Plant traits related to precipitation sensitivity of species and communities in semiarid shortgrass prairie

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Summary

- Understanding how plant communities respond to temporal patterns of precipitation in water-limited ecosystems is necessary to predict interannual variation and trends in ecosystem properties, including forage production, biogeochemical cycling, and biodiversity.
- In North American shortgrass prairie, we measured plant abundance, functional traits related to growth rate and drought tolerance, and aboveground net primary productivity to identify: species-level responsiveness to precipitation (precipitation sensitivity S_{spp}) across functional groups; S_{spp} relationships to continuous plant traits; and whether continuous trait—S_{spp} relationships scaled to the community level.
- Across 32 plant species, we found strong bivariate relationships of both leaf dry matter content (LDMC) and leaf osmotic potential Ψ_{osm} with S_{spp}. Yet, LDMC and specific leaf area were retained in the lowest Akaike information criterion multiple regression model, explaining 59% of S_{spp}. Most relationships between continuous traits and S_{spp} scaled to the community level but were often contingent on the presence/absence of particular species and/or land management at a site.
- Thus, plant communities in shortgrass prairie may shift towards slower growing, more stress-resistant species in drought years and/or chronically drier climate. These findings highlight the importance of both leaf economic and drought tolerance traits in determining species and community responses to altered precipitation.

Introduction

Water is a vital resource for terrestrial ecosystem processes, such as photosynthesis and net primary productivity (Del Grosso *et al.*, 2008). Changes in water availability due to interannual variation and directional shifts in precipitation can cause fluctuations in the abundance of different plant species within communities (Carson & Pickett, 1990; Collins *et al.*, 2012). The response of each species within a community to wet or dry years is driven by physiological and competitive constraints on its sensitivity to soil moisture fluctuations. Species' responses within a community combine to yield variation in ecosystem services, such as forage quantity (French, 2017), livestock production (Bailey, 2005), habitat for wildlife (Ceradini & Chalfoun, 2017), biogeochemical cycling (Xu *et al.*, 2013; Du *et al.*, 2018), and invasion resistance (Byers, 2002).

Many terrestrial ecosystems are likely to experience chronically altered amounts of precipitation in the future, with some systems becoming wetter and others drier depending on geographic location (IPCC, 2013; Greene & Seager, 2016). Through impacts on individual species, these changes in precipitation regimes can shift plant community structure (Wilcox *et al.*, 2016), which can feed back to impact how ecosystems respond to global change drivers (Smith *et al.*, 2009). The challenge becomes predicting which species will perform well and which poorly as precipitation varies and climates change. Although much work has focused on characteristics that control plant abundance and affinities across spatial gradients of resource availability (Bartlett *et al.*, 2012; Belluau & Shipley, 2017, 2018; Shipley *et al.*, 2017; Wright *et al.*, 2017), our understanding of the characteristics that regulate plants' temporal responses to precipitation remains surprisingly limited.

Researchers and naturalists have long focused on categorical traits that describe an organism's functional group determined by a species' growth habit (e.g. graminoids, forbs, shrubs) and/or life span (e.g. annuals versus perennials) to gain insight into different plant strategies for resource capture, growth, and reproduction (Clements, 1916; Simberloff & Dayan, 1991). More recently,

considerable attention has been paid to morphological and physiological plant traits (e.g. specific leaf area (SLA), leaf osmotic potential), allowing for examination of differences in plant characteristics within as well as across functional groups (Reich *et al.*, 2007; Violle *et al.*, 2007; Verheijen *et al.*, 2016). Global patterns show consistent tradeoffs between traits that allow rapid resource acquisition (e.g. large thin leaves, high leaf nitrogen (N)) and those that increase leaf longevity or hydraulic safety (e.g. leaf density, osmotic potential) (Bartlett *et al.*, 2012; Moles *et al.*, 2014; Díaz *et al.*, 2016; Ocheltree *et al.*, 2016; Wright *et al.*, 2017). Relationships between these traits and precipitation or water availability across locations, however, are less robust (Wright *et al.*, 2004; Ordoñez *et al.*, 2009; Kattge *et al.*, 2011). For example, traits associated with the leaf economic spectrum, such as SLA and leaf N concentrations, have weak positive relationships with precipitation and water availability at regional and global scales (Wright *et al.*, 2005; Moles, 2018), and leaf-level traits related to drought tolerance (e.g. osmotic potential at full turgor) and water use efficiency (e.g. carbon (C) isotope discrimination) are more strongly correlated with measures of aridity (Diefendorf *et al.*, 2010; Bartlett *et al.*, 2012; Blackman *et al.*, 2014).

Traits that explain species' existence across climatic gradients likely have evolutionary significance (Ehleringer & Monson, 1993; Ma *et al.*, 2018) and could be useful for predicting how species may respond to precipitation variability or change over time. Thus, a logical application of spatial trait–climate relationships is to use them to predict how temporal variation in precipitation will influence plant species' abundances and community composition. Yet, observations suggest ecosystem processes may not change through time as they do across spatial gradients of precipitation (Lauenroth & Sala, 1992; Huxman *et al.*, 2004). Spatial relationships may not reflect how species and communities will change due to interannual fluctuations in rainfall because legacy effects of the previous year's precipitation can create water availability scenarios mismatched with the current year's precipitation (Sala *et al.*, 2012). Additionally, species abundance shifts with chronic changes in water availability may not be in accordance with spatial patterns because many ecosystem attributes (e.g. soil and biogeochemical properties) can take decades or centuries to change in a manner that would reflect spatial patterns (Burke *et al.*, 1997). These limitations are borne out by recent evidence showing that trait variation over environmental gradients is often not predictive of temporal relationships between species' function/survival and environmental conditions (Sandel *et al.*, 2010; Laughlin *et al.*, 2018).

An exciting way forward is to focus within communities and ecosystems and link plant traits with species' performance under varying weather conditions (Garnier *et al.*, 2007; Jung *et al.*, 2014; Májeková *et al.*, 2014). Previous research has established a set of traits related to drought tolerance and, conversely, rapid growth under high resource conditions (Craine *et al.*, 2001; Wright *et al.*, 2002; Bartlett *et al.*, 2012; Frenette-Dussault *et al.*, 2013). Yet, we lack direct tests of how this set of traits influences species' capacities to persist and grow across years with widely varying precipitation. By focusing on long records of temporal variation in precipitation responses within a group of co-

occurring and competing species, we aim to improve understanding of which traits regulate plant responses to precipitation and which species are likely to succeed under different precipitation regimes (Shipley *et al.*, 2016).

