7-2022

Water Availability Dictates How Plant Traits Predict Demographic Rates

Alice E. Stears
University of Wyoming, astears@uwyo.edu

Peter B. Adler
Utah State University

Dana M. Blumenthal
USDA, Agricultural Research Service

Julie A. Kray
USDA, Agricultural Research Service

Kevin E. Mueller
Cleveland State University, k.mueller89@csuohio.edu

ARTICLE

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

Water availability dictates how plant traits predict demographic rates

Alice E. Stears[1] | Peter B. Adler[2] | Dana M. Blumenthal[3] |
Julie A. Kray[3] | Kevin E. Mueller[4] | Troy W. Ocheltree[5] |
Kevin R. Wilcox[6] | Daniel C. Laughlin[1]

[1]Botany Department and Program in Ecology, University of Wyoming, Laramie, Wyoming, USA

[2]Department of Wildland Resources and the Ecology Center, Utah State University, Logan, Utah, USA

[3]USDA-ARS Rangeland Resources Research Unit, Fort Collins, Colorado, USA

[4]Department of Biological, Geological and Environmental Sciences, Cleveland State University, Cleveland, Ohio, USA

[5]Warner College of Natural Resources, Colorado State University, Fort Collins, Colorado, USA

[6]Department of Ecosystem Science and Management, University of Wyoming, Laramie, Wyoming, USA

Correspondence
Alice E. Stears
Email: astears@uwyo.edu

Handling Editor: Nathan Jared Boardman Kraft

Abstract

A major goal in ecology is to make generalizable predictions of organism responses to environmental variation based on their traits. However, straightforward relationships between traits and fitness are rare and likely to vary with environmental context. Characterizing how traits mediate demographic responses to the environment may enhance the predictions of organism responses to global change. We synthesized 15 years of demographic data and species-level traits in a shortgrass steppe to determine whether the effects of leaf and root traits on growth and survival depended on seasonal water availability. We predicted that (1) species with drought-tolerant traits, such as lower leaf turgor loss point (TLP) and higher leaf and root dry matter content (LDMC and RDMC), would be more likely to survive and grow in drier years due to higher wilting resistance, (2) these traits would not predict fitness in wetter years, and (3) traits that more directly measure physiological mechanisms of water use such as TLP would best predict demographic responses. We found that graminoids with more negative TLP and higher LDMC and RDMC had higher survival rates in drier years. Forbs demonstrated similar yet more variable responses. Graminoids grew larger in wetter years, regardless of traits. However, in both wet and dry years, graminoids with more negative TLP and higher LDMC and RDMC grew larger than less negative TLP and low LDMC and RDMC species. Traits significantly mediated the impact of drought on survival, but not growth, suggesting that survival could be a stronger driver of species' drought response in this system. TLP predicted survival in drier years, but easier to measure LDMC and RDMC were equal or better predictors. These results advance our understanding of the mechanisms by which drought drives population dynamics, and show that abiotic context determines how traits drive fitness.

KEYWORDS
demographic rates, drought, global change, grasslands, plant traits

INTRODUCTION

As climate change leads to higher frequency and intensity of extreme weather events, it becomes increasingly important to identify how organisms respond to abiotic stressors. It is well known that traits can affect growth, survival, and reproduction (Adler et al., 2014; Kunstler et al., 2020), but we are only now beginning to learn how these effects depend on environmental context (Worthy et al., 2020). Models using traits to predict responses to changing climate must explicitly determine how trait effects on performance change according to climatic variation. Most work to date has relied on morphological traits, but traits that directly measure resource use may be superior predictors of demographic performance. Understanding how the effect of physiological and morphological traits on demographic rates varies across environmental gradients will allow for precise predictions of occurrence and performance across global ecosystems and in future climate scenarios (Laughlin et al., 2020). Here, we examined how plant leaf and root traits predict growth and survival rates of grassland species according to interannual variation in water availability in a North American shortgrass steppe ecosystem, while accounting for individual plant size and local neighborhood interactions.

Although climate models predict that some regions will receive more precipitation in concentrated, extreme events, other regions such as western North America will receive less moisture overall or have longer periods of drought punctuated by extreme precipitation events (Ummenhofer & Meehl, 2017). Communities with lower mean annual precipitation often have lower community-weighted mean (CWM) specific leaf area (SLA) (Cornwell & Ackerly, 2009). Higher SLA species also increase in abundance in wetter years in communities with low mean precipitation (Wilcox et al., 2021). Other studies observed little to no variation in CWM traits after drought, but have identified changes in functional diversity (FD) in dry sites (Luo et al., 2019) or after experimentally induced drought (Griffin-Nolan, Blumenthal, et al., 2019). In North American shortgrass steppe, plant species with low leaf osmotic potential (a primary determinant of turgor loss point; Bartlett, Scoffoni, Sack, 2012), high leaf dry matter content (LDMC), and low SLA are relatively insensitive to interannual precipitation variability (Wilcox et al., 2021). Correlations among these and other traits indicate trade-offs between drought resistance and rapid resource acquisition (Blumenthal et al., 2020). Additional work has found that species are more likely to survive drought if they have traits correlated with a conservative resource acquisition strategy (Luong et al., 2021). Determining how traits affect growth and survival can help to provide a mechanistic understanding of population responses to interannual climate variation, as

well as improve our understanding of drought-tolerance mechanisms in grassland plants.

Individual-level impacts of abiotic variation are observed first in the physiological responses of plants to stress, such as wilting in response to decreased water availability (Bartlett, Scoffoni, Ardy, et al., 2012; Bartlett et al. 2016). After a plant's physiological ability to withstand or escape drought is surpassed, death or decreased fecundity negatively impacts population sizes (Koerner & Collins, 2014). Community composition may then shift, in turn altering the competitive and facilitative interactions between individuals within that community (Ploughe et al., 2019). In extreme cases, this process can lead to either species extirpation or recruitment of formerly absent species to the local species pool, changing both the functional and phylogenetic diversity of the community. Evaluating the underlying demographic mechanisms and plant–plant interactions that are driving community dynamics will allow us to predict how plant phenotypes mediate the impacts of future climate change on plant demographic rates.

Many morphological traits are correlated along an axis representing resource acquisition strategy from fast (e.g., high SLA, low LDMC) to slow (e.g., low SLA, high LDMC) (Reich, 2014). Of these economic traits, we expect that LDMC is most relevant to a plant's ability to survive water stress because it measures leaf structure and allocation of carbon to leaf tissue (Hodgson et al., 2011). Species with higher LDMC have higher allocation to cell wall structure and more densely packed leaf cells, and therefore are more likely to maintain cell turgor under water stress (Poorter et al., 2009; Wilcox et al., 2021). High LDMC species also have higher lignin content, probably due to a higher number of leaf vessels and thicker cell walls, which also confers the ability to maintain water transport under more negative water potentials (Blumenthal et al., 2020). Finally, high LDMC species generally have more nonstructural carbohydrates (NSCs), which provide osmotic resistance to wilting (Griffin-Nolan, Ocheltree, et al. 2019).

Traits that more directly measure physiological processes such as cavitation resistance or osmotic potentials might be especially useful for identifying patterns of individual plant responses to soil water availability. One such trait is leaf turgor loss point (TLP), a measure of the water potential within a leaf at which leaf cells begin to lose turgor and the leaf loses function (Bartlett, Scoffoni, Ardy, et al., 2012; Bartlett et al., 2016). Plants with more negative TLP have greater physiological drought tolerance because they can withstand more negative water potentials before experiencing a reduction in leaf cell turgor, stomatal and hydraulic conductance, and gas exchange (Bartlett, Scoffoni, Ardy, et al., 2012). Recent

methodological advances use a vapor pressure osmometer to identify leaf osmotic potential, or leaf cell solute potential at full hydration, which is correlated with TLP in woody species (Bartlett, Scoffoni, Sack, 2012) and herbaceous species in western North American grasslands (Griffin-Nolan, Ocheltree, et al. 2019). In semiarid shortgrass steppe, TLP is predictive of species occurrences in response to drought, with lower TLP species less likely to decline in abundance in drier years (Wilcox et al., 2021). In this ecosystem, low TLP is also correlated with other traits such as high LDMC and low leaf nitrogen and phosphorous, which indicate drought tolerance and a resource conservative growth strategy (Blumenthal et al., 2020). However, the extent to which TLP mediates the effect of drought on plant survival and growth is not known. We also lack robust evidence to show that traits more closely measuring physiological processes are better than more traditional economic traits for predicting plant responses.

