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Rooting depth and xylem vulnerability are independent woody plant traits jointly selected by aridity, seasonality, and water table depth

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Summary

- Evolutionary radiations of woody taxa within arid environments were made possible by multiple trait innovations including deep roots and embolism-resistant xylem, but little is known about how these traits have coevolved across the phylogeny of woody plants or how they jointly influence the distribution of species.
- We synthesized global trait and vegetation plot datasets to examine how rooting depth and xylem vulnerability across 188 woody plant species interact with aridity, precipitation seasonality, and water table depth to influence species occurrence probabilities across all biomes.
- Here we show that xylem resistance to embolism and rooting depth are independent woody plant traits that do not exhibit a trade-off. Resistant xylem and deep roots increase occurrence probabilties in arid, seasonal climates over deep water tables. Resistant xylem and shallow roots increase occurrence probabilities in arid, non-seasonal climates over deep water tables. Vulnerable xylem and deep roots increase occurrence probabilities in arid, non-seasonal climates over shallow water tables. Vulnerable xylem and shallow roots increase occurrence probabilities in humid climates.
- Traits related to water uptake and transport explain biogeographic-scale species occurrences, suggesting that responses of deeply rooted vegetation may be buffered if evaporative demand changes faster than water table depth under climate change.

Keywords: cavitation, drought avoider, drought resistant, embolism, species distribution modeling, water availability

‘*Species that show deviations from statistical correlations (and there are always many such species) may tell us more about the adaptive value of particular characteristics than species that fit the correlation*.’ (Sherwin Carlquist, 1975, p. 1)

Introduction

Hotter droughts are expected to become more frequent and severe under most climate change scenarios (Spinoni *et al.*, 2018; Hammond *et al.*, 2022) and they have already resulted in widespread tree mortality (Bauman *et al.*, 2022; Hartmann *et al.*, 2022; McDowell *et al.*, 2022). Understanding which plant species are winners and losers under scenarios of decreasing water availability is critical for improving predictions of vegetation dynamics (Hammond *et al.*, 2019) and ecosystem restoration success (Laughlin *et al.*, 2017). Rooting depth and xylem vulnerability to drought-induced embolism are strongly linked to how woody plant species respond to moisture availability (Aubin *et al.*, 2016; Volaire, 2018) because the physiological link between water uptake and xylem conductance is vital to maintaining photosynthesis in arid climates and during dry seasons. However, little is known about how these traits have coevolved within woody taxa, nor do we know the joint effects of these traits on species distributions and potential responses to global change.

