

RESEARCH ARTICLE

Drought response in herbaceous plants: A test of the integrated framework of plant form and function

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Abstract

1. Multidimensional trait frameworks are increasingly used to understand plant strategies for growth and survival. However, it is unclear if frameworks developed at a global level can be applied in local communities and how well these frameworks—based largely on plant morphological traits—align with plant physiology and response to stress.
2. We tested the ability of an integrated framework of plant form and function to characterise seedling trait variation and drought response among 22 grasses and forbs common in a semi-arid grassland. We measured above-ground and below-ground traits, and survival to explore how drought response is linked to three trait dimensions (resource conservation, microbial collaboration, and plant size) associated with the framework as well as non-morphological dimensions (e.g. physiological traits) that are under-represented in global trait frameworks.
3. We found support for three globally-recognised axes representing trade-offs in strategies associated with tissue investment (leaf nitrogen, leaf mass per area, root tissue density), below-ground resource uptake (root diameter, specific root length), and size (shoot mass). However, in contrast to global patterns, above-ground and below-ground resource conservation gradients were oppositely aligned: root tissue density was positively correlated with leaf N rather than leaf mass per area. This likely reflects different investment strategies of annual and perennial herbaceous species, as fast-growing annual species invested in lower density roots and less nitrogen-rich leaves to maximise plant-level carbon assimilation. Species with longer drought survival minimised water loss through small above-ground size and low leaf-level transpiration rates, and drought survival was best predicted by a principal component axis representing plant size.
4. Contrary to our expectations, drought survival in seedlings did not align with the conservation or collaboration axes suggesting that seedlings with different

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functional strategies can achieve similar drought survival, as long as they minimise water loss. Our results also show that within local communities, expected trait relationships could be decoupled as some plant groups achieve similar performance through different trait combinations. The effectiveness of species mean trait values in predicting drought response highlights the value of trait-based methods as a versatile tool for understanding ecological processes locally across various ecosystems.

KEYWORDS

grassland, leaf traits, plant size, plant survival, resource acquisition, resource conservation, root traits, water-use efficiency

1 | INTRODUCTION

Species traits are increasingly used to understand plant strategies for growth, survival and reproduction, which strongly influence ecological processes at multiple scales (Bruehlheide et al., 2018; Díaz et al., 2016; Laughlin et al., 2021). Over the last few decades, these approaches have evolved beyond a focus on above-ground traits (Díaz et al., 2016; Wright et al., 2004) to consider multiple dimensions of below-ground function, including root construction and collaboration with symbiotic microbes (Bergmann et al., 2020). In a recent rendition of this multidimensional approach, Weigelt et al. (2021) found global evidence for an “integrated framework of plant form and function” that couples well-established economic trade-offs in leaves and roots (resource conservation gradient) with independent plant size and root collaboration trait gradients (Figure 1). While compelling, functional tests of this multidimensional framework are needed to determine its relevance for plant response to environmental variation—including its applicability at local spatiotemporal scales and the implications of multiple dimensions in relation to singular functions such as drought response. Here we explore whether drought response may be driven by several established trait dimensions (e.g. conservation and size) as well as non-morphological dimensions (e.g. physiological traits) that remain conspicuously absent from trait frameworks.

Plant strategy frameworks have described evolutionarily successful trait combinations at global scales (Carmona et al., 2021; Díaz et al., 2016; Weigelt et al., 2021), yet trait composition at smaller scales may diverge from these patterns. In contrast to the large-scale environmental factors that drive trait trade-offs at global scales, trait diversity patterns at the community scale appear to be structured by local factors such as microenvironment and biotic interactions (Bruehlheide et al., 2018). Species within a community may therefore possess diverse strategies with different trait combinations that allow survival in the same environment. Correspondingly, recent tests of plant strategy frameworks demonstrate mixed success in explaining demographic rates and community processes at smaller scales (Balazs et al., 2020; Fort et al., 2017). Core functional trade-offs may also be absent in some communities (e.g. herbaceous, temperate deciduous) if they lack variation in traits such as

leaf lifespan and plant stature that tend to drive broad morphological differences among species (e.g. Funk & Cornwell, 2013). It is thus essential to evaluate the relevance of global trait frameworks at local scales and how well these frameworks predict species and community response to environmental stressors.

While plant strategy frameworks aim to link trait trade-offs to different functional strategies for acquiring and processing resources, a critical but often overlooked possibility is that multiple dimensions contribute simultaneously to a given function (Umaña et al., 2021; Worthy et al., 2020). With respect to drought response, for example, Reich (2014) proposed that species that cope well with drought tend to have denser tissues, grow and move water slowly, and use less water overall. However, evidence from dryland systems suggests that a range of different strategies can enable survival in water-limited environments. Many arid and semi-arid environments are home to fast-growing species possessing a drought-escape strategy characterised by high leaf N concentration, high photosynthetic capacity and early flowering (Franks, 2011; Nguyen et al., 2016). Furthermore, plants may respond to drought with vastly different root responses, altering their root architecture to grow toward deeper pools of soil moisture or proliferating shallow roots to more efficiently acquire surface moisture (Gupta et al., 2020). These strategies could achieve the same function (i.e. enhancing water uptake) via different root attributes, which may weaken trait-environment and trait-performance relationships. Leaf-level water-use efficiency (WUE), a key physiological trait reflecting transpiration and photosynthetic rates, typically shows inconsistent relationships with root traits (Ávila-Lovera et al., 2022; Funk, Larson, & Ricks-Oddie, 2021) but has been found to align with the ‘fast’ end of the conservation gradient in some groups of species including legumes and desert annuals (Adams et al., 2016; Huxman et al., 2008), although this varies across populations, water treatments and ontogenetic stages (e.g. Funk, Larson, & Vose, 2021). With the exception of WUE, many water-use strategies (i.e. resource conservation, rooting depth, root construction and collaboration) are reflected to some degree in the different dimensions of Weigelt's (Weigelt et al., 2021) trait framework, which provides a foundation to test multidimensional linkages between morphological plant strategy, water use and drought response. As many regions get drier with climate change

Relationships between traits and drought survival in herbaceous seedlings based on three established functional gradients