Precipitation sensitivity, often represented as the relationship of abundance or biomass with annual precipitation (Smith *et al.*, 2017), is an important attribute that describes how plant populations and communities may fluctuate through time. Additionally, knowledge of how traits influence precipitation sensitivity should facilitate prediction of plant community shifts as ecosystems become wetter or drier (Lavorel & Garnier, 2002; Suding *et al.*, 2008; Tatarko & Knops, 2018). If species' responses to precipitation can be predicted from traits, chronic changes to precipitation may also lead to predictable changes in traits of the entire community (i.e. average species-level traits weighted by species abundance). For example, if species with greater SLA are linked with greater precipitation sensitivity, we might predict that species with greater SLA would become more abundant under chronically wetter conditions, leading to a community with greater SLA. Yet, there are many reasons that scaling from the species to community level may not be so straightforward. Shifts in community traits may be dependent on the assemblage or relative abundance of species within the starting community (Fukami *et al.*, 2005). Also, compensation or asynchrony among species (Isbell *et al.*, 2009) complicates simple species-to-community scaling of traits. Therefore, it will be important to test whether community-level traits shift with precipitation in the same way that species-level sensitivity varies across traits.

Here, we combine long-term data describing community and species performance (aboveground net primary productivity (ANPP), species' abundance) and species' traits for 32 species in a North American shortgrass prairie to address the following questions: (1) How does precipitation sensitivity vary across species, growth habit (e.g. forbs, graminoids, shrubs/subshrubs), and life span (e.g. annuals, perennials)? (2) Which leaf economic and drought tolerance traits are correlated with a species' precipitation sensitivity? (3) Do functional groups differ in which traits explain sensitivity? (4) Do traits that predict species-level variation in precipitation sensitivity also vary with precipitation at the community level? Associated with these questions, we tested the overarching prediction that species and communities with 'fast', resource-acquisitive traits (e.g. annuals) are more sensitive to fluctuating precipitation over time than species and communities with 'slow', resource-conservative traits (e.g. perennials, and species with greater drought tolerance and water use efficiency; following Reich (2014)). Addressing these questions will provide insight into how altered precipitation regimes may impact grassland plant communities, and how various plant species/groups cope with altered precipitation.

Materials and Methods

Site description

Data were collected at the USDA-ARS Central Plains Experimental Range (CPER) site near Nunn, CO, USA (40°49′N,

107°46′W), part of the Long-Term Agroecosystem Research (LTAR) Network. The 6270 ha research site is divided into 45 different pastures that vary in the duration, timing, and/or intensity of grazing. Mean annual temperature is 8.4°C, with maximum temperatures in July averaging 30.6°C and minimum average temperatures in January of −11.0°C (Milchunas *et al.*, 1994). Mean annual precipitation at the site is 343.7 mm, yet interannual variation is high (SD = 92.5 mm, 1939–2017; Lauenroth & Bradford, 2006). The majority of precipitation occurs from late spring through early fall, when temperatures are warm enough to facilitate plant growth (Lauenroth & Bradford, 2006; Irisarri *et al.*, 2016). Soils at the site are primarily fine-sandy loams. Vegetation is dominated by the warm-season (C$_4$) perennial grass species, *Bouteloua gracilis* [Willd. Ex Kunth]; in grazed pastures, *B. gracilis* has a mean relative canopy cover of 60% (SD = 14%) and in ungrazed areas it has a mean relative canopy cover of 29% (SD = 18%; Augustine *et al.*, 2017). Subdominant species are *Carex duriuscula* C.A. Mey (C$_3$ sedge), *Bouteloua dactyloides* [Nutt.] J.T. Columbus (C$_4$ perennial grass), *Pascopyrum smithii* [Rydb.] Á. Löve (C$_3$ perennial grass), *Sphaeralcea coccinea* [Nutt.] Rydb. (perennial forb), *Artemisia fridgida* Willd. (subshrub), and *Opuntia polycantha* Haw. (cactus). Annual species, such as *Vulpia octoflora* [Walter] Rydb., can make up more than 50% of herbaceous plant production during certain years but are typically less abundant (Dufek *et al.*, 2018).

Quantifying plant traits

From 2014 to 2017, we collected plant trait information for 32 common species (Table 1), chosen based on their rankings from mean long-term abundance in both grazed and ungrazed locations across the CPER. The only common species omitted was *Opuntia polyacantha*, a cactus for which measurement of many leaf traits was not feasible nor comparable. Species were characterized as graminoids, forbs, and shrub/subshrubs and as annuals and perennials based on the USDA PLANTS Database (USDA, 2015). Here, we focus on 11 plant traits that we identified *a priori* as likely to influence precipitation sensitivity by either mediating a plant's ability to withstand water stress or to grow rapidly. Focal traits included: SLA, leaf nitrogen (N, %), leaf phosphorus (P, %), stem specific density, leaf osmotic potential Ψ_{osm}, leaf thickness, leaf pubescence, leaf dry matter content (LDMC), leaf area, plant height, and $\Delta^{13}C$ (the $\delta^{13}C$ ratio of leaves expressed relative to the $\delta^{13}C$ ratio of the atmosphere, a proxy for C-isotope discrimination and water use efficiency during photosynthesis). Leaf $\Delta^{13}C$ was calculated following (Farquhar *et al.*, 1989):

$$\Delta^{13}C = \frac{\frac{\delta^{13}C_{air}-\delta^{13}C_{leaf}}{1+\delta^{13}C_{leaf}}}{1000}$$

Eqn 1

where $\delta^{13}C_{air} = -9.19‰$ was measured on site. Note that several of these traits have been related to the ability of species to grow rapidly and their ability to withstand environmental stressors (e.g. LDMC; Wilson *et al.*, 1999; Saura-Mas & Lloret, 2007). Measurement of plant traits followed methods outlined by Pérez-Harguindeguy *et al.* (2013, 2016); see Supporting

Table 1 Metrics describing sensitivity to interannual variation in precipitation S_{spp} of 32 species at the Central Plains Experimental Range in northern Colorado, USA.

Species	Growth habit	Life span	S_{spp}	SE of S_{spp}
Tragopogon dubius	Forb	Perennial	2.2	1.1
Oenothera albicaulis	Forb	Annual	2.0	0.78
Lappula occidentalis	Forb	Annual	1.7	0.59
Cryptantha minima	Forb	Annual	1.3	0.69
Plantago patagonica	Forb	Annual	1.2	0.38
Vulpia octoflora	Graminoid	Annual	1.2	0.40
Lepidium densiflorum	Forb	Annual	1.1	0.50
Chamaesyce glyptosperma	Forb	Annual	0.90	0.59
Bromus tectorum	Graminoid	Annual	0.69	0.94
Astragalus gracilis	Forb	Perennial	0.69	1.0
Artemisia frigida	Shrub/subshrub	Perennial	0.64	0.35
Thelesperma filifolium	Forb	Perennial	0.63	0.50
Oenothera suffrutescens	Forb	Perennial	0.61	0.54
Chenopodium leptophyllum	Forb	Annual	0.39	0.51
Salsola tragus	Forb	Annual	0.38	0.50
Psoralidium tenuiflorum	Forb	Perennial	0.30	0.40
Pascopyrum smithii	Graminoid	Perennial	0.22	0.26
Cirsium undulatum	Forb	Perennial	0.21	0.81
Elymus elymoides	Graminoid	Perennial	0.17	0.38
Sporobolus cryptandrus	Graminoid	Perennial	0.17	0.25
Sphaeralcea coccinea	Forb	Perennial	0.14	0.14
Eriogonum effusum	Shrub/subshrub	Perennial	0.072	0.23
Bouteloua gracilis	Graminoid	Perennial	−0.0017	0.070
Bouteloua dactyloides	Graminoid	Perennial	−0.013	0.22
Carex duriuscula	Graminoid	Perennial	−0.065	0.13
Aristida purpurea	Graminoid	Perennial	−0.069	0.23
Picradeniopsis oppositifolia	Forb	Perennial	−0.12	0.41
Liatris punctata	Forb	Perennial	−0.15	0.53
Ericameria nauseosa	Shrub/subshrub	Perennial	−0.30	0.90
Gutierrezia sarothrae	Shrub/subshrub	Perennial	−0.44	0.45
Hesperostipa comata	Graminoid	Perennial	−0.48	0.26
Lithospermum incisum	Forb	Perennial	−1.2	1.3