We evaluated whether species-level plant functional traits related to water use helped to explain patterns in species growth and survival, two critical components of fitness for perennial plants, across 15 years of variation in previous-year growing-season water availability in a Colorado shortgrass steppe ecosystem. We integrated long-term demographic data, climate records, and species-level trait measurements to develop statistical models that quantify how traits predict survival and growth, and determine how that relationship changes according to interannual water availability. These models also account for the effects of competition and individual plant size, which generally impact plants' response to drought and can explain variation in vital rate responses to drought across individuals of the same species (Adler et al., 2018; Tredennick et al., 2018). We predicted that (1) species with low TLP and high tissue DMC (dry matter content) will have higher growth and survival rates in drier years than species with high TLP and low tissue DMC, but that (2) these traits will not impact growth and survival as strongly in wet years because water is less limiting (Figure 1). We also predicted that (3) traits related to water use, such as TLP and LDMC, will be better predictors of growth and survival in response to drought when compared with traits that are less related to water use such as SLA (Reich, 2014; Wright et al., 2004). Furthermore, TLP, the trait we analyzed that most directly measures mechanism, will better predict survival than other easy-to-measure traits, because it is a more direct measurement of physiological processes that impact growth and survival.

METHODS

Demographic data

We monitored growth and survival for eight graminoid and eight forb species (Appendix S1: Table S1) in
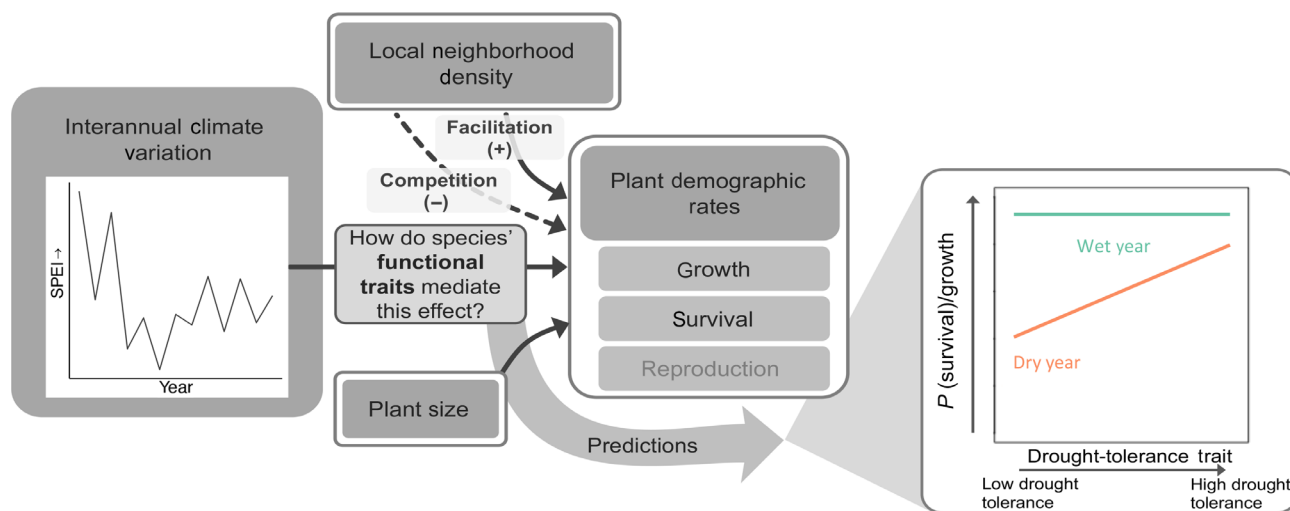
FIGURE 1 The demographic rates of growth, survival, and reproduction are impacted by environment, interactions with neighbors, and size. We focus here on plant growth and survival. The impact of environmental variation on an organism's demographic rates is likely to be mediated by the traits of that organism. This is especially true for traits that are related to environmental conditions that are most limiting or stress-inducing in a given habitat. In the semiarid steppe, traits related to water use might be more important for plant growth and survival in very dry years, and relatively less important in wetter years. The "predictions" figure shows how a trait related to drought tolerance may mediate the effect of climate on growth and survival. Specifically, we predicted that water-use traits impact survival or growth rates in dry years, but are not important in wetter years when a plant is not experiencing severe water stress.

24, 1-m^2 chart-quadrats from 1997 to 2010 at the Central Plains Experimental Research location (CPER) in Nunn, Colorado, USA (40.8° N/110.8° W) (Chu et al., 2013). This North American shortgrass steppe is at 1650 m elevation and is dominated by *Bouteloua gracilis* and *Bouteloua dactyloides*. It receives an annual average of 340 mm of precipitation, and has a mean annual temperature of 8°C (Appendix S2: Section S1). The chart-quadrat method maps each plant in each year, but does not uniquely identify each individual. Plants with a sizable basal area are mapped as polygons, whereas grasses and forbs with few stems are mapped as points. Graminoids in this analysis were measured as polygons, and forbs as points, so we use these functional groups in place of "polygon" or "point." Points representing forbs do not indicate plant size, so we can only measure growth for graminoids. We extracted growth and survival from a digitized version of this map dataset using "tracking algorithms" in R (version 4.0.3) (Lauenroth & Adler, 2008; R Core Team, 2021). Individuals were allowed to be "dormant" for up to 1 year (Appendix S2: Section S2).

Climate data

The standardized precipitation–evapotranspiration index (SPEI) is a drought metric that uses temperature and precipitation data to estimate evapotranspiration. More negative SPEI values correspond to drier conditions. We calculated SPEI for a four-month interval corresponding to the growing season at CPER using climate data from the Global SPEI database (Vicente-Serrano et al., 2010; Appendix S2: Section S3). "Wet" and "dry" years have positive and negative SPEI values, respectively. SPEI varied substantially above and below the mean (mean SPEI = 0) over the period of study (Appendix S1: Figure S1).

Trait data

We measured leaf and root traits for the 16 species in the demographic dataset. Five to 10 mature, healthy individuals of each species were sampled for each trait. Most values used in this analysis were collected at the CPER. However, several additional species were measured at the USDA-ARS High Plains Grasslands Research Station (HPGRS), a northern mixed-grass prairie 60 km from the CPER. Trait samples were collected from CPER and HPGRS between 2014 and 2018, and the associated data has been published (Blumenthal et al., 2020). For species without trait data from CPER or HPGRS, we used species-level trait values measured in 2018 and 2019 at Hays, KS, Miles City, MT, and Dubois, ID. Please refer to

Appendix S1: Table S1 for sampling details. Species explained significant variation in traits (e.g., SLA ($p < 0.01$, $F = 4.78$, $df = 58$), whereas trait sampling location did not ($p = 0.13$, $F = 2.53$, $df = 1$)). We calculated species mean values for seven traits: SLA, LDMC and RDMC, leaf TLP, specific root length (SRL), average root diameter (RDiam), and root tissue density (RTD) (Appendix S2: Section S4).

