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(Article begins on next page)

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# Growth form and lifespan mediate the role of traits in short-term drought response: A global study on herbaceous species

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**Abstract**

Increased weather variability is expected to increase the frequency of extreme short-term drought events with detrimental effects on habitats globally. Plants have evolved stress tolerance strategies involving trade-offs in resource conservation, mycorrhizal collaboration, and plant size, yet how these strategies promote drought resistance across different groups of herbaceous plants is unknown. Leveraging 63 globally distributed sites from Drought-Net's International Drought Experiment, we identified traits linked to drought resistance in 661 populations of 421 species after one season of extreme drought. We assessed how nine traits, site precipitation, and drought severity affected percent cover changes across annuals, perennials, graminoids, and forbs. We examined interactions among traits and environmental factors influencing drought resistance. Traits from different gradients predicted drought response, particularly forbs utilized traits across conservation, collaboration, and size gradients, diverging from the traditional fast-slow trait paradigm. Trait interactions mediated drought response; root traits predicted performance only in concert with other traits. Environmental variables influenced trait effects on drought resistance, notably for annuals in less stressful sites suggesting drought-escape strategies in annuals may be advantageous only under mild stress. Our study highlights variability in traits predicting drought response across species groups, emphasizing species context, environmental stress, and trait selection in research and management.

## Introduction

Global climate shifts are causing increasingly variable weather patterns, characterized by drier conditions in some regions and more frequent, intense episodes of extreme precipitation in others[1,2]. Extreme short-term droughts are projected to increase in frequency and intensity, causing significant impacts on plant communities with consequences for ecological and social systems[3,4]. Plants have evolved a range of drought survival strategies, which are linked to morphological, physiological, and phenological traits, all contributing to performance and fitness[5]. Analyzing the effectiveness of these strategies in the face of extreme short-term drought conditions can provide a framework to better understand and predict plant responses to changing climate[6,7].

Trait-based approaches have the potential to predict responses to pulse dynamics[8] and biomass-altering disturbances, such as drought[9]. Trait frameworks can be useful for conceptualizing trade-offs among traits involved in these responses[10]. Weigelt et al.[11] proposed a novel framework which includes gradients related to resource conservation, mycorrhizal collaboration, and plant size that describe gradual linear changes between opposing ecological strategies. The conservation gradient is defined by the leaf[12] and root[13] economics spectra. One end of the gradient is comprised of 'fast' traits linked to resource acquisition and shorter lifespan, while the other end features 'slow' traits related to conserving resources and longer lifespans. Along the collaboration gradient, root traits of plants are characterized by a 'do it yourself' strategy versus an 'outsourcing to fungal partners' strategy for acquiring resources[14]. In the latter, trade-offs are between root diameter, which provides habitat for mycorrhizal fungal colonization, and mass-specific root length (or surface area) which facilitates nutrient foraging and acquisition via long, thin absorptive roots[14]. Lastly, there are size gradients associated with

plant vegetative height and rooting depth - taller plants compete better for light and deeper roots access water from deep soil[15], but both of these strategies require greater resource investment.

A range of phenotypic strategies will likely confer drought resistance. With respect to the resource conservation gradient, species with slow resource-return traits, such as thicker and denser leaves and roots, may help minimize water loss and increase drought survival[7,16]. Across the collaboration and plant size gradients, multiple traits can enhance water uptake including greater investment in root surface area[17,18], mycorrhizal associations to access water beyond root depletion zones, or 1st and 2nd order roots (or tap roots) in deep soils[7,19]. The gradients of conservation and collaboration are orthogonal to each other and to plant size. This suggests that plants may adopt a specific conservation strategy while varying their collaboration and size strategies, creating a multifaceted approach to drought adaptation[11]. In support of this idea, recent studies have demonstrated that plants combine traits in unexpected ways (e.g., acquisitive aboveground traits with conservative belowground traits[20]) to increase growth, survival, and fecundity[21,22] and that different combinations of traits optimize these performance metrics across environments[23,24].

We used a network of short-term extreme drought experiments (International Drought Experiment or IDE) broadly distributed across grasslands and shrublands (Fig. 1, Table S1) to address our first aim of determining which traits or combination(s) of traits are related to drought resistance for a diverse set of herbaceous plant species. We define drought resistance here as lower reductions in plant cover with drought. Based on plant economic theory, we hypothesized that traits aligned with the slow end of the resource conservation gradient would increase drought resistance[12]. While root traits are a recent addition to trait strategy frameworks, we hypothesized that belowground traits aligned with resource conservation (e.g., thicker, robust roots) would

more often be associated with increased drought resistance than aboveground traits[15,25]. Additionally, we posited that traits could combine in complex ways to achieve similar drought resistance, supporting alternative design theory[26,27]. We hypothesized that traits from different trade-off gradients or allocation strategies would interact such that the association of one trait on cover change was mediated by another trait. For example, mass-based leaf nitrogen content could interact with rooting depth where plants with higher drought resistance combine a 'slow' resource conservation strategy, lower leaf nitrogen, with a size gradient strategy, higher rooting depth. Lastly, we hypothesized that how traits are associated with cover change may differ with drought severity and with mean annual rainfall[28,29].