Nomenclature from USDA PLANTS as of 1 February 2020.

Information Table S1 for additional information about these traits and how they were measured. Traits were log$_{10}$ or square-root transformed to maximize normality (Table S1). Since Ψ_{osm} is inherently negative, the absolute value was taken before transformation. As such, the directionality of these values is the opposite of raw values (i.e. larger values indicate greater drought tolerance). Mean trait values for each species are publicly available on Dryad (https://doi.org/10.5061/dryad.8sf7m0cjr).

Estimating species' sensitivity to interannual variation in precipitation

To address questions 1–3, we assessed sensitivity to interannual variation in precipitation for all 32 species for which trait

information was collected. Calculating sensitivity from intact local communities provides the advantage of incorporating competition effects into the measure. Using species-level absolute foliar cover data from a long-term grazing study (see following section), species' sensitivities were estimated as the within-species proportional change in cover per millimeter of interannual variation of rainfall. The proportional change was assessed instead of the absolute change in order to minimize the potential for a strong bias of the metric towards dominant species. To this end, species absolute cover values were standardized as $Cover_{std} = (x - \overline{x})/\overline{x}$, where x is the absolute cover value of a species in a particular year, and $\overline{x}$ is the average absolute cover of a species across all years. Then, the slope between standardized cover values and water-year precipitation (1 September–31 August) was used as the sensitivity of that species to precipitation S_{spp}. We used the inverse of the SE around this slope to weight trait–sensitivity regressions to minimize the impact of less robust sensitivity estimates. Because species are not uniformly abundant across grazing regimes (Porensky $et\ al.$, 2017), we calculated sensitivity separately using data from two pastures having light or no grazing and from two pastures having moderate to heavy grazing. When species were present in both sets of pastures, sensitivity and the SE of sensitivity were averaged across the sets.

We assessed the performance of species sensitivity estimates by scaling them up to the community level and comparing with a commonly used sensitivity metric – see review by Smith $et\ al.$ (2017). To this end, we used species abundance data in 15 separate plots across CPER that were independent from the plots used to calculate sensitivity (see following section). We did this by calculating the community-weighted sensitivity for each plot: $S_{comm} = \sum_{i=1}^{n} S_{spp i} \times p_i$, where $S_{spp i}$ is the sensitivity value for species i, and p_i is the relative abundance of species i in a plot. Next, we regressed S_{comm} with the sensitivity of ANPP data (slope between ANPP and water-year precipitation) for the same 15 additional plots. ANPP measurements from the shrub species $Artemisia\ frigida$ were excluded from this analysis because of difficulties obtaining precise measurements of ANPP for this species. Overall, this exercise produced robust support for S_{spp} as a useful metric to estimate precipitation sensitivity at the species level (see Fig. S1 and caption for further details).

Plant species abundance and primary productivity measurements

Species abundance measurements from the long-term grazing intensity (LTGI) study were used to estimate species-level precipitation sensitivity values and to calculate community-weighted means of functional traits. LTGI is comprised of four pastures with similar loamy soils that have experienced different levels of grazing (none, light, moderate, and heavy) during May–October since 1939 (Klipple & Costello, 1960). From 2003 to 2014, species-level plant foliar cover (aerial cover of all vegetation) was measured in each of the four pastures in sixty 0.1 m² plots using modified Daubenmire cover classes (Daubenmire, 1959). Plot locations within a pasture varied slightly from year to year

(5–10 m in random cardinal direction), so we averaged foliar cover across plots in each year to obtain pasture-level estimates of species cover. All plots where cover was measured were protected from grazing throughout the growing season using moveable exclosures. Exclosures were relocated annually prior to cattle entering the pasture, so plots were subjected to grazing in all years except for the year of measurement.

Species abundance and ANPP from three other data sets at CPER were used to assess the robustness of species-level precipitation sensitivity estimates calculated from the LTGI study (Fig. S1). The first data set describes species abundance and ANPP in 10 moderately grazed areas initiated in 1939. Within these, basal coverage measurements (aerial coverage of stems 1 cm from ground level) were taken from 1992 to 2015. Species abundance estimates were obtained by averaging across basal cover measurements taken in 20 quadrats (0.1 m² each) within each exclosure and paired area. ANPP in this data set was collected annually from 1992 to 2015 in six 0.25 m² plots located within small moveable grazing exclosure cages (as already mentioned for LTGI). The other two data sets describe species-level ANPP in five separate areas from 1983 to 2016 (minus 2009–2013 when data were not collected). Species-level ANPP, averaged across fifteen 0.25 m² quadrats sampled within each study area, were summed in each plot and averaged across plots to yield ANPP. Collectively, these additional ANPP estimates, from 15 separate plots in total, were used to assess the robustness of the relationship between precipitation sensitivity and ANPP at the community scale.

Calculating community-weighted traits

To assess how traits are altered by precipitation at the community level, we calculated community-weighted trait values T_{comm}:

$$T_{comm} = \sum_{i=1}^{n} T_i p_i \qquad \text{Eqn 2}$$

T, trait value of species i; p_i, relative abundance of species i; n, number of species measured in the pasture. T_{comm} for each trait was calculated annually using pasture-level species foliar cover from the LTGI data set and regressed with water-year precipitation. Summed relative abundance of the 32 species for which we had plant trait information was > 90% in all years and all areas we examined.

Statistical analyses

To assess variability in precipitation sensitivity among functional groups (question 1), S_{spp} values were compared among growth habit (graminoid, forb, shrub/subshrub) and life span (annual, perennial) via a type III ANOVA. S_{spp} values were weighted by the inverse of the standard error of the slope of each species (1/SE of S_{spp}); this resulted in a hypothesis test that emphasized species with more precise estimates of S_{spp}. We also ran unweighted models for comparison, and results were qualitatively similar. Specifically, the same traits were generally retained as predictors

in 'best' models of S_{spp} (see below), but unweighted models had less explanatory power.

