

Drought-tolerant grassland species are generally more resistant to competition

Hailey E. Mount¹  | Melinda D. Smith²  | Alan K. Knapp²  |
 Robert J. Griffin-Nolan³  | Scott L. Collins⁴  | David H. Atkins¹  | Alice E. Stears¹  |
 Daniel C. Laughlin¹ 

¹Department of Botany and Graduate Program in Ecology and Evolution, University of Wyoming, Laramie, Wyoming, USA

²Department of Biology and Graduate Degree Program in Ecology, Colorado State University, Fort Collins, Colorado, USA

³Department of Biological Sciences, California State University, Chico, California, USA

⁴Department of Biology, University of New Mexico, Albuquerque, New Mexico, USA

Correspondence

Hailey E. Mount
Email: hmount@uwyo.edu

Funding information

National Institute of Food and Agriculture, Grant/Award Number: 2019-67019-29459; National Science Foundation-Macrosystems Biology Program, Grant/Award Number: 1137342, 1137363, 1137378, 1655499 and 1856383

Handling Editor: Giovanna Battipaglia

Abstract

1. Plant populations are limited by resource availability and exhibit physiological trade-offs in resource acquisition strategies. These trade-offs may constrain the ability of populations to exhibit fast growth rates under water limitation and high cover of neighbours. However, traits that confer drought tolerance may also confer resistance to competition. It remains unclear how fitness responses to these abiotic conditions and biotic interactions combine to structure grassland communities and how this relationship may change along a gradient of water availability.
2. To address these knowledge gaps, we estimated the low-density growth rates of populations in drought conditions with low neighbour cover and in ambient conditions with average neighbour cover for 82 species in six grassland communities across the Central Plains and Southwestern United States. We assessed the relationship between population tolerance to drought and resistance to competition and determined if this relationship was consistent across a precipitation gradient. We also tested whether population growth rates could be predicted using plant functional traits.
3. Across six sites, we observed a positive correlation between low-density population growth rates in drought and in the presence of interspecific neighbours. This positive relationship was particularly strong in the grasslands of the northern Great Plains but weak in the most xeric grasslands. High leaf dry matter content and a low (more negative) leaf turgor loss point were associated with high population growth rates in drought and with neighbours in most grassland communities.
4. Synthesis: A better understanding of how both biotic and abiotic factors impact population fitness provides valuable insights into how grasslands will respond to extreme drought. Our results advance plant strategy theory by suggesting that drought tolerance increases population resistance to interspecific competition in grassland communities. However, this relationship is not evident in the driest grasslands, where above-ground competition is likely less important. Leaf dry matter content and turgor loss point may help predict which populations will establish and persist based on local water availability and neighbour cover, and

these predictions can be used to guide the conservation and restoration of biodiversity in grasslands.

KEY WORDS

community assembly, drought tolerance, functional traits, grasslands, plant community dynamics, population growth rates, resistance to competition

1 | INTRODUCTION

Plant species responses to water availability will determine the future of grassland ecosystems under the increasing intensity and frequency of extreme drought events (Breshears et al., 2016; Smith, 2011). Our ability to predict these outcomes is confounded by idiosyncratic plant–plant interactions that mediate community responses across different environmental conditions (Brooker, 2006; Plough et al., 2019) and resource availabilities (Grant et al., 2014; Maestre et al., 2009). According to the Huxman-Smith model, grassland sensitivity to drought, measured as relative reductions in above-ground net primary productivity (ANPP), is expected to vary inversely with mean annual precipitation (Huxman et al., 2004; Knapp et al., 2015). However, long-term changes in precipitation patterns drive changes in the functional composition of plant communities that could either increase or decrease drought sensitivity in these communities (Griffin-Nolan, Blumenthal, et al., 2019). Disentangling how species traits and local biotic and abiotic conditions combine to influence population growth will improve our ability to predict the future of grassland community composition and ecosystem function under climate change (Germain et al., 2018; Volaire, 2018).

Long-standing ecological theory proposes that adaption to local conditions will cause population growth to be primarily limited by abiotic drivers in resource-limited conditions and by competitive interactions in productive conditions (Darwin, 1859; Louthan et al., 2015; Maestre et al., 2009). Therefore, we expect to see variation in strategies and population fitness depending on the intensity of competition and the availability of resources (Berger & Ludwig, 2014; Liancourt et al., 2013). However, plant strategy theories disagree about how interactions between traits and the environment at the population level structure communities (Craine, 2005; Grace, 1990; Grime, 2006; Tilman, 1994). Grime (2001) proposed that stress-tolerant species will exhibit positive population growth despite limited resources, whereas competitive species will exhibit positive population growth in productive conditions where resources are primarily limited by biotic interactions. This theory predicts a trade-off between fitness in resource-limited conditions and fitness in productive conditions where interspecific competition is high. Tilman (1988) proposed an alternative theory that stress-tolerant species are more competitive because of their greater ability to persist at low resource levels. In this case, we would expect a positive relationship where species with high fitness under drought would also exhibit high

fitness in a dense community because of their enhanced ability to compete for water. Given these contrasting theoretical expectations, it is unclear if drought tolerance is positively or negatively correlated with competitive ability in water-limited ecosystems such as semi-arid grasslands.

Fitness differences among species are likely driven by differences in phenotypic traits. Plant species variation along a fast-to-slow economic spectrum of resource acquisition and conservation (Grime, 2001; Reich, 2014; Wright et al., 2004) may explain the physiological mechanisms driving variation in population responses to drought and competition. Plants either allocate resources to acquisitive tissues that can be cheaply produced or to longer-lived tissues that incur a higher construction cost (Onoda et al., 2017; Shipley et al., 2006). Root construction costs face a similar dilemma, but with an additional orthogonal collaboration trade-off where they either produce thick roots with more cortex for enhanced mycorrhizal colonization or thin roots that seek out resources on their own (Bergmann et al., 2020). From Grime's perspective, a species is more competitive if it acquires resources first, and so acquisitive traits are associated with a competitive strategy. If acquisitive traits make species more competitive and less drought tolerant, this could underlie a trade-off in fitness between abiotic and biotic drivers across grasslands. However, from Tilman's perspective, if conservative traits increase the competitive ability of stress-tolerant plants in water-limited environments, this may explain a positive relationship between fitness under drought and with neighbour competition. Thus, it is unclear if selection on traits to cope with water limitation will prevent grassland species from having high fitness in more productive conditions, or if conservative traits confer both drought tolerance and resistance to neighbour competition.

Grasslands in the Central Plains and Southwestern United States provide an excellent study system to test for the relationship between tolerance to abiotic and biotic stresses within and between grassland types that span a broad precipitation gradient (Figure 1). We used 5 years of plant cover estimates as a measure of species abundance from six different grasslands in the Extreme Drought in Grasslands Experiment (EDGE) to investigate the relationship between population fitness under drought and competition. We asked three questions: (1) What is the relationship between tolerance to drought and resistance to competition in grasslands? (2) How does this relationship differ between communities along a precipitation gradient? (3) Do traits explain the relationship between population fitness under drought and with neighbours?