A second aim of this work was to explore how trait-performance relationships vary across species groups and elucidate strategies used for drought resistance. We hypothesized that species with different growth forms (e.g., graminoids, forbs) and lifespans (e.g., annuals, perennials) would respond differently to short-term drought, complicating the development of a global framework for drought response. For example, grasses may develop extensive fine roots for optimal water uptake in shallow soil layers, compared to more deeply rooted forbs[30,31], and these morphological differences may underlie the relatively larger negative effects of drought on grasses than forbs[32]. Annual and perennial species may respond to short-term drought using different strategies to enhance performance. Perennial species are generally expected to adopt a drought-resistant strategy corresponding to the slow end of the conservation gradient, but this group appears to employ a variety of strategies in response to drought[33,34]. By contrast, annual species may employ a drought-escape strategy characterized by traits associated with the fast end of the conservation gradient designed to maximize growth rate and expedite flowering and reproduction[5,35].

## Results

*Traits from different gradients predict drought response in forbs*

Leaf N, height, and root tissue density (RTD) were significant predictors of cover change, however these relationships were largely restricted to forbs (Figs. 2, S1-S9). Specifically, higher drought resistance (lower reductions in plant cover with drought) in forbs was positively associated with height, leaf N (particularly perennial forbs), and RTD. The positive association between leaf N and drought resistance was also observed when all plant groups were pooled (Fig. 2).

*Interactions between traits on different gradients mediate short-term drought response*

We found evidence that traits aligned with different trade-off gradients interact to drive species' drought resistance (Figure S10). Taller plants with higher leaf N showed higher drought resistance in perennials and the all-species group (Fig. 3), representing an interaction between the plant size and resource conservation gradients. Additionally, plants with higher belowground biomass allocation (RMF) and higher leaf N were more drought resistant in annuals and the all-species group (Fig. 3). In contrast, plants with lower RMF showed greater drought resistance if they diluted their leaf N. Finally, we found interactions between the resource conservation and collaboration gradients, where forbs could achieve higher drought resistance with a conservative strategy of low SRL and high RTD or an acquisitive strategy of high SRL and low RTD (Figs. 3, S10).

*Environmental factors mediate the effects of some traits on drought resistance*

Overall, drought severity index and mean annual precipitation were weak predictors of drought resistance (Figs S1-S9). Drought resistance was higher for annuals in sites with higher MAP (Figs. 2, S1). However, we found that environmental variables mediated the effects of traits on drought resistances, particularly in less stressful sites. Drought resistance was higher for plants in the annual, forb, and all-species groups with higher leaf N in sites that experienced a less severe drought (higher DSI, Fig. 4). Similarly, taller annuals were more drought resistant in sites with higher mean annual precipitation (Fig. 4)

## Discussion

Few studies have examined how trait frameworks predict drought resistance while taking a whole-plant perspective across such a broad range of species and sites[9]. Our study demonstrates that forbs employ diverse drought strategies, combining traits from conservation, collaboration, and size gradients[11] in ways that challenge the traditional 'fast-slow' spectrum, though these patterns vary with environmental context. Leaf N concentration and height, two acquisitive (fast) traits, were related to drought resistance in forbs, which is consistent with a drought-escape strategy[5,35]. This suggests a benefit to fast-growing species that can escape drought by completing their life cycle in a short time, thus speeding up their phenology. High leaf N can also enhance water-use efficiency as greater investment in ribulose-1,5-bisphosphate carboxylase/oxygenase (rubisco) increases carboxylation efficiency[36]. Drought resistant forbs, however, also displayed high root tissue density, a conservative (slow) trait that may characterize robust taproots particularly in perennial forbs, suggesting these species leverage traits from both ends of the conservation gradient. These findings highlight that the capacity to deploy contrasting short-term strategies - coupling acquisitive traits for rapid growth with conservative

151 root investments - may stabilize ecosystem function during intermittent drought[37], but prolonged
152 drought could force shifts toward either extreme, decoupling trait coordination patterns observed
153 under transient stress[38,39].

154 Taller forbs were less negatively impacted by short-term drought, which contradicts
155 studies that report an advantage of small size under drought and in arid environments[37,40-43], as
156 lower leaf area leads to less water transpired. Taller forbs may resist drought by possessing
157 deeper roots, which is supported by positive correlations between height and rooting depth,
158 particularly in annual forbs ($r = 0.22$, Table S8). However, rooting depth was not a significant
159 predictor of percent cover change in any plant group (Figs. 2, S1). Our inability to detect
160 significant effects of rooting depth on drought response may stem from difficulties in accurately
161 measuring this trait, but the ability of this trait to predict how species will respond to drought has
162 already been called into question. For example, using simulations, Nippert and Holdo[44] showed
163 that the distribution, functional plasticity, and hydraulic conductivity of roots all influence
164 aboveground biomass such that shifts in root distribution to surface soils without changes in
165 rooting depth may outweigh the importance of having deeper roots.