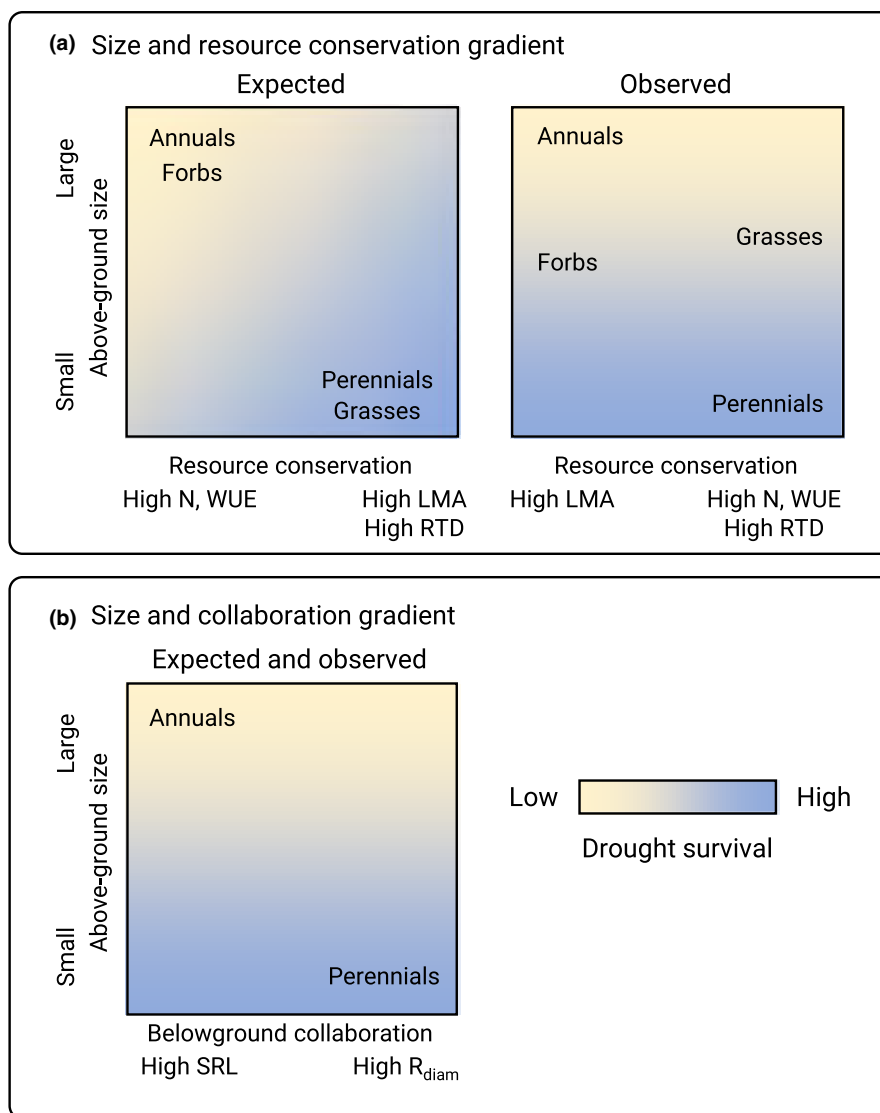


FIGURE 1 The integrated framework of plant form and function (Weigelt et al., 2021) predicts trait coordination along three gradients: resource conservation, below-ground collaboration and plant size. The conservation gradient reflects a trade-off between traits associated with high metabolic activity (fast) and those associated with high structural investment in tissues (slow). The collaboration gradient reflects a trade-off between thin roots that efficiently take up resources (do it yourself strategy) and thicker roots that 'outsource' resource uptake to mycorrhizal partners. (a) We expected that species with high drought survival (shown in blue) would be small (low above-ground biomass) with robust tissues (high resource conservation). We also expected annual and forb species to be larger and to display traits associated with faster resource acquisition relative to perennial and grass species. These predictions were generally not supported. Above-ground and below-ground trade-offs associated with resource conservation were oppositely aligned: root tissue density (a 'slow' root trait) was positively correlated with leaf N concentration (a 'fast' leaf trait) in contrast to expectations. Perennials were smaller and displayed longer drought survival relative to annuals as expected; however, perennials were aligned with the 'fast' end of the above-ground conservation gradient instead of the 'slow' end. Furthermore, size and drought survival did not differ among forbs and grasses. (b) Because species can use different root strategies to acquire water, and potentially avoid drought, we expected that species with high drought survival could fall anywhere along the collaboration gradient. We also predicted that annual species would display higher specific root length while perennials have larger root diameter. Both of these predictions were supported by our data.

(Cook et al., 2018), we need to develop generalisable yet comprehensive frameworks that predict how species and communities respond to drought.

Using trait frameworks to predict ecological processes requires consideration of both the limiting resources and life stages that

shape plant survival and performance. Seedling emergence and survival can pose substantial bottlenecks for recruitment in arid and semi-arid environments (Larson et al., 2015), and traits that predict success at these early ontogenetic stages may differ from those for adult plants (Gibert et al., 2016; Larson & Funk, 2016a). For example,

height has been used as an above-ground size trait in economic frameworks because tall plants generally have a longer time to reproduction, greater longevity, and a greater capacity to compete for light (Díaz et al., 2016; Westoby et al., 2002). However, vegetative height and longevity vary relatively little among seedlings and herbaceous species and, more critically, may be less relevant metrics for understanding drought response—where stem and leaf biomass may have more direct links to transpiration loss. Similarly, while rooting depth has been used to characterise access to below-ground resources, other traits that characterise the volume of soil explored (such as root length density or root mass fraction) may also predict drought response (Comas et al., 2013; Freschet & Roumet, 2017; Funk, Larson, & Ricks-Oddie, 2021). Indeed, Weigelt et al. (2021) found a weak correlation between height and rooting depth and concluded that above- and below-ground biomass allocation may better represent trait coordination in plant size.

In this study, we tested the ability of a multidimensional trait framework developed at a global scale (Weigelt et al., 2021) to characterise trait trade-offs and drought response among seedlings of diverse herbaceous species co-occurring at a local scale. We measured above-ground and below-ground traits, and drought survival in seedlings of 22 grasses and forbs common in California grasslands. We predicted that species surviving longest with a finite amount of water would have trait values aligned with the 'slow' end of the conservation gradient and smaller above-ground size (Figure 1a), as smaller investment in stem and leaf area may reduce water loss via transpiration (Blumenthal et al., 2021; Eziz et al., 2017). We predicted that higher leaf-level WUE would align with the 'fast' end of the conservation gradient (Figure 1a) as more N invested in photosynthetic machinery may draw down intercellular CO_2 concentrations and reduce transpiration loss (Wright et al., 2001), offering an alternative mechanism of drought survival. Given evidence that plants can effectively acquire water using different root strategies (Freschet, Roumet, et al., 2021), we predicted that species with high drought survival can fall anywhere along the collaboration gradient (Figure 1b). We also controlled for phylogeny in our analyses and, based on previous work demonstrating strong drought resistance in many grasses (Blumenthal et al., 2021; Voltaire et al., 2014), we expected to identify higher leaf-level WUE and denser tissues as attributes related to higher drought survival in grasses, relative to forbs (Figure 1a,b). As annuals need to establish quickly and complete their life cycle in one growing season, we predicted that annual seedlings would be larger and have more resource-acquisitive traits compared to perennials (e.g. Funk & Wolf, 2016; Larson et al., 2016), making them more susceptible to drought mortality (Figure 1a,b).