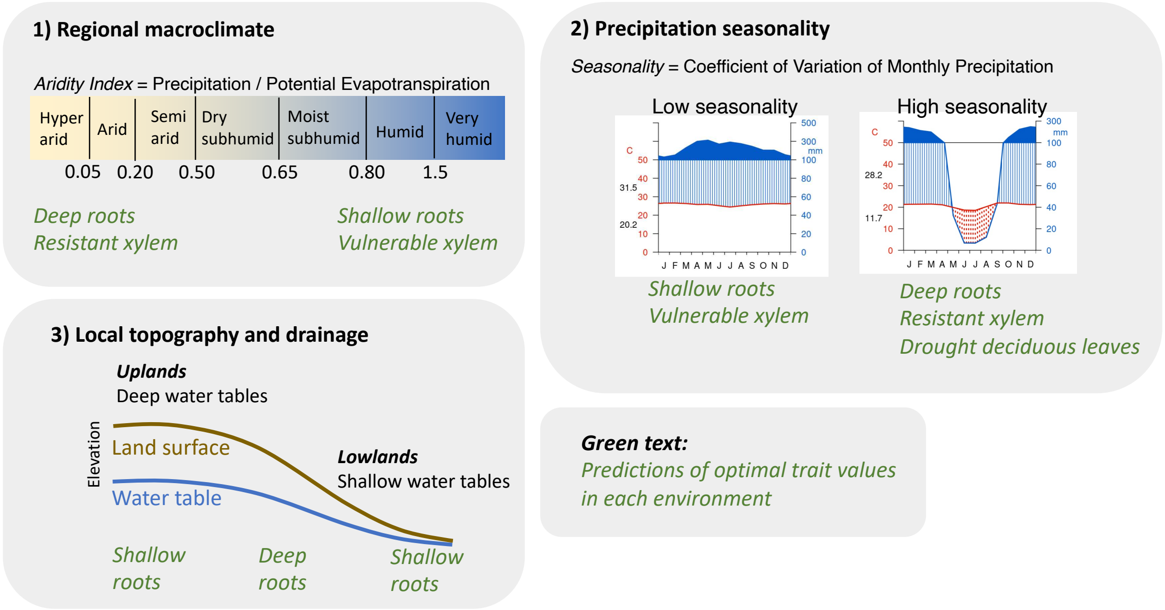
Survival in water-limited landscapes can be achieved by resisting, avoiding, or escaping dehydration caused by low soil water potentials (May & Milthorpe, 1962; Fischer & Maurer, 1978; Levitt, 1980; Volaire, 2018). First, drought resistance (also called drought tolerance) is achieved by constructing xylem that can resist embolism formation and maintain water conductance to enable CO_2 uptake even under extreme negative xylem pressure. Woody plants vary widely in their vulnerability to embolism (Hacke *et al.*, 2001; Maherali *et al.*, 2004; Choat *et al.*, 2012), which can be quantified by P_{50}, the xylem pressure (MPa) at which xylem conductance is reduced to 50% of its maximum. Species with lower P_{50} values (i.e., more negative values) are more resistant to embolism. Second, drought avoidance can be achieved by constructing root systems that access deeper soil water in the unsaturated vadose zone or directly from the water table in the saturated zone (Loheide *et al.*, 2005; Ryel *et al.*, 2008). Maximum rooting depth varies widely among woody plants (Canadell *et al.*, 1996; Jackson *et al.*, 1996). Deep root systems evolved for a variety of reasons, including anchorage, support, and increasing the available soil volume, but here we explore its vital role in water uptake. Shallow-rooted species rely on rainfall directly, whereas deep-rooted species can access water from deeper and older sources of water (Miguez-Macho & Fan, 2021). Both phreatophytic species that tap into water tables and deeply-rooted xerophytic plants that access vadose zone soil water can avoid the drought-induced reductions in soil water potential near the soil surface (Ryel *et al.*, 2008; Miguez-Macho & Fan, 2021). In arid climates, species that develop only shallow roots confront drought directly and must be able to resist embolism formation. If "roots grow only as deeply as needed" (Schenk & Jackson, 2002, p. 481), then in humid climates plants should grow shallow roots, and may even need to restrict their roots to the shallow oxygenated zone to prevent anoxia (Jackson *et al.*, 1996; Fan *et al.*, 2017; Tumber-Dávila *et al.*, 2022). Third, drought escape can be achieved by completing a short life cycle during the wet growing season or by deciduous leaf senescence in the dry season.

The large carbon investment into growth and maintenance of deep roots must be offset by carbon gains made possible by having such deep roots, otherwise the strategy would be unlikely to have evolved (Seyfried *et al.*, 2005). The construction costs of deep roots could possibly be offset by lower stem xylem construction costs, and evidence for a trade-off between rooting depth and xylem resistance to embolism was demonstrated across 12 species in a humid tropical forest, where shallow-rooted species were more tolerant of low water potentials (Brum *et al.*, 2019). However, the relationship between rooting depth and xylem vulnerability across global-scale climatic gradients has never been rigorously quantified. There are well-known examples of deep-rooted species in arid climates that also exhibit remarkably resistant stem xylem (Jackson *et al.*, 2000; Seyfried *et al.*, 2005), suggesting that the carbon costs of constructing both deep roots and resistant xylem are offset by the carbon gains that are achieved by simultaneously avoiding and resisting dehydration.

Rooting depth and xylem vulnerability may jointly influence species distributions along gradients of water availability in complex ways (Fig. 1A). Water limitation in plants is affected by the regional macroclimate, precipitation seasonality, and local topography and drainage gradients (Schwinning & Ehleringer, 2001; Fan *et al.*, 2017; Grossiord *et al.*, 2020). Climatic aridity is defined by both the total precipitation relative to potential evapotranspiration, as well as the occurrence of dry seasons during the year. From a hydrological perspective, water from ‘uplands’ (defined as well-drained topographic positions independent of elevation above sea level) flows into local topographic depressions creating shallow water tables in ‘lowlands’ (defined as poorly drained topographic depressions independent of elevation above sea level) (Fig. 1A) (Nobre *et al.*, 2011; Fan *et al.*, 2017). Water table depth is largely independent of regional climate because it is primarily under hydrologic control (Sousa *et al.*, 2022), and plant species responses to regional drought may depend on water table depth (Sousa *et al.*, 2020). For example, phreatophytic plants growing in arid riparian areas experience severe atmospheric vapor pressure deficits yet have ample access to soil water. Conversely, plants growing in coarse, shallow, or excessively drained soils within humid regions will experience local soil water deficits despite receiving high amounts of precipitation. In previous studies, species with low P_{50} were associated with arid regional climates (Larter *et al.*, 2017; Laughlin *et al.*, 2020a) and upland topographical positions (Oliveira *et al.*, 2019). Plants with shallow roots tend to occur in humid climates and waterlogged soil, whereas both shallow and deep-rooted species occur in well-drained soil in arid climates (Schenk & Jackson, 2005; Fan *et al.*, 2017). Determining the joint response of both traits to gradients of regional aridity, seasonality, and local water table depth will improve our understanding of vegetation response to drought.