166 Given the central role of roots in water uptake, we hypothesized that root traits would be
167 strong predictors of drought response. However, our findings indicate that root traits generally
168 predicted performance only in concert with other traits. Being taller was particularly
169 advantageous in combination with high leaf N, and the benefits of high leaf N were amplified
170 when more biomass was allocated belowground. Root tissue density, which enhanced drought
171 resistance in forbs, mediated the effect of specific root length, such that species could achieve
172 resistance through either high SRL and low RTD (thinner, less dense roots) or the opposite
173 strategy. This supports the idea that multiple strategies can yield similar performance

outcomes,[23,24] and may explain discrepancies across studies that focus on single root traits or report weak relationships between root traits and performance[9,37,45,46]. Alternatively, root traits may play a larger role in long-term drought responses, rather than short-term extreme drought as analyzed here. While many of our trait values were sourced from site PIs or trait databases, several root traits (e.g., N, RMF) are underrepresented in databases and were estimated through imputation. Databases and imputation do not capture the plasticity that species may exhibit in response to variation in water availability in the field[47]. Incorporating trait plasticity in future studies, in addition to better representation of sites from Africa, Asia, and South America, will be crucial for understanding its impacts on resource acquisition, drought resistance, and the predictive power of trait-based approaches[41,48].

Our results demonstrate that the relationship between plant traits and drought resistance is highly context-dependent, with environmental conditions altering which strategies confer resilience. Specifically, the positive effect of leaf N on drought resistance in annuals and forbs was evident only under mild stress (low DSI), and taller annuals were more drought resilient only at wetter sites. These results suggest that the drought-escape strategy characteristic of many annuals is advantageous primarily under moderate stress, while at drier sites or under severe drought, more conservative traits likely play a greater role in drought resistance. Traits not examined here, such as osmotic potential, root distribution, or root hair abundance, may become increasingly important as stress intensifies[41,49]. Our finding that complex interactions among traits and environmental variables shape drought resistance underscores the context dependency of trait-performance relationships, echoing and extending recent work in this area[23,24,50].

Trait–performance relationships were generally weaker or absent in graminoids and perennials, which may reflect the influence of additional factors such as stored reserves, clonal

growth, or unmeasured traits buffering their short-term drought responses[51]. The performance of perennial species in particular may require longer-term observation to capture how storage and economic traits interact to mitigate drought effects. In contrast, annuals exhibited stronger links between traits and drought response, possibly because their fitness is more directly tied to immediate environmental conditions[52]. While our study did not incorporate intraspecific trait variation, local-scale variation and plastic responses may contribute to the variability observed in graminoid and perennial groups[38,41]. Overall, these findings suggest that growth form and lifespan are important considerations when interpreting drought sensitivity, and that integrating these factors will be critical for improving predictions of species and community responses to increasing drought stress.

Our study, the first to leverage a globally distributed network of sites to identify how traits predict short-term drought response across a range of habitats and plant species types, demonstrates that traits can predict plant performance in some plant species groups and that trait-performance relationships vary across environments and with drought severity. There is a growing consensus that the choice of trait matters in deciphering species growth strategies[53,54], and our results suggest further context dependency in how trait frameworks can be applied to understand ecological processes. While individual traits contributed to drought resistance, our findings also highlight that interactions among key traits can further enhance plant performance under stress. Although this analysis does not delve into the mechanisms by which abiotic and biotic factors drive variation in drought resistance across plots within sites, it opens up promising avenues for future research. Within-site analyses provide an exciting opportunity to explore how microclimate, soil texture, drought history, and functional composition of neighboring plants, for example, influence drought performance on community-level scales. In order to fully capture the

variability of plant trait responses to drought, combined understanding from detailed local-scale studies and globally replicated experiments is pivotal.

## Methods

*Experimental design*

We measured changes in plant species cover in response to experimentally-imposed, short-term drought in Drought-Net's International Drought Experiment (IDE). The IDE is a coordinated, distributed experiment, where precipitation inputs are reduced passively across a range of grassland and shrubland sites in order to generate proportionally similar levels of drought severity[55]. Precipitation reductions were determined individually for each site in order to impose statistically extreme levels (comparable to a 1-in-100 year drought at each site) based on historical precipitation records from the site or by using the Terrestrial Precipitation Analysis Tool[56]. Precipitation levels were reduced with passive rain-out shelters (with v-shaped or corrugated roofs), which work especially well in ecosystems with small-statured plants[57]. Cover was estimated using the Daubenmire[58] method for each species separately in each plot at each site. Cover could be greater than 100% for a plot and the original cover estimates were used to calculate cover change. All sites participating in the IDE are required to use the same Drought-Net experimental protocols (https://droughtnet.weebly.com).