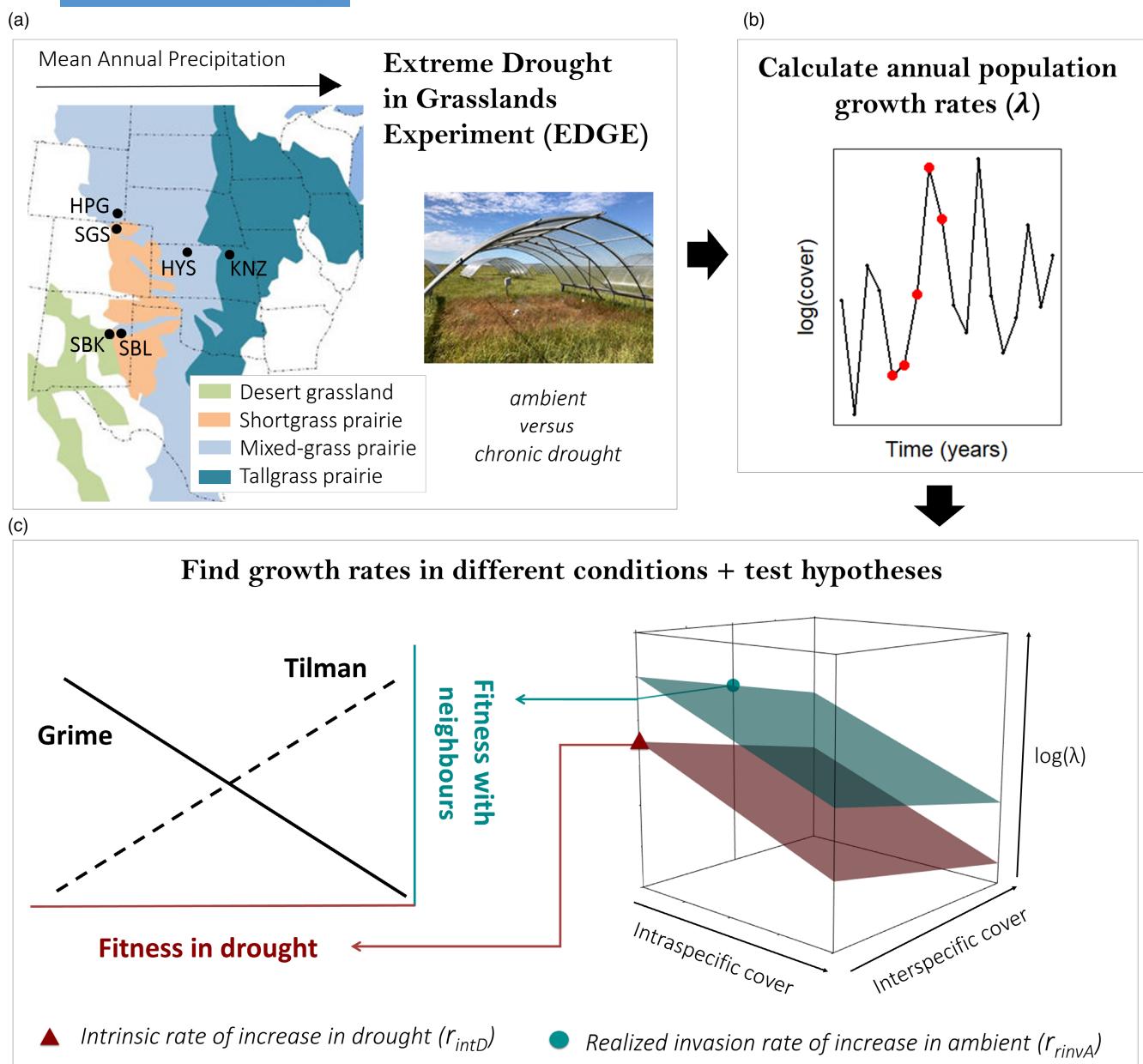


FIGURE 1 Conceptual diagram of the methodologies used in this paper (see Section 2 for details) and hypotheses being tested. (a) Cover estimates were collected over 5 years for species in ambient conditions and extreme chronic drought (50% annual precipitation reduction). We used rainout shelters (photo from <https://robertgriffin-nolan.weebly.com/grassland-sensitivity-to-extreme-drought.html>) to experimentally impose the extreme drought across six sites (map adapted from Griffin-Nolan et al., 2018). (b) Cover estimates were used to calculate annual population growth rates for each species in each grassland type in each annual transition. (c) A model of species annual population growth rate predicted by intraspecific and interspecific cover in each treatment was used to calculate estimates of intrinsic population growth rates (r) in different conditions. We relate the r in drought and r with higher neighbour cover to determine the relationship between these drivers and their effect on population fitness. We tested two hypotheses for how biotic interactions with neighbours may be related to drought tolerance. Grime's CSR model predicts that species with high fitness under drought will have low fitness in a highly competitive environment with neighbours (solid line). Alternatively, Tilman's theory predicts that species able to draw down the limiting resource will maintain high growth rates despite neighbour competition (dashed line).

2 | MATERIALS AND METHODS

2.1 | Extreme Drought in Grasslands Experiment

Approximately 320 plant species were monitored in the EDGE project across six grassland types, including tallgrass prairie, southern

mixed-grass prairie, northern mixed-grass prairie, northern short-grass prairie, southern shortgrass prairie and desert grassland (Baur et al., 2021; Carroll et al., 2021; Griffin-Nolan, Blumenthal, et al., 2019; Knapp et al., 2015; Lagueux et al., 2021; Yue et al., 2019; Table 1). Twenty 36-m² plots were established across a topographically uniform area at each site and split into four 2 m × 2 m subplots

TABLE 1 Summary of key attributes of the six different grassland sites. Mean annual precipitation (MAP), growing season precipitation (GSP) and mean annual temperature (MAT) are 30-year averages between 1982 and 2012 (Knapp et al., 2015). The final column lists the number of species analysed at each site in this analysis.

Site	Location	Grassland type	MAP (mm)	GSP (mm)	MAT (°C)	Dominant species	Final # species
SBK	Sevilleta Wildlife Refuge, NM	Desert	246	163	13.4	<i>Bouteloua eriopoda</i>	11
SBL	Sevilleta Wildlife Refuge, NM	Southern Shortgrass	246	163	13.4	<i>Bouteloua gracilis</i> <i>Bouteloua eriopoda</i>	13
SGS	Central Plains Experimental Range, CO	Northern Shortgrass	375	293	9.5	<i>Bouteloua gracilis</i>	17
CHY	High Plains Grassland Research Station, WY	Northern Mixed grass	400	303	7.9	<i>Bouteloua gracilis</i> <i>Pascopyrum smithii</i>	26
HYS	Hays Agricultural Research Center, KS	Southern Mixed grass	584	426	12.3	<i>Pascopyrum smithii</i> <i>Bouteloua gracilis</i> <i>Sporobolus asper</i>	29
KNZ	Konza Prairie Biological Station, KS	Tallgrass	892	652	13	<i>Andropogon gerardii</i> <i>Sorgastrum nutans</i>	17

with a 1 m buffer on every side. Plots were hydrologically isolated from the surrounding soil matrix using aluminium flashing and 6-mil plastic barriers installed to a depth of at least 20 cm. Ten control plots at each site received ambient rainfall over the experimental period, and 10 treatment plots experienced a 66% reduction in growing season precipitation (equivalent to roughly 40%–50% over the whole year) using greenhouse rainout shelters equipped with strips of clear corrugated polycarbonate. Permission for fieldwork was granted by the land managers at each location (Table 1). Additional site and experimental design details are available in Griffin-Nolan, Blumenthal, et al. (2019) (Figure 1a). We limited our analyses to 82 species that had >50 observations in both the control and drought treatments, totaling 113 species-site combinations (Table S1). The absolute cover of all species in four 1 × 1 m quadrats was estimated yearly from 2012 to 2017 (Figure 1a,b). There was variation in total cumulative cover of all species at the quadrat-level by grassland, treatment and year (Figure S1), but accounting for variation in year as a random effect was not possible because these models did not converge.