To assess traits as predictors of S_{spp} (question 2), bivariate relationships between trait values and S_{spp} (weighted by 1/SE of S_{spp}) were assessed using regression. S_{spp} was square-root transformed (after adding a constant) to improve normality within multiple regression models. Forward, backward, and bi-directional stepwise regression using Akaike information criterion (AIC) was used to identify key plant traits for predicting S_{spp} across species. All three methods of model selection yielded identical final models, so we report output from the bi-directional selection process only. Leaf $\Delta^{13}C$ was not included in the stepwise regression because leaf $\Delta^{13}C$ is not comparable across C_3 and C_4 species.

To augment findings from stepwise selection, we also conducted path analysis to simultaneously assess direct and indirect relationships of traits with S_{spp}. Path analysis was selected instead of structural equation modeling because we desired to examine linkages among trait measurement variables and between trait measurements and S_{spp}. To this end, we selected the following a priori model based on the following rationale: (1) we wished to test the direct influence of the strongest bivariate trait S_{spp} relationships – LDMC, Ψ_{osm}, and SLA; (2) we wished to examine whether the importance of LDMC was mediated through SLA or Ψ_{osm}, or if its effect was independent of these other traits; (3) leaf thickness was included because it, along with leaf density, is an important component of both SLA and LDMC. This rationale resulted in the following model: $S_{spp} \sim \Psi_{osm}$ + SLA + LDMC + Leaf Thickness; SLA ~ LDMC + Leaf Thickness; Ψ_{osm} ~ LDMC; Leaf Thickness ~~ LDMC. In this set of formulas, '~' represents regressed on and '~~' represents covariance. Because of collinearity concerns (Petraitis et al., 1996), we checked correlations for the two potential relationships not represented in our a priori model. Neither SLA ↔ Ψ_{osm} nor Leaf Thickness ↔ Ψ_{osm} showed particularly strong correlations (Fig. S2).

To assess variability in trait–S_{spp} relationships among functional groups (question 3), we conducted bidirectional stepwise AIC model selection for each trait–sensitivity combination with life span-by-trait (Trait × Life) and growth habit-by-trait (Trait × Habit) interaction terms in the model. Significant life span and growth habit terms in the resulting 'best' models (models with lowest AIC during bidirectional selection process) were used as indicators of whether trait–sensitivity relationships differed across growth habit and life span. Additionally, we examined model terms retained in any model within two AICs of 'best' models.

We used linear regression to assess linkages between community-weighted means of functional traits T_{comm} and water-year precipitation (question 4). As was the case for species-level sensitivity calculations, this was done separately for pastures receiving no or light grazing, and those receiving moderate to heavy grazing.

All analyses were done in R (R Core Team, 2020), and scripts are publicly available on GitHub (https://github.com/wilcoxkr/Precip_sensitivity_traits_2020). Data used to calculate sensitivity metrics and mean trait values for each species are publicly available (see data availability statement associated with this article).

Results

Sensitivity of plant growth to annual precipitation (September–August; S_{spp}) was calculated for 32 species: 10 graminoids, 18 herbaceous forbs, and 4 shrubs or subshrubs; 10 were annual species and 22 were perennials. S_{spp} represents the proportional change in species abundance (relative to its average absolute abundance) for every 1 mm change in water-year precipitation. For example, a species with an S_{spp} value of 1.0 would increase by 10% with an increase of 10 mm water-year precipitation, or double with an increase of 100 mm. S_{spp} ranged from +2.2 to −1.2% mm^{-1}. For most species S_{spp} was positive (Table 1), reflecting greater abundance in high-rainfall years and lower abundance in low-rainfall years. We found strong differences in S_{spp} between annual and perennials, with perennial species having, on average, 86% lower sensitivity than annual species ($F_{1,28} = 19.0$, $P < 0.01$, Fig. 1). We found no significant differences in S_{spp} among growth habit ($F_{2,28} = 0.99$, $P = 0.38$, Fig. 1).

Trait–S_{spp} relationships

Of the 11 traits we examined, we identified six statistically significant ($P < 0.05$) cross-species correlations between plant traits and S_{spp} (Fig. 2). Species having greater SLA, leaf N, and leaf P generally had higher S_{spp} (Fig. 3a–c). Alternately, species having greater stem specific density, more negative leaf osmotic potential (Ψ_{osm} – note that the values in Fig. 2 are opposite in sign to raw Ψ_{osm} values), and greater LDMC generally had lower S_{spp} (Fig.
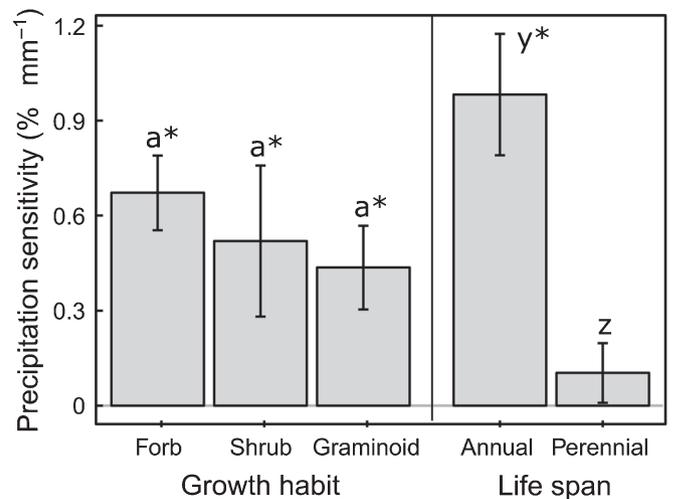

Fig. 1 Least-squared means from the model comparing precipitation sensitivity S_{spp} across growth habit and life span, which was weighted by the inverse of the standard error of a species' S_{spp}. Letters within panels indicate significant differences among growth habit or life spans. Asterisks indicate that S_{spp} is significantly different than zero. Bars represent ± 1 SE from the mean. The threshold for statistical significance was set at α = 0.05.

3d,e,h). LDMC was the trait most strongly correlated with S_{spp} ($r = -0.67$). We did not find significant correlations between S_{spp} and leaf thickness, pubescence, leaf area, plant height, or leaf carbon-isotope discrimination ($\Delta^{13}C$; Fig. 3f,g,i–k).

Owing to covariance among leaf traits (Fig. S2), the pairwise correlations between leaf traits and S_{spp} are not necessarily independent of one another. Bidirectional stepwise model selection based on AIC was used to determine the set of traits that best predicted S_{spp}. We found that LDMC and SLA together represented the model with the lowest AIC, explaining 59% of the variation in S_{spp}. Within this model, both LDMC and SLA were significant predictors ($P < 0.01$) whose modeled effects were largely independent (variance inflation factor VIF = 1.02 for LDMC and SLA). Leaf N and leaf P were included in preceding models during selection that had AIC values within 2 of the final model (Table S2), so these were similarly useful predictors of S_{spp}. Leaf N and leaf P were not highly collinear (VIF < 2.5 for leaf P and leaf N).