While there are over 140 sites participating in the IDE, we chose a subset of the sites (n = 63 sites; Fig. 1; Table S1) owing to a combination of availability of pre- and post-treatment plant cover data, complete identification of plant species, and trait data. Like most grasslands and shrublands, many of these sites (62%) have a history of management (Table S1). Only ten of these sites have active management: mowing (4), burning (4), and grazing (1). We chose not to

include plant cover or trait data for woody species present at the sites. Cover change of woody species can be difficult to measure and their traits vary greatly across different life stages[59,60]; we could not be certain the life stage associated with traits from trait databases[61,62]. In our dataset that included woody species, 53% of populations excluded by outlier trait analysis were woody populations suggesting more extreme trait values for woody species. Further, due to their larger size and stored energy, woody species may be buffered from drought-induced effects in a single year[63, 64].

All sites included in this study experienced approximately one year of experimental drought treatment and had both pre- and post-drought species cover data available. Mean annual precipitation (MAP) was reported by site PIs for each of their sites[55]. The magnitude of drought experienced by each site differed, so we calculated an index to represent the actual severity of drought imposed at each site during the experimental period. Following Smith et al.[55], we calculated the amount of precipitation each site received in the year prior to plant cover collection, corrected based on the number of days drought shelters were in place. We then multiplied this value by the site-reported percent reduction in precipitation imposed by the drought treatment to estimate the total amount of precipitation received at each site ($Precipitation_{DROUGHT}$). We then compared the estimated precipitation received to MAP and calculated the deviation from this number: Drought Severity Index (DSI) = ($Precipitation_{DROUGHT}$ – MAP)/MAP[55]. More negative values of DSI correspond to more severe drought (Table S1).

*Cover change quantification*

We used a BACI (before, after, control, impact) design to determine the relative percent change in cover for each species at each site following ~ one year of drought[65]. We quantified

the change in percent cover due to drought effects by subtracting the change in percent cover within control plots from the change in cover in droughted plots [($Drought_{AFTER}$ – $Drought_{BEFORE}$) – ($Control_{AFTER}$ – $Control_{BEFORE}$)][66]. If a population was absent at one time point, before or after the drought, but present at the other, its cover was set at zero when absent. Input percent cover values were means of each species across all replicated plots within each site. Outlier values of cover change (± 3 SD from mean) were removed to prevent their skew on model interpretation (2.5% of values). Final percent cover change values represent the effects of drought on droughted plots relative to control plots. Positive values indicate increased percent cover in drought compared to control plots whereas negative values indicate decreased percent cover in drought compared to control plots. Cover change varied between -21% and 21% across populations (Table S2).

*Functional traits*

Nine traits were included in this study, namely height, mass-based leaf nitrogen content (Leaf N), mass-based root nitrogen content (Root N), root mass fraction (RMF), rooting depth, mean fine root diameter, fine root tissue density (RTD), specific leaf area (SLA), and fine specific root length (SRL) (Table S2). Mean root diameter, RTD, and SRL values were from fine root samples, those less than or equal to two mm in diameter. Values of root N came from total root samples. Different data sources often report different measurements of SLA, with petiole included, unknown status of petiole inclusion, or petiole excluded. We included any observation regardless of measurement type to maximize data coverage. If multiple types of measurements were available, we took the average. The traits were selected in order to balance above- and

288 belowground traits, organ-level and biomass allocation traits, and to capture integrated whole-
289 plant strategies and trait trade-offs[11].

290 Trait data were gathered for species in a stepwise manner (Table S3). First, IDE principal
291 investigators were queried for trait data that corresponded to species in their local site;
292 measurements made according to[67]. Second, trait databases were queried including TRY[68],
293 AusTraits[69], Global Root Traits (GRooT)[70], and observed values from CoRRE[71]. TRY, GRooT
294 and CoRRE are global databases while AusTraits only includes data for Australian plant species.
295 CoRRE is focused on grassland species and combines data from across other databases including
296 TRY, BIEN[72], AusTraits, TiP Leaf[73], and the China Plant Trait Database[74]. From AusTraits and
297 GRooT, we used database supplied mean values for each species. For TRY and CoRRE, we
298 calculated mean values when there were multiple database submissions for a given trait of a
299 species. More specifically for TRY, we first calculated the mean within datasets and then within
300 species. Lastly, we conducted comprehensive literature searches to populate remaining missing
301 trait data for species when possible (Table S3). We only included trait data for species from
302 studies without experimental manipulations and those coming from mature individuals, omitting
303 traits from seedlings.