In this paper, we combined species-level trait data with two macroclimatic gradients and one local gradient in water availability and asked the following two research questions: (1) Are P_{50} and maximum rooting depth correlated across the phylogeny of woody plants? and (2) Are species occurrences along regional aridity, seasonality, and local water table depth gradients jointly explained by species P_{50} and maximum rooting depth? We demonstrate that there is no evidence for a trade-off between drought resistance and avoidance and that each combination of xylem vulnerability and rooting depth values differentially optimizes occurrence probabilities along multiple gradients of water availability.

(A) Three drivers of water limitation



(B) Geographic distribution of plots

(C) Whittaker biome distribution of plots

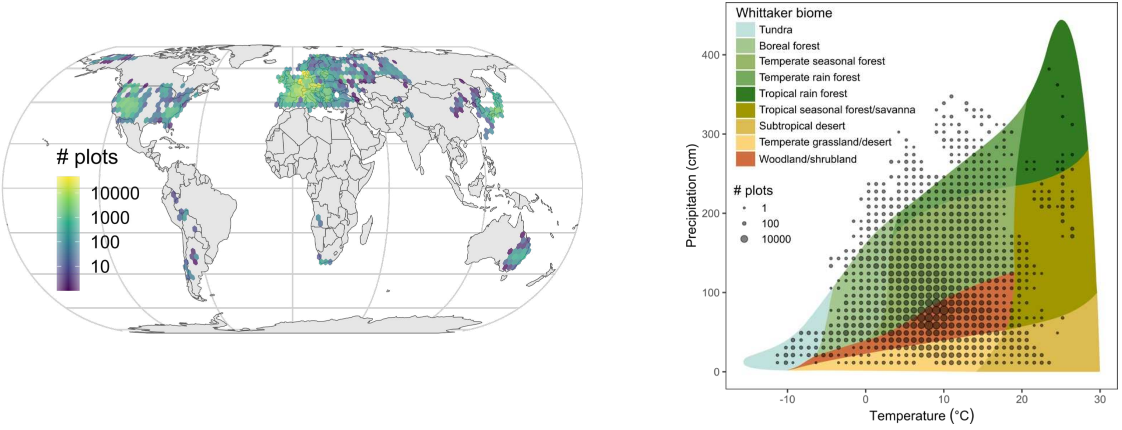


Figure 1. (A) Gradients of regional aridity (macroclimate), precipitation seasonality, and local water table depth drive variation of water limitation in plants. Green text reports predictions of optimal trait values along each environmental gradient. Note rooting depth is predicted to be highest at intemediate water table depth (Fan et al. 2017) (B) Biogeographic distribution of vegetation plots from the sPlot 3.0 database around the planet illustrated as density of plots per hexagonal grid cell. (C) Bioclimatic distribution of vegetation plots within Whittaker biome defined by mean annual temperature and total annual precipitation.

Material and Methods

Dataset compilation

We combined the Xylem Functional Traits (XFT) database (Choat *et al.*, 2012) with recently published data to quantify average P_{50} trait data at the species level (Table S1). We discarded vulnerability curves that were non-sigmoidal in shape or were generated using the air-injection method (Cochard *et al.*, 2013). We merged this P_{50} dataset with the Root Systems of Individual Plants (RSIP) database based on species (Tumber-Dávila *et al.*, 2022). We calculated maximum rooting depth for each species as the absolute maximum rooting depth recorded for that species in the database. This estimates the potential rooting depth of a species and is analogous to maximum height, another size-dependent trait and key indicator of plant ecological strategies (Díaz *et al.*, 2022). Maximum rooting depth is meaningful because it captures the potential for individuals of a species to construct deep roots. This potential may be more informative than individual trait values, which are highly plastic and noisy, for explaining species occurrence across environmental gradients. Maximum rooting depth was strongly correlated with the median of individual plant rooting depths across species ($r = 0.85$), and models that used median rooting depth were qualitatively indistinguishable from models that used maximum rooting depth. After standardizing species names according to the World Flora Online taxonomic backbone (Miller & Ulate, 2017) and filtering out two outlying measurements of maximum rooting depth that were < 0.3 m, the database contained 903 species (2458 observations) with average P_{50} and 1089 species (2716 observations) with maximum rooting depth. We merged the datasets based on species names and found that both traits have been measured on 207 woody species (Table S1). For these 207 species, there were 871 observations of P_{50} and 950 observations of rooting depth (Table S1).