Statistical analysis

We used a generalized linear mixed model (GLMM) framework to identify how the effect of trait values on growth and survival varies with drought intensity, as well as to assess the relative ability of each trait to predict these demographic rates. All variables in all survival and growth models were centered and scaled. We created separate growth and survival models for each trait, because we were interested in the relative ability of each trait to predict drought tolerance along a gradient of SPEI, as opposed to their relative importance for demographic rates directly. Both growth and survival models followed a similar covariate structure, shown below (Equation 1). In both model frameworks, the covariates of most interest are SPEI, trait, and an SPEI-by-trait interaction.

$$\begin{aligned} \text{Response variable} &\sim \alpha + \gamma_{\text{species}} + \delta_{\text{quad}} + \tau_{\text{year}} \\ &+ \ln\left[\text{size}_t\left(\beta_{\text{species}} + \beta_1\right)\right] + \text{trait}\beta_2 + \text{SPEI}\beta_3 + \text{nearEdge}\beta_4 \quad (1) \\ &+ \text{neighborhoodDensity}\beta_5 + (\text{trait} \times \text{SPEI})\beta_6 + \varepsilon \end{aligned}$$

To model survival, we used the *lme4* package in R statistical software to fit GLMMs with a binomial error distribution and a logit link function (Bates et al., 2015). All survival models used a binary response variable indicating survival in the next year (year$_{t+1}$). We modeled graminoid and forb survival separately because data for size, an important predictor of variation in survival within species, was only available for graminoids. To model growth, we used *lme4* to fit GLMMs using a Gaussian error distribution. We measured growth as ln(basal area in year$_{t+1}$) as a function of ln(basal area in year$_t$). Growth models were only constructed for graminoids, because we did not have size information for forbs. All growth and survival models for both forbs and graminoids included fixed terms for SPEI, neighborhood density in the current year (year$_t$), a "nearEdge" term indicating proximity of ≤5 cm to the quadrat edge, trait value, and an interaction between trait and SPEI (Equation 1). They also included a random intercept for species (γ_{species}) to account for variation in the effects of

fixed covariates on response variables across species. All models also included a random intercept for quadrat (δ_{quad}) to account for non-independence of observations within the same quadrat, and a random intercept for year (δ_{year}) to account for nonindependence of samples observed in the same year.

All graminoid growth and survival models included a fixed term for individual plant size. All graminoid growth models and most graminoid survival models also included a random slope for individual size that varied according to species ($\ln[size_t \; (\beta_{species} + \beta_1)]$), which accounted for the fact that larger individuals have a higher growth and survival probability than small individuals of the same species, but also allowed for variation in response for each species. This random slope term was not included in graminoid survival models using RTD and SRL because it led to singular model fit. All models included fixed covariates for conspecific local neighborhood density and proximity to quadrat edge (Equation 1) to account for factors in addition to species-level trait values and climate that either impacted demographic rates or contributed to measurement error. The "nearEdge" model term is a binary variable indicating whether an individual was growing within 5 cm of the quadrat edge, and accounts for edge effects, as well as potential underestimation of neighborhood density or individual size due to proximity to the edge. Local neighborhood density, which incorporates effects of competition/facilitation on demographic rates (Figure 1), was calculated for each individual in each year (Appendix S2: Section S5). We estimated only intraspecific competition, because the fact that forbs and graminoids were measured differently made it difficult to produce a reasonable estimate of interspecific competition. Additionally, interspecific competition has been shown to be weaker than intraspecific competition in dry grassland systems (Chu et al., 2016; Laughlin et al., 2018).

We used the Akaike information criterion (AIC) to determine the best random effect structure for each trait model by comparing the F-statistics of models with all possible random effect structures. We then used an analogous process to determine the best fixed effect structure (Bolker et al., 2009). We used the *mixed()* function in the *afex* R package to calculate *p*-values for coefficients using likelihood ratio tests (Singmann et al., 2021). We used the size and significance of the trait-by-SPEI interaction coefficient to assess the sign and magnitude of a trait's ability to predict drought tolerance. We then used to two methods to compare the relative ability of traits to predict drought tolerance. First, we used a value we called ΔAIC. It was impossible to use AIC to compare the fit across models because data for each trait were not available for all species, so each model had a different sample size.

Instead, we used AIC to compare each model to a model of the same structure, but without the trait and trait-by-environment interaction coefficients (this we called ΔAIC; where ΔAIC = $AIC_{No\text{-traits}} - AIC_{traits}$). This comparison indicated how including traits as covariates improved the model. The more positive the ΔAIC between the trait model and the no-trait model, the more support for the ability of that trait to predict survival or growth in response to drought. Negative ΔAIC values indicated that including a trait did not improve model fit. Second, we used likelihood ratio tests (LRTs) as an additional method to quantify the difference between models with or without traits. A significant χ^2 value ($p < 0.05$) from an LRT indicated that including trait values significantly changes model fit. If, for example, including values for trait A resulted in a positive ΔAIC and/or a significant LRT result, while including values for trait B did not, trait A is a better predictor of the response variable than trait B.

RESULTS

Graminoid survival

We detected significant negative main effects of local neighborhood conspecific density and significant positive main effects of individual plant size on survival probability across all trait models (Table 1 and Figure 2a,b; Appendix S1: Table S3). Plants with more conspecific neighbors were less likely to survive, and larger plants were more likely to survive than smaller plants of the same species. There was a consistently negative main effect of SPEI on survival that showed that plants had higher survival in drier years, but this effect was only significant in root trait models. RTD was the only trait with a significant main effect on survival. Every trait except RTD significantly interacted with SPEI to impact survival (Table 1). The traits with the strongest interactions based on the absolute value of the interaction coefficient were LDMC, RDMC, TLP, and RDiam, in that order (Table 1 and Figure 3a,d,g,j). There was also a significant interaction between SRL and SPEI, but the coefficient was small (Table 1). Species with low TLP and high LDMC, RDMC, and RDiam were more likely to survive in drier years (Figure 3a,d,g,j). The opposite was true of species with high TLP and low LDMC, RDMC, and RDiam. ΔAIC and LRT values indicated that LDMC, RDMC, TLP, and RDiam best predicted survival across a gradient of SPEI. SRL, RTD, and SRL also had positive ΔAIC values and significant LRTs, although ΔAIC values were smaller and LRTs less insignificant than for other traits (Table 1). Fixed effects explained 33%–61% of variation in

TABLE 1 Graminoid survival model coefficients.

Model term	Trait model						
	TLP	LDMC	SLA	RDMC	RTD	SRL	RDiam
Size$_t$	0.95**	0.94**	0.96**	0.78**	1.19**	1.20**	0.86**
Neighbors	−0.61**	−0.62**	−0.60**	−0.61**	−0.43**	−0.43**	−0.59**
nearEdge	0.003	−0.001	0.01	−0.003	0.08	0.08	0.02
SPEI:trait	0.15**	−0.26**	−0.08**	−0.21**	0.01	−0.05**	−0.15**
SPEI	−0.08	−0.09	−0.07	−0.11	−0.23*	−0.23*	−0.19*
Trait	−0.04	0.26	−0.07	−0.02	0.36**	0.14	−0.04
τ_{00}	0.13$_{quad}$	0.12$_{quad}$	0.13$_{quad}$	0.13$_{quad}$	0.11$_{quad}$	0.11$_{quad}$	0.12$_{quad}$
	0.11$_{year}$	0.12$_{year}$	0.09$_{year}$	0.08$_{year}$	0.14$_{year}$	0.14$_{year}$	0.08$_{year}$
	1.22$_{spp.}$	1.70$_{spp.}$	1.27$_{spp.}$	0.48$_{spp.}$	0.06$_{spp.}$	0.40$_{spp.}$	0.58$_{spp.}$
τ_{01}	0.37$_{size \times spp}$	0.30$_{size \times spp}$	0.37$_{size \times spp}$	0.15$_{size \times spp}$	...	...	0.17$_{size \times spp}$
ρ_{01}	−0.95$_{spp.}$	−0.97$_{spp.}$	−0.96$_{spp.}$	−0.85$_{spp.}$	...	...	−0.88$_{spp.}$
Residual variance	3.29	3.29	3.29	3.29	3.29	3.29	3.29
n	18,827	18,829	18,827	18,474	16,618	16,618	17,190
Marginal/Conditional R^2	0.38/0.63	0.41/0.62	0.38/0.63	0.33/0.50	0.61/0.64	0.60/0.67	0.38/0.55
AIC	14,823.8	14,749.4	14,861.9	14,774.8	13,334.3	13,346.4	13,502.5
ΔAIC[a]	48.79	123.18	10.64	87.60	5.06	2.99	46.13
LRT: χ^2 (df) (p-value)[b]	52.79(2)** (p < 0.001)	127.2(2)** (p < 0.001)	14.6(2)** (p = 0.001)	91.6(2)** (p < 0.001)	9.1(2)* (p = 0.011)	7.0(2)* (p = 0.030)	50.1(2)** (p < 0.001)