304 Missing trait values were imputed using Bayesian hierarchical probabilistic matrix
305 factorization (BHPMF[75]). This methodology imputes trait values based on taxonomic hierarchy
306 of the species and correlation structure of the traits. Prior to imputation, all traits were $\log_{10}$- and
307 z-transformed, then 50 imputations were performed, and the mean of these imputations was
308 taken[76]. Imputation was performed using the default settings of the *GapFilling* function in the
309 BHPMF[77] package in R programming language[78]. Cross-validation was used during imputation
310 such that observed data was randomly removed and imputed values were created for all

311 populations, including those with observed measurements. This methodology allowed for
312 estimation of the quality of the imputed values; observed values were regressed with their
313 imputed values and $R^2$ values were evaluated. Imputed trait values were of high quality with $R^2$
314 values ranging from 0.89 to 0.99 (Figure S12).
315 Finally, we removed outlier trait values (± 3 SD from mean). Overall few trait data were
316 removed, with 2.5% of rooting depth values being the highest percentage of data removed for
317 any trait. If a species had observed cover data at multiple IDE study sites, we assigned the same
318 trait values for all its occurrences. The R package Taxonstand[79] was used to verify species'
319 names were used consistently. Interspecific trait variation differed across traits, with some traits
320 (leaf N, root N, SLA, SRL) showing wider ranges across species than others (height, rooting
321 depth, RMF, RTD, mean root diameter, Table S2).
322 We evaluated the effects of the nine traits, site MAP and DSI, and selected trait-trait and
323 trait-environment interactions on percent cover change for 661 populations, from 421 species,
324 across 63 IDE sites. We were also interested in understanding how these effects differed
325 depending on lifespan (annuals: n = 178; perennials: n = 462), and growth form (graminoids: n =
326 251; forbs n = 410). Thus, we analyzed responses for nine plant groups: Annuals, Perennials,
327 Graminoids, Forbs, Annual Forbs, Perennial Graminids, Perennial Forbs, and All species (Tables
328 S2, S4-S7). The annual group consisted of grasses (n = 44), forbs (n = 124), and legumes (n =
329 10) while the perennial group included grasses (n = 174), forbs (n = 224), legumes (n = 33), and
330 graminoids (n = 31; sedges or rushes). Populations classified as biennial (10) or uncertain
331 lifespan (11) were excluded from strictly annual or perennial plant groups. Analysis of the
332 annual graminoids (n = 50) was not completed due to limited sample size.
333

*Analyses*

We fit linear mixed-effects models using a Bayesian approach to each of the eight data sets to analyze trait effects on changes in percent cover between control and droughted plots of widely distributed sites. Additionally, we fit models to each data set to evaluate how interactions of traits associated with different trade-off gradients and allocation strategies are related to drought resistance, specifically, interactions of leaf N versus height and rooting depth (conservation versus size[11,12]), leaf N versus RMF (conservation versus allocation[11,12,17]), and RTD and SRL (conservation versus collaboration[11,13,14]). We also wanted to understand how the association of these traits with drought resistance was dependent on the environment. To do so, we fit models where the trait was interacting with MAP and DSI, separate models for leaf N, height, rooting depth, RMF, RTD, and SRL. All models were fitted using the brms package[80] with traits or trait combination, MAP, and DSI as fixed effects or trait-environment interactions as fixed effects along with site and species as random effects. All predictors were centered and scaled prior to analysis. Fixed effects were given diffuse normal priors for slopes and default Student-t priors for intercepts; random effects were also given default Student-t priors. For each model, we ran four independent chains with random initial values for 2,000 iterations and a warm-up period of 1,000 iterations. All parameters were assessed for convergence (Rhat = 1) and were considered significant if their 95% credible interval did not overlap zero. For each of the plant groups, we checked whether predictor variables were correlated with all correlations between -0.48 and 0.39 (Table S8).

**Data Availability**

All data are available on GitHub: https://github.com/sjworthy/IDE.Traits. A Zenodo doi will be obtained for the GitHub material upon manuscript acceptance.

**Code Availability**

All code is available on GitHub: https://github.com/sjworthy/IDE.Traits. A Zenodo doi will be obtained for the GitHub material upon manuscript acceptance.