2.2 | Population growth rates

Percent cover was used as a measure of population size for each species at the quadrat level. The population growth rate at time t (λ_t) was calculated as the total cover (C) of a species at time $t+1$ divided by the total cover at time t :

$$\lambda_t = \frac{C_{t+1}}{C_t} \quad (1)$$

The natural logarithm of λ_t (often denoted as the intrinsic rate of increase: r) for a species in a quadrat describes whether the population increased (positive value) or decreased (negative value) in the transition from year t to $t+1$. This method integrates the growth, survival and reproduction of individuals into a single estimate of population fitness for plants (Laughlin et al., 2020). Population growth rates were calculated for each species in each quadrat in

each annual transition (Figure 1b). Because we use species cover instead of counts of individuals to measure population size, intraspecific cover is equal to the cumulative cover of a species in a quadrat. Interspecific cover in each quadrat is defined as the cumulative cover of all non-focal species in a quadrat.

2.3 | Population growth rate responses

Estimates of population growth at low density are important for understanding fitness responses to contrasting conditions (Adler et al., 2006; Angert et al., 2009; Chesson, 2000; Germain et al., 2018). Using the intercept of models that relate population growth to intraspecific cover, they provide a standardized metric to quantify and compare population fitness after controlling for intraspecific density dependence (Angert et al., 2009; Chesson, 2000). We calculated low-density growth rates for populations of each species at each site to assess fitness in two different conditions: mean neighbour abundance under ambient rainfall and minimum neighbour abundance under extreme drought. Minimum and mean neighbour abundances were averaged across all 5 years of the experiment. We compared these low-density growth rates to assess differences in fitness when experiencing stress from abiotic or biotic drivers.

To estimate these growth rates, we fit linear models predicting r for each species in each grassland as a function of drought treatment, intraspecific neighbourhood cover and interspecific neighbourhood cover (Figure 1c) pooled across years using the following equation:

$$r = \beta_0 + \beta_1 D + \beta_2 N_a + \beta_3 N_e + \beta_4 N_d + \beta_5 N_i + \epsilon \quad (2)$$

where D is a binary variable representing the ambient treatment ($D=0$) or the chronic drought treatment ($D=1$), N_a is the natural log of intraspecific plant cover in time t and N_e is the natural log of interspecific plant cover in time t . We estimated our population growth rates in the absence of density dependence using the modelled relationships between population growth and intraspecific cover when intraspecific

cover was set to zero. This metric estimates the potential growth rate of a focal population in the absence of neighbours. We observed an inverse relationship between r and intraspecific cover in most species-site combinations, indicating strong negative density dependence, but relationships between r and interspecific cover varied by species, grassland and treatment (Figure S2).

We estimated intrinsic growth rates in drought (r_{intD}) to assess the inherent population fitness in the absence of competition in the drought treatments for each species in each grassland (Figure 1). These values were computed by solving for r in our growth rate models for each species when intraspecific cover was set to zero, interspecific cover was set to the minimum observed and $D=1$ for the drought treatment (Equation 2). For many species, an interspecific cover of zero was not recorded, so the minimum observed values of interspecific cover were used instead to avoid extrapolating beyond the observed data.

We also calculated realized invasion growth rates (r_{inv}) to assess the population fitness at low intraspecific abundance in the presence of average observed interspecific neighbour abundance. These values were computed by solving for r when intraspecific cover was set to zero, interspecific cover was set to the mean of total interspecific cover and $D=0$ for ambient conditions. r_{inv} differs from the low-density invasion growth rates used in modern coexistence theory, which were beyond the scope of this analysis because these are calculated at equilibrium abundance of neighbours estimated using experimentally derived competition model coefficients (Chesson, 2000; Germain et al., 2018; Grainger et al., 2019). Our metric provides an analogous empirical measure of the effects of competition on population fitness. In summary, two population growth rates were estimated for the 113 species-site combinations: (1) intrinsic growth rate in drought (r_{intD}) and (2) realized invasion growth rates in ambient (r_{invA}) (Figure 1).

2.4 | Functional traits

We tested for the influence of 11 different functional traits on the two measures of population growth. Species-level trait data were assembled from several publications and trait databases, and these 11 were selected based on their importance to known physiological trade-offs. Leaf dry matter content (LDMC; g g^{-1}), average individual leaf area (cm^2) and leaf turgor loss point (TLP; MPa) provide insight into water use and desiccation tolerance (Griffin-Nolan, Ocheltree, et al., 2019; Májeková et al., 2021; Stears et al., 2022; Wilcox et al., 2021). Leaf nitrogen concentration (%), specific leaf area (SLA; $\text{cm}^2 \text{g}^{-1}$) and leaf tissue density (LTD; $\text{cm}^3 \text{g}^{-1}$) are key traits that reflect physiological constraints associated with the leaf economic spectrum and other resource use strategies (Pierce et al., 2007; Poorter & Evans, 1998; Westoby, 1998). Root nitrogen (%), root tissue density (RTD; $\text{cm}^3 \text{g}^{-1}$), root diameter (mm) and specific root length (SRL; mg^{-1}) describe below-ground root structure and function (Bergmann et al., 2020; Kong et al., 2015; Lozano et al., 2020). Additionally, average maximum height (mm) was investigated because of the important role height plays in structuring local plant communities along a productivity gradient (Brown & Cahill, 2019).

Due to the large influence regional climate can have on trait-environment interactions (Kelly et al., 2021; Wright et al., 2005), trait data were compiled for each species at the site level where available (Table S1). Trait values measured at, or nearby, EDGE sites were considered the closest estimate for species traits. For this, we used a mix of unpublished and open-access trait data from individual researchers (Blumenthal et al., 2020; Craine et al., 2011; Farrell, 2018; Laughlin et al., 2010; Stears et al., 2022; Tucker, 2010). Grassland communities that did not have data available at the local scale were filled in by progressively broader estimates using regional averages and eventually global estimates provided by the TRY database as needed (Kattge et al., 2019; Table S2). Commonly measured traits such as SLA and other leaf traits exhibited more coverage across all species than difficult-to-measure traits such as root traits. Overall, 21 populations had values for all traits, and 52% of all populations had values for at least five. There were 11 species that did not have any trait values from the public databases accessed and were excluded from the trait analyses (see Table S1).