Path analysis was used to detect direct and indirect effects of multiple key drought tolerance and economic traits (Fig. 3). The *a priori* model we selected was not a significantly poor fit to the data ($\chi^2 = 0.10$, df = 2, $P = 0.95$). This analysis showed strong independent regressions of SLA ($z = 2.3$, $P = 0.02$) and LDMC ($z = -2.1$, $P = 0.04$) with S_{spp}, whereas Ψ_{osm} and leaf thickness direct regressions with S_{spp} were not significant ($z = 0.87$, $P = 0.39$ and $z = 0.01$, $P = 1.0$, respectively). Leaf thickness and LDMC were both strongly negatively related with SLA (thickness: $z = -6.4$, $P < 0.01$; LDMC: $z = -5.6$, $P < 0.01$). LDMC was also positively related to Ψ_{osm} ($z = 5.2$, $P < 0.01$).

Effects of traits, growth habit, and life span on precipitation sensitivity S_{spp}

We examined whether trait values were a significant predictor in trait–S_{spp} models that also included growth habit and life span. We found that life span was important in most of the trait–S_{spp}
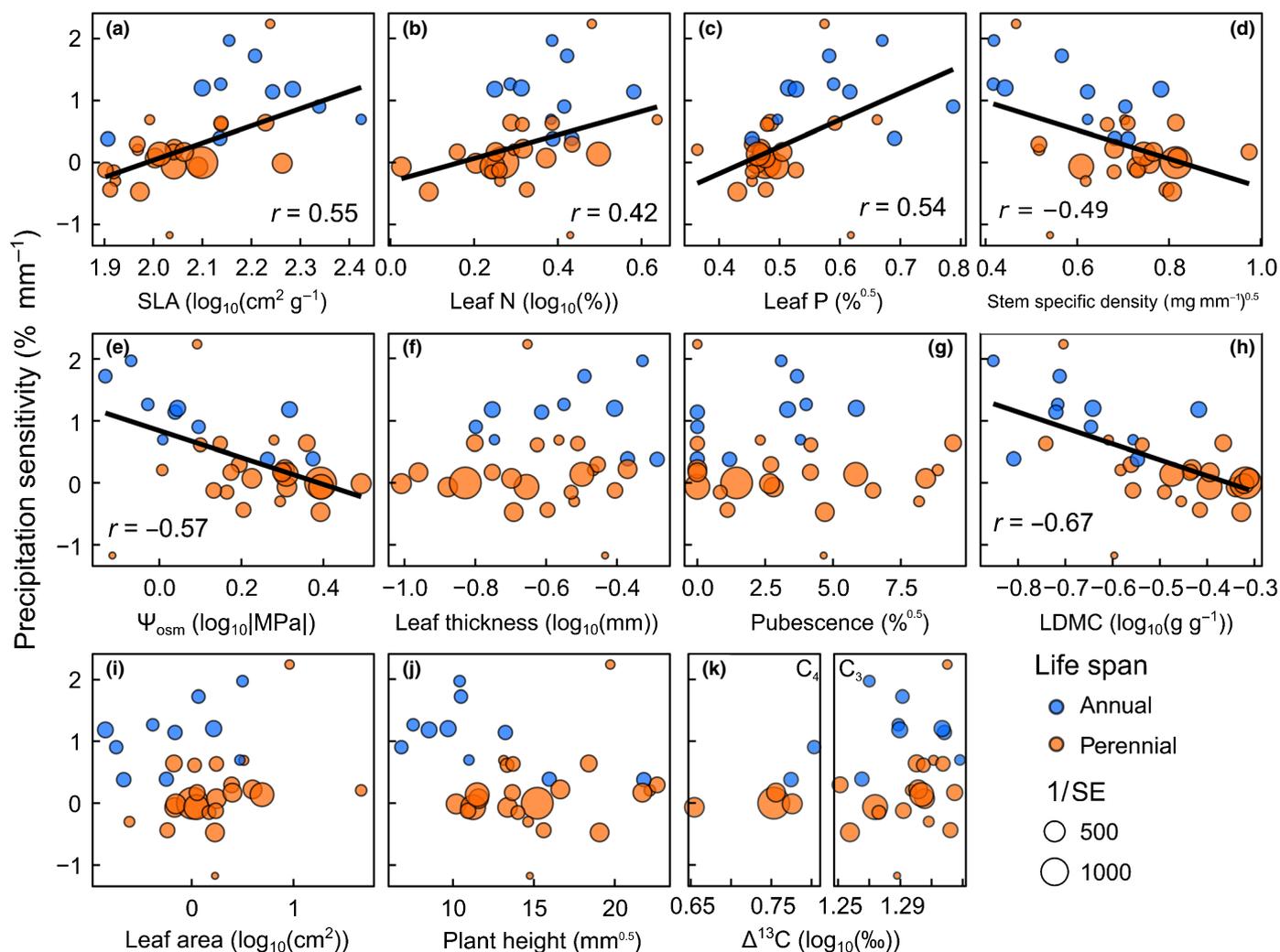

Fig. 2 Interspecific bivariate relationships between precipitation sensitivity S_{spp} and plant trait values. Regressions are weighted by the inverse of the SE of a species' sensitivity value. Colors represent different life spans. Different panels show different plant traits: (a) specific leaf area (SLA); (b) leaf nitrogen (leaf N); (c) leaf phosphorus (leaf P); (d) stem specific density; (e) leaf osmotic potential (Ψ_{osm}); (f) leaf thickness; (g) pubescence; (h) leaf dry matter content (LDMC); (i) individual leaf area; (j) plant height; (k) leaf $\Delta^{13}C$. Nonsignificant regression lines ($\alpha = 0.05$) are not shown. The regression for leaf $\Delta^{13}C$ was performed separately for species with C_3 and C_4 photosynthetic pathways.
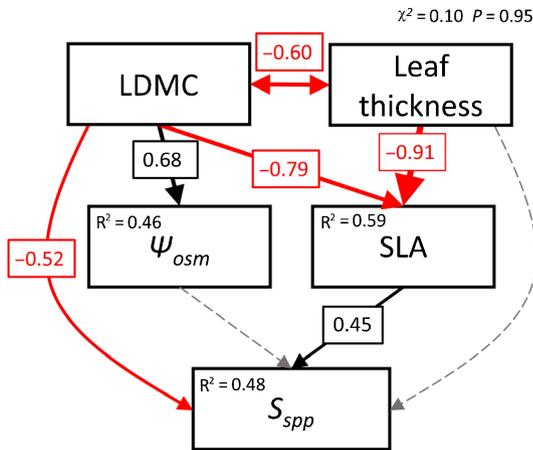
$\chi^2 = 0.10$ $P = 0.95$