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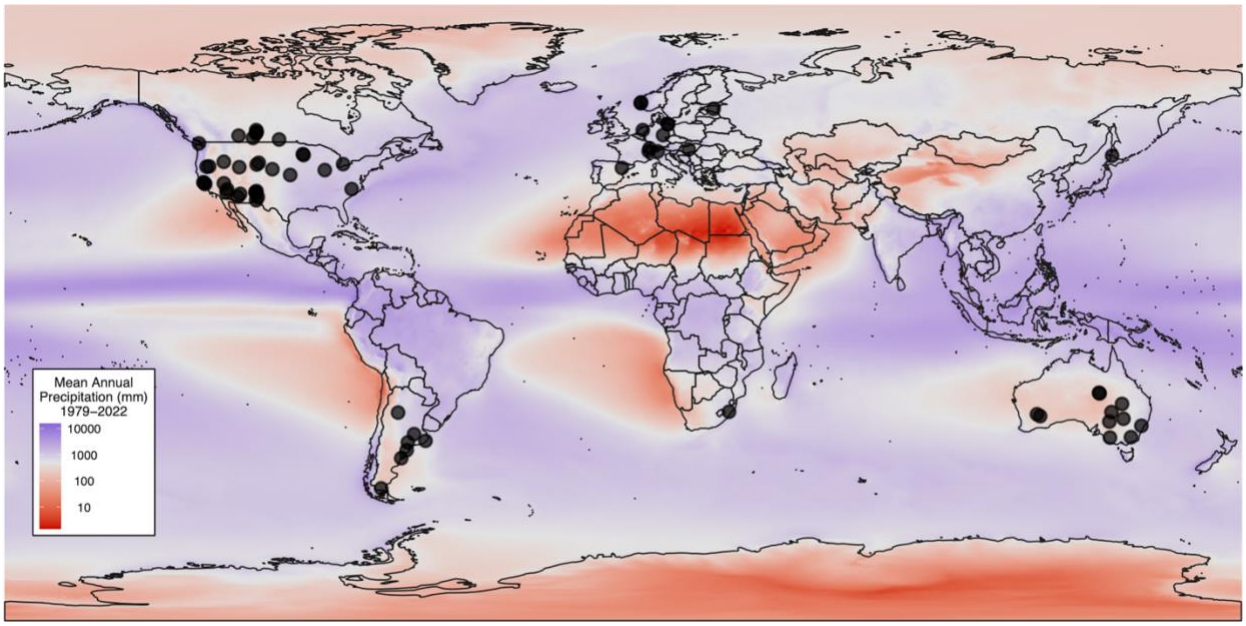
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572 **Figure 1**. Global distribution of the 63 study sites (dots) and mean annual precipitation (mm)

573 from 1979 to 2022 at 0.25° resolution[81,82].




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**Figure 2.** Relationships where traits or environmental variables had a significant effect on percent cover change. Higher drought resistance was associated with higher leaf N when all plant groups were pooled and for forbs. Additionally, taller forbs or those with higher root tissue density were associated with higher drought resistance. Annuals from sites with higher mean annual precipitation also had higher drought resistance. Trend lines represent conditional effects of the trait or environmental variable, colored envelopes represent 95% credible intervals, and opaque gray points are observed data points where darker points indicate overlap among points. Values on the x-axes are back-transformed. $R^2$ values representing the percent of variance in percent cover change explained by the full model are provided for each plant group.