We extracted vegetation plots from the sPlot 3.0 database (Bruelheide *et al.*, 2019) that contained at least one of the 207 species with P_{50} and rooting depth data and had a location uncertainty of 1 km or less (508,443 plots). Of the 207 species, 188 were present in at least one plot (1,733,795 occurrences). The selected plots were broadly distributed worldwide and throughout Whittaker's bioclimatic space (Fig. 1B-C). Vegetation plots were assigned to ecoregions using Olson's updated ecoregion map (Olson *et al.*, 2001; Dinerstein *et al.*, 2017). We defined regional species pools as all of our species that were detected within an ecoregion, and we defined species absences as species that were present in the regional species pool but not detected in the plot itself (Laughlin *et al.*, 2021). For each plot, we extracted the aridity index (the ratio of precipitation-to-potential evapotranspiration) from the Global Aridity Index and Potential Evapo-Transpiration Climate Database (Zomer *et al.*, 2008; Trabucco & Zomer, 2018), water table depth (WTD) from the 'wtd' database (Döll & Fiedler, 2008; Fan *et al.*, 2013), and precipitation seasonality (the CV of monthly precipitation) from WorldClim (Fick & Hijmans, 2017). The aridity index estimates macroclimatic water availability, where ratios <0.65 indicate arid climates and >0.65 indicate humid climates (Fig 1A). Water table depth varies independently of climate (in this dataset, the correlation coefficient between aridity and WTD is $r = 0.13$) and is thought to be a major driver of rooting depth distributions (Fan *et al.*, 2017).

Of the 207 species for which rooting depth and P_{50} were available, 105 were evergreen and 102 were deciduous (Table S1). We focus on drought resistance and avoidance in this paper because only a few deciduous species in our dataset were drought-deciduous escapers; the vast majority were cold-deciduous species. Nevertheless, we evaluate deciduous and evergreen species to understand their effects on the overall model results.

Data Analysis

To answer question 1, we extracted a fully resolved phylogeny based on the PhytoPhylo megaphylogeny (Qian & Jin, 2016) using the R package V.PhyloMaker version 0.1.0 (Jin & Qian, 2019). We calculated Pagel's λ under a Brownian motion model of evolution to quantify the phylogenetic signal for each trait (Pagel, 1999) using the phylosig function in the R package phytools version 1.2.0 (Revell 2012). We quantified the phylogenetic covariance between the two traits by fitting phylogenetic generalized least squares (PGLS) regression and a phylogenetic correlation structure to account for the non-independence of species across the phylogeny (Revell & Harmon, 2022). Ancestral state reconstruction used maximum likelihood estimates under a Brownian motion model of evolution. The phylogeny was plotted using the R package phytools (Revell, 2012).

To answer question 2, we compared two generalized linear mixed effects models of species presence–absence data using the binomial family and logit link. Both models included species random intercepts to account for the fact that trait data were species-level averages and not measured at the intraspecific level at each location, and ecoregion random intercepts to account for the different numbers of observations in each ecoregion. Model 1 was an environment-only model that included linear and quadratic fixed effects terms for aridity, seasonality, and WTD, and interactions among their linear terms. Model 2 included both the environment and traits, where P_{50}, rooting depth, aridity, seasonality, and WTD, their squared terms, and interactions among linear terms up to a five-way interaction, were included as fixed effects. Aridity index and the absolute value of P_{50} were square root transformed, seasonality, WTD and rooting depth were log transformed, and all predictors were mean-centered and scaled to a standard deviation of 1 prior to fitting the models.

For example, in Model 1:

$$y_i \sim \text{Bernoulli}(p_i)$$

$$p_i = \text{logit}^{-1}\big(\beta_0 + \beta_1\text{arid}_i + \beta_2\text{arid}_i{}^2 + \beta_3\text{WTD}_i + \beta_4\text{WTD}_i{}^2 + \beta_5\text{seas}_i + \beta_6\text{seas}_i{}^2$$
$$+ \beta_7\text{arid}_i\text{WTD}_i + \, + \beta_8\text{arid}_i\text{seas}_i + \beta_9\text{WTD}_i\text{seas}_i + \beta_{10}\text{arid}_i\text{WTD}_i\text{seas}_i$$
$$+ \eta_{j[i]} + \gamma_{k[i]}\big)$$