2.5 | Data analysis

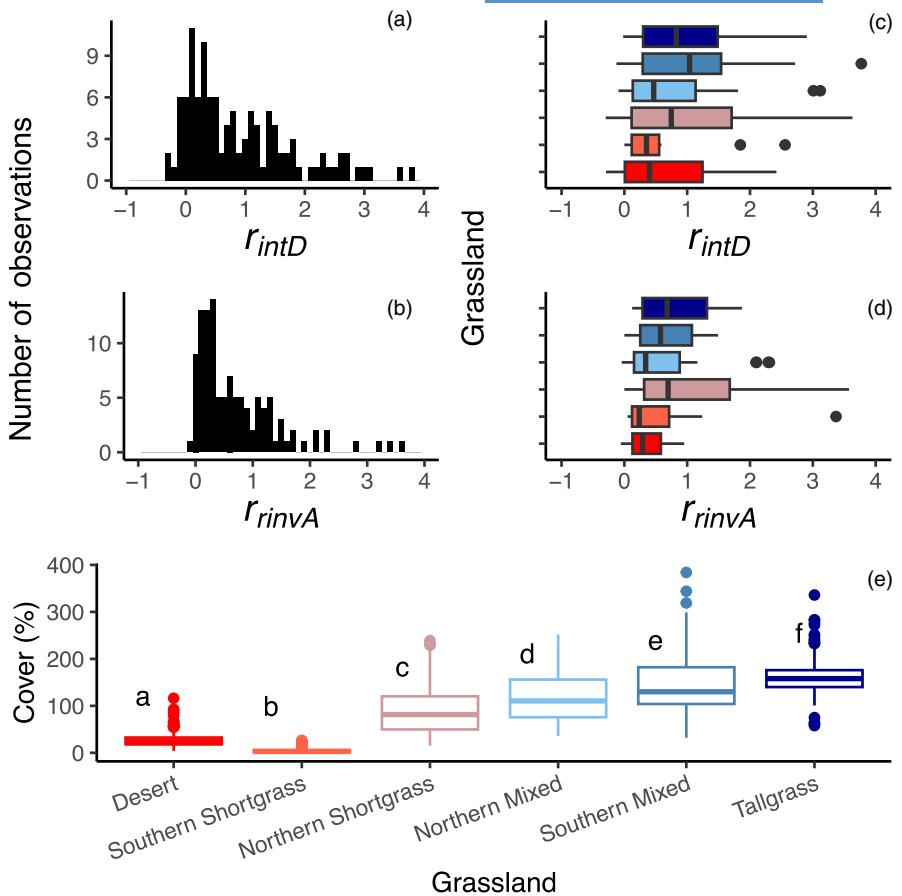
All analyses were conducted in R version 4.1.3 (R Core Team, 2022). We first report summary statistics describing the distribution of calculated values of r in the different abiotic and biotic conditions to demonstrate the range of variation across the species-site combinations. To answer our first question, we computed a correlation coefficient from a linear model to test for a negative relationship between fitness under drought and fitness with neighbour competition. To explore this relationship, we used an ordinary least squares regression and weighted each observation by the certainty we had in our estimates of r , measured as $\frac{1}{\text{SE}}$ of each model, where SE = standard error of the model. Because we did not necessarily expect one of the variables to solely influence the other, we compared this regression model to a major axis regression (Warton et al., 2012), but found no qualitative differences between methods, so we only report the ordinary least squares linear regression model results. To answer the second question, we used an F-test to assess the goodness-of-fit for a model with and without grassland type included as a factor in the linear regression model. To answer the third question, we used ANCOVAs to determine the influence of focal species traits, local environment and the interaction of these predictors on the variation between population responses to drought and neighbour cover.

3 | RESULTS

3.1 | Variation in fitness across grasslands

Species exhibited variation in intrinsic growth rates under extreme drought (Figure 2A) and in their realized invasion growth rates in ambient conditions (Figure 2B). The positive skew in these two population growth rate estimates indicates that most species exhibited

FIGURE 2 Range of variation in the two calculated population growth rates across all populations. Frequency distributions of (A) r_{intD} (intrinsic growth rate in drought) and (B) r_{rinvA} (realized invasion growth rates in ambient). (C and D). Box plots illustrate the lack of variation in population growth rates by grassland type. (E) Cumulative cover increased along the precipitation gradient across grasslands (lowercase letters indicate significantly different cover among sites).



positive population growth at low density. The growth rates were generally positive because they represent potential growth rates in the absence of intraspecific neighbours. There were no significant differences among grasslands in estimates of r_{intD} ($F_{5,106}=0.84$, $p=0.52$) or r_{rinvA} ($F_{5,107}=1.87$, $p=0.11$; Figure 2C,D). However, cumulative cover in subplots increased across the precipitation gradient at the grassland sites ($R^2=0.66$, $F_{5,2208}=854.6$, $p<0.001$; Figure 2E).

3.2 | Correlations between drought tolerance and resistance to competitors

There was a positive relationship between population growth rates in drought conditions with low neighbour cover and in ambient conditions with average neighbour cover ($r=0.59$, $F_{1,109}=58.96$, $p<0.001$; Figure 3a). In other words, drought-tolerant populations were also more resilient to higher competition from neighbours. A majority of the populations fell below the 1:1 line, further suggesting that populations were more often better able to tolerate drought than neighbour cover (Figure 3a).

We also found a strong correlation between population growth in drought and higher neighbour cover when considering grassland ($r=0.66$, $F_{11,99}=8.56$, $p<0.001$; Figure 3b). The strength of the positive correlation differed by grassland (r_{intD} -by-Grassland type interaction term: $F_{5,99}=3.49$, $p=0.006$, Table S3), and including grassland as a predictor improved the goodness-of-fit of our models compared

to those without grassland as a predictor ($F_{10,99}=2.64$, $p=0.007$; Figure 3b). Most sites exhibited a positive relationship between abiotic and biotic tolerances, while the two driest sites had the weakest correlations, where growth rates were reduced much more by neighbours than by drought (Figure 3b). We additionally tested to see if there were differences in this relationship between perennial and short-lived species but found that including an interaction with lifespan did not further improve the goodness-of-fit of this model (Figure S3).

3.3 | Traits as predictors of population growth rates

Focal species traits, grassland type and trait-by-grassland type interaction affected population growth rates to varying degrees depending on the focal trait. LDMC and TLP emerged as key traits for predicting population growth rates in drought with low neighbour abundance and population growth rates in ambient conditions with higher neighbour cover in ANCOVA models (Figure 4). LDMC had an overall positive effect on both fitness in drought ($R^2=0.19$, $F_{11,64}=2.64$, $p=0.007$; Figure 4a) and fitness with neighbour competition ($R^2=0.18$, $F_{11,65}=2.5$, $p=0.012$; Figure 4b). In the three sites with the most available TLP data, species with lower (more negative) TLP values—indicative of higher drought tolerance—had higher fitness in drought ($R^2=0.21$, $F_{10,43}=2.37$, $p=0.025$; Figure 4c)

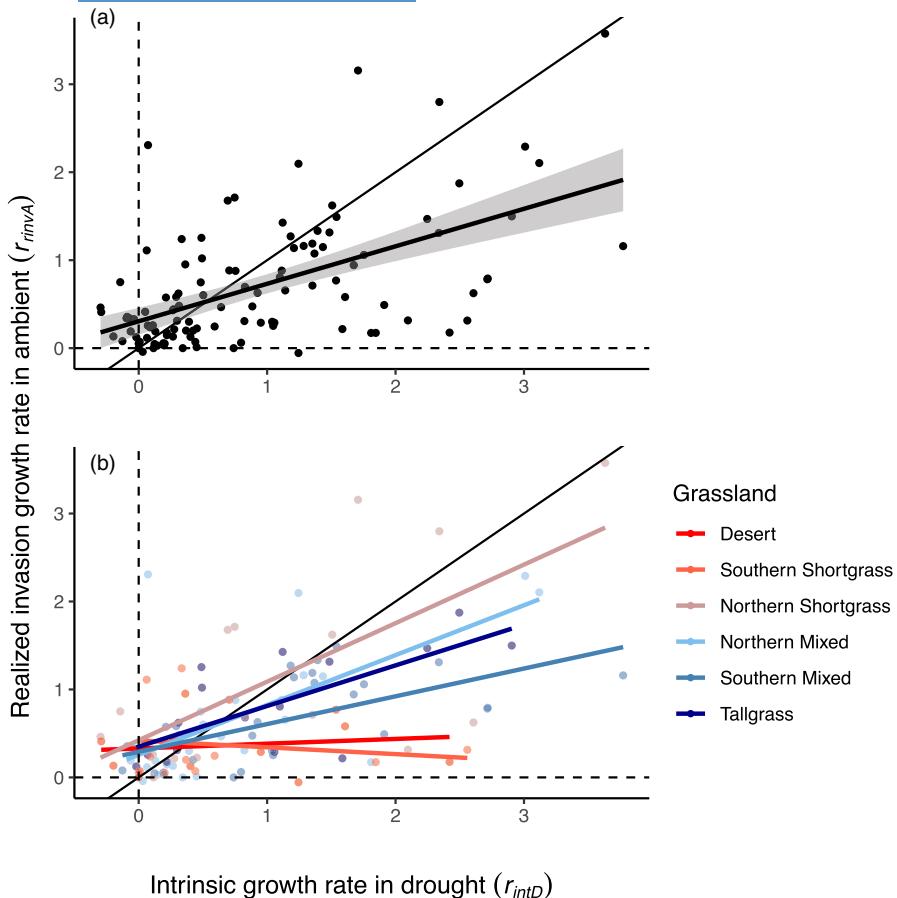


FIGURE 3 (a) Across all grasslands, there is a positive relationship between intrinsic population growth rates under drought (r_{intD}) and population growth rates with neighbours (r_{invA}). (b) The linear model was significantly improved by including an interaction with grassland type. In both plots, points represent the modelled low-density population growth rate under drought or with neighbours for a single species-site combination averaged across all years. These were derived from linear models predicting fitness from Equation 2 (see text) and weighted by the certainty in our growth rate estimates. A majority of these points fall below the black 1:1 line. The coloured lines in (b) represent fitted regression models in each grassland community that span a precipitation gradient from the most xeric site in red to the most mesic site in dark blue.