Fig. 3 Path analysis assessing direct and indirect relationships between key economic and drought-tolerance traits and species sensitivity to interannual variation in precipitation S_{spp}. Traits assessed were leaf dry matter content (LDMC), leaf thickness, leaf osmotic potential (Ψ_{osm}), and specific leaf area (SLA). Black and red solid arrows represent positive and negative effects, respectively. Gray dashed lines represent nonsignificant effects at $\alpha = 0.05$. Numbers within lines and line thickness represent magnitude of standardized effect sizes. Directional arrows travel from predictor variables to dependent variables, whereas double-ended arrows represent covariance accounted for within the model. Note that the absolute value of leaf osmotic potential was used in this analysis (i.e. greater values indicate greater drought tolerance).

models but that traits had additional predictive value. For most of the traits that were robust predictors of S_{spp} by themselves, trait variation within growth habit and/or within life span was a useful predictor of S_{spp} (statistically significant for SLA and LDMC; marginally significant for leaf N, Ψ_{osm}, and stem specific density; Table 2). By contrast, the relationship between leaf P and S_{spp} was driven primarily by differences between annuals and perennials. Notably, when accounting for differences between life span and/or growth habit, we found some evidence that the five traits that did not show a significant univariate relationship with S_{spp} all explained additional variance in S_{spp}. For example, the size of individual leaves (leaf area) was positively correlated with S_{spp} within both annuals and perennials, but leaf area was not a significant predictor across all species (Fig. 2i). Significant Trait × Life terms for pubescence and plant height ($P = 0.02$ and $P = 0.05$, respectively) indicate that the effects of these traits on S_{spp} differed for annual versus perennial species (Fig. 2g,j). Pubescence had a more positive slope with S_{spp} for annual (0.11 ± 0.16; slope $\pm$ 95% confidence interval) versus perennial species ($7.0 \times 10^{-4} \pm 6.0 \times 10^{-2}$). Plant height had a more negative slope with S_{spp} for annual species (-0.066 ± 0.067) than for perennial species (0.019 ± 0.049).

Community-weighted traits

Finally, we aimed to assess how community-weighted traits might respond to temporal variation in precipitation (response traits *sensu* Lavorel & Garnier, 2002). To gauge the strength of each trait as a community response trait, we calculated standardized slopes between T_{comm} and water-year precipitation in four

adjacent pastures with similar soils. We found that all traits except stem specific density and plant height had significant T_{comm}–precipitation slopes in either light-to-no grazing or moderate-to-heavy grazed communities. Interestingly, the magnitude of the slope varied with grazing for leaf N, leaf thickness, and leaf pubescence (Fig. 4), likely reflecting the low occurrence of species with high N, thick leaves in moderate to heavily grazed areas, and low occurrence of species with pubescent leaves in areas with no or light grazing.

Discussion

In this study, we examined how temporal sensitivity to precipitation varied among species, growth habit, and life span, which traits were robust predictors of that sensitivity, and whether these traits were also predictors of community-level responses. Our major findings were: (1) annual species were, on average, almost an order of magnitude more sensitive to interannual variation in precipitation than perennial species were (Fig. 1); (2) SLA and LDMC together explained 59% of the variation in sensitivity across 32 species, yet these two trait–sensitivity relationships were largely orthogonal to each other; (3) at the community level, leaf economic traits, stem traits, and traits related to drought tolerance (e.g. leaf Ψ_{osm}) were related to interannual variation of precipitation, but responses depended on grazing regime and abundance of particular species. Together, these results highlight the importance of both economic and drought-tolerance traits, and the potential ability of trait-based approaches to help scientists and managers predict species and community-level responses to weather variability and climate change.

Precipitation sensitivity S_{spp} among functional groups

Regional and global assessments suggest that, across ecosystems, the sensitivity of net primary productivity to interannual variability in precipitation is dependent on climate, with more mesic ecosystems being less sensitive to fluctuations of precipitation across years (Huxman *et al.*, 2004; Sala *et al.*, 2012; Biederman *et al.*, 2016). However, case studies have provided evidence that the type of vegetation present within an ecosystem can also have strong impacts on the sensitivity of an ecosystem to precipitation fluctuations (Xu *et al.*, 2013; Scott *et al.*, 2014; Wilcox *et al.*, 2015). We predicted that such variability in the precipitation sensitivity of plant communities should be a function of both categorical plant traits (e.g. growth habit and life span) and continuous plant traits (e.g. leaf economic traits). Our results support this prediction. For example, the lower sensitivity of perennial species to year-to-year variation in precipitation in the shortgrass steppe is likely a function of the fact that the leaves, stems, and roots of perennials tend to have traits associated with a 'slower' strategy for growth and resource acquisition (relative to annuals). Additionally, species mortality and limited germination cues due to water stress likely limit abundance of annual species in dry years. Consistent with this interpretation, we observed that, both within and across plant functional groups, species with

Table 2 P values of terms included in the lowest Akaike information criterion (AIC) models ('best' models) of sensitivity to interannual variation in precipitation S_{spp} from bidirectional stepwise model selection for each trait.

Trait name	Trait	Life span	Growth habit	Trait × Life	Trait × Habit	R^2
SLA†	**< 0.01**	**0.02**	**0.04**	—	—	0.60
Leaf N†	*0.10*	**< 0.01**	—	(0.31)	—	0.44
Leaf P†	(0.72)	**< 0.01**	—	—	—	0.46
Ψ_{osm}†	*0.08*	**< 0.01**	0.16	(0.37)	0.17	0.52
LDMC†	**0.03**	**< 0.01**	—	(0.23)	—	0.52
Leaf Δ^{13}C‡	*0.05*	**< 0.01**	0.16	(0.32)	0.19	0.55
Leaf thickness	0.11	**< 0.01**	0.22	0.11	(0.09)	0.52
Pubescence	*0.09*	0.57	*0.07*	**0.02**	*0.08*	0.55
Height	0.08	**< 0.01**	(0.24)	*0.05*	—	0.51
Leaf area	*0.05*	**< 0.01**	—	(0.85)	—	0.48
SSD†	*0.05*	**< 0.01**	0.16	(0.28)	0.19	0.49