where y_i is the *i*th presence-absence record, p_i is the expected occurrence probability, the β's are regression coefficients, η_j is a random intercept for species *j* drawn from a normal distribution, $N(0, \sigma_\eta)$, and γ_k is a random intercept for ecoregion *k* drawn from a normal distribution, $N(0, \sigma_\gamma)$. This models a two-dimensional surface of P_{50} and rooting depth and its interaction with a three-dimensional surface of aridity, seasonality, and WTD. The shape of the trait surface changes in relation to aridity, seasonality, and WTD, accounting for trait-by-environment interactions that cause different trait combinations to be selected in different environments. We compared models 1 and 2 using a likelihood ratio test to determine the importance of traits for explaining species occurrences when environmental variables were already in the model. The R syntax of Model 2 using the bam function in the R package mgcv 1.8.41 (Wood, 2011) was as follows: pres ~ arid * wtd * ps * p50 * rd + arid^2 + wtd^2 + ps^2 + p50^2 + rd^2 + s(spp, bs = "re") + s(eco, bs = "re"). We plotted 90% confidence intervals using posterior simulations from the fitted model.

We plotted model predictions of occurrence probabilities at different combinations of environment and trait values. We plotted conditional effects of each trait by illustrating the effects of one trait, while holding the other trait at its mean value, at different combinations of high (95th percentile) or low (5th percentile) aridity, seasonality, and water table depth. To illustrate trait-by-trait interactions, we plotted landscapes of occurrence probabilities across a two-dimensional surface of P_{50} and rooting depth at different combinations of aridity, seasonality, and water table depth. To test the four hypotheses directly, we fixed the two traits at their 5th and 95th percentiles to represent four plant strategies and plotted landscapes of occurrence probabilities along a two-dimensional surface of aridity and WTD at two levels of seasonality. The average occurrence probability across this large dataset is approximately 5%, so predicted probabilities vary above and below this mean value. All analyses used R version 4.2.2.

Results

Phylogenetic correlation

Mean P_{50} and maximum rooting depth exhibited significant phylogenetic signal (Fig. 2), although the signal was weaker for rooting depth (P_{50}: Pagel's $\lambda = 0.91$, $P < 0.001$; rooting depth: Pagel's $\lambda = 0.58$, $P < 0.01$). These two traits were uncorrelated (Fig. 3) across the phylogeny of woody plants (PGLS slope = 0.06, SE = 0.07, $t = 0.95$, $P = 0.35$), and inspection of intraspecific trait ranges provided no indication that these traits were correlated (Figure S1). Deciduous and evergreen species were well distributed throughout this two-dimensional trait space, but deciduous species had on average more vulnerable xylem than evergreen species (Fig. 3).