Our models use species trait means rather than traits collected under different water environments, as the 'holy grail' of trait-based ecology (e.g. Funk et al., 2017) is to leverage trait databases (which primarily include species-level averages) to infer function (e.g. response to climate change). Thus, our approach uses data collected under control or ambient conditions to see how well they predict drought survival. This research further contributes to the field of functional ecology by examining how key physiological traits related

to water and carbon use align with global frameworks and evaluating the applicability of these frameworks to drought survival predictions at local scales.

2 | METHODS

Twenty-two herbaceous species were selected based upon their prevalence within grassland communities in southern California (USA) with the goal of including variation in growth forms ($n=12$ grass, $n=10$ forbs) and life history ($n=11$ annuals, $n=11$ perennials). Seeds were collected from local seed farms in Irvine, California or purchased commercially. We grew three sets of plants in a common garden: one for above-ground trait measurements, one for below-ground trait measurements and one to quantify survival in response to a prolonged drought.

2.1 | Above-ground trait measurements

Seeds were germinated on moist filter paper in petri dishes and then transplanted into moistened potting soil (one plant per pot; Sunshine Mix #1, Sun Gro Horticulture). Germination occurred in early January, which coincides with the start of the growing season in Southern California. Plants were grown in full sun at Chapman University (Orange, California) and watered daily to saturation. With the relatively short growth period (6 weeks), we did not supplement potting soil with any additional fertiliser and observed no signs of nutrient limitation. We planted five replicate pots per species but had fewer replicates for some species due to mortality: *Bromus carinatus* ($n=2$), *Grindelia camporum* ($n=3$), *Leymus condensatus* ($n=4$). Pots were blocked by replicate (one replicate for each species) and blocks were rotated every week.

Sampling occurred after 5–6 weeks, when the leaves were large enough for above-ground measurements. Gas exchange measurements were conducted using a LI-6400 portable photosynthesis system (LI-COR, Lincoln, NE, USA) between 8:00 and 13:00. Because physiological traits can change throughout the day and across days in response to ambient conditions, plants were sampled randomly within replication blocks. Chamber conditions were controlled at 25°C, with CO_2 at 400 $\mu\text{L L}^{-1}$, light at 1800 $\mu\text{mol photon m}^{-2}\text{s}^{-2}$, and relative humidity at 52%–62%. Photosynthetic rate (A_{area} ; $\mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$) and transpiration rate (E , $\text{mol m}^{-2}\text{s}^{-1}$) values were corrected to account for differences in leaf area in the chamber. Water use efficiency (WUE; $\mu\text{mol CO}_2 \text{ mmol}^{-1} \text{H}_2\text{O}$) was calculated as A_{area} divided by transpiration rate. Following the gas exchange measurements, at least three leaves were harvested from each plant to determine leaf mass per area (LMA; g m^{-2}) and leaf nitrogen concentration (N, %). The harvested leaves were scanned (CanoScan LiDE 210) to obtain total leaf area (ImageJ) and dried at 60°C for at least 48 h to obtain leaf mass. Dried leaf material was ground (Thomas Wiley Mill, 40 mesh screen), and leaf N concentration was determined using an elemental analyser (ECS 4010 CHNSO Analyser, Costech Analytical Technologies, Inc.).

2.2 | Below-ground trait measurements

A second set of seeds was germinated using the methods described above. Seedlings were then transplanted, one plant per pot, into a 1:1:1 sand-perlite-vermiculite mixture that facilitated harvesting of the intact root system. Upon transplanting, each pot received 240 mL of distilled water and 360 mL of a nutrient solution matching that of typical coastal sage scrub soil (Padgett & Allen, 1999). We planted five replicate pots per species. Pots were grown in full sun at Chapman University, watered daily to saturation and harvested between March and May.

Plants were harvested after 4–6 weeks of growth to allow for maximum root development before roots exceeded pot boundaries. Root systems were washed and scanned using WinRHIZO image analysis (Regent Instruments, Inc., Quebec, QC, Canada) to obtain total root length and average root diameter (R_{diam} ; mm), as in Freschet, Pagès, et al. (2021). Above- and below-ground biomasses were dried at 60°C for at least 48 h to obtain shoot mass (g; including all above-ground biomass), root mass (g), root mass fraction (g root g^{-1} plant), specific root length (SRL; m root g^{-1} root) and root tissue density (RTD, g root cm^{-3} root). Root length density was calculated as total root length divided by pot soil volume (cm root cm^{-3} soil). While pots can influence plant growth and root architecture at high plant biomass: rooting volume ratios, the maximum ratio observed in this study (0.023 g L^{-1} soil) was two orders of magnitude lower than the recommended threshold of 1 g L^{-1} soil for pot experiments (Poorter et al., 2012). Most roots systems were below 0.01 g L^{-1} and no root systems were severely pot-bound.

2.3 | Drought survival experiment

A third set of seeds was germinated and transplanted following the same methods as the above-ground pots. Plants were grown in full sun at Chapman University and watered daily to saturation for 6 weeks. During the sixth week, we stopped watering plants to simulate a drought. The plants were monitored for eight additional weeks during the simulated drought, and plant mortality was assessed using the six stages of leaf wilting described by Engelbrecht and Kursar (2003); see Table S2. The same person assessed all plant species for consistency. All plants achieved stage six (death) within 8 weeks of drought. Water was added to a subset of plants to confirm that they were dead rather than dormant. Mean survival was calculated across all individuals within a species ($n=3$ to 8 individuals).

2.4 | Analysis

All analyses were completed using R (<http://www.r-project.org>, version 4.0.3). The full set of traits available for analysis are summarised in Figure 2. Species mean traits were checked for assumptions of multivariate normality and linearity prior to analysis when applicable.