Note: *p < 0.05; **p < 0.01. Exact p-values, test statistics, and degrees of freedom are shown in Appendix S1: Table S3; τ_{00} = rand. intercept variance; τ_{01} = rand. slope variance; ρ_{01} = correlation of rand. slope, and intercept.

Abbreviations: LDMC, leaf dry matter content; RDiam, average root diameter; RDMC, root dry matter content; RTD, root tissue density; SLA, specific leaf area; SPEI, standardized precipitation–evapotranspiration index; SRL, specific root length; TLP, leaf turgor loss point.

[a]Compares the Akaike information criterion (AIC) of a model with fixed effects for trait and trait:envi interaction to a model without these effects.

[b]Results from a likelihood ratio test comparing models with or without trait and trait:envi effects.

graminoid survival, whereas fixed and random effects combined explained 50%–67% of variation (Table 1).

Graminoid growth

All models of plant growth had a significant negative main effect of local neighborhood conspecific density, and a significant positive main effect of individual size in the current year on size in the next year (Table 2 and Figure 2c–e; Appendix S1: Table S4). When plants are small, they are likely to become larger in the next year. However, when they exceed a moderate size in the current year, they shrink in the next year (Figure 2d,e). There was a positive main effect of SPEI on growth for all models, although it was only significant for models with TLP, LDMC, SLA, and RDMC. RTD was the only trait with a significant main effect on growth. Species with lower RTD were significantly more likely to grow larger in the next year. There were not any significant interactions between traits and SPEI (Table 2 and Figure

3b,e,h,k,n). Both our metrics indicated that including trait main effects and a trait-by-SPEI interactions did not improve models of graminoid growth. All models had negative ΔAIC values, as well as insignificant χ^2 values from LRTs (Table 2). Fixed effects explained 16%–24% of variation in growth, whereas both fixed and random effects combined explained 38%–53% of variation (Table 2).

Forb survival

There were no significant main effects of local neighborhood conspecific density, SPEI, or traits on forb survival (Table 3; Appendix S1: Table S5). However, survival was affected by a significant interaction between SPEI and LDMC, RDMC, SLA, SRL, and RTD (Table 3 and Figure 3f,i,o; Appendix S1: Figure S2C,F). In drier years, survival was higher for species with high LDMC and RDMC. In wetter years, survival was higher for species with low LDMC and RDMC. There was a weaker interaction between TLP and SPEI in
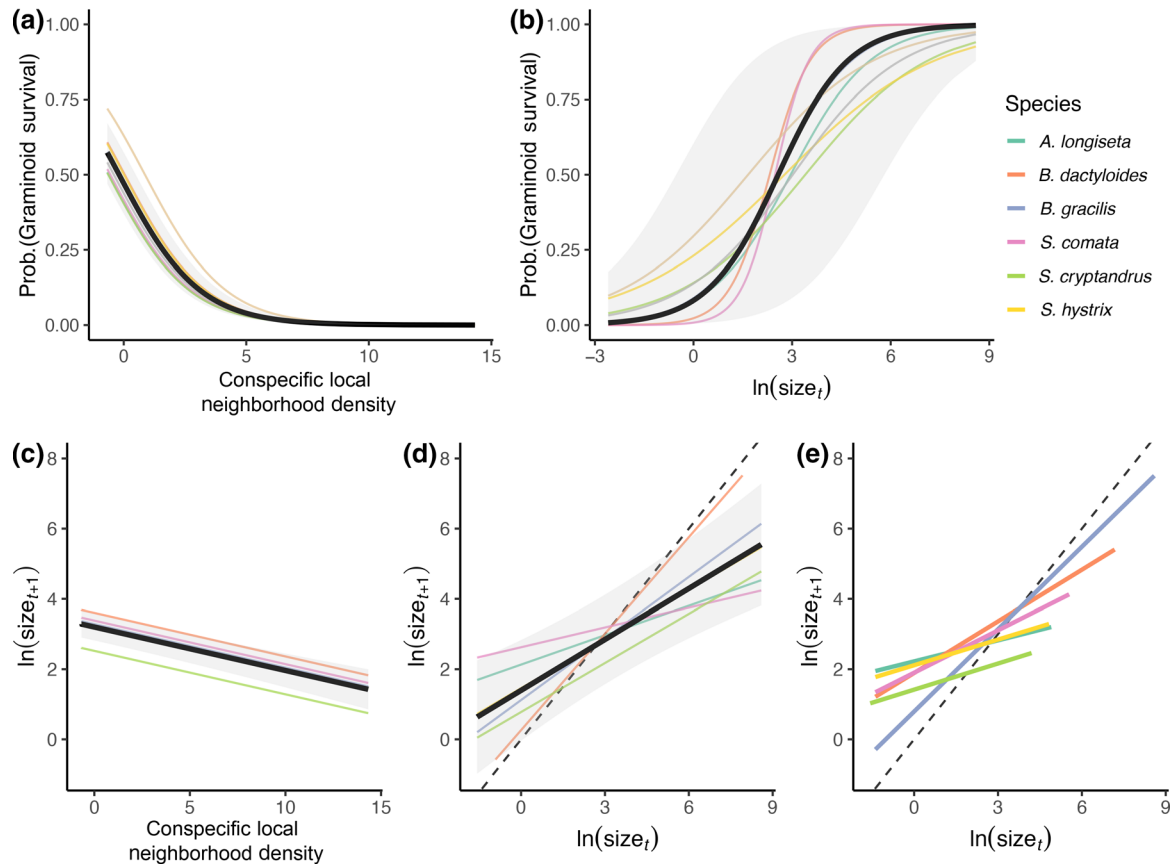
FIGURE 2 The effect of local neighborhood density (a) and size in year$_t$ (b) on graminoid survival in models using leaf dry matter content (LDMC) as the trait predictor. (a) Across all graminoid species, higher local neighborhood crowding by individuals of the same species corresponds with lower survival. (b) Larger individuals are more likely to survive to the next year than smaller individuals of the same species. (c, d) Values from models using turgor loss point (TLP) as the trait predictor. (c) Across all graminoid species, higher local neighborhood crowding by individuals of the same species corresponds to smaller size$_{t+1}$. (d) This model predicts that as ln(size$_t$) increases, a plant will become larger in year$_{t+1}$ until it reaches a midpoint in size$_t$, at which point it will plateau in size. (e) In the raw data, as opposed to model predictions shown in (a–d), there is a positive linear relationship between ln(size$_t$) and ln(size$_{t+1}$) for each graminoid, although there is a size above which plants are more likely to shrink than grow in year$_t$. Dashed lines in (d) and (e) show a 1:1 relationship between ln(size) and ln(size$_{t+1}$). Dark lines show the overall effect of each covariate on survival. The 95% CI for the predictor is shown in light gray. Colored lines incorporate random species effects to show the effects of competition or size$_t$ by species.

models of forb survival than in graminoids. Forb survival was uniformly higher in wetter years. Visualizations of the interactions between SPEI and LDMC and RDMC for forb survival were consistent with those for graminoids. However, the interaction between SLA and SPEI, in which low SLA species had high survival in drier years and low survival in wetter years, was opposite the pattern in graminoids. Although ΔAICs were small and LRTs were mostly insignificant, these two metrics indicated that including traits and trait-by-SPEI interactions in models using LDMC, RDMC, and SLA improved our ability to predict change in survival across variation in SPEI (Table 3). The uncertainty in forb survival estimates was much larger than for graminoids (Figure 3c,f,i,l,o; Appendix S1: Figure S2). Fixed effects explained <1% of the variation

in forb survival, whereas fixed and random effects combined explained 53%–69% of variation.

DISCUSSION

Effects of climate change on species composition will primarily be manifested through demography, yet it is not tractable to develop unique demographic predictions for every species. If traits predict demographic responses to environmental variation, then generalizable predictions across species may be possible. Here, we determined how leaf and root traits mediated the effect of drought on perennial growth and survival in a shortgrass steppe ecosystem, and found that (1) traits are better predictors of survival than growth across a gradient of SPEI, (2) TLP is
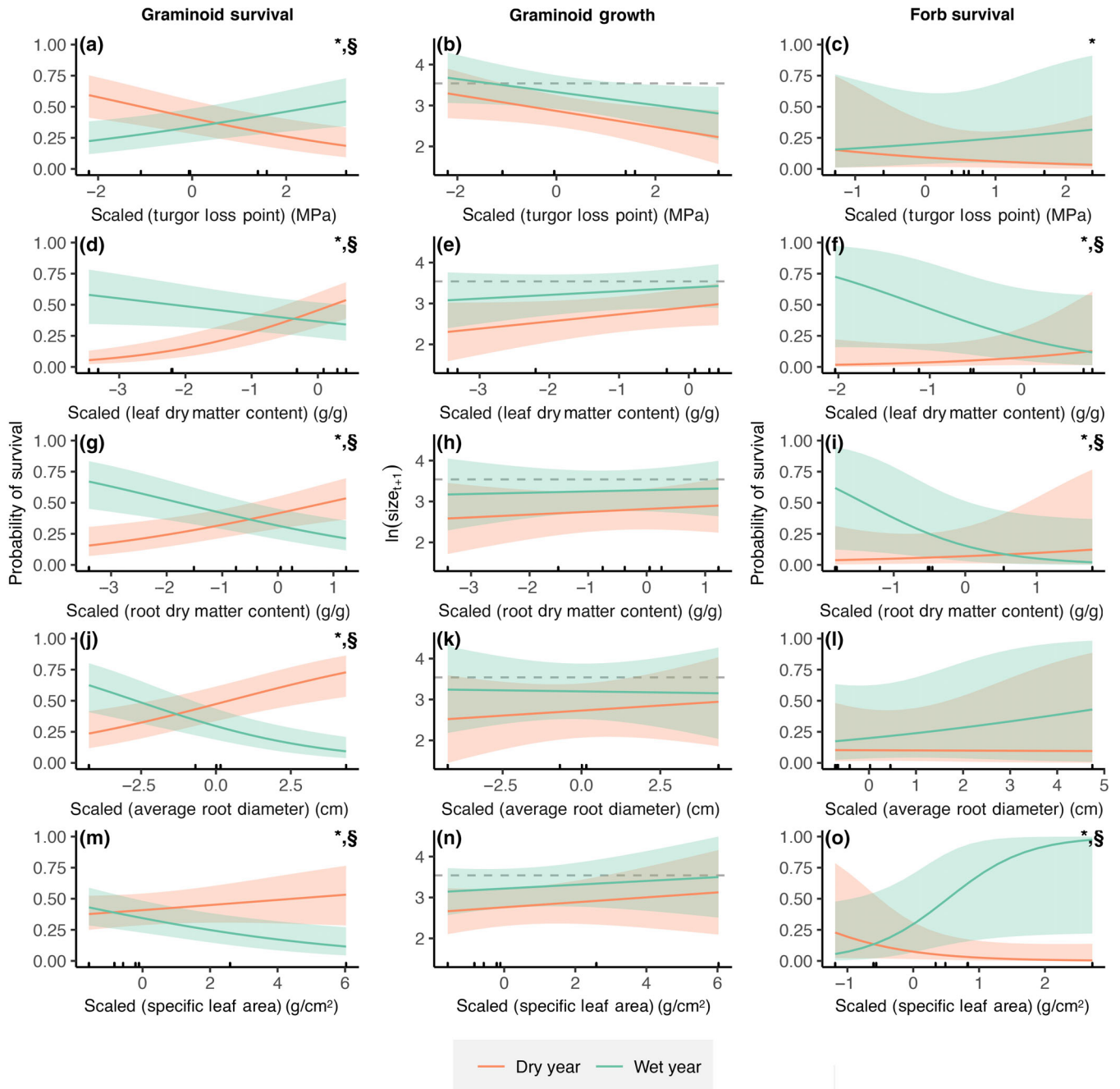
FIGURE 3 Survival probabilities and ln(size$_{t+1}$) for wet years and dry years, calculated using the 97.5th and 2.5th quantiles of the distribution of standardized precipitation–evapotranspiration index (SPEI) values. (a) Low turgor loss point (TLP) graminoid species are more likely to survive than high TLP species in dry years (low SPEI), whereas in wet years (high SPEI) species with a high TLP are more likely to survive than low TLP species ($\beta_{TLP \times SPEI}$ =0.95; $p < 0.001$; $\chi^2 = 16.45$; $df = 1$). (d, g) A similar trend in graminoid survival is predicted by the models that includes leaf dry matter content (LDMC) ($\beta_{LDMC \times SPEI}$ =0.94; $p < 0.001$; $\chi^2 = 17.06$; $df = 1$) and RDMC ($\beta_{RDMC \times SPEI} = 0.78$; $p < 0.001$; $\chi^2 = 17.36$; $df = 1$). Note that the scale of TLP is inverse to that of LDMC and root dry matter content (RDMC). (j, m) There are significant interactions between SPEI and RDiam ($\beta_{RDiam \times SPEI}$ =0.86; $p < 0.001$; $\chi^2 = 14.58$; $df = 1$) and SLA ($\beta_{SLA \times SPEI}$ =0.96; $p < 0.001$; $\chi^2 = 17.12$; $df = 1$). However these two traits models have much lower ΔAIC values than other trait models. (b, e, h, k, n) There are no significant interactions between the effects of any trait and SPEI on size$_{t+1}$ (Appendix S1: Table S4). Horizontal dashed lines in (b, e, h, k, n) indicate the average plant size in year$_t$. (c, f, i, l, o) Trends for forb survival were similar to those for graminoids, although model fit is weaker and interactions between trait and environment are less significant for all traits (Appendix S1: Table S5). Black bars on the x-axis indicate species-level trait values, and bands around each line indicate 95% CIs. *$p < 0.05$ for this trait:SPEI interaction. § ΔAIC for this model is positive and the likelihood ratio test (LRT) is significant.

TABLE 2 Graminoid growth model coefficients.

Model term	Trait model						
	TLP	LDMC	SLA	RDMC	RTD	SRL	RDiam
$Size_t$	0.51**	0.51**	0.51**	0.51**	0.56**	0.56**	0.48**
Neighbors	−0.12**	−0.12**	−0.12**	−0.12**	−0.13**	−0.13**	−0.13**
nearEdge	−0.003	−0.004	−0.004	−0.004	−0.03	−0.03	−0.02
SPEI:trait	0.01	−0.02	−0.004	−0.01	0.01	0.003	−0.02
SPEI	0.12*	0.13*	0.12*	0.12*	0.12	0.12	0.12
Trait	−0.17	0.13	0.05	0.05	−0.20*	−0.09	0.02
τ_{00}	0.02_{quad}	0.02_{quad}	0.02_{quad}	0.02_{quad}	0.02_{quad}	0.02_{quad}	0.02_{quad}
	0.03_{year}	0.03_{year}	0.03_{year}	0.03_{year}	0.04_{year}	0.04_{year}	0.04_{year}
	$0.72_{spp.}$	$0.62_{spp.}$	$0.53_{spp.}$	$0.52_{spp.}$	$0.34_{spp.}$	$0.49_{spp.}$	$0.76_{spp.}$
τ_{01}	$0.06_{size \times spp}$	$0.06_{size \times spp}$	$0.06_{size \times spp}$	$0.06_{size \times spp}$	$0.08_{size \times spp}$	$0.07_{size \times spp}$	$0.09_{size \times spp}$
ρ_{01}	$-0.09_{spp.}$	$-0.86_{spp.}$	$-0.81_{spp.}$	$-0.78_{spp.}$	$-0.74_{spp.}$	$-0.48_{spp.}$	$-0.76_{spp.}$
Residual variance	1.44	1.44	1.44	1.44	1.44	1.44	1.44
n	9497	9497	9497	9497	8802	8802	9018
Marginal/ Conditional R^2	0.23/0.38	0.23/0.40	0.20/0.40	0.20/0.41	0.24/0.49	0.19/0.53	0.16/0.44
AIC	30,597.8	30,597.4	30,600.2	30,599.3	28,430.6	28,433.7	29,107.7
ΔAIC^a	−10.78	−10.40	−13.16	−12.25	−9.55	−12.66	−12.39
LRT: χ^2 (df) (p-value)[b]	3.0(2) ($p = 0.22$)	2.6(2) ($p = 0.27$)	0.6(2) ($p = 0.73$)	0.5(2) ($p = 0.76$)	4.4(2) ($p = 0.11$)	0.8(2) ($p = 0.65$)	0.7(2) ($p = 0.69$)

Note: *$p < 0.05$; **$p < 0.01$. Exact p-values, test statistics, and degrees of freedom are shown in Appendix S1: Table S4; τ_{00} = rand. intercept variance; τ_{01} = rand. slope variance; ρ_{01} = correlation of rand. slope, and intercept.

Abbreviations: LDMC, leaf dry matter content; RDiam, average root diameter; RDMC, root dry matter content; RTD, root tissue density; SLA, specific leaf area; SPEI, standardized precipitation–evapotranspiration index; SRL, specific root length; TLP, leaf turgor loss point.

[a]Compares the Akaike information criterion (AIC) of a model with fixed effects for trait and trait:envi interaction to a model without these effects.

[b]Results from a likelihood ratio test comparing models with or without trait and trait:envi effects.

an important predictor of graminoid survival in this semiarid grassland, (3) surprisingly, RDMC and LDMC (from this point forward collectively referred to as DMC) are more related to survival than TLP in both graminoids and forbs, and (4) survival is not uniformly higher for all species in wet years. These findings are an important step toward understanding the context-dependent impacts of traits on demographic rates, and demonstrate the relative importance of different traits for predicting demographic responses to variation in water availability.

Trait-by-environment effects on growth and survival

Population-level response to precipitation in shortgrass steppe species (as measured by changes in percent-cover and ANPP) can be predicted by species-level values of TLP, LDMC, SLA, and leaf N and P (Wilcox et al., 2021). We found that change in graminoid survival in response to water availability can be explained by TLP and LDMC,

but also RDMC and RDiam. The effect of traits on demographic rates is not uniform across the spectrum of water availability. Although a certain suite of traits may increase survival in drier years, that advantage does not necessarily translate to higher survival in wetter years. For example, species with traits that were predicted to be drought tolerant (low TLP, high DMC) were more likely to survive in drier years, but less likely to survive in wetter years than species at the other end of the trait spectrum (Figure 3a,d,g). This result contributes to growing evidence that environmental context determines when and how traits impact fitness, and expands this framework beyond woody plants to herbaceous grassland species (Anderegg et al., 2016; Kunstler et al., 2020). However, the interaction in survival models between water-related traits and SPEI differs from our prediction of consistently high survival in wetter years regardless of a species' traits. Instead, survival declines for low TLP and high LDMC species (Figure 3). This pattern may indicate a trade-off between drought tolerance and competitive ability, in which drought-tolerant species suffer

T A B L E 3 Forb survival model coefficients.

Model term	Trait model						
	TLP	LDMC	SLA	RDMC	RTD	SRL	RDiam
Neighbors	−0.28	−0.30	−0.29	−0.29	−0.26	−0.27	−0.24
nearEdge	−0.03	−0.03	−0.11	−0.05	0.10	0.09	0.002
SPEI:trait	0.17	−0.46**	0.70**	−0.40**	−0.36*	0.21*	0.06
SPEI	0.23	0.34	0.42	0.23	0.29	0.29	0.20
Trait	−0.10	−0.15	0.28	−0.43	0.13	0.04	0.11
τ_{00}	0.55_{quad}	0.51_{quad}	0.56_{quad}	0.52_{quad}	0.63_{quad}	0.66_{quad}	0.56_{quad}
	0.44_{year}	0.31_{year}	0.34_{year}	0.34_{year}	0.51_{year}	0.66_{year}	0.53_{year}
	$3.20_{spp.}$	$2.54_{spp.}$	$3.00_{spp.}$	$3.10_{spp.}$	$3.10_{spp.}$	$5.70_{spp.}$	$3.47_{spp.}$
Residual variance	3.29	3.29	3.29	3.29	3.29	3.29	3.29
n	551	551	551	551	438	464	507
Marginal/Conditional R^2	0.01/0.57	0.05/0.53	0.04/0.56	0.05/0.57	0.03/0.57	0.01/0.69	0.01/0.58
AIC	643.4	636.8	636.8	637.0	544.0	551.4	621.2
ΔAIC[a]	−2.14	8.72	4.49	4.34	1.61	−2.90	−3.56
LRT: χ^2 (df) (p-value)[b]	1.9(2) ($p = 0.40$)	12.7(2)** ($p = 0.002$)	8.5(2)* ($p = 0.014$)	8.3(2)* ($p = 0.015$)	5.6(2) ($p = 0.06$)	1.1(2) ($p = 0.58$)	0.4(2) ($p = 0.80$)

Note: *$p < 0.05$; **$p < 0.01$; Exact p-values, test statistics, and degrees of freedom are shown in Appendix S1: Table S5; τ_{00} = rand. intercept variance.

Abbreviations: LDMC, leaf dry matter content; RDiam, average root diameter; RDMC, root dry matter content; RTD, root tissue density; SLA, specific leaf area; SPEI, standardized precipitation–evapotranspiration index; SRL, specific root length; TLP, leaf turgor loss point.

[a]Compares the Akaike information criterion (AIC) of a model with fixed effects for trait and trait:envi interaction to a model without these effects.

[b]Results from a likelihood ratio test comparing models with and without trait and trait:envi effects.

from competition with less drought-tolerant species in wetter years. This aligns with substantial evidence supporting a trade-off between stress-tolerance and competitive ability (Craine, 2007; Grime, 1979). Additional support for a drought-tolerance–competition trade-off is provided by the negative main effect of SPEI on graminoid survival in the rootDiam model. This higher survival in dry years regardless of root diameter could be due to increased facilitation in more stressful conditions (Maestre et al., 2009).

Although the effect of traits on forb survival varied according to water availability, these interactions were weakly significant (Figure 3). The significant interaction between DMC and SPEI in models of forb survival align with results for graminoid survival. However, unlike with graminoids, the TLP-by-SPEI interaction is weak and the SLA-by-SPEI interaction is strongly significant. Although it is possible that SLA is more correlated with drought-sensitivity for forbs than graminoids, it is also possible that our small sample size and lack of information about forb size impacted our results. Additionally, lower precision in estimation of TLP from forb leaf osmotic potential may have impacted the accuracy of TLP models (Griffin-Nolan, Ocheltree, et al. 2019).

Root tissue density was the only trait that predicted graminoid growth. Although the effect of TLP and DMC on growth was not significant, low TLP and high DMC species generally had higher growth than high TLP and low DMC species, consistent with the pattern observed in graminoid survival models. Unlike in models of survival, there were no significant interactions between traits and SPEI (Figure 3). Therefore, species with trait values considered to be more drought tolerant grew larger regardless of drought intensity. Previous work in the same grassland found that abundances of species with a similar suite of drought-tolerant traits were less sensitive to precipitation change than drought-intolerant species (Wilcox et al., 2021). Our results generally aligned with this finding. Although the abundance of drought-intolerant species was more sensitive to precipitation change (Wilcox et al., 2021), drought-tolerant species may still have higher absolute growth irrespective of water availability, as seen in our results (Figure 2b,e). This is because they are better suited to the average conditions of this habitat. The shortgrass steppe is nearly always water limited, and so drought tolerance is generally a very favorable strategy. Additionally, the heightened precipitation sensitivity of drought-intolerant species may be driven by the fact that many of the drought-intolerant species in this system are annuals, which are adapted to spike in abundance in years that are well suited to their growth strategy (Blumenthal et al., 2020; Wilcox et al., 2021). Our analysis included only

perennial species, and those perennials that are drought intolerant may be generally less likely to grow in this water-limited system. However, our growth model results should be interpreted with a degree of caution, because there were multiple potential sources of error in the growth-measurement process. Although accurately identifying whether a plant survived is relatively straightforward, there is substantial room for error when mapping basal area in the field, translating a basal area outline from a quadrat to a datasheet, and then to a digital shapefile.

Relative predictive ability of traits

Leaf TLP is a good predictor of herbaceous plant survival and growth in this shortgrass steppe ecosystem (Figure 3a–c), where water availability is highly variable and limits plant growth. TLP is used as an indicator of physiological drought tolerance, and has been linked to drought tolerance in tropical trees (Bartlett, Scoffoni, Ardy, et al., 2012), but there is mixed evidence for its utility as a predictor of drought tolerance in grasslands. TLP has been linked to precipitation sensitivity in North American grasslands (Blumenthal et al., 2020; Griffin-Nolan, Ocheltree, et al. 2019; Wilcox et al., 2021), but was not indicative of whole-plant drought tolerance in European grassland species (Májeková et al., 2019). Our analysis further tests the relationship of TLP to drought tolerance in graminoids and forbs, and represents the first test of TLP to predict demographic responses to variation in drought. Species with a more negative TLP can experience more negative water potentials before wilting, and we found that they have a higher survival probability in drier years than species with higher TLP. Species with more negative TLP are also more likely to grow larger than species with high TLP, regardless of water availability.

Tissue DMC was a better predictor of growth and survival in response to drought than TLP. This is surprising because TLP is a direct measure of a plant's capacity to maintain leaf turgor under water stress, and has been shown to be a good indicator of physiological drought tolerance (Bartlett, Scoffoni, Ardy, et al., 2012). Although LDMC and RDMC have been linked to drought tolerance, they are less directly related to plant water status than TLP, and are correlated with functional strategies beyond drought tolerance. These results may indicate that structural, rather than osmotic, resistance to wilting is a more successful strategy in this environment. The proportionally higher carbon investment in leaf and root structure in high DMC species impedes wilting, even when soil water availability is low enough to overcome osmotic wilting resistance. Although the relative

importance of these traits for predicting demographic responses to drought may differ in other systems, this result is encouraging from a methodological standpoint because LDMC and RDMC are much easier to measure than TLP.

Identifying traits that predict demographic responses to environmental stress represents a key step in formulating frameworks of population and community dynamics under environmental change (Laughlin et al., 2020). Our results challenge the idea that traits that more closely measure physiological mechanism are always superior predictors of individual-level responses to abiotic conditions. Specifically, we have shown that easy-to-measure plant traits such as DMC explain significant variation in demographic responses to drought across 16 herbaceous species in a North American grassland. More importantly, these results advance our understanding of the environment-dependent effect of traits on demographic rates, and reinforce the notion that demographic rates can respond in distinct ways to environmental variation and can have differing contributions to population-level responses to the environment.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

ORCID
Alice E. Stears https://orcid.org/0000-0002-1325-6641
Peter B. Adler https://orcid.org/0000-0002-4216-4009
Dana M. Blumenthal https://orcid.org/0000-0001-7496-0766
Kevin E. Mueller https://orcid.org/0000-0002-0739-7472
Troy W. Ocheltree https://orcid.org/0000-0002-7707-5639
Kevin R. Wilcox https://orcid.org/0000-0001-6829-1148
Daniel C. Laughlin https://orcid.org/0000-0002-9651-5732

REFERENCES

Adler, P. B., R. Salguero-Gómez, A. Compagnoni, J. S. Hsu, J. Ray-Mukherjee, C. Mbeau-Ache, and M. Franco. 2014. "Functional Traits Explain Variation in Plant Lifehistory Strategies." *Proceedings of the National Academy of Sciences of the United States of America* 111: 740–5.

Adler, P. B., D. Smull, K. H. Beard, R. T. Choi, T. Furniss, A. Kulmatiski, J. M. Meiners, A. T. Tredennick, and K. E. Veblen. 2018. "Competition and Coexistence in Plant Communities: Intraspecific Competition Is Stronger than Interspecific Competition." *Ecology Letters* 21: 1319–29.

Aestears. 2022. "aestears/CO-Sgs-paper: Actually ready for publication! (v1.0.1)." Zenodo. https://doi.org/10.5281/zenodo.6647755.

Anderegg, W. R. L., T. Klein, M. Bartlett, L. Sack, A. F. A. Pellegrini, B. Choat, and S. Jansen. 2016. "Meta-Analysis Reveals that Hydraulic Traits Explain Cross-Species Patterns of Drought-Induced Tree Mortality across the Globe." *Proceedings of the National Academy of Sciences of the United States of America* 113: 5024–9.

Bartlett, M. K., T. Klein, S. Jansen, B. Choat, and L. Sack. 2016. "The Correlations and Sequence of Plant Stomatal, Hydraulic, and Wilting Responses to Drought." *Proceedings of the National Academy of Sciences of the United States of America* 113: 13098–103.

Bartlett, M. K., C. Scoffoni, R. Ardy, Y. Zhang, S. Sun, K. Cao, and L. Sack. 2012. "Rapid Determination of Comparative Drought Tolerance Traits: Using an Osmometer to Predict Turgor Loss Point." *Methods in Ecology and Evolution* 3: 880–8.

Bartlett, M. K., C. Scoffoni, and L. Sack. 2012. "The Determinants of Leaf Turgor Loss Point and Prediction of Drought Tolerance of Species and Biomes: A Global Meta-Analysis." *Ecology Letters* 15: 393–405.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67: 1–48. https://doi.org/10.18637/jss.v067.i01.

Blumenthal, D. M., K. E. Mueller, J. A. Kray, T. W. Ocheltree, D. J. Augustine, and K. R. Wilcox. 2020. "Traits Link Drought Resistance with Herbivore Defence and Plant Economics in Semi-Arid Grasslands: The Central Roles of Phenology and Leaf Dry Matter Content." *Journal of Ecology* 108: 2336–51.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J. S. S. White. 2009. "Generalized Linear Mixed Models: A Practical Guide for Ecology and Evolution." *Trends in Ecology and Evolution* 24: 127–35.

Chu, C., A. R. Kleinhesselink, K. M. Havstad, M. P. McClaran, D. P. Peters, L. T. Vermeire, H. Wei, and P. B. Adler. 2016. "Direct Effects Dominate Responses to Climate Perturbations in Grassland Plant Communities." *Nature Communications* 7: 1–10.

Chu, C., J. Norman, R. Flynn, N. Kaplan, W. K. Lauenroth, and P. B. Adler. 2013. "Cover, Density, and Demographics of Shortgrass Steppe Plants Mapped 1997–2010 in Permanent Grazed and Ungrazed Quadrats." *Ecology* 94: 1435.

Cornwell, W. K., and D. D. Ackerly. 2009. "Community Assembly and Shifts in Plant Trait Distributions across an Environmental Gradient in Coastal California." *Ecological Monographs* 79: 109–26.

Craine, J. M. 2007. "Plant Strategy Theories: Replies to Grime and Tilman: Forum." *Journal of Ecology* 95: 235–40.

Griffin-Nolan, R. J., D. M. Blumenthal, S. L. Collins, T. E. Farkas, A. M. Hoffman, K. E. Mueller, T. W. Ocheltree, M. D. Smith, K. D. Whitney, and A. K. Knapp. 2019. "Shifts in Plant Functional Composition Following Long-Term Drought in Grasslands." *Journal of Ecology* 107: 2133–48.

Griffin-Nolan, R. J., T. W. Ocheltree, K. E. Mueller, D. M. Blumenthal, J. A. Kray, and A. K. Knapp. 2019. "Extending the Osmometer Method for Assessing Drought Tolerance in Herbaceous Species." *Oecologia* 189: 353–63.

Grime, J. P. 1979. *Plant Strategies and Vegetation Processes*. New York: John Wiley & Sons, Ltd.

Hodgson, J. G., G. Montserrat-Martí, M. Charles, G. Jones, P. Wilson, B. Shipley, M. Sharafi, et al. 2011. "Is Leaf Dry Matter Content a Better Predictor of Soil Fertility than Specific Leaf Area?" *Annals of Botany* 108: 1337–45.

Koerner, S. E., and S. L. Collins. 2014. "Interactive Effects of Grazing, Drought, and Fire on Grassland Plant Communities in North America and South Africa." *Ecology* 95: 98–109.

Kunstler, G., A. Guyennon, S. Ratcliffe, N. Rüger, P. Ruiz-Benito, D. Z. Childs, J. Dahlgren, et al. 2020. "Demographic Performance of European Tree Species at their Hot and Cold Climatic Edges." *Journal of Ecology* 109: 1041–54.

Lauenroth, W. K., and P. B. Adler. 2008. "Demography of Perennial Grassland Plants: Survival, Life Expectancy and Life Span." *Journal of Ecology* 96: 1023–32.

Laughlin, D. C., J. R. Gremer, P. B. Adler, R. M. Mitchell, and M. M. Moore. 2020. "The Net Effect of Functional Traits on Fitness." *Trends in Ecology and Evolution* 35: 1037–47.

Laughlin, D. C., R. T. Strahan, P. B. Adler, and M. M. Moore. 2018. "Survival Rates Indicate that Correlations between Community-Weighted Mean Traits and Environments Can Be Unreliable Estimates of the Adaptive Value of Traits." *Ecology Letters* 21: 411–21.

Luo, W., X. Zuo, R. J. Griffin-Nolan, C. Xu, W. Ma, L. Song, K. Helsen, et al. 2019. "Long Term Experimental Drought Alters Community Plant Trait Variation, Not Trait Means, across Three Semiarid Grasslands." *Plant and Soil* 442: 343–53.

Luong, J. C., K. D. Holl, and M. E. Loik. 2021. "Leaf Traits and Phylogeny Explain Plant Survival and Community Dynamics in Response to Extreme Drought in a Restored Coastal Grassland." *Journal of Applied Ecology* 58: 1670–80.

Maestre, F. T., R. M. Callaway, F. Valladares, and C. J. Lortie. 2009. "Refining the Stress-Gradient Hypothesis for Competition and Facilitation in Plant Communities." *Journal of Ecology* 97: 199–205.

Májeková, M., J. Martínková, and T. Hájek. 2019. "Grassland Plants Show no Relationship between Leaf Drought Tolerance and Soil Moisture Affinity, but Rapidly Adjust to Changes in Soil Moisture." *Functional Ecology* 33: 774–85.

Ploughe, L. W., E. M. Jacobs, G. S. Frank, S. M. Greenler, M. D. Smith, and J. S. Dukes. 2019. "Community Response to Extreme Drought (CRED): A Framework for Drought-Induced Shifts in Plant–Plant Interactions." *New Phytologist* 222: 52–69.

Poorter, H., Ü. Niinemets, L. Poorter, I. J. Wright, and R. Villar. 2009. "Causes and Consequences of Variation in Leaf Mass per Area (LMA): A Meta-Analysis." *New Phytologist* 182: 565–88.

R Core Team. 2021. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Reich, P. B. 2014. "The World-Wide "Fast-Slow" Plant Economics Spectrum: A Traits Manifesto." *Journal of Ecology* 102: 275–301.

Singmann, H., B. Bolker, J. Westfall, F. A. Aust, and M. S. Ben-Shachar. 2021. "afex: Analysis of Factorial Experiments." https://CRAN.R-project.org/pacakge-afex.

Stears, Alice A., P. Adler, D. Blumenthal, J. Kray, K. Mueller, T. Ocheltree, K. Wilcox, and D. Laughlin. 2022. "Water Availability Dictates How Plant Traits Predict Demographic Rates." Dryad, Dataset. https://doi.org/10.5061/dryad.31zcrjdp5.

Tredennick, A. T., B. J. Teller, P. B. Adler, G. Hooker, and S. P. Ellner. 2018. "Size-by-Environment Interactions: A Neglected Dimension of species' Responses to Environmental Variation." *Ecology Letters* 21: 1757–70.

Ummenhofer, C. C., and G. A. Meehl. 2017. "Extreme Weather and Climate Events with Ecological Relevance: A Review." *Philosophical Transactions of the Royal Society B: Biological Sciences* 372: 20160135.

Vicente-Serrano, S. M., S. Beguería, and J. I. López-Moreno. 2010. "A Multiscalar Drought Index Sensitive to Global Warming: The Standardized Precipitation Evapotranspiration Index." *Journal of Climate* 23: 1696–718.

Wilcox, K. R., D. M. Blumenthal, J. A. Kray, K. E. Mueller, J. D. Derner, T. Ocheltree, and L. M. Porensky. 2021. "Plant Traits Related to Precipitation Sensitivity of Species and Communities in Semiarid Shortgrass Prairie." *New Phytologist* 229: 2007–19.

Worthy, S. J., D. C. Laughlin, J. Zambrano, M. N. Umaña, C. Zhang, L. Lin, M. Cao, and N. G. Swenson. 2020. "Alternative Designs and Tropical Tree Seedling Growth Performance Landscapes." *Ecology* 101: 1–12.

Wright, I. J., P. B. Reich, J. Flexas, E. Garnier, P. K. Groom, J. Gulias, K. Hikosaka, et al. 2004. "The Worldwide Leaf Economics Spectrum." *Nature* 428: 821–7.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Stears, Alice E., Peter B. Adler, Dana M. Blumenthal, Julie A. Kray, Kevin E. Mueller, Troy W. Ocheltree, Kevin R. Wilcox, and Daniel C. Laughlin. 2022. "Water Availability Dictates How Plant Traits Predict Demographic Rates." *Ecology* e3799. https://doi.org/10.1002/ecy.3799