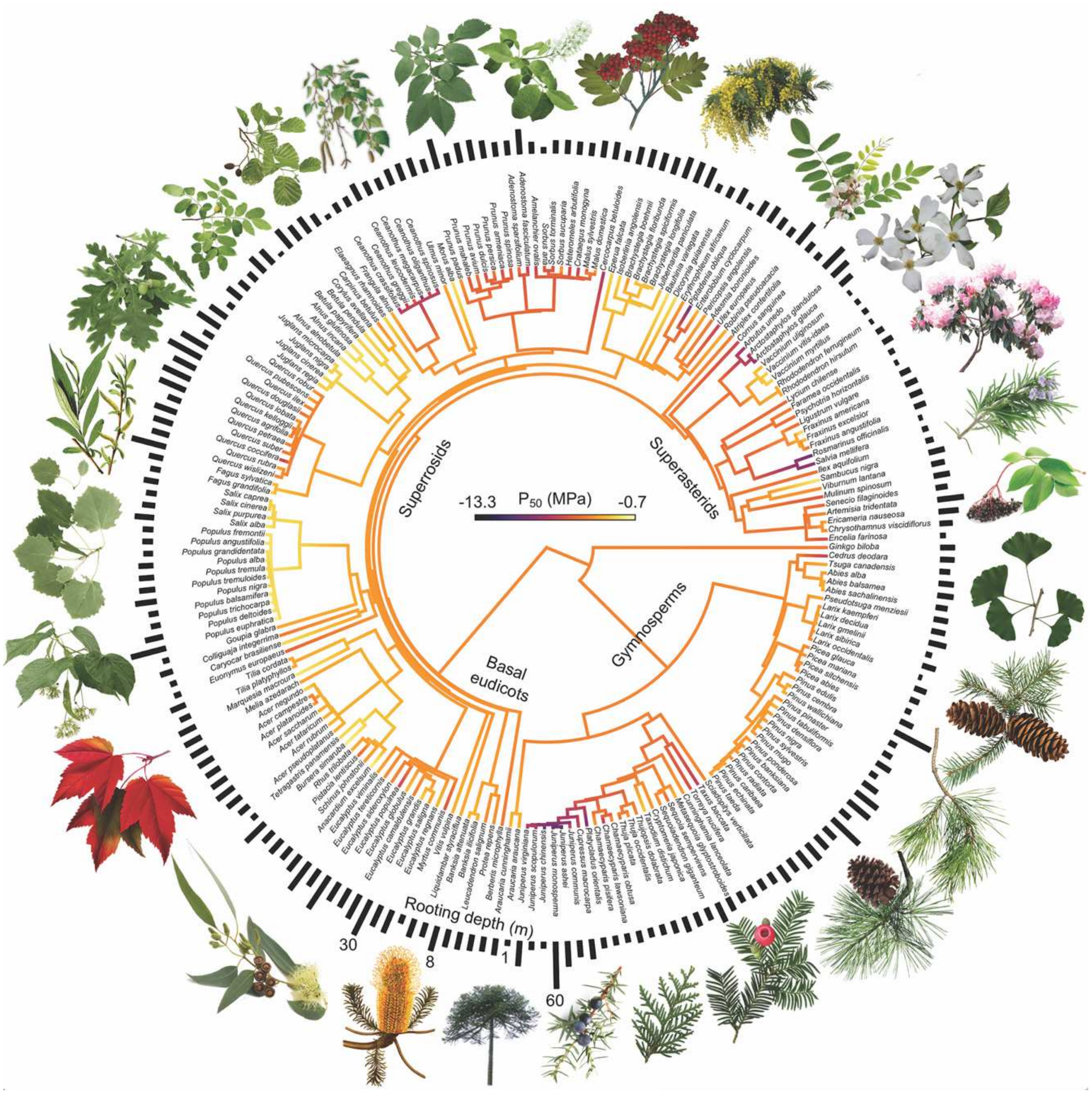


Figure 2. Xylem vulnerability to embolism (P_{50}) mapped onto the phylogeny of woody plants, where the color of the internal tree branches show vulnerability based on maximum likelihood-based ancestral state reconstruction. Dark colors indicate more resistant xylem and light colors indicate more vulnerable xylem (see legend in the center). The outer bars represent maximum rooting depth (log-scale) for each species, where longer bars represent deeper roots (see lower left for rooting depth scale legend). Pictures of representative species of major clades are illustrated around the phylogeny.