We first created a phylogenetic tree of all study species using the National Center for Biotechnology Information (NCBI) database (taxize

package; Chamberlain & Szöcs, 2013). Trait data was matched to the phylogeny ('match_data' tool from De Bello et al., 2021) and we calculated the phylogenetic signal of each trait using Blomberg K tests (phytools package; Revell, 2012). Trait specific standard errors were included in these randomisation tests where relevant. To aid interpretation of phylogenetic signal, we also evaluated differences in trait values between grasses and forbs (growth form, which represented the deepest split in the phylogenetic tree) and among annuals and perennials (life history); we did this for each trait using two-factor analysis of variance (ANOVA) with post hoc tests using Tukey contrasts.

To identify key dimensions of trait variation, we conducted principal component analysis (PCA) using two approaches; one without accounting for phylogeny and one using the function `phyl.pca` from the package `phytools` to account for phylogeny. Prior to analysis, we scaled values of five traits from the Weigelt framework (LMA, leaf N, SRL, R_{diam} , RTD) and our metric of plant size (shoot mass). After conducting each ordination, we explored whether drought survival and additional water use or access traits were related to these trade-offs (including WUE, A_{area} , E, RMF) by estimating their correlation to each PC axis (overlaid in PC space). We did not include two traits (root mass, root length density) in this assessment due to their high correlation and functional redundancy with shoot mass ($r>0.80$). To aid in interpretation, we also estimated bivariate correlations and phylogenetically controlled correlations among all traits plus drought survival. For phylogenetically controlled values, we calculated corrected correlation coefficients from fitted phylogenetic generalised least-squares models for each bivariate trait combination (following Weigelt et al., 2021). For both ordination and correlations, phylogenetically controlled models were fit using an optimised value of lambda (between 0 and 1).

We used mixed effects models to determine how traits influenced drought survival. We used the `lme4` package in R (Bates, 2010) to fit one model predicting the number of days until mortality following severe drought (survival) as a function of species' scores along the first three PC axes with species as a random effect. We then fit a second model predicting survival as a function of all scaled traits and species as a random effect. We used a backward stepwise regression approach for each model to eliminate random and fixed effects until reaching a final model (`lmerTest` package in R, Kuznetsova et al., 2017). For final models, we used the `confint` function to generate 95% confidence intervals for regression coefficients and estimated both conditional (fixed effects) and marginal (fixed + random effects) R^2 values (performance package in R).

3 | RESULTS

3.1 | Trait and survival differences across growth form and life history groups

Plant size varied substantially across species (shoot mass varied 30-fold) while other seedling traits were less variable (e.g. LMA only varied 2-fold across species). Only five of twelve traits showed phylogenetic signal, all related to physiology or size (A_{area} , WUE, E, shoot

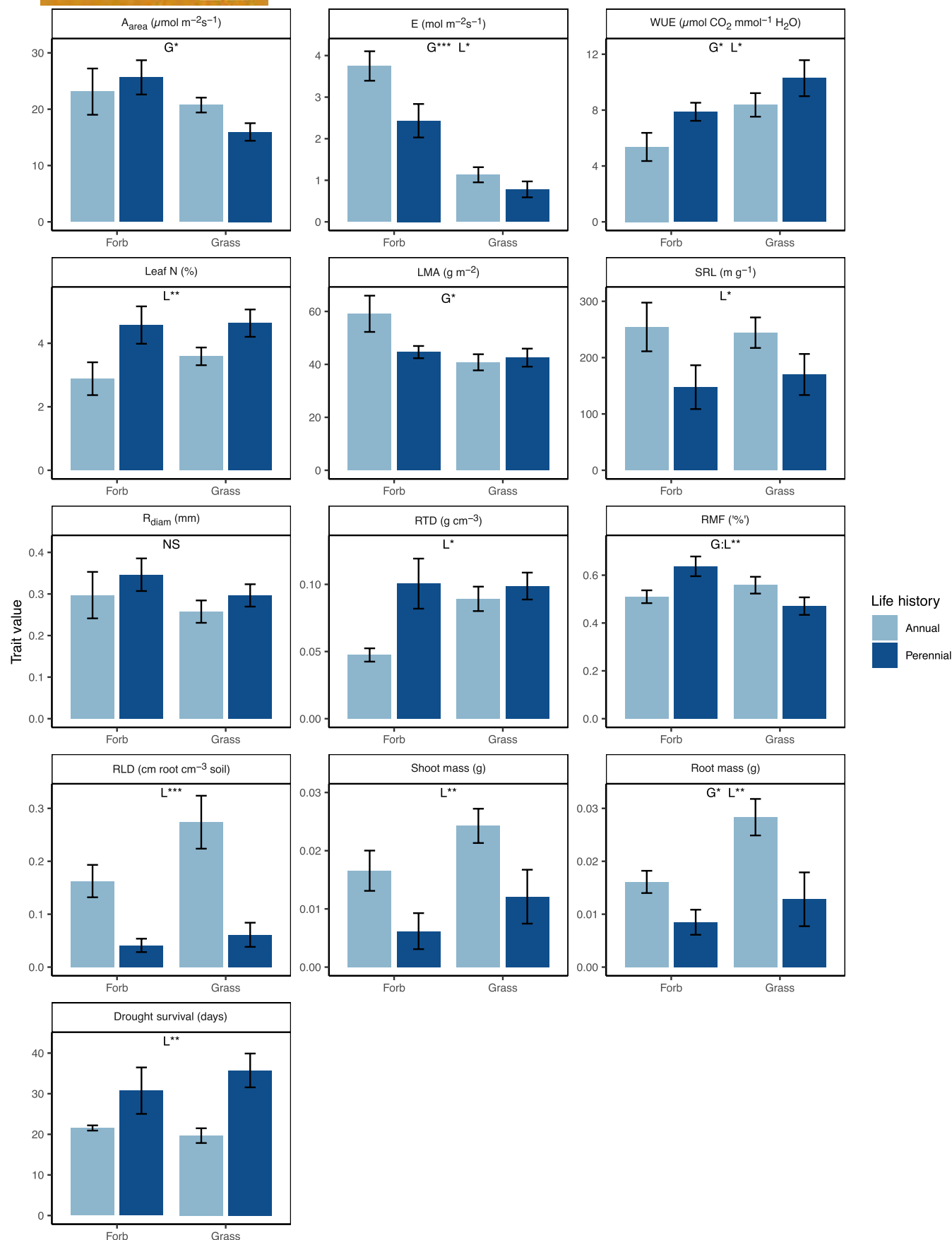


FIGURE 2 Trait data for five annual forbs, six annual grasses, five perennial forbs, and six perennial grasses summarised by growth form (G, grass or forb) and life history (L, annual or perennial). Means and standard errors are shown for all 12 traits estimated in the analysis, plus drought survival (number of days until death following drought). Where applicable, significant differences in life history and growth form are noted (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). See Table S3 for complete ANOVA results. Trait abbreviations are provided in the text.