Bold values indicate $P < 0.05$; italic values indicate $0.05 < P < 0.1$. SLA, specific leaf area; N, nitrogen; P, phosphorus; Ψ_{osm}, leaf osmotic potential; C, carbon; LDMC, leaf dry matter content; SSD, stem specific density.
See Supporting Information Table S1 for details of the trait names. Values in parentheses are terms that were not in lowest AIC model but were in models within two AICs of lowest AIC model. —, terms that were removed from all models within two AICs of lowest AIC model.
†Traits that were significantly related to S_{spp} without life span and growth habit in the model.
‡C_4 species were removed from the leaf Δ^{13}C model.
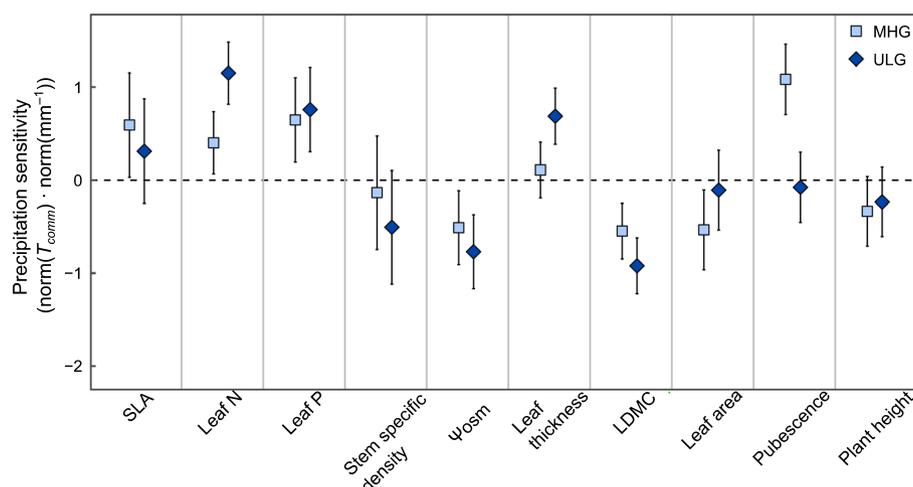

Fig. 4 Standardized slopes from relationships of water-year precipitation (PPT) with community-weighted traits T_{comm}. PPT–T_{comm} regressions were done separately in pastures without grazing or having light grazing (ULG; dark diamonds) and in pastures with moderate or heavy grazing (MHG, light squares). Traits assessed, from left to right, were specific leaf area (SLA), leaf nitrogen (leaf N), leaf phosphorus (leaf P), stem specific density, leaf osmotic potential (Ψ_{osm}), leaf thickness, leaf dry matter content (LDMC), individual leaf area, pubescence, and plant height. All values used in regressions were normalized by their means for comparison across traits. Error bars represent 95% confidence intervals. Transformations are as in Fig. 2; note that the sign of leaf Ψ_{osm} was reversed such that greater positive values represent greater drought tolerance.

low SLA, high LDMC, and/or more negative leaf Ψ_{osm} were less sensitive to interannual variability in precipitation.

Other unmeasured traits likely also contributed to the patterns we observed. For example, the lower sensitivity of perennial species may be a function of their ability to utilize carbohydrates stored from previous years' growth, which can buffer individuals in years when soil moisture levels are suboptimal (White, 1973). Additionally, perennial species are often more deeply rooted than annual species, which can allow organisms to avoid drought (Nippert & Knapp, 2007). By contrast, annual species have greater aboveground growth rates when environments are favorable (Hsiao & Acevedo, 1974), as reflected here in high values

for SLA and leaf nutrient concentrations. This is likely also due to low root:shoot ratios and the lack of belowground carbohydrate storage for future growing seasons (De Souza & Da Silv, 1987). In addition to differences among functional groups, the resolution of these data allowed us to assess species-level relationships between continuous traits and S_{spp}.

Interspecific patterns of precipitation sensitivity S_{spp} and continuous traits

We found that S_{spp} was best predicted by both leaf economic and drought-tolerance traits. The strongest bivariate relationship

between a continuous trait and S_{spp} was with LDMC (Fig. 2), a trait that provides information both about drought tolerance and leaf economics. This contention is supported by our path analysis results, which show robust separate paths from LDMC and SLA to S_{spp}. This is likely because LDMC is associated with thicker and more rigid cell walls within the leaf, which allows for maintenance of cell function under low leaf water potentials (Monson & Smith, 1982). In this way, LDMC provides information about a species' ability to tolerate dry conditions. Increased C costs associated with this safety infrastructure can result in slower growth rates, compared with species having thinner, less rigid cell walls. As such, LDMC also informs about a species' position along the leaf economic spectrum. Additional evidence that both leaf economic and drought-tolerance traits are important for determining precipitation sensitivity are, first, high correlation coefficients of leaf osmotic potential, SLA, and leaf P and, second, that LDMC and SLA were both included in the model with the lowest AIC and greatest R^2 during the stepwise model selection process (Table S2). Although LDMC and SLA are often closely related, they can provide different information about drought tolerance and growth rate, perhaps particularly in this ecosystem, where an inverse relationship between LDMC and thickness weakens their correlation (Blumenthal et al., 2020). The counterintuitive relationship between LDMC and thickness in this ecosystem is likely because species with high LDMC (contributing to low SLA) also have thin leaves (contributing to high SLA). These trends occur within functional groups but are most clearly seen across functional groups: perennial forbs and legumes in this ecosystem often have thicker, but less dense leaves, whereas perennial grasses have thinner, but more dense leaves (Blumenthal et al., 2020).

The codependence of S_{spp} on leaf economic and drought-tolerance traits is likely due to 'fast' species being better able to increase growth in wet years, whereas species able to tolerate drought continue functioning in dry years. So, a species' S_{spp} may be driven by either leaf economic or drought-tolerance traits. For example, Oenothera albicaulis, prairie evening primrose, was the annual species with the highest S_{spp}, yet it had an intermediate SLA value. We suspect the reason for its high S_{spp} value was due to a lack of hydraulic safety infrastructure, indicated by low LDMC, low stem specific density, and less negative Ψ_{osm}, or alternately due to a lack of germination in dry years. The independent effects of LDMC and SLA shown in our 'best' model and path analysis (Fig. 3) suggest that LDMC provides information about the drought tolerance of species within this system, which is separate from its effects through leaf economics. S_{spp} is determined by species' responses in both wet (via ability to fully take advantage of excess soil water) and dry (via ability to maintain abundance despite low water availability) years. It follows that both drought tolerance and leaf economic traits are important for determining S_{spp}, as we see here. We also note that we tested an alternate path analysis model structure that switched the directionality between LDMC and Ψ_{osm}, such that $\Psi_{osm} \rightarrow$ LDMC, and this led to a model that was a poor fit to the data ($\chi^2 = 6.23$, df = 2, $P = 0.04$), but the effect sizes were qualitatively similar to our a priori model. We suggest that the robustness of the path analysis findings despite changes in

model structure provides additional evidence that LDMC is associated with S_{spp} due to its linkages with both the leaf economic spectrum and drought resistance.