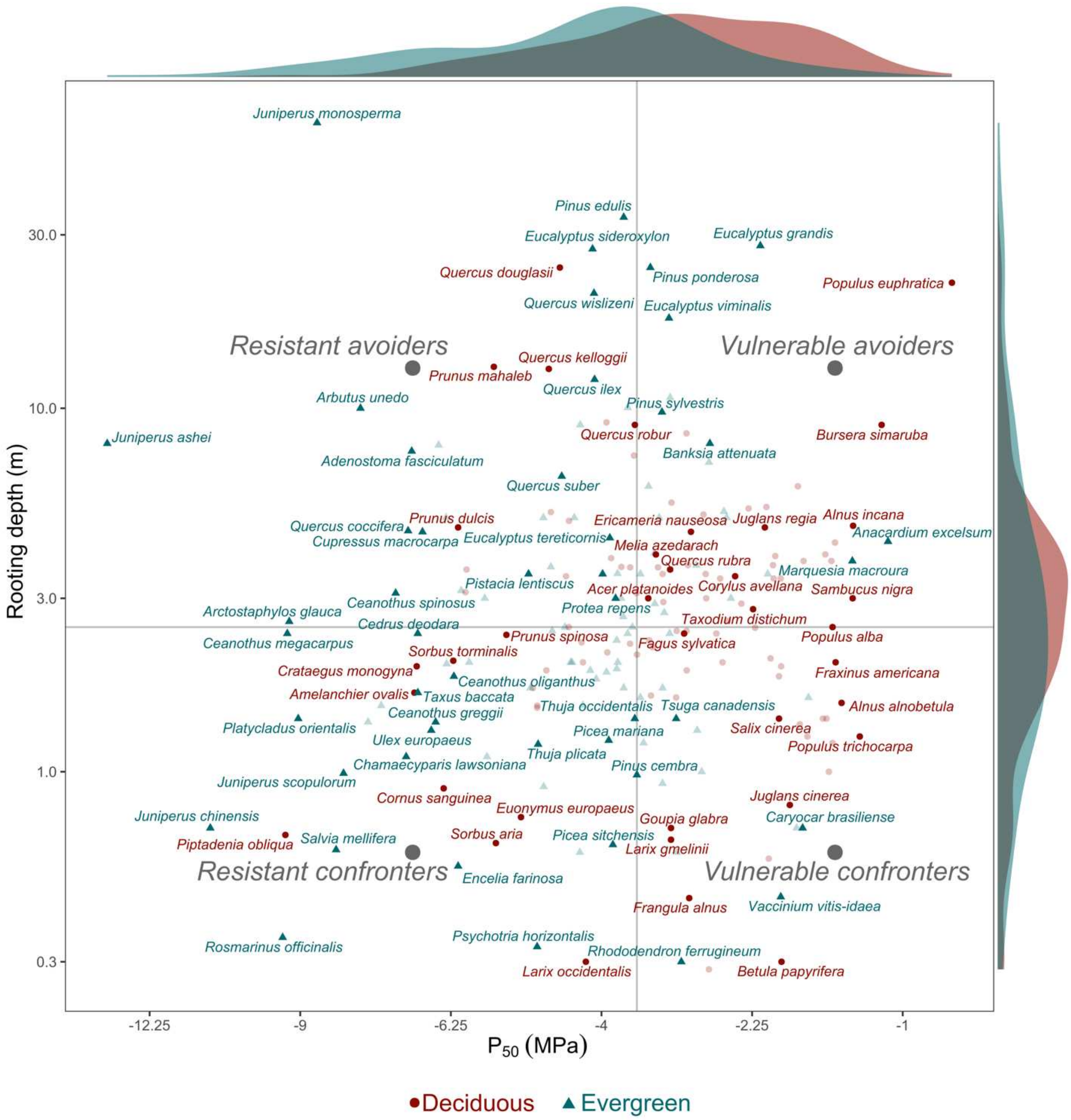


Figure 3. Distribution of species in the bivariate trait space defined by maximum observed rooting depth and mean P_{50}. Deciduous species are red and evergreen species are blue. Vertical and horizontal lines denote the 50th percentiles of the traits. Species names associated with bold symbols were selected by an algorithm to represent as much as the occupied trait space as possible because not all names could easily fit. The four grey points represent the 5th and 95th percentiles of the trait distributions (-7.0 and -1.5 MPa for P_{50}; 12.9 and 0.6 m for rooting depth) to represent each of the four plant strategies described in Figure 1B (see Methods). The curves depict the distribution of values across each of the two trait axes for each leaf type.

Models of occurrence probabilities

The generalized linear mixed effects model that included traits (see Model 2 results in Table S2) explained 16.7% of the deviance (marginal $R^2 = 0.24$; conditional $R^2 = 0.70$). A likelihood ratio test (LRT) determined that traits were a significant improvement to the model that only included environmental data as predictors (LRT $\chi^2_{21} = 188{,}143$; $P < 0.0001$) (see Model 1 results in Table S3). Traits exhibited no significant main effects (i.e., the trait effects depended on the environment), and the quadratic term for rooting depth was not significant. Nearly all trait-by-environment interactions were significant (Table S2).

P_{50} interacted with aridity, seasonality, and water table depth (Fig. 4, Table S2). The effect of P_{50} on probability of occurrence switched from negative to positive from arid to humid climates, where the probability of occurrence of species resistant to embolism increased in more arid climates (Fig 4A,B). In arid climates with shallow water tables, low P_{50} values increased occurrence probability in seasonal environments, whereas high P_{50} values increased occurrence probabilities in non-seasonal environments (Fig 4C).

Rooting depth interacted weakly with aridity, seasonality, and water table depth (Fig. 4, Table S2). The effect of rooting depth on probability of occurrence switched from positive to negative in arid to humid climates, where the probability of occurrence of species that avoid drought by constructing deep roots increased in more arid climates (Fig. 4E,F). The interaction was weak because the importance of shallow roots in humid climates increased slightly in sites with shallower water tables (Fig 4F,H).

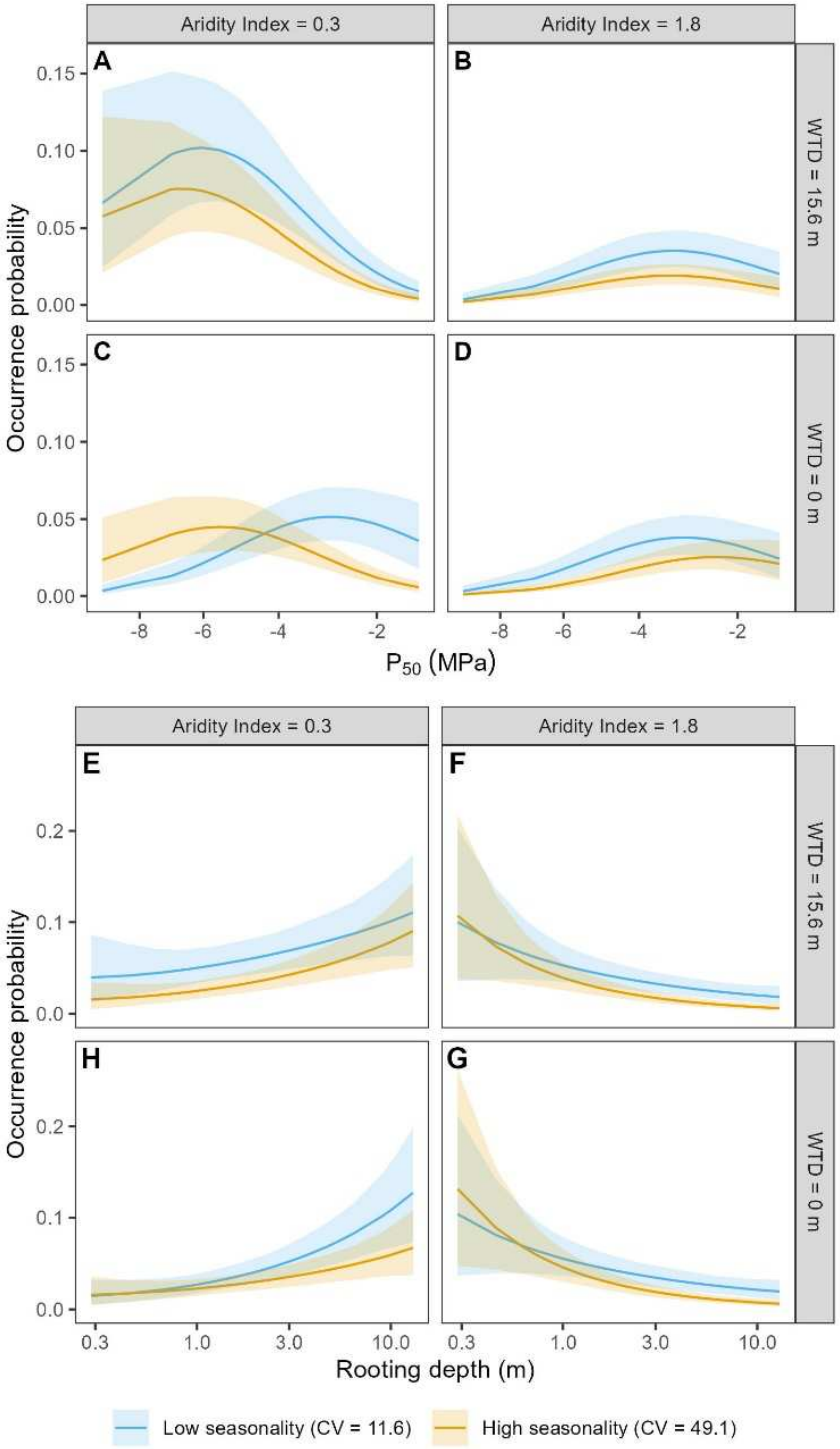


Figure 4. (A-D) Effects of P_{50} on occurrence probability (with rooting depth held at its average value, 2.6 m) at the 5th and 95th percentiles of the aridity index, seasonality, and water table depth (WTD). (E-H) Effects of rooting depth on occurrence probability (with P_{50} held at its average value, -3.6 MPa) at the 5th and 95th percentiles of the aridity index, seasonality, and water table depth (WTD). Note that the 5th percentile of WTD was close to zero meters.

Trait-by-environment interactions generated highly contingent occurrence landscapes. Landscapes of probabilities illustrate the trait values and environments that optimize species occurrence probabilities and can be viewed through two perspectives: first, as functions of aridity, seasonality, and water table depth for each of the four plant strategies (Figure 5); and second, as functions of P_{50} and rooting depth in different combinations of aridity, seasonality, and water table depth (Figure 6).

Each strategy was most likely to occur in different environments. First, resistant avoiders (low P_{50} and deep roots) were most likely to occur in arid and seasonal climates in sites with deep water tables (Figures 5A, 6A). Second, vulnerable confronters (high P_{50} and shallow roots) were most likely to occur in humid climates at any water table depth (Figures 5D, 6B, 6D). Third, resistant confronters (low P_{50} and shallow roots) were most likely to occur in arid and non-seasonal environments in sites with deep water tables (Figure 5C). Fourth, vulnerable avoiders (high P_{50} and deep roots) were most likely to occur in arid and non-seasonal climates in sites with shallow water tables (Figure 5B, 6C).

Trends in occurrence probabilities for deciduous species were qualitatively similar to full model results (Figure S2). However, resistant confronters and vulnerable avoiders with evergreen leaves exhibited relatively flat occurrence landscapes, suggesting that the full model results for these two strategies were driven by deciduous species.