mass and root mass; Figures S1 and S2). These patterns largely reflected differences between forbs and grasses: grasses had higher root mass and were more water-use efficient than forbs, while forbs had higher photosynthetic and transpiration rates (Figure 2, Figures S1 and S2, Table S3). While grasses displayed lower LMA than forbs (Figure 2), this did not correspond to a significant phylogenetic signal. Relative to perennials, annual species displayed seedling trait values associated with drought escape: high water uptake (high specific root length, high root length density, high root mass, low root tissue density), high carbon acquisition (high shoot mass) and low water conservation (high E, low WUE and leaf N concentration; Figure 2, Table S3).

There was a large range in seedling survival time to prolonged drought among the 22 species, with the annual grass *Festuca perennis* surviving for 12 days and perennial species *Sisyrinchium bellum* and *Muhlenbergia rigens* surviving for 52 days. There was a significant phylogenetic signal for drought survival ($p=0.006$, Figure S1), and perennial seedlings survived the drought an average of 13 days longer than annuals (Figure 2).

3.2 | Alignment with the integrated framework of plant form and function

Our analysis of six traits associated with the conservation, collaboration and plant size gradients (Figure 3) showed some similarities and differences to the global-database analysis in Weigelt et al. (2021). The first three axes explained 45.6%, 21% and 14.8% of the variation among species, respectively. Traits associated with the above-ground (leaf N, LMA) and below-ground (root tissue density) conservation gradients loaded strongly onto PC1 (Figure 3, Table S4). We found the expected trade-off between LMA and leaf N; however, in contrast to results from Weigelt et al. (2021), root tissue density was positively aligned with leaf N rather than LMA (supported by bivariate correlations, Table S5). The collaboration gradient—characterised by a trade-off between SRL and root diameter—aligned best with PC2, though substantial variation was also shared with PC1. While root diameter loaded primarily on PC2 ($r=0.80$), SRL was more strongly associated with PC1 ($r=0.81$), reflecting its negative relationships with both root diameter and root tissue density, respectively (Figure S4). Finally, plant size (shoot mass) aligned strongly with PC3. Although some bivariate trait correlations were influenced by phylogeny (Table S5), controlling for phylogeny did not alter PCA results (optimised Lambda <0.001 ; Figure S3, Table S4).

We then examined how four additional water use and acquisition traits (A_{area} , E, WUE, and root mass fraction) mapped onto the PCA along with drought survival (number of days until death). Photosynthetic rate was not strongly correlated with any PC axes. However, both water-use efficiency (WUE) and root mass fraction (RMF) were associated with the conservation gradient on PC1 ($r=-0.49$ and $r=-0.52$, respectively). Specifically, species with denser roots (high RTD) tended to have higher WUE ($r=0.46$), while

species with higher leaf N tended to allocate more biomass to roots (high RMF, $r=0.59$; Table S5). Transpiration rate (E) loaded more evenly on both PC1 and PC2 ($r=0.39$ and $r=-0.49$, respectively), yet aligned most strongly with the trade-off between RTD and LMA (higher transpiration rates associated with high LMA but low RTD; Tables S4 and S5). In contrast, drought survival loaded most heavily on PC3 ($r=-0.64$), reflecting a strong negative relationship with the size gradient.

In line with correlational analyses, the mixed model that included PCs as fixed effects (based only on six traits from Weigelt et al., 2021) showed that survival during extreme drought was best predicted by PC3, which negatively affected survival (Figure 4a, Table S6). PC3 was the only axis retained in the final model and explained 36.5% of the variation in drought survival (marginal $R^2=0.945$). However, a second model based on individual traits (including four additional water use and acquisition traits) identified both shoot mass and leaf-level transpiration rate as significant drivers of drought survival (Figure 4b, Table S6). Out of 10 traits, shoot mass and transpiration rate were the only traits retained in the final model and explained 49.8% of the variation in drought survival (marginal $R^2=0.944$). These traits were unrelated (Figure 4c), suggesting that both small plant size and low transpiration rate were independently associated with longer seedling survival under drought (Figure 4d,e). Notably, the seven species with longest survival times were all perennial grasses and forbs which tended to have small size, low transpiration rates or both.

4 | DISCUSSION

We tested the ability of a globally integrated, multidimensional trait framework (Weigelt et al., 2021) to characterise trait variation at the local level among a diverse group of co-occurring herbaceous species. Overall, we found support for the expected trade-offs with one exception; above-ground and below-ground resource conservation gradients were oppositely aligned as fast-growing annual species tended to have low root tissue density (a 'fast' root trait), but high LMA and low leaf N concentration ('slow' leaf traits). Water use and acquisition traits (water-use efficiency, transpiration rate and root mass fraction) showed some alignment with traits on the conservation gradient. However, drought survival was most closely aligned with the plant size gradient, as smaller plants survived longer in response to severe drought. Weak relationships between drought survival and most traits along the conservation and collaboration gradients suggest that seedlings with different functional strategies can achieve similar drought survival, as long as they minimise water loss through small size or low transpiration rates.