Qualitatively, these results align with previous observations across spatial gradients. For example, global gradients of leaf economic traits and climate (e.g. Ordoñez et al., 2009; Wright et al., 2017) show that traits related to 'fast' growth strategies often are more common in wetter ecosystems, and traits related to 'slow' growth strategies exist in drier ecosystems. Also, previous studies have shown drought tolerance traits are typically more successful (Markesteijn et al., 2011) and abundant (Bartlett et al., 2012; Belluau & Shipley, 2017) in more arid locations. However, patterns between precipitation and traits that are relatively weak across space (Wright et al., 2004; Ordoñez et al., 2009; Kattge et al., 2011) turn out to be quite strong through time within this semiarid ecosystem. So, though our findings support the contention that economic traits should be useful for understanding water relations within ecosystems (Reich, 2014), and that rapid resource acquisition and growth is an important strategy for coping with variable water availability, they also highlight the need for simultaneously considering drought tolerance to robustly assess community-level effects of altered water availability. Additionally, these strong interspecific relationships of both drought and leaf economic traits with S_{spp} suggest that we can predict both which species will be most responsive in terms of productivity and which will be most resistant to drought. Our findings also suggest that LDMC may be one of the most useful traits for understanding semiarid ecosystems, as previously observed for mesic and arid ecosystems (Wilson et al., 1999; Laliberté et al., 2012; Frenette-Dussault et al., 2013; Májeková et al., 2014). Thus, we found broad support for our prediction that precipitation sensitivity can be linked to both leaf economics traits and drought-resistance traits, and that these linkages are orthogonal to one another.

Trait–S_{spp} relationships within and among functional groups

One challenge of using plant traits to predict the functioning of plant communities is the possibility that the traits most strongly related to function differ between plant functional groups. We found that, even when accounting for differences in S_{spp} across growth habit and/or life span, variation of continuous traits were important predictors for S_{spp}, especially for SLA and LDMC (Fig. 2; Table 2). Another clearer pattern in our findings was that shorter plants were more sensitive to interannual precipitation shifts, but only among annual species (Fig. 2; Table 2). This could reflect the reliance of short annual species, which tend to have shallow roots (e.g. V. octoflora; Augustine et al., 2017), on consistent precipitation across the growing season, whereas short perennials can have substantial root networks (e.g. B. gracilis; Liang et al., 1989).

These findings are also important for predicting ecosystem states and functioning under shifts in environmental conditions. Many demographic vegetation components within Earth system models use plant functional groups to represent changes in

vegetation and their subsequent control on ecosystem processes – see review by Fisher *et al.* (2018) – whereas others represent vegetation shifts using continuous traits to represent individuals (Scheiter *et al.*, 2013). Our findings support the suggestion that both continuous traits and functional groups should be incorporated into projections of future ecosystem states and functioning (e.g. Butler *et al.*, 2017). Additionally, our findings that drought-tolerance traits were related much more strongly to temporal patterns of rainfall than those found typically across space lead us to suggest caution when using spatial gradients of traits and environmental conditions to predict community shifts under global changes.

Are cross-species trait–sensitivity patterns indicative of shifts in community-level traits?

Similar to species-level responses, we found that many of the community-weighted traits we examined were related to interannual variation in precipitation (Fig. 4). Wet years led to greater community-weighted values for many 'fast' traits, whereas dry years led to greater values for LDMC and Ψ_{osm}, in each case reflecting greater abundance of species with those traits. However, the robustness of T_{comm}–precipitation relationships varied in areas having different grazing pressures, suggesting that community-scale responses to precipitation may be mediated by other factors, such as land management. For example, in the lightly/ungrazed pastures (Fig. 4, dark diamonds), increases in *Thelesperma filifolium* (a species with high leaf N and relatively high S_{spp}) in wet years contributed to a substantial increase in community-weighted leaf N. Alternately, in the areas with moderate and heavy grazing (Fig. 3, light squares), we found a much weaker relationship between community-weighted leaf N and precipitation because *T. filifolium* is typically not abundant in areas of higher grazing pressure (Milchunas, 2011; Porensky *et al.*, 2017). In moderately and heavily grazed pastures, we found that pubescence was a strong response trait, indicative of increased community-weighted pubescence in wetter years, and vice versa in dry years. This is likely linked to the abundance of *Artemisia frigida*, a very pubescent subshrub that is relatively sensitive to precipitation (Table 1) and abundant in areas of high grazing pressure. These location-specific differences in response traits highlight the need to understand the initial plant community composition to determine its trajectory under varying or changing precipitation.

It is important to note that these variations in community-weighted traits do not incorporate intraspecific variation, which will likely also be an important component of how community traits respond to altered precipitation. Based on previous work showing predictive power of interspecific drought-tolerance traits despite the presence of trait plasticity (Bartlett *et al.*, 2014), we contend that interspecific rankings are still useful for assessing directionality of shifts in community traits to occur under altered precipitation. We posit that these relationships may be more pronounced when intraspecific responses to altered precipitation are also incorporated, yet additional investigation of these trends is needed.

Conclusions

Here, we focused on one of the less studied areas in trait-based ecology by assessing the role of plant traits as predictors of species and community performance through time in intact communities. We found that multiple physiological and morphological plant traits were strongly linked with species-level sensitivity to precipitation, explaining variation in sensitivity both within and among functional groups. In this semiarid grassland, plant strategies for coping with highly variable precipitation appear to fall along two different spectrums, one describing a species' leaf economic spectrum and the other describing its drought tolerance. Both of these trait categories seem to be important in determining a species' response to altered precipitation. These results provide insight into how species and plant communities might respond to fluctuations or directional shifts in water availability. For example, under chronically increased precipitation and in wet years, we predict that plant communities may shift to those having more species lacking drought-tolerance characteristics and more species having characteristics for fast growth. In conjunction with information of how traits link with ecosystem functioning, this will aid in making predictions of shifts in ecosystem functioning with statistical and process-based models, as well as aid land managers with risk mitigation. For example, although climate records for this region do not show trends in average annual precipitation (Ray *et al.*, 2008), they do show substantially higher occurrence of severe drought (Lukas *et al.*, 2014). As such, we may see increased abundance of species and communities with low SLA, high LDMC, and less negative Ψ_{osm} in these ecosystems, which may result in relatively greater ecosystem function in dry years. So, ensuring the presence of drought-resistant species within landscapes should be a priority for sustainability of ecosystem function and services under more frequent drought. Additionally, care should be taken when applying broad trait–environment relationships, since the identity of traits that change under altered resource levels may vary among functional groups/ecosystems. Based on these findings, we suggest that continuous traits can add value to more traditional functional group categorization schemes and improve our understanding of how communities respond to fluctuations in water availability. Both drought tolerance and economic traits should be considered when predicting future community structure.

Author contributions

KRW and DMB conceived of this study, DMB, JAK, KEM and TO collected and cleaned trait data, LMP and JDD collected and cleaned cover data, KRW analyzed data, and KRW, DMB, JAK, KEM, JDD, TO and LMP wrote and edited the manuscript.cd/cd   H:/journals/W3G/NPH/17000/K:\sps-soft\WileyML_3G\suser\zip.exe   APPSupport.zip *.td *.3f *.hyp *.m2t *.bak *.batdel AppSup.bat

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Regression between sensitivity of aboveground net primary productivity and weighted species sensitivity.

Fig. S2 Correlation matrix among traits.

Table S1 Details of plant traits collected in this study.

Table S2 AIC trace of bi-directional stepwise selection.

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