and fitness with neighbour competition ($R^2=0.18$, $F_{10,43}=2.14$, $p=0.042$; Figure 4d). Other above-ground traits—SLA, leaf nitrogen content, leaf tissue density and height—as well as one below-ground trait, SRL, were also significant predictors of population growth with neighbour cover (Table S4). Neither leaf area nor any of the other root traits explained significant variation in population growth rates (Table S4).

4 | DISCUSSION

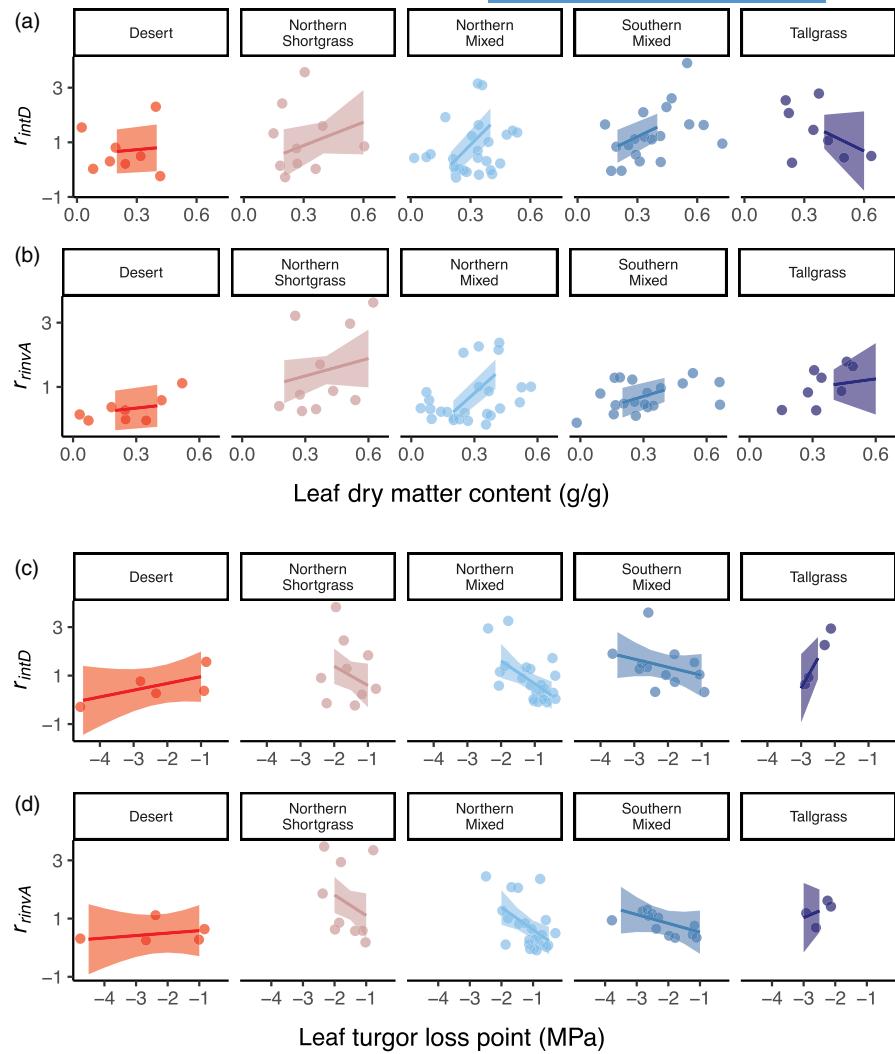
We used repeated monitoring data from an experiment that imposed 4 years of chronic drought across six grassland sites to test for the effects of water limitation and neighbourhood competition on population fitness among 113 plant populations, and we determined if traits could explain the relationship between tolerance to drought and resistance to neighbour competition. Our results suggest that (1) there is a positive correlation between tolerance to drought and resistance to competition; (2) this relationship is weakest in the driest grasslands, which may be expected given that there is reduced above-ground competition in drier sites; and (3) LDMC and TLP explained variation in population growth rates both under drought and with neighbour cover, a result that aligns with other studies on coordinated trait evolution in grasslands.

First, we found compelling evidence for a coordinated relationship between tolerance to drought and resistance to interspecific

competition in grasslands. In other words, populations with high annual growth rates under drought were also likely to have high annual growth rates when growing with interspecific neighbours. Our findings support the prediction that species that tolerate resource limitation are also more competitive in resource-limited habitats (Tilman, 1988; Figure 1). Moreover, there is evidence to suggest that the hydraulic pathways in grasses may be decoupled from acquisitive resource strategies like high photosynthetic capacity (Májeková et al., 2021; Ocheltree et al., 2016), which could explain the generally positive relationship we found in these grass-dominated ecosystems. We acknowledge, however, that for species with positive growth rates in drought, we could not distinguish between it being due to high performance under low water availability or whether it was a result of another indirect factor that coincided with the drought treatment, such as changes in below-ground fungal community composition (Lagueux et al., 2021). Similarly, resistance to competition (i.e. a positive population growth rate with neighbour cover) could result either from facilitation by other species in the community (Liancourt et al., 2005; Liancourt & Dolezal, 2021; Plouge et al., 2019; Soliveres & Maestre, 2014) or another factor that coincided with higher neighbour abundance, such as increased nutrient availability.

Second, stronger coordination between population growth rates in drought and with neighbours was found in grasslands with average to high precipitation along the precipitation gradient encompassed by the grassland sites studied, while the weakest correlations

FIGURE 4 ANCOVA model results are shown for the predicted relationship between population growth rates in drought (r_{intD}) or with neighbours (r_{invA}) given focal species leaf dry matter content (LDMC) (a and b) or leaf turgor loss point (TLP) (c and d), grassland and the interaction between trait and grassland. Higher values of LDMC and more negative values of TLP both indicate increased drought tolerance. Grasslands are coloured along the precipitation gradient from red to blue. Points illustrate observed data, and shaded regions are 95% confidence intervals.



were found in the grasslands with the lowest mean annual precipitation. These drier grasslands had the lowest cumulative cover, which likely reduces species interactions above-ground. Although we could not differentiate competitive ability and facilitation in these communities, it may be that drier grasslands exert stronger selection on drought tolerance than for species interactions. Supporting this, at the desert grassland, there was far greater variation in population fitness under drought than variation in population fitness with neighbours, indicating poorer responses to competition at this site.