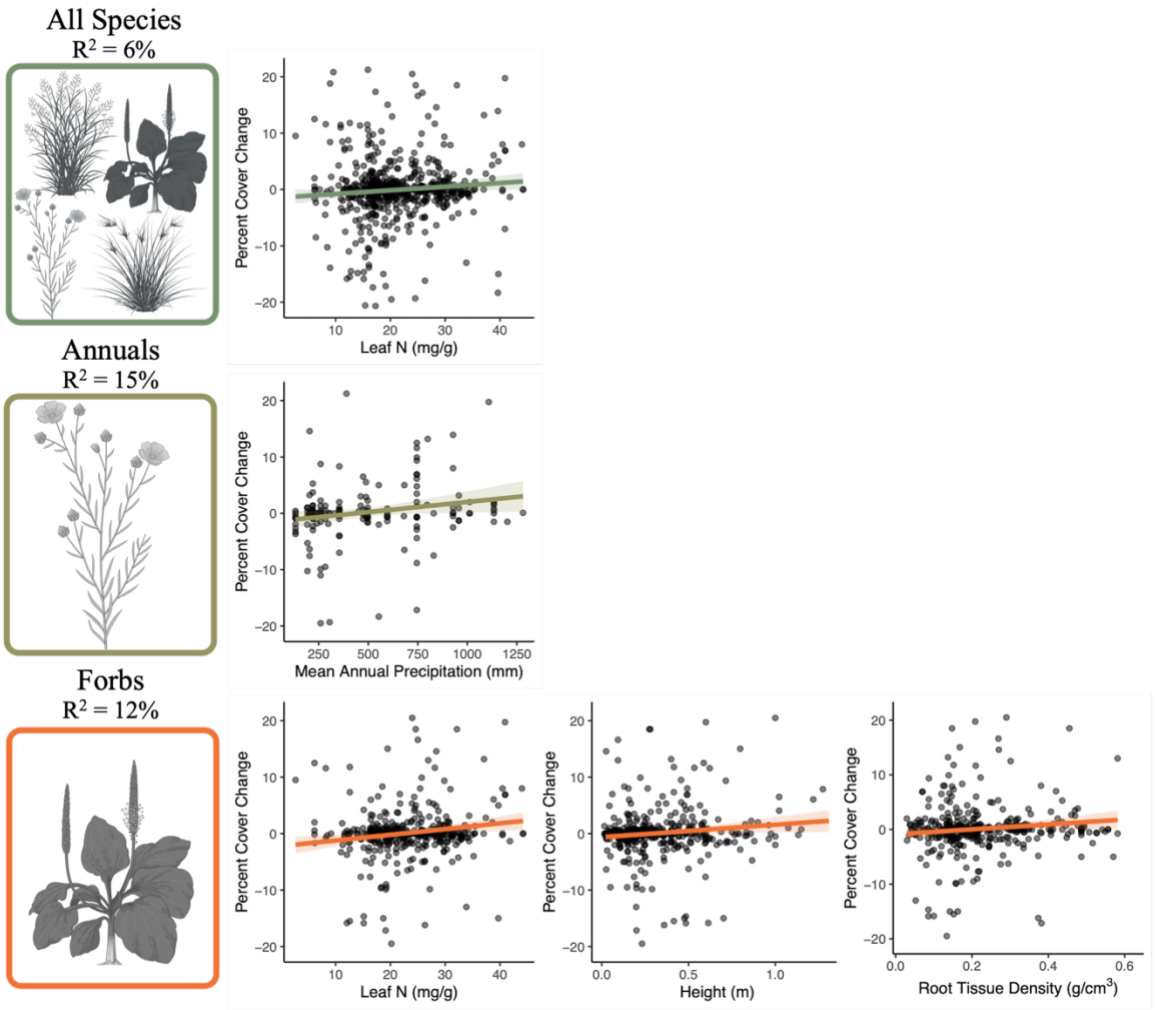
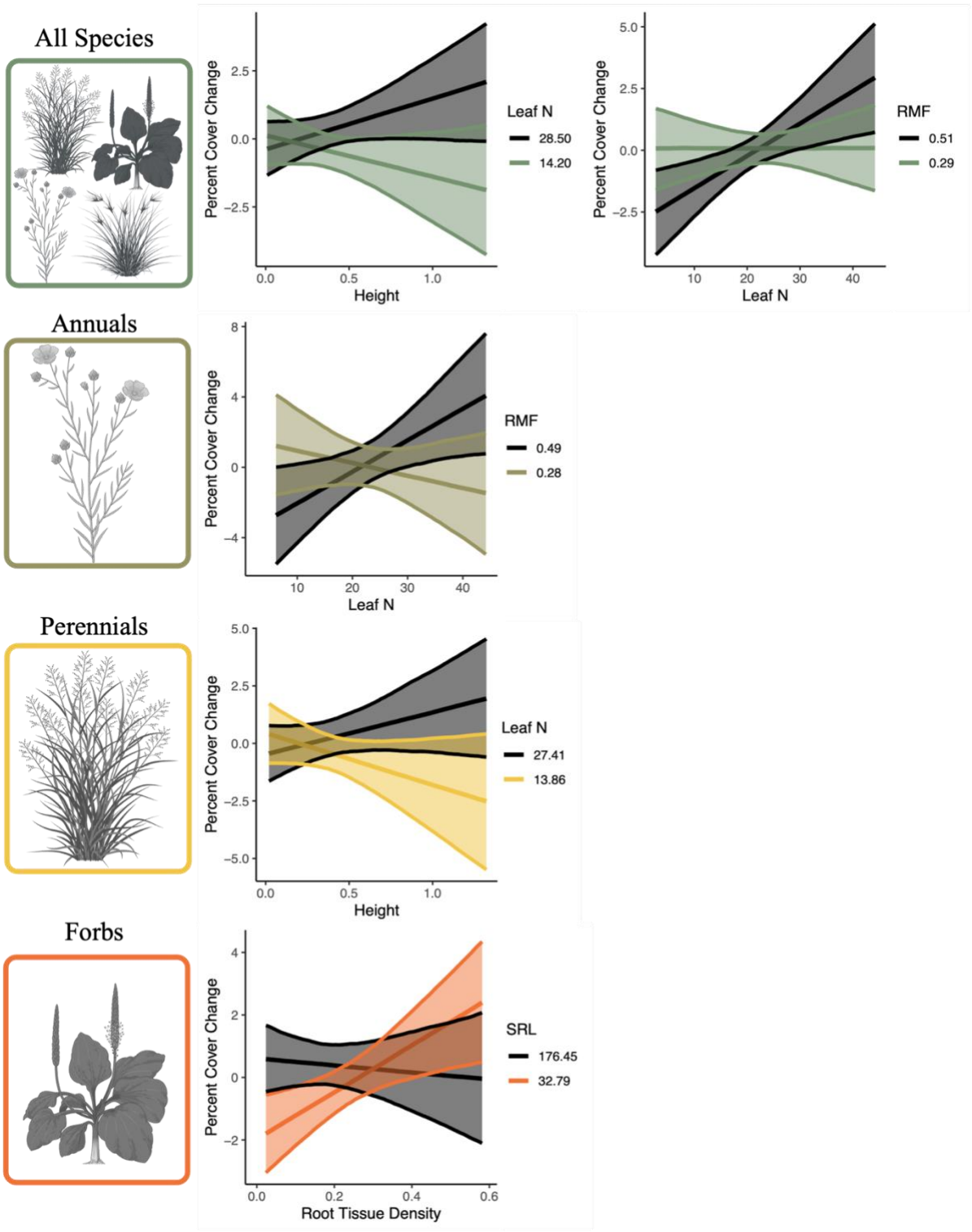