4.1 | Evidence for integrated function in herbaceous species

Across a diverse group of herbaceous, semi-arid species, we found a unified dimension of 'conservation' traits; however, in contrast to

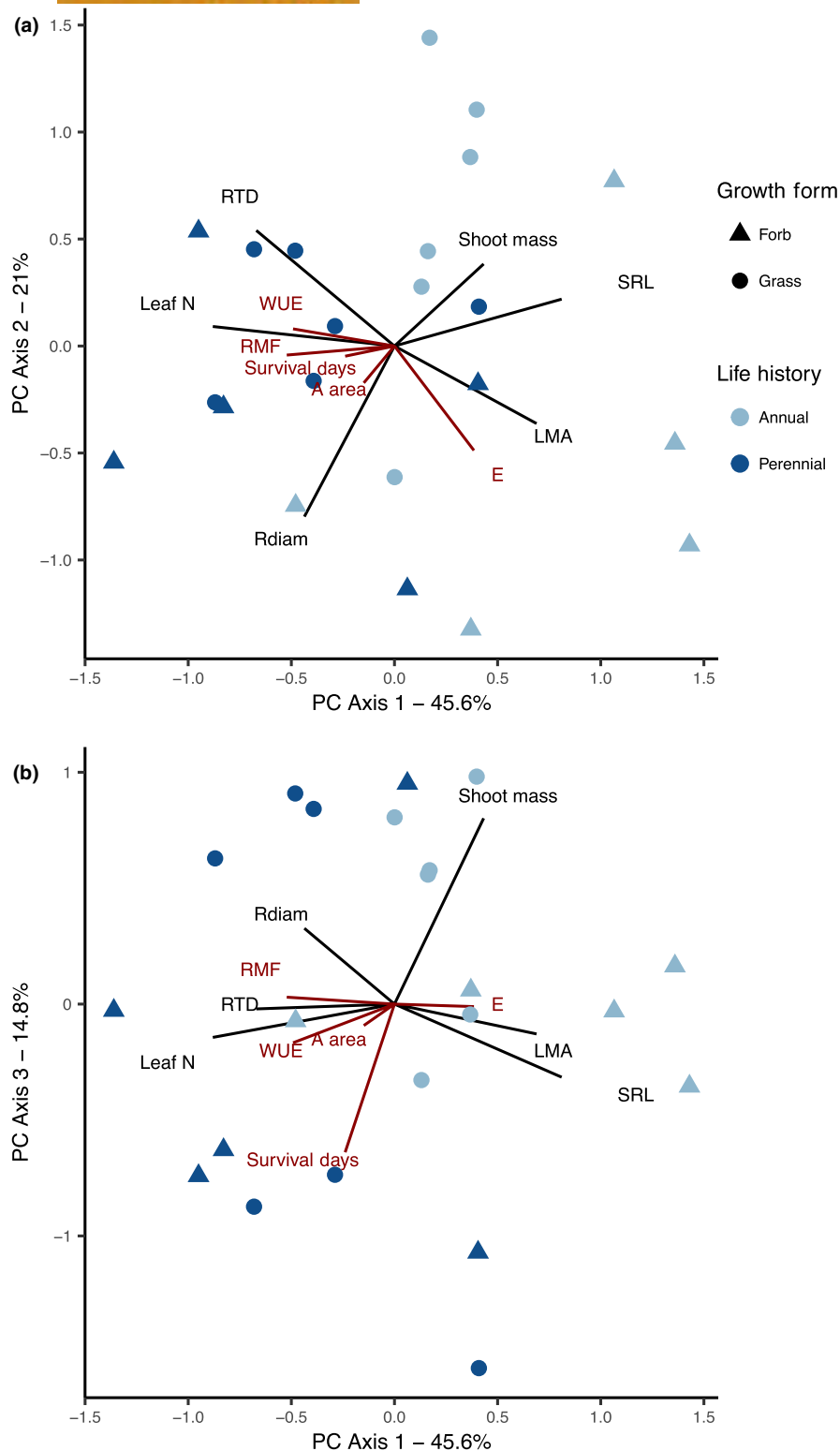


FIGURE 3 The (a) first and second axes and (b) first and third axes from a PCA including six traits from the integrated framework of plant form and function. Segments indicate the direction and strength of correlation between each trait and axis. Correlations with area-based photosynthetic rate (A_{area}), transpiration rate (E), root mass fraction (RMF), water-use efficiency (WUE), and drought survival are overlaid in red. Points are species in trait space. Annuals are in light blue, perennials in dark blue. Forbs are triangles, grasses are circles. Trait abbreviations are provided in the text.

global patterns observed by Weigelt et al. (2021), 'fast' and 'slow' ends of the conservation gradient were oppositely aligned for above- and below-ground traits. We observed an unexpected positive relationship between leaf N and root tissue density, which appeared to reflect different investment strategies of annual and perennial species in this system. Perennials invested in conservative below-ground structures more than annuals, as evidenced by higher root tissue density and

lower specific root length, but they also displayed higher leaf N. While high concentrations of leaf N are typically associated with 'fast' resource acquisition, evidence from several herbaceous communities in California suggest that fast-growing annual species often dilute leaf N concentration in favour of making more leaves (Funk & Wolf, 2016; Welles & Funk, 2021). In these herb-dominated systems, a large mass of low N leaves can serve a critical role of outcompeting neighbours

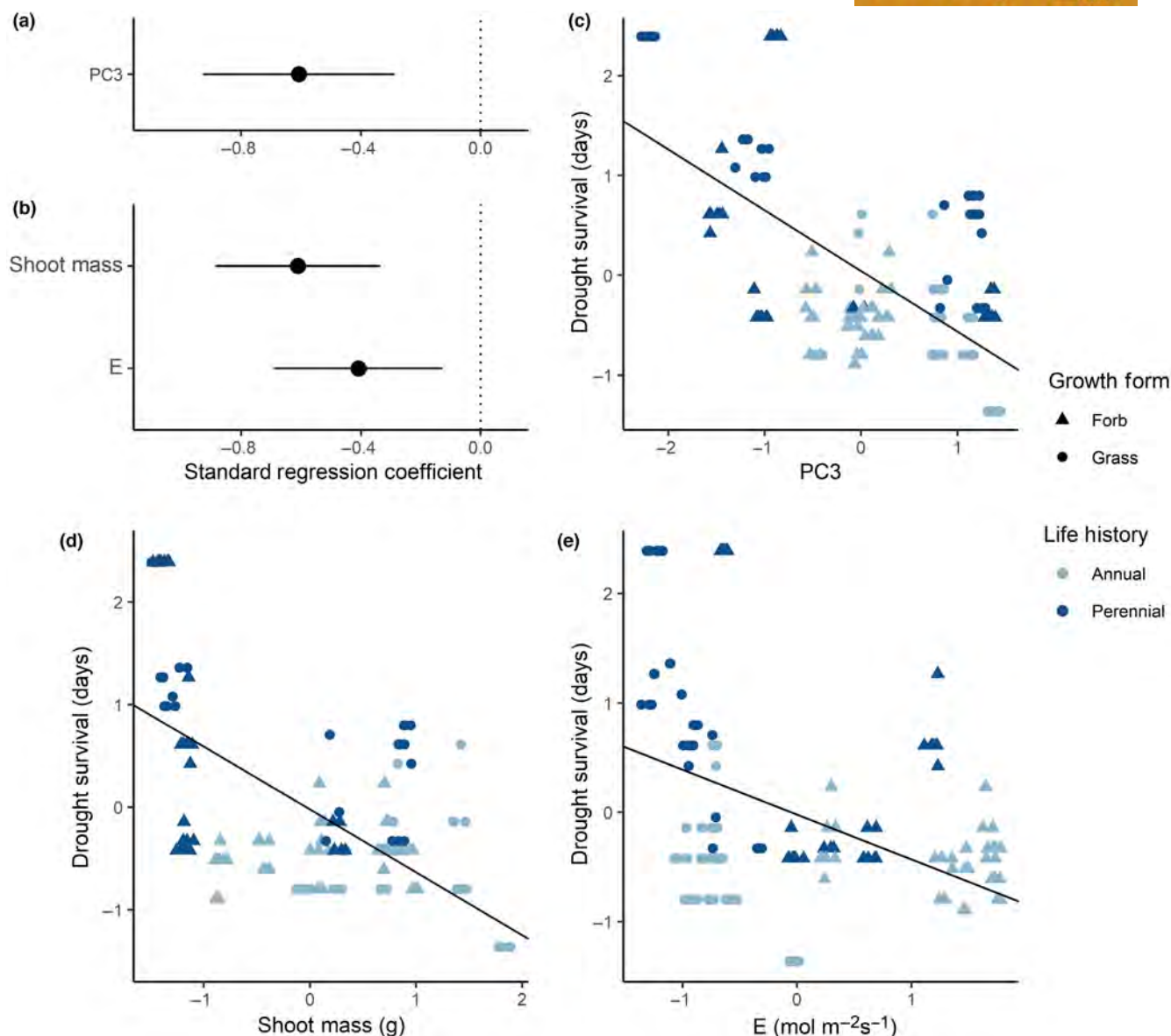


FIGURE 4 Results from two mixed models predicting survival as a function of PC scores (see Figure 3) or traits, with species as a random effect. (a) The standardised effect of PC3 scores on survival following drought, with bars representing 95% confidence intervals. PC1 and PC2 were not retained in the final model following stepwise backward regression (full results in Table S6). (b) The standardised effects of shoot mass and E (transpiration rate) on survival following drought (eight other traits not retained in the final model). Bars represent 95% confidence intervals (full results in Table S6). (c–e) Bivariate plots of species' mean values of drought survival versus PC3, shoot mass and transpiration rate ($n = 105$ individual plants; see Table S6 for all bivariate correlations). Annual species are in light blue, perennials in dark blue. Forbs are triangles, grasses are circles.

for light and result in high plant-level carbon assimilation. The combination of higher shoot mass and lower leaf N for annual species in the current study supports this idea. By investing in less dense roots and low N leaves to achieve a 'fast' strategy, annual plants decoupled the expected above and below-ground conservation gradients in this system. This also concurs with the idea that annual species can show different trait-performance and trait-environment relationships than expected based on analyses of woody and perennial herbaceous species (Kurze et al., 2021).

In agreement with expectations, the collaboration gradient, reflecting a trade-off between specific root length and root diameter,

was orthogonal to the conservation gradient. However, specific root length was correlated with two axes, reflecting strong negative relationships with both root tissue density (PC1) and root diameter (PC2). Ma et al. (2018) demonstrated that the inverse relationship between specific root length and root diameter can be strongly influenced by root tissue density. We found that, for a given diameter, roots with lower tissue density could achieve higher specific root length (Figure S4), enabling the plant to explore more soil per gram of biomass invested in the root. The multivariate links between these three root traits suggest that rooting strategies in herbaceous plants are a blend of both resource acquisition

(through symbiotic collaboration or soil exploration) and conservation (through tissue construction), with specific root length as a trait mediating both aspects.

Finally, we found support for a separate plant size gradient, as shoot mass loaded strongly on a third axis, supporting the predictions of Weigelt et al. (2021). Whole-plant strategic frameworks use plant height as a metric of size (Díaz et al., 2016; Westoby, 1998) and Weigelt et al. (2021) used plant height and rooting depth to characterise two independent size gradients. However, due to varying above-ground morphology in herbaceous plants (e.g. rosette, tillers), adult height does not accurately reflect above-ground investment in these species, which is why we selected shoot mass rather than height. In our study, shoot mass was negatively correlated with leaf-level WUE and leaf N concentration, supporting the idea that these herbaceous plants display a trade-off between maximising plant-level carbon assimilation through large leaf area per plant versus investing in photosynthetic proteins to enhance leaf-level carbon assimilation and WUE. Although the relative allocation of biomass below-ground can vary in magnitude depending on the species, environment and ontogeny (e.g. Husáková et al., 2016; Larson & Funk, 2016b; Poorter & Bongers, 2006), above-ground and below-ground biomass were strongly positively correlated in our experiment ($r=0.88$). Above-ground and below-ground biomass may thus be better metrics than height and rooting depth to characterise plant size gradients, especially for herbaceous plants.

4.2 | How do physiological traits and drought response align with the integrated framework?

As predicted, the size gradient was a strong predictor of drought survival in our experiment; small seedlings (low shoot mass) survived the drought longer than large seedlings. Over-investing in resource-acquiring tissues can be a detrimental strategy when resources are scarce (Reich, 2014). Large, fast-growing herbaceous plants require higher internal water concentration to maintain the turgor pressure necessary for proper nutrient distribution and growth (Green & Cummins, 1974), leaving plants with high leaf mass more vulnerable during drought conditions. In our experiment, drought-sensitive annual seedlings had larger root biomass and greater root length density (root length per volume of soil) relative to perennials suggesting that they should be able to access more below-ground resources to support the larger shoot mass. While bigger seedlings (e.g. more leaf area, stem length) are more sensitive to initial drought (Lopez-Iglesias et al., 2014; Oriens et al., 1999; Poorter & Markesteijn, 2008), as we observed here, this may not hold in older plants where larger root systems can access deeper, moister soil layers, particularly in field environments as opposed to pot-based experimental systems (Zwicke et al., 2015).

Only one of our water-use traits, transpiration rate, appeared to impact survival. Transpiration rate was weakly negatively correlated with survival ($r=-0.40$) and was one of the two traits, along with shoot mass, that predicted drought survival in our trait model. This

suggests that seedlings can resist drought by reducing transpiration at either the leaf level (lower E) or at the whole plant level (small size). Water-use efficiency aligned with high leaf nitrogen concentration, as predicted, but was not associated with drought survival. The relationship between WUE and plant performance in arid environments can vary significantly, influenced by factors such as the type of WUE metric (instantaneous versus time-integrated), drought strategies of selected species, environmental conditions, and season (e.g. Donovan et al., 2009; Ehleringer et al., 1992; Nicotra & Davidson, 2010). While WUE did not predict survival across the 22 species in our study, WUE was higher in grasses and perennial species and may have contributed to drought survival alongside other traits. Thus, WUE may contribute to a plant's ability to withstand drought, but not enough to predict survival.

In contrast to our predictions, species surviving longest with a finite amount of water did not have trait values aligned with the conservation gradient. With respect to above-ground conservation traits, leaf N and LMA only varied two-fold across species, which may not have been enough variation to influence performance outcomes under drought (Funk & Cornwell, 2013). Below-ground, perennial species displayed more robust roots (higher root tissue density, lower specific root length) than annual species, which did not survive as long as perennials under drought. However, root traits did not predict survival, possibly because root traits can combine in complex ways to influence water uptake (Freschet, Roumet, et al., 2021). The root 'collaboration' gradient emphasises that plants can effectively acquire resources whether thin-rooted (via soil exploration) or thick-rooted (via microbial symbioses). Both strategies can have trade-offs, for example thinner roots may be vulnerable to desiccation, while thicker roots may grow slowly and miss resource patches (Lopez-Iglesias et al., 2014; Ma et al., 2018; Poorter & Markesteijn, 2008). These complex trade-offs, along with the multidimensional nature of rooting strategies identified here (via both conservation and collaboration gradients, Figure 3) may explain the poor alignment between root traits and drought survival. While further research is needed to elucidate how root trait gradients link to performance and ecosystem functioning (Weemstra et al., 2016), this idea of complex trade-offs below-ground supports our expectation that species with high drought survival can fall anywhere along the collaboration gradient.

We focused on commonly used physiological and morphological traits that can influence growth and survival in seedlings; however, other traits are known to govern plant response to water availability. For example, several studies in California grassland have found that species with larger seeds are more robust to drought stress (Harrison & LaForgia, 2019; Larson et al., 2020); however, resources provided in large seeds may be more critical when drought occurs earlier in a plant's lifetime (after germination, but prior to full autotropism). Other studies have highlighted the importance of hydraulic traits such as turgor loss point, which has been linked with higher survival rates in dry years for graminoids (Stears et al., 2022). While turgor loss point correlates with some resource-use traits (e.g. root tissue density, leaf dry matter content, Stears et al., 2022), this is not

a general pattern across herbaceous species (Májeková et al., 2021). Future work should consider direct measurements of leaf hydraulics when exploring drought responses in herbaceous species, with attention placed on seedlings—whose small sizes are challenging to work with, but are also a critical indicator of species vulnerability to drought.

In our research, we employed mean trait values of species as indicators of drought response. This approach aligns with the broader objective of trait-based ecology, which is to leverage widely accessible trait data at population and species levels for deducing community and ecosystem functions across various scales (e.g. Funk et al., 2017). However, plant traits exhibit plasticity in response to water availability, enhancing their adaptability to drought conditions (Funk, Larson, & Ricks-Oddie, 2021; Heschel et al., 2002; Nicotra & Davidson, 2010). While examining trait plasticity in response to drought was beyond the remit of our study, we acknowledge that understanding this plasticity is valuable for more accurately predicting drought responses.

Finally, traits related to drought strategies may be determined to some degree by a species' evolutionary history. In addition to including a mix of annual and perennial species, many herbaceous communities contain a large fraction of grasses. The phylogenetic split between monocots and dicots resulted in some trait divergence between the groups. If traits display a phylogenetic signal, taxonomic identity may be useful in identifying drought response based on members of a community (Larson et al., 2020; Luong et al., 2021). Here, we found a strong evolutionary signal for survival under drought. Shoot mass and transpiration rate, the traits that best predicted survival, also showed evolutionary signal. Thus, while we observed many differences in the traits of broad functional groups (e.g. based on life history, growth form), studies must also consider finer patterns of evolutionary history to understand when and how species have adapted to drought.

5 | CONCLUSIONS

Our findings support the idea that multiple dimensions are required to capture trait variation within communities; consequently, a single axis of variation is unlikely to represent plant function comprehensively—even when including physiological and structural traits from all plant organs. An integrated framework of plant form and function, previously generated with global-scale data, applied surprisingly well to a relatively small group of herbaceous species from a semi-arid grassland system, although above-ground and below-ground traits associated with the resource conservation gradient were decoupled. The size gradient emerged as the most direct predictor of survival under drought, suggesting that this framework has the potential to capture plant drought response in application. Species traits have been associated with plant abundances across broad environmental gradients, and are easier to assess than direct performance or survival measures, especially given the expansion of online trait databases. If we can continue to

develop strong links between plant traits and drought response at finer scales, we will be in a better position to anticipate the impacts of a changing climate on vegetation.

AUTHOR CONTRIBUTIONS

Jennifer L. Funk and Julie E. Larson conceived and designed the experiments. Jennifer L. Funk, Julie E. Larson, Megan D. Blair, Monica A. Nguyen and Ben J. Rivera performed the experiments and/or analysed the data. Jennifer L. Funk, Julie E. Larson and Megan D. Blair wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to report.

DATA AVAILABILITY STATEMENT

Data and code are available in the following Zenodo archive: <https://doi.org/10.5281/zenodo.10388020> (Funk, 2023).

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SUPPORTING INFORMATION

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

Table S1. List of species used for the study, their abbreviations, growth form, and phenology.

Table S2. The six stages of leaf wilting.

Table S3. *p*-values from the analysis of variance examining effects of growth form and phenology on functional traits.

Table S4. Pearson correlations between each trait and PC axis.

Table S5. Phylogenetically-informed correlation coefficients and Pearson correlation coefficients among traits and plant survival under drought.

Table S6. Output from two mixed models predicting plant survival time under drought as a function of PC axes or traits.

Figure S1. Phylogenetic tree for study species and the distribution of aboveground traits across the tree.

Figure S2. Phylogenetic tree for study species and the distribution of belowground traits across the tree.

Figure S3. Phylogenetically-informed PCA.

Figure S4. Relationships among root diameter, specific root length, and root tissue density.

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