Third, traits explained some of the coordination in population growth rates under drought and with neighbour competition. High LDMC and low TLP generally increased fitness under drought and fitness with neighbours in grasslands, and these traits are strongly linked to drought tolerance. This highlights the critical role that leaf-level drought tolerance plays in not only environmental filtering but also in plant-plant interactions in water-limited systems. Studies on drought and herbivory have found a similar coordination between drought tolerance and biotic interactions, specifically herbivory resistance (Blumenthal et al., 2020). These studies have also pointed to LDMC as a critical predictor of this coordinated relationship. Thus, LDMC continues to be an important trait for understanding

community assembly in grassland systems and could be excellent for selecting species that will succeed in restoration projects or that will be at risk from climate change. Although we found root traits were poor predictors of fitness, with more local root trait data, it may be possible to link these traits to fitness differences as well. Our work suggests that traits known to increase drought tolerance concurrently increase competitive resistance in most grasslands. Future work should investigate the connection between traits and population fitness at smaller scales to explicitly disentangle the effects of competitive ability and facilitation on structuring this relationship.

In summary, plant populations that maintain high growth rates in drought also maintain high growth rates with increased interspecific neighbour cover, but this coordination is weakest in extremely xeric grasslands. Dry grasslands may experience stronger selection for drought tolerance than resistance to competitive interactions. By determining which traits allow species to tolerate both abiotic and biotic stressors, we can predict how changes in precipitation and neighbour abundance may affect grassland communities. This provides a general framework for identifying populations that are most likely to successfully establish and persist in a restoration project. An enhanced understanding of how population fitness is related to both

abiotic and biotic drivers will improve our predictions of community assembly in a rapidly changing world.

AUTHOR CONTRIBUTIONS

Hailey E. Mount and Daniel C. Laughlin conceived of and designed this study. Melinda D. Smith, Alan K. Knapp, Robert J. Griffin-Nolan and Scott L. Collins provided the data used for the analysis, and further assistance was provided by Alice E. Stears and David H. Atkins. Hailey E. Mount analysed the data and wrote the initial draft of the manuscript. All authors provided comments on the final manuscript.

ACKNOWLEDGEMENTS

Funding was provided by a USDA-NIFA grant (2019-67019-29459) to D.C.L., and by the NSF Macrosystems Biology Program (DEB-1137378, 1137363 and 1137342) to M.D.S., A.K.K. and S.L.C., with continuing support to S.L.C. from DEB-1655499 and DEB-1856383. We thank the scientists and technicians at each of the LTER field sites in the EDGE project that collected the cover data. We also thank Dr. Dana Blumenthal and the USDA-ARS crew, Dr. Sally Tucker, Dr. Anna Farrell, contributors to the SEV-LTER Plant Traits Database and others who made their data available through the TRY database.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14243>.

DATA AVAILABILITY STATEMENT

Data and R scripts used in these analyses are archived and publicly available on Zenodo: <https://doi.org/10.5281/zenodo.10198333> (Mount, 2023) and data are also archived on Dryad Digital Repository: <https://doi.org/10.5061/dryad.1jwstqk1x> (Mount et al., 2023).

ORCID

Hailey E. Mount  <https://orcid.org/0000-0001-6767-6636>
 Melinda D. Smith  <https://orcid.org/0000-0003-4920-6985>
 Alan K. Knapp  <https://orcid.org/0000-0003-1695-4696>
 Robert J. Griffin-Nolan  <https://orcid.org/0000-0002-9411-3588>
 Scott L. Collins  <https://orcid.org/0000-0002-0193-2892>
 David H. Atkins  <https://orcid.org/0000-0002-1565-9356>
 Alice E. Stears  <https://orcid.org/0000-0002-1325-6641>
 Daniel C. Laughlin  <https://orcid.org/0000-0002-9651-5732>

REFERENCES

Adler, P. B., HilleRisLambers, J., Kyriakidis, P. C., Guan, Q., & Levine, J. M. (2006). Climate variability has a stabilizing effect on the coexistence of prairie grasses. *Proceedings of the National Academy of Sciences of the United States of America*, 103(34), 12793–12798. <https://doi.org/10.1073/pnas.0600599103>

Angert, A. L., Huxman, T. E., Chesson, P., & Venable, D. L. (2009). Functional tradeoffs determine species coexistence via the storage effect. *Proceedings of the National Academy of Sciences of the United States of America*, 106(28), 11641–11645. <https://doi.org/10.1073/pnas.0904512106>

Baur, L., Collins, S., Muldavin, E., Rudgers, J. A., & Pockman, W. T. (2021). Data from: Extreme drought in grassland ecosystems (EDGE) seasonal biomass and seasonal and annual NPP data at the Sevilleta National Wildlife Refuge, New Mexico ver 209676. Environmental Data Initiative <https://doi.org/10.6073/pasta/6d4a2def5f8f42866dc6c7d39740ee21>

Berger, J. D., & Ludwig, C. (2014). Contrasting adaptive strategies to terminal drought-stress gradients in Mediterranean legumes: Phenology, productivity, and water relations in wild and domesticated *Lupinus luteus* L. *Journal of Experimental Botany*, 65(21), 6219–6229. <https://doi.org/10.1093/jxb/eru006>

Bergmann, J., Weigelt, A., van der Plas, F., Laughlin, D. C., Kuyper, T. W., Guerrero-Ramirez, N., Valverde-Barrantes, O. J., Bruehlheide, H., Freschet, G. T., Iversen, C. M., Kattge, J., McCormack, M. L., Meier, I. C., Rillig, M. C., Roumet, C., Semchenko, M., Sweeney, C. J., Van Ruijven, J., York, L. M., & Mommer, L. (2020). The fungal collaboration gradient dominates the root economics space in plants. *Science Advances*, 6(27), eaba3756. <https://doi.org/10.1126/sciadv.aba3756>

Blumenthal, D. M., Mueller, K. E., Kray, J. A., Ocheltree, T. W., Augustine, D. J., & Wilcox, K. R. (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(6), 2336–2351. <https://doi.org/10.1111/1365-2745.13454>

Breshears, D. D., Knapp, A. K., Law, D. J., Smith, M. D., Twidwell, D., & Wonkka, C. L. (2016). Rangeland responses to predicted increases in drought extremity. *Rangeland*, 38(4), 191–196. <https://doi.org/10.1016/j.rala.2016.06.009>

Brooker, R. W. (2006). Plant–plant interactions and environmental change. *New Phytologist*, 171(2), 271–284. <https://doi.org/10.1111/j.1469-8137.2006.01752.x>

Brown, C., & Cahill, J. F. (2019). Vertical size structure is associated with productivity and species diversity in a short-stature grassland: Evidence for the importance of height variability within herbaceous communities. *Journal of Vegetation Science*, 30(5), 789–798. <https://doi.org/10.1111/jvs.12785>

Carroll, C. J. W., Slette, I. J., Griffin-Nolan, R. J., Baur, L. E., Hoffman, A. M., Denton, E. M., Gray, J. E., Post, A. K., Johnston, M. K., Yu, Q., Collins, S. L., Luo, Y., Smith, M. D., & Knapp, A. K. (2021). Is a drought a drought in grasslands? Productivity responses to different types of drought. *Oecologia*, 197(4), 1017–1026. <https://doi.org/10.1007/s00442-020-04793-8>

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, 31(1), 343–366. <https://doi.org/10.1146/annurev.ecolsys.31.1.343>

Craine, J. M. (2005). Reconciling plant strategy theories of Grime and Tilman. *Journal of Ecology*, 93(6), 1041–1052. <https://doi.org/10.1111/j.1365-2745.2005.01043.x>

Craine, J. M., Nippert, J. B., Towne, E. G., Tucker, S., Kembel, S. W., Skibbe, A., & McLauchlan, K. K. (2011). Functional consequences of climate change-induced plant species loss in a tallgrass prairie. *Oecologia*, 165(4), 1109–1117. <https://doi.org/10.1007/s00442-011-1938-8>

Darwin, C., 1809–1882. (1859). *On the origin of species by means of natural selection, or preservation of favoured races in the struggle for life*. John Murray. <https://search.library.wisc.edu/catalog/9934839413602122>

Farrell, A. K. (2018). Effects of management on functional diversity in restored tallgrass Prairie Plant communities. Northern Illinois University.

Germain, R. M., Mayfield, M. M., & Gilbert, B. (2018). The ‘filtering’ metaphor revisited: Competition and environment jointly structure

invasibility and coexistence. *Biology Letters*, 14(8), 4. <https://doi.org/10.1098/rsbl.2018.0460>

Grace, J. B. (1990). On the relationship between plant traits and competitive ability. In *Perspective on plant competition* (pp. 51–65). Academic Press.

Grainger, T. N., Levine, J. M., & Gilbert, B. (2019). The invasion criterion: A common currency for ecological research. *Trends in Ecology & Evolution*, 34(10), 925–935. <https://doi.org/10.1016/j.tree.2019.05.007>

Grant, K., Kreyling, J., Heilmeier, H., Beierkuhnlein, C., & Jentsch, A. A. (2014). Extreme weather events and plant-plant interactions: Shifts between competition and facilitation among grassland species in the face of drought and heavy rainfall. *Ecological Research*, 29(5), 991–1001. <https://doi.org/10.1007/s11284-014-1187-5>

Griffin-Nolan, R. J., Blumenthal, D. M., Collins, S. L., Farkas, T. E., Hoffman, A. M., Mueller, K. E., Ocheltree, T. W., Smith, M. D., Whitney, K. D., & Knapp, A. K. (2019). Shifts in plant functional composition following long-term drought in grasslands. *Journal of Ecology*, 107(5), 2133–2148. <https://doi.org/10.1111/1365-2745.13252>

Griffin-Nolan, R. J., Carroll, C. J. W., Denton, E. M., Johnston, M. K., Collins, S. L., Smith, M. D., & Knapp, A. K. (2018). Legacy effects of a regional drought on aboveground net primary production in six central US grasslands. *Plant Ecology*, 219, 505–515. <https://doi.org/10.1007/s11258-018-0813-7>

Griffin-Nolan, R. J., Ocheltree, T. W., Mueller, K. E., Blumenthal, D. M., Kray, J. A., & Knapp, A. K. (2019). Extending the osmometer method for assessing drought tolerance in herbaceous species. *Oecologia*, 189(2), 353–363. <https://doi.org/10.1007/s00442-019-04336-w>

Grime, J. P. (2001). *Plant strategies, vegetation processes, and ecosystem properties* (2nd ed.). John Wiley and Sons.

Grime, J. P. (2006). Trait convergence and trait divergence in herbaceous plant communities: Mechanisms and consequences. *Journal of Vegetation Science*, 17(2), 255–260. <https://doi.org/10.1111/j.1654-1103.2006.tb02444.x>

Huxman, T. E., Smith, M. D., Fay, P. A., Knapp, A. K., Shaw, M. R., Loik, M. E., Smith, S. D., Tissue, D. T., Zak, J. C., Weltzin, J. F., Pockman, W. T., Sala, O. E., Haddad, B. M., Harte, J., Koch, G. W., Schwinnig, S., Small, E. E., & Williams, D. G. (2004). Convergence across biomes to a common rain-use efficiency. *Nature*, 429(6992), 651–654. <https://doi.org/10.1038/nature02561>

Kattge, J., Bönnisch, G., Díaz, S., Lavorel, S., Prentice, L. C., & Leadley, P. (2019). TRY plant trait database – Enhanced coverage and open access. *Global Change Biology*, 26(1), 119–188.

Kelly, R., Healy, K., Anand, M., Baudraz, M. E. A., Bahn, M., Cerabolini, B. E. L., Cornelissen, J. H. C., Dwyer, J. M., Jackson, A. L., Kattge, J., Niinemets, Ü., Penuelas, J., Pierce, S., Salguero-Gómez, R., & Buckley, Y. M. (2021). Climatic and evolutionary contexts are required to infer plant life history strategies from functional traits at a global scale. *Ecology Letters*, 24(5), 970–983. <https://doi.org/10.1111/ele.13704>

Knapp, A. K., Carroll, C. J. W., Denton, E. M., La Pierre, K. J., Collins, S. L., & Smith, M. D. (2015). Differential sensitivity to regional-scale drought in six central US grasslands. *Oecologia*, 177(4), 949–957. <https://doi.org/10.1007/s00442-015-3233-6>

Kong, D., Wang, J., Kardol, P., Wu, H., Zeng, H., Deng, X., & Deng, Y. (2015). *The root economics spectrum: Divergence of absorptive root strategies with root diameter* [Preprint]. Biodiversity and Ecosystem Function: Terrestrial. <https://doi.org/10.5194/bgd-12-13041-2015>

Lagueux, D., Jumpponen, A., Porras-Alfaro, A., Herrera, J., Chung, Y. A., Baur, L. E., Smith, M. D., Knapp, A. K., Collins, S. L., & Rudgers, J. A. (2021). Experimental drought re-ordered assemblages of root-associated fungi across north American grasslands. *Journal of Ecology*, 109(2), 776–792. <https://doi.org/10.1111/1365-2745.13505>

Laughlin, D. C., Gremer, J. R., Adler, P. B., Mitchell, R. M., & Moore, M. M. (2020). The net effect of functional traits on fitness. *Trends in Ecology & Evolution*, 35(11), 1037–1047. <https://doi.org/10.1016/j.tree.2020.07.010>

Laughlin, D. C., Leppert, J. J., Moore, M. M., & Sieg, C. H. (2010). A multi-trait test of the leaf-height-seed plant strategy scheme with 133 species from a pine forest flora. *Functional Ecology*, 24(3), 493–501. <https://doi.org/10.1111/j.1365-2435.2009.01672.x>

Liancourt, P., Callaway, R. M., & Michalet, R. (2005). Stress tolerance and competitive ability determine the outcome of biotic interactions. *Ecology*, 86(6), 1611–1618. <https://doi.org/10.1890/04-1398>

Liancourt, P., & Dolezal, J. (2021). Community-scale effects and strain: Facilitation beyond conspicuous patterns. *Journal of Ecology*, 109(1), 19–25. <https://doi.org/10.1111/1365-2745.13458>

Liancourt, P., Spence, L. A., Song, D. S., Lkhagva, A., Sharkhuu, A., Boldgiv, B., Helliker, B. R., Petraitis, P. S., & Casper, B. B. (2013). Plant response to climate change varies with topography, interactions with neighbors, and ecotype. *Ecology*, 94(2), 444–453. <https://doi.org/10.1890/12-0780.1>

Louthan, A. M., Doak, D. F., & Angert, A. L. (2015). Where and when do species interactions set range limits? *Trends in Ecology & Evolution*, 30(12), 780–792. <https://doi.org/10.1016/j.tree.2015.09.011>

Lozano, Y. M., Aguilar-Trigueros, C. A., Flaig, I. C., & Rillig, M. C. (2020). Root trait responses to drought depend on plant functional group. *Ecology*, 37(11), 2224–2235 [preprint]. <https://doi.org/10.1111/1365-2435.13656>

Maestre, F. T., Callaway, R. M., Valladares, F., & Lortie, C. J. (2009). Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology*, 97(2), 199–205. <https://doi.org/10.1111/j.1365-2745.2008.01476.x>

Májeková, M., Hájek, T., Albert, Á. J., de Bello, F., Doležal, J., Götzenberger, L., Janeček, Š., Lepš, J., Liancourt, P., & Mudrák, O. (2021). Weak coordination between leaf drought tolerance and proxy traits in herbaceous plants. *Functional Ecology*, 35(6), 1299–1311. <https://doi.org/10.1111/1365-2435.13792>

Mount, H. E. (2023). Hmount/EDGE_thesis: v1.0.0 (v1.0.0). Zenodo. <https://doi.org/10.5281/zenodo.1019833>

Mount, H. E., Smith, M. D., Knapp, A. K., Griffin-Nolan, R. J., Collins, S. L., Atkins, D. H., Stears, A. E., & Laughlin, D. C. (2023). Data from: Drought tolerant grassland species are generally more resistant to competition. Dryad Digital Repository. <https://doi.org/10.5061/dryad.1jwstqk1x>

Ocheltree, T. W., Nippert, J. B., & Prasad, P. V. V. (2016). A safety vs efficiency trade-off identified in the hydraulic pathway of grass leaves is decoupled from photosynthesis, stomatal conductance and precipitation. *New Phytologist*, 210(1), 97–107. <https://doi.org/10.1111/nph.13781>

Onoda, Y., Wright, I. J., Evans, J. R., Hikosaka, K., Kitajima, K., Niinemets, Ü., Poorter, H., Tsoens, T., & Westoby, M. (2017). Physiological and structural tradeoffs underlying the leaf economics spectrum. *New Phytologist*, 214(4), 1447–1463. <https://doi.org/10.1111/nph.14496>

Pierce, S., Ceriani, R. M., DE Andreis, R., Luzzaro, A., & Cerabolini, B. (2007). The leaf economics spectrum of Poaceae reflects variation in survival strategies. *Plant Biosystems-An International Journal Dealing with all Aspects of Plant Biology*, 141(3), 337–343. <https://doi.org/10.1080/11263500701627695>

Plougher, L. W., Jacobs, E. M., Frank, G. S., Greenler, S. M., Smith, M. D., & Dukes, J. S. (2019). Community response to extreme drought (CRED): A framework for drought-induced shifts in plant-plant interactions. *New Phytologist*, 222(1), 52–69. <https://doi.org/10.1111/nph.15595>

Poorter, H., & Evans, J. R. (1998). Photosynthetic nitrogen-use efficiency of species that differ inherently in specific leaf area. *Oecologia*, 116, 26–37. <https://doi.org/10.1007/s004420050560>

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org>

Reich, P. B. (2014). The world-wide 'fast-slow' plant economics spectrum: A traits manifesto. *Journal of Ecology*, 102(2), 275–301. <https://doi.org/10.1111/1365-2745.12211>

Shipley, B., Lechowicz, M. J., Wright, I., & Reich, P. B. (2006). Fundamental trade-offs generating the worldwide leaf economic spectrum. *Ecology*, 87(3), 535–541. <https://doi.org/10.1890/05-1051>

Smith, M. D. (2011). An ecological perspective on extreme climatic events: A synthetic definition and framework to guide future research: Defining extreme climate events. *Journal of Ecology*, 99(3), 656–663. <https://doi.org/10.1111/j.1365-2745.2011.01798.x>

Soliveres, S., & Maestre, F. T. (2014). Plant–plant interactions, environmental gradients and plant diversity: A global synthesis of community-level studies. *Perspectives in Plant Ecology, Evolution and Systematics*, 16(4), 154–163. <https://doi.org/10.1016/j.ppees.2014.04.001>

Stears, A. E., Adler, P. B., Blumenthal, D. M., Kray, J. A., Mueller, K. E., Ocheltree, T. W., Wilcox, K. R., & Laughlin, D. C. (2022). Water availability dictates how plant traits predict demographic rates. *Ecology*, 103(11), e3799. <https://doi.org/10.1002/ecy.3799>

Tilman, D. (1988). *Plant strategies and the dynamics and structure of plant communities* (Vol. 26). Princeton University Press; JSTOR. <https://doi.org/10.2307/j.ctvx5w9ws>

Tilman, D. (1994). Competition and biodiversity in spatially structured habitats. *Ecology*, 75(1), 2–16. <https://doi.org/10.2307/1939377>

Tucker, S. S. (2010). *Morphological and physiological traits as indicators of drought tolerance in tallgrass prairie plants*. Pittsburgh State University.

Volaire, F. (2018). A unified framework of plant adaptive strategies to drought: Crossing scales and disciplines. *Global Change Biology*, 24(7), 2929–2938. <https://doi.org/10.1111/gcb.14062>

Warton, D. I., Duursma, R. A., Falster, D. S., & Taskinen, S. (2012). smatr 3 - an R package for estimation and inference about allometric lines. *Methods in Ecology and Evolution*, 3(2), 257–259. <https://doi.org/10.1111/j.2041-210X.2011.00153.x>

Westoby, M. (1998). A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, 199(2), 213–227. <https://doi.org/10.1023/A:1004327224729>

Wilcox, K. R., Blumenthal, D. M., Kray, J. A., Mueller, K. E., Derner, J. D., Ocheltree, T., & Porensky, L. M. (2021). Plant traits related to precipitation sensitivity of species and communities in semiarid short-grass prairie. *New Phytologist*, 229(4), 2007–2019. <https://doi.org/10.1111/nph.17000>

Wright, I. J., Reich, P. B., Cornelissen, J. H. C., Falster, D. S., Groom, P. K., Hikosaka, K., Lee, W., Lusk, C. H., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Warton, D. I., & Westoby, M. (2005). Modulation of leaf economic traits and trait relationships by climate: Modulation of leaf traits by climate. *Global Ecology and Biogeography*, 14(5), 411–421. <https://doi.org/10.1111/j.1466-822x.2005.00172.x>

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., ... Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, 428(6985), 821–827. <https://doi.org/10.1038/nature02403>

Yue, X., Zuo, X., Yu, Q., Xu, C., Lv, P., Zhang, J., Knapp, A. K., & Smith, M. D. (2019). Response of plant functional traits of *Leymus chinensis* to extreme drought in Inner Mongolia grasslands. *Plant Ecology*, 220(2), 141–149. <https://doi.org/10.1007/s11258-018-0887-2>

SUPPORTING INFORMATION

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

Figure S1. Total cumulative cover in quadrats at each grassland type varied by year and between treatments.

Figure S2. Models of annual instantaneous rates of increase (r) measured as $\log(\lambda)$ over increasing log-transformed intra-specific or interspecific cover for the species in each grassland type.

Figure S3. Boxplots showing the results of t-tests where we found no differences in (a) population growth rates under drought ($t_{(110)} = -0.37$, $p = 0.71$), nor (b) population growth rates with neighbors ($t_{(111)} = -0.04$, $p = 0.97$). (c) Both perennial and short-lived species exhibit a similar positive trend consistent with the relationship we identified. Lifespan did not improve the goodness of fit of our models including just the trait and grassland interaction ($F_{(11,88)} = 0.78$, $p = 0.66$).

Table S2. The proportion of trait data that was available from plants measured at or near the site, regional values or averages, and global values if applicable.

Table S3. Results of an ANOVA testing for effects of intrinsic population growth rates under drought (r_{intD}), grassland type, and the interaction of r_{intD} and grassland type on population growth rates with neighbors (r_{rinvA}).

Table S4. Results for all ANCOVA tests on the effects of traits, environment, and their interaction on the population growth rates under drought or with higher neighbor cover.

Table S1. All of the compiled trait data for the species–grassland combinations includes life history traits, maximum height (mm), leaf traits, root traits, and the sources of data.

How to cite this article: Mount, H. E., Smith, M. D., Knapp, A. K., Griffin-Nolan, R. J., Collins, S. L., Atkins, D. H., Stears, A. E., & Laughlin, D. C. (2024). Drought-tolerant grassland species are generally more resistant to competition. *Journal of Ecology*, 112, 416–426. <https://doi.org/10.1111/1365-2745.14243>