**Figure 3.** Interaction plots displaying the predicted effects of significant two-way interactions between traits. Two significant interactions were found when all plant groups were pooled: height (m) × leaf N (mg $g^{-1}$, $R^2$ = 5%) and leaf N (mg $g^{-1}$) × root mass fraction (RMF, g $g^{-1}$, $R^2$ = 5%). The interaction between leaf N and RMF ($R^2$ = 13%) was also significant for annuals while the interaction between height and leaf N ($R^2$ = 6%) was also significant for perennials. For forbs, root tissue density (g $cm^{-3}$) significantly interacted with specific root length (SRL, m $g^{-1}$) to effect percent cover change ($R^2$ = 8%). Trend lines represent relationships between percent cover change and the x-axis trait at minimum (colored line) and maximum (black line) values of the other trait; colored envelopes represent 95% credible intervals. Values of the two traits are back-transformed.


All Species
Percent Cover Change
Height
Leaf N
28.50
14.20
Leaf N
RMF
0.51
0.29
Annuals
RMF
0.49
0.28
Perennials
Leaf N
27.41
13.86
Forbs
SRL
176.45
32.79
Root Tissue Density

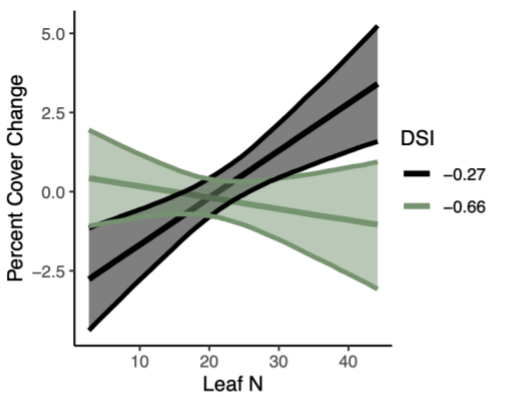
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**Figure 4.** Interaction plots displaying the predicted effects of significant two-way interactions between traits and the environmental variables drought severity index (DSI) and mean annual precipitation (MAP). All species ($R^2$ = 6%), annual ($R^2$ = 17%), and forb ($R^2$ = 11%) plant groups had a significant interaction between leaf N (mg $g^{-1}$) and DSI. More negative values of DSI correspond to more severe drought. There was also a significant interaction between height (m) and MAP (mm) for the annual species group ($R^2$ = 12%). Trend lines represent relationships between percent cover change and the x-axis trait at minimum (colored line) and maximum (black line) values of the environmental variable; colored envelopes represent 95% credible intervals. Values of the trait and environmental variables are back-transformed.

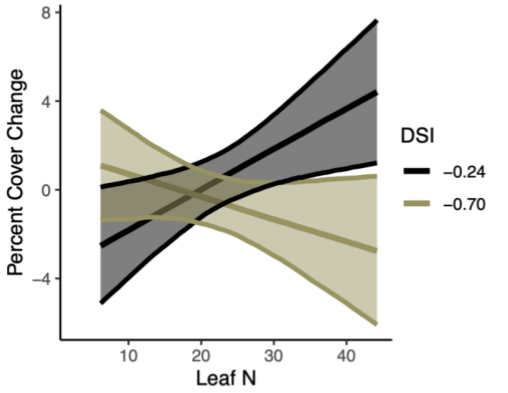
All Species

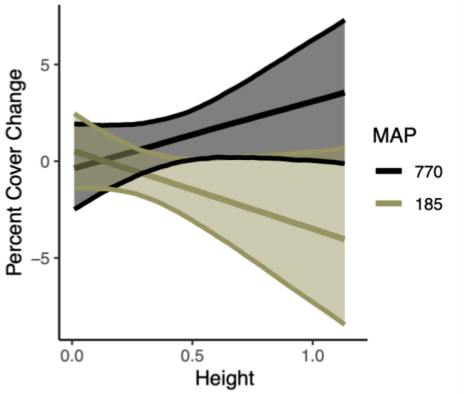





Annuals

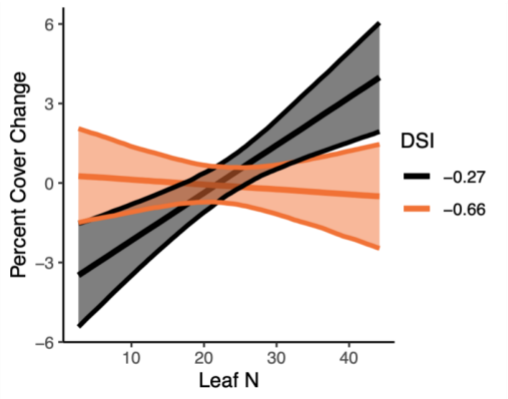





Forbs






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