

1 **Water availability dictates how plant traits predict demographic rates**

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

41 **Keywords:** demographic rates, drought, plant traits, global change, grasslands

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

56 While climate models predict that some regions will receive more precipitation in
57 concentrated, extreme events, other regions such as western North America will receive less
58 moisture overall or have longer periods of drought punctuated by extreme precipitation events
59 (Ummenhofer and Meehl 2017). Communities with lower mean annual precipitation often have
60 lower community-weighted mean (CWM) specific leaf area (SLA) (Cornwell and Ackerly
61 2009). Higher SLA species also increase in abundance in wetter years in communities with low
62 mean precipitation (Wilcox et al. 2021). Other studies observed little to no variation in CWM
63 traits after drought, but have identified changes in functional diversity (FD) in dry sites (Luo et
64 al. 2019) or after experimentally-induced drought (Griffin-Nolan et al. 2019a). In North

65 American shortgrass steppe, plant species with low leaf osmotic potential (a primary determinant
66 of turgor loss point (Bartlett et al. 2012b)), high leaf dry matter content (LDMC) and low SLA
67 are relatively insensitive to interannual precipitation variability (Wilcox et al. 2021). Correlations
68 among these and other traits indicate tradeoffs between drought resistance and rapid resource
69 acquisition (Blumenthal et al. 2020). Additional work has found that species are more likely to
70 survive drought if they have traits correlated with a conservative resource acquisition strategy
71 (Luong et al. 2021). Determining how traits affect growth and survival can help provide a
72 mechanistic understanding of population responses to interannual climate variation, as well as
73 improve our understanding of drought-tolerance mechanisms in grassland plants.

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

85 Many morphological traits are correlated along an axis representing resource acquisition
86 strategy from fast (e.g. high SLA, low LDMC) to slow (e.g. low SLA, high LDMC) (Reich
87 2014). Of these economic traits, we expect that LDMC is most relevant to a plant's ability to

88 survive water stress because it measures leaf structure and allocation of carbon to leaf tissue
89 (Hodgson et al. 2011). Species with higher LDMC have higher allocation to cell wall structure
90 and more densely-packed leaf cells, and thus are more likely to maintain cell turgor under water
91 stress (Poorter et al. 2009, Wilcox et al. 2021). High LDMC species also have higher lignin
92 content, likely due to a higher number of leaf vessels and thicker cell walls, which also confers
93 the ability to maintain water transport under more negative water potentials (Blumenthal et al.
94 2020). Finally, high LDMC species generally have more non-structural carbohydrates (NSCs),
95 which provide osmotic resistance to wilting (Griffin-Nolan et al. 2019b).

96 Traits that more directly measure physiological processes such as cavitation resistance or
97 osmotic potentials might be especially useful for identifying patterns of individual plant
98 responses to soil water availability. One such trait is leaf turgor loss point (TLP), a measure of
99 the water potential within a leaf at which leaf cells begin to lose turgor and the leaf loses function
100 (Bartlett et al. 2012a, 2016). Plants with more negative TLP have greater physiological drought
101 tolerance because they can withstand more negative water potentials before experiencing a
102 reduction in leaf cell turgor, stomatal and hydraulic conductance, and gas exchange (Bartlett et
103 al. 2012a). Recent methodological advances use a vapor pressure osmometer to identify leaf
104 osmotic potential, or leaf cell solute potential at full hydration, which is correlated with TLP in
105 woody species (Bartlett et al. 2012b) and herbaceous species in western North American
106 grasslands (Griffin-Nolan et al. 2019b). In semiarid shortgrass steppe, TLP is predictive of
107 species occurrences in response to drought, with lower TLP species less likely to decline in
108 abundance in drier years (Wilcox et al. 2021). In this ecosystem, low TLP is also correlated with
109 other traits such as high LDMC and low leaf nitrogen and phosphorous, which indicate drought
110 tolerance and a resource conservative growth strategy (Blumenthal et al. 2020). However, the

111 extent to which TLP mediates the effect of drought on plant survival and growth is not known.
112 We also lack robust evidence to show that traits more closely measuring physiological processes
113 are better than more traditional economic traits for predicting plant responses.

114 We evaluated whether species-level plant functional traits related to water use help
115 explain patterns in species growth and survival, two critical components of fitness for perennial
116 plants, across 15 years of variation in previous-year growing-season water availability in a
117 Colorado shortgrass steppe ecosystem. We integrated long-term demographic data, climate
118 records, and species-level trait measurements to develop statistical models that quantify how
119 traits predict survival and growth, and determine how that relationship changes according to
120 inter-annual water availability. These models also account for the effects of competition and
121 individual plant size, which generally impact plants' response to drought and can explain
122 variation in vital rate responses to drought across individuals of the same species (Adler et al.
123 2018, Tredennick et al. 2018). We predicted that (1) species with low TLP and high tissue DMC
124 (dry matter content) will have higher growth and survival rates in drier years than species with
125 high TLP and low tissue DMC, but that (2) these traits will not impact growth and survival as
126 strongly in wet years because water is less limiting (Fig. 1). We also predicted that (3) traits
127 related to water use, such as TLP and LDMC, will be better predictors of growth and survival in
128 response to drought when compared to traits that are less related to water use such as SLA
129 (Wright et al. 2004, Reich 2014). Further, TLP, the trait we analyzed that most directly measures
130 mechanism, will better predict survival than other easy-to-measure traits, since it is a more direct
131 measurement of physiological processes that impact growth and survival.

132 **Methods: Demographic Data** We monitored growth and survival for eight graminoid
133 and eight forb species (Appendix S1:Table S1) in 24, 1-m² chart-quadrats from 1997 to 2010 at

134 the Central Plains Experimental Research location (CPER) in Nunn, Colorado, USA (40.8
135 °N/110.8 °W) (Chu et al. 2013). This North American shortgrass steppe is at 1650 m elevation
136 and is dominated by *Bouteloua gracilis* and *Bouteloua dactyloides*. It receives an annual average
137 of 340 mm of precipitation, and has a mean annual temperature of 8 °C (Appendix S2: Section
138 S1). The chart-quadrat method maps each plant in each year, but does not uniquely identify each
139 individual. Plants with a sizeable basal area are mapped as polygons, while grasses and forbs
140 with few stems are mapped as points. Graminoids in this analysis were measured as polygons,
141 and forbs as points, so we use these functional groups in place of “polygon” or “point.” Points
142 representing forbs do not indicate plant size, so we can only measure growth for graminoids. We
143 extracted growth and survival from a digitized version of this map dataset using "tracking
144 algorithms" in R (version 4.0.3) (Lauenroth and Adler 2008, R Core Team 2021). Individuals
145 were allowed to be ‘dormant’ for up to one year (Appendix S2: Section S2).

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

153 **Trait Data** We measured leaf and root traits for the 16 species in the demographic
154 dataset. Five to ten mature, healthy individuals of each species were sampled for each trait. A
155 majority of the values used in this analysis were collected at the CPER. However, several
156 additional species were measured at the USDA-ARS High Plains Grasslands Research Station

157 (HPGRS), a northern mixed-grass prairie 60 km from the CPER. Trait samples were collected
 158 from CPER and HPGRS between 2014 and 2018, and the associated data has been published
 159 (Blumenthal et al. 2020). For species without trait data from CPER or HPGRS, we used species-
 160 level trait values measured in 2018 and 2019 at Hays, KS, Miles City, MT and Dubois, ID. See
 161 Appendix S1: Table S1 for sampling details. Species explained significant variation in traits (e.g.
 162 SLA ($P < 0.01$, $F = 4.78$, $df = 58$), while trait sampling location did not ($P = 0.13$, $F = 2.53$, $df =$
 163 1). We calculated species mean values for seven traits: specific leaf area (SLA), leaf and root
 164 dry matter content (LDMC and RDMC), leaf turgor loss point (TLP), specific root length (SRL),
 165 average root diameter (RDiam), and root tissue density (RTD) (Appendix S2: Section S4).

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

175 **Equation 1**

176 $Response\ variable \sim \alpha + \gamma_{species} + \delta_{quad} + \tau_{year} + \ln[size_t(\beta_{species} + \beta_1)] +$
 177 $trait\beta_2 + SPEI\beta_3 + nearEdge\beta_4 + neighborhoodDensity\beta_5 + (trait \times SPEI)\beta_6 + \epsilon$

178 To model survival, we used the lme4 package in R statistical software to fit GLMMs with
 179 a binomial error distribution and a logit link function (Bates et al. 2015). All survival models use
 180 a binary response variable indicating survival in the next year ($year_{t+1}$). We modeled graminoid

181 and forb survival separately because data for size, an important predictor of variation in survival
182 within species, was only available for graminoids. To model growth, we used lme4 to fit
183 GLMMs using a Gaussian error distribution. We measured growth as $\ln(\text{basal area in year}_{t+1})$ as
184 a function of $\ln(\text{basal area in year}_t)$. Growth models were only constructed for graminoids, since
185 we did not have size information for forbs. All growth and survival models for both forbs and
186 graminoids included fixed terms for SPEI, neighborhood density in the current year (year_t), a
187 “nearEdge” term indicating proximity of ≤ 5 cm to the quadrat edge, trait value, and an
188 interaction between trait and SPEI (Eqn. 1). They also included a random intercept for species
189 (γ_{species}) to account for variation in the effects of fixed covariates on response variables across
190 species. All models also included a random intercept for quadrat (δ_{quadr}) to account for non-
191 independence of observations within the same quadrat, and a random intercept for year (δ_{year})
192 to account for non-independence of samples observed in the same year.

193 All graminoid growth and survival models included a fixed term for individual plant size.
194 All graminoid growth models and most graminoid survival models also included a random slope
195 for individual size that varied according to species ($\ln[\text{size}_t (\beta_{\text{species}} + \beta_I)]$), which accounts for the
196 fact that larger individuals have a higher growth and survival probability than small individuals
197 of the same species, but also allows for variation in response for each species. This random slope
198 term was not included in graminoid survival models using RTD and SRL because it led to
199 singular model fit. All models included fixed covariates for conspecific local neighborhood
200 density and proximity to quadrat edge (Eqn. 1) to account for factors in addition to species-level
201 trait values and climate that either impact demographic rates or contribute to measurement error.
202 The “nearEdge” model term is a binary variable indicating whether an individual was growing
203 within 5 cm of the quadrat edge, and accounts for edge effects, as well as potential under-

204 estimation of neighborhood density or individual size due to proximity to the edge. Local
205 neighborhood density, which incorporates effects of competition/facilitation on demographic
206 rates (Fig. 1), was calculated for each individual in each year (Appendix S2: Section S5). We
207 estimated only intra-specific competition, since the fact that forbs and graminoids were measured
208 differently made it difficult to produce a reasonable estimate of inter-specific competition.
209 Additionally, inter-specific competition has been shown to be weaker than intra-specific
210 competition in dry grassland systems (Chu et al. 2016, Laughlin et al. 2018).

211 We used AIC to determine the best random effect structure for each trait model by
212 comparing the F-statistics of models with all possible random effect structures. We then used an
213 analogous process to determine the best fixed effect structure (Bolker et al. 2009). We used the
214 `mixed()` function in the “afex” R package to calculate *P*-values for coefficients using Likelihood
215 Ratio Tests (Singmann et al. 2021). We used the size and significance of the trait-by-SPEI
216 interaction coefficient to assess the sign and magnitude of a trait’s ability to predict drought
217 tolerance. We then used two methods to compare the relative ability of traits to predict
218 drought tolerance. First, we used a value we call ΔAIC . It was impossible to use AIC to compare
219 fit across models because data for each trait was not available for all species so each model had a
220 different sample size. Instead, we used AIC to compare each model to a model of the same
221 structure, but without the trait and trait-by-environment interaction coefficients (what we call
222 ΔAIC ; $\Delta AIC = AIC_{\text{No-traits}} - AIC_{\text{traits}}$). This comparison indicates how including traits as
223 covariates improved the model. The more positive the ΔAIC between the trait model and the no-
224 trait model, the more support for the ability of that trait to predict survival or growth in response
225 to drought. Negative ΔAIC values indicate that including a trait did not improve model fit.
226 Second, we used likelihood ratio tests (LRTs) as an additional method to quantify the difference

227 between models with and without traits. A significant χ^2 value ($P < 0.05$) from an LRT
228 indicates that including trait values significantly changes model fit. If, for example, including
229 values for trait A resulted in a positive ΔAIC and/or a significant LRT result, while including
230 values for trait B did not, trait A is a better predictor of the response variable than trait B.

231 **Results: *Graminoid Survival*** We detected significant negative main effects of local
232 neighborhood conspecific density and significant positive main effects of individual plant size on
233 survival probability across all trait models (Table 1; Fig. 2: A-B; Appendix S1: Table S3). Plants
234 with more conspecific neighbors were less likely to survive, and larger plants were more likely to
235 survive than smaller plants of the same species. There was a consistently negative main effect of
236 SPEI on survival which shows that plants had higher survival in drier years, but this effect was
237 only significant in root trait models. RTD was the only trait with a significant main effect on
238 survival. Every trait except RTD significantly interacted with SPEI to impact survival (Table 1).
239 The traits with the strongest interactions based on the absolute value of the interaction coefficient
240 were LDMC, RDMC, TLP, and RDiam, in that order (Table 1; Fig. 3: D, G, A & J). There was
241 also a significant interaction between SRL and SPEI, but the coefficient was small (Table 1).
242 Species with low TLP and high LDMC, RDMC and RDiam were more likely to survive in drier
243 years (Fig. 3: A, D, G, & J). The opposite was true of species with high TLP and low LDMC,
244 RDMC and RDiam. ΔAIC and LRT values indicated that LDMC, RDMC, TLP, and RDiam best
245 predicted survival across a gradient of SPEI. SRL, RTD, and SRL also had positive ΔAIC values
246 and significant LRTs, although ΔAIC values were smaller and LRTs less insignificant than for
247 other traits (Table 1). Fixed effects explained 33- 61% of variation in graminoid survival, while
248 fixed and random effects combined explained 50- 67% of variation (Table 1).

249 **Graminoid Growth** All models of plant growth had a significant negative main effect of
250 local neighborhood conspecific density, and a significant positive main effect of individual size
251 in the current year on size in the next year (Table 2; Fig. 2 C-E; Appendix S1: Table S4). When
252 plants are small, they are likely to become larger in the next year. However, when they exceed a
253 moderate size in the current year, they shrink in the next year (Fig. 2: D-E). There was a positive
254 main effect of SPEI on growth for all models, although it was only significant for models with
255 TLP, LDMC, SLA, and RDMC. RTD was the only trait with a significant main effect on growth.
256 Species with lower RTD were significantly more likely to grow larger in the next year. There
257 were not any significant interactions between traits and SPEI (Table 2, Fig. 3: B, E, H, K & N).
258 Both our metrics indicated that including trait main effects and a trait-by-SPEI interactions did
259 not improve models of graminoid growth. All models had negative Δ AIC values, as well as
260 insignificant χ^2 values from LRTs (Table 2). Fixed effects explained 16-24% of variation in
261 growth, while both fixed and random effects combined explained 38-53% of variation (Table 2).

262 **Forb Survival** There were no significant main effects of local neighborhood conspecific
263 density, SPEI, or traits on forb survival (Table 3; Appendix. S1: Table S5). However, survival
264 was affected by a significant interaction between SPEI and LDMC, RDMC, SLA, SRL, and
265 RTD (Table 3; Fig. 3: F, I & O; Appendix S1: Figs. S2: F & C). In drier years, survival was
266 higher for species with high LDMC and RDMC. In wetter years, survival was higher for species
267 with low LDMC and RDMC. There was a weak interaction between TLP and SPEI in models
268 of forb survival than in graminoids. Forb survival was uniformly higher in wetter years.
269 Visualizations of the interactions between SPEI and LDMC and RDMC for forb survival were
270 consistent with those for graminoids. However, the interaction between SLA and SPEI, where
271 low SLA species had high survival in drier years and low survival in wetter years, was opposite

272 the pattern in graminoids. Although Δ AICs were small and LRTs were mostly insignificant,
273 these two metrics indicated that including traits and trait-by-SPEI interactions in models using
274 LDMC, RDMC, and SLA improved our ability to predict change in survival across variation in
275 SPEI (Table 3). The uncertainty in forb survival estimates was much larger than for graminoids
276 (Fig. 3: C, F, I, L & O; Appendix. S1: Fig. S2). Fixed effects explained less than 1% of variation
277 in forb survival, while fixed and random effects combined explained 53-69% of variation.

278 **Discussion:** Effects of climate change on species composition will primarily be manifested
279 through demography, yet it is not tractable to develop unique demographic predictions for every
280 species. If traits predict demographic responses to environmental variation, then generalizable
281 predictions across species may be possible. Here, we determined how leaf and root traits
282 mediated the effect of drought on perennial growth and survival in a shortgrass steppe
283 ecosystem, and found that (1) traits are better predictors of survival than growth across a gradient
284 of SPEI, (2) TLP is an important predictor of graminoid survival in this semiarid grassland, (3)
285 surprisingly, RDMC and LDMC (hereafter collectively referred to as DMC) are more related to
286 survival than TLP in both graminoids and forbs, and (4) survival is not uniformly higher for all
287 species in wet years. These findings are an important step toward understanding the context-
288 dependent impacts of traits on demographic rates, and demonstrate the relative importance of
289 different traits for predicting demographic responses to variation in water availability.

290 *Trait-by-environment effects on growth and survival:* Population-level response to
291 precipitation in shortgrass steppe species (as measured by changes in percent-cover and ANPP)
292 can be predicted by species-level values of TLP, LDMC, SLA, and leaf N and P (Wilcox et al.
293 2021). We found that change in graminoid survival in response to water availability can be
294 explained by TLP and LDMC, but also RDMC and RDiam. The effect of traits on demographic

295 rates is not uniform across the spectrum of water availability. While a certain suite of traits may
296 increase survival in drier years, that advantage does not necessarily translate to higher survival in
297 wetter years. For example, species with traits that were predicted to be drought tolerant (low
298 TLP, high DMC) were more likely to survive in drier years, but less likely to survive in wetter
299 years than species at the other end of the trait spectrum (Fig. 3: A, D & G). This result
300 contributes to growing evidence that environmental context determines when and how traits
301 impact fitness, and expands this framework beyond woody plants to herbaceous grassland
302 species (Anderegg et al. 2016, Kunstler et al. 2020). However, the interaction in survival models
303 between water-related traits and SPEI differs from our prediction of consistently high survival in
304 wetter years regardless of a species' traits. Instead, survival declines for low TLP and high
305 LDMC species (Fig. 3). This pattern may indicate a trade-off between drought tolerance and
306 competitive ability, where drought tolerant species suffer from competition with less drought
307 tolerant species in wetter years. This aligns with substantial evidence supporting a trade-off
308 between stress-tolerance and competitive ability (Grime 1979, Craine 2007). Additional support
309 for a drought-tolerance-competition trade-off is provided by the negative main effect of SPEI on
310 graminoid survival in the rootDiam model. This higher survival in dry years regardless of root
311 diameter could be due to increased facilitation in more stressful conditions (Maestre et al. 2009).

312 While the effect of traits on forb survival varied according to water availability, these
313 interactions were weakly significant (Fig. 3). The significant interaction between DMC and SPEI
314 in models of forb survival align with results for graminoid survival. However, unlike with
315 graminoids, the TLP-by-SPEI interaction is weak and the SLA-by-SPEI interaction is strongly
316 significant. While it is possible that SLA is more correlated with drought-sensitivity for forbs
317 than graminoids, it is also possible that our small sample size and lack of information about forb

318 size impacted our results. Additionally, lower precision in estimation of TLP from forb leaf
319 osmotic potential may have impacted the accuracy of TLP models (Griffin-Nolan et al. 2019b).

320 RTD was the only trait that predicted graminoid growth. Although the effect of TLP and
321 DMC on growth was not significant, low TLP and high DMC species generally had higher
322 growth than high TLP and low DMC species, consistent with the pattern observed in graminoid
323 survival models. Unlike in models of survival, there were no significant interactions between
324 traits and SPEI (Fig. 3). Thus, species with trait values considered to be more drought tolerant
325 grew larger regardless of drought intensity. Previous work in the same grassland found that
326 abundances of species with a similar suite of drought tolerant traits were less sensitive to
327 precipitation change than drought intolerant species (Wilcox et al. 2021). Our results generally
328 align with this finding. While the abundance of drought-intolerant species is more sensitive to
329 precipitation change (Wilcox et al. 2021), drought-tolerant species may still have higher absolute
330 growth irrespective of water availability, as seen in our results (Fig. 2: B, E) . This is because
331 they are better suited to the average conditions of this habitat. The shortgrass steppe is nearly
332 always water-limited, and so drought tolerance is generally a very favorable strategy.

333 Additionally, the heightened precipitation sensitivity of drought-intolerant species may be driven
334 by the fact that many of the drought-intolerant species in this system are annuals, which are
335 adapted to spike in abundance in years that are well-suited to their growth strategy (Blumenthal
336 et al. 2020, Wilcox et al. 2021). Our analysis included only perennial species, and those
337 perennials that are drought intolerant may be generally less likely to grow in this water-limited
338 system. However, our growth model results should be interpreted with a degree of caution, since
339 there were multiple potential sources of error in the growth-measurement process. While
340 accurately identifying whether a plant survived is relatively straightforward, there is substantial

341 room for error when mapping basal area in the field, translating a basal area outline from a
342 quadrat to a datasheet, and then to a digital shapefile.

343 *Relative predictive ability of traits:* Leaf TLP is a good predictor of herbaceous plant
344 survival and growth in this shortgrass steppe ecosystem (Fig. 3: A-C), where water availability
345 is highly variable and limits plant growth. TLP is used as an indicator of physiological drought
346 tolerance, and has been linked to drought tolerance in tropical trees (Bartlett et al. 2012a), but
347 there is mixed evidence for its utility as a predictor of drought tolerance in grasslands. TLP has
348 been linked to precipitation sensitivity in North American grasslands (Griffin-Nolan et al. 2019b,
349 Blumenthal et al. 2020, Wilcox et al. 2021), but was not indicative of whole-plant drought
350 tolerance in European grassland species (Májeková et al. 2019). Our analysis further tests the
351 relationship of TLP to drought tolerance in graminoids and forbs, and represents the first test of
352 TLP to predict demographic responses to variation in drought. Species with a more negative TLP
353 can experience more negative water potentials before wilting, and we found they have a higher
354 survival probability in drier years than species with higher TLP. Species with more negative TLP
355 are also more likely to grow larger than species with high TLP, regardless of water availability.

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

364 soil water availability is low enough to overcome osmotic wilting resistance. Although the
365 relative importance of these traits for predicting demographic responses to drought may differ in
366 other systems, this result is encouraging from a methodological standpoint since LDMC and
367 RDMC are much easier to measure than TLP.

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

378 **Author Contributions:** AES and DCL designed the study. DMB, JAK, KEM, TWO, and KRW
379 collected trait data, and PBA compiled demographic data. AES performed analysis with DCL,
380 DMB, and PBA contributing. AES wrote the manuscript with contributions from all authors.

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493 **Tables**

494 **Table 1.** Graminoid survival model coefficients

	<i>Trait Model</i>						
	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*spp}	0.30 _{size*spp}	0.37 _{size*spp}	0.15 _{size*spp}			0.17 _{size*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
Marg./Cond. 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^{\dagger}	48.79	123.18	10.64	87.60	5.06	2.99	46.13
LRT: χ^2 (df) (P-val) ^{††}	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)

495 Note: * $P < 0.05$; ** $P < 0.01$; Exact P -values, test statistics, and degrees of freedom are shown in

496 Appendix S1: Table S3; τ_{00} = rand. intercept variance; τ_{01} = rand. slope variance; ρ_{01} =

497 correlation of rand. slope & intercept; \dagger = compares the AIC of a model with fixed effects for

498 trait and trait:envi interaction to a model without these effects.; $\dagger\dagger$ = Results from a likelihood

499 ratio test comparing models with and without trait and trait:envi effects. Key to traits: TLP (leaf

500 turgor loss point), LDMC (leaf dry matter content), SLA (specific leaf area), RDMC (root dry

501 matter content), RTD (root tissue density), SRL (specific root length), RDiam (average root
 502 diameter)

503

504 **Table 2.** Graminoid growth model coefficients

	<i>Trait Model</i>						
	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}						
	0.03 _{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*spp}	0.06 _{size*spp}	0.06 _{size*spp}	0.06 _{size*spp}	0.08 _{size*spp}	0.07 _{size*spp}	0.09 _{size*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	9,497	9,497	9,497	9,497	8,802	8,802	9,018
Marg./Cond.	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
R ²							
AIC	30,597.8	30,597.4	30,600.2	30,599.3	28,430.6	28,433.7	29,107.7
ΔAIC [†]	-10.78	-10.40	-13.16	-12.25	-9.55	-12.66	-12.39
LRT: χ ² (df)	3.0(2)	2.6(2)	0.6(2)	0.5(2)	4.4(2)	0.8(2)	0.7(2)
(P-val) ^{††}	(P=0.22)	(P=0.27)	(P=0.73)	(P=0.76)	(P=0.11)	(P=0.65)	(P=0.69)

505 *Note:* * $P < 0.05$; ** $P < 0.01$; Exact P -values, test statistics, and degrees of freedom are shown in

506 Appendix. S1: Table S4; τ₀₀ = rand. intercept variance; τ₀₁ = rand. slope variance; ρ₀₁ =

507 correlation of rand. slope & intercept; † = compares the AIC of a model with fixed effects for

508 trait and trait:envi interaction to a model without these effects.; †† = Results from a likelihood

509 ratio test comparing models with and without trait and trait:envi effects.

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513 **Table 3.** Forb survival model coefficients

	<i>Trait Model</i>						
	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
Marg./Cond. 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^\dagger	-2.14	8.72	4.49	4.34	1.61	-2.90	-3.56
LRT: χ^2 (df)(P-val) ^{††}	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)

514 Note: * $P < 0.05$; ** $P < 0.01$; Exact P -values, test statistics, and degrees of freedom are shown in

515 Appendix S1: Table S5; τ_{00} = rand. intercept variance; † = compares the AIC of a model with

516 fixed effects for trait and trait:envi interaction to a model without these effects.; $^\dagger^\dagger$ = Results

517 from a likelihood ratio test comparing models with and without trait and trait:envi effects.

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523 **Figure Captions**

524 **Figure 1.** The demographic rates of growth, survival, and reproduction are impacted by
525 environment, interactions with neighbors, and size. We focus here on plant growth and survival.
526 The impact of environmental variation on an organism's demographic rates is likely mediated by
527 the traits of that organism. This is especially true for traits that are related to environmental
528 conditions that are most limiting or stress-inducing in a given habitat. In semiarid steppe, traits
529 related to water use might be more important for plant growth and survival in very dry years, and
530 relatively less important in wetter years. The “predictions” figure shows how a trait related to
531 drought-tolerance may mediate the effect of climate on growth and survival. Specifically, we
532 predicted that water-use traits impact survival or growth rates in dry years, but are not important
533 in wetter years when a plant is not experiencing severe water stress.

534 **Figure 2.** The effect of local neighborhood density (**A**) and size in year_t (**B**) on graminoid
535 survival in models using LDMC as the trait predictor. (**A**) Across all graminoid species, higher
536 local neighborhood crowding by individuals of the same species corresponds with lower
537 survival. (**B**) Larger individuals are more likely to survive to the next year than smaller
538 individuals of the same species. (**C-D**) use values from models using TLP as the trait predictor.
539 (**C**) Across all graminoid species, higher local neighborhood crowding by individuals of the
540 same species corresponds to smaller size_{t+1}. (**D**) This model predicts that as $\ln(\text{size}_t)$ increases, a
541 plant will become larger in year_{t+1} until it reaches a mid-point in size_t, at which point it will

542 plateau in size. **(E)** In the raw data (as opposed to model predictions shown in **A-D**) there is a
 543 positive linear relationship between $\ln(\text{size}_t)$ and $\ln(\text{size}_{t+1})$ for each graminoid, although there is
 544 a size above which plants are more likely to shrink than grow in year_t. Dashed lines in **(D)** and
 545 **(E)** show a 1:1 relationship between $\ln(\text{size})$ and $\ln(\text{size}_{t+1})$. Dark lines show the overall effect of
 546 each covariate on survival. The 95% CI for the predictor is shown in light grey. Colored lines
 547 incorporate random species effects to show the effects of competition or size_t by species.

548 **Figure 3:** Survival probabilities and $\ln(\text{size}_{t+1})$ for wet years and dry years, calculated using the
 549 97.5th and 2.5th quantiles of the distribution of SPEI values. **(A)** Low TLP graminoid species are
 550 more likely to survive than high TLP species in dry years (low SPEI), while in wet years (high
 551 SPEI) species with a high TLP are more likely to survive than low TLP species
 552 ($\beta_{TLP*SPEI} = 0.95$; $P < 0.001$; $\chi^2 = 16.45$; $df = 1$). **(D, G)** A similar trend in graminoid survival is
 553 predicted by the models that includes LDMC ($\beta_{LDMC*SPEI} = 0.94$; $P < 0.001$; $\chi^2 = 17.06$; $df = 1$) and
 554 RDMC ($\beta_{RDMC*SPEI} = 0.78$; $P < 0.001$; $\chi^2 = 17.36$; $df = 1$). Note the scale of TLP is inverse to that
 555 of LDMC and RDMC. **(J, M)** There are significant interactions between SPEI and RDiam
 556 ($\beta_{RDiam*SPEI} = 0.86$; $P < 0.001$; $\chi^2 = 14.58$; $df = 1$) and SLA ($\beta_{SLA*SPEI} = 0.96$; $P < 0.001$; $\chi^2 = 17.12$;
 557 $df = 1$). However these two traits models have much lower Δ AIC values than other trait models.
 558 **(B, E, H, K, N)** There are no significant interactions between the effects of any trait and SPEI on
 559 size_{t+1} (Appendix S1: Table S4). Horizontal dashed lines in **(B, E, H, K, N)** indicate the average
 560 plant size in year_t. **(C, F, I, L, O)** Trends for forb survival were similar to those for graminoids,
 561 although model fit is weaker and interactions between trait and environment are less significant
 562 for all traits (Appendix S1: Table S5). Black bars on the x-axis indicate species-level trait values,
 563 and bands around each line indicate 95% CIs. $*$ ($P < 0.05$) for this trait:SPEI interaction; \S Δ AIC
 564 for this model is positive and the LRT is significant.