that incorporating the

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effects of climate variability and its effects on soil water availability enhances our ability to understand past and potential future vegetation dynamics in dryland ecosystems.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Ordination of plots by functional type for all sites.
Appendix S2. Temporal trends in grass, shrub, and cactus abundance at all sites.
Appendix S3. Cover as a function of cover in the previous time step for all sites.
Appendix S4. Predicted vs. observed values from linear mixed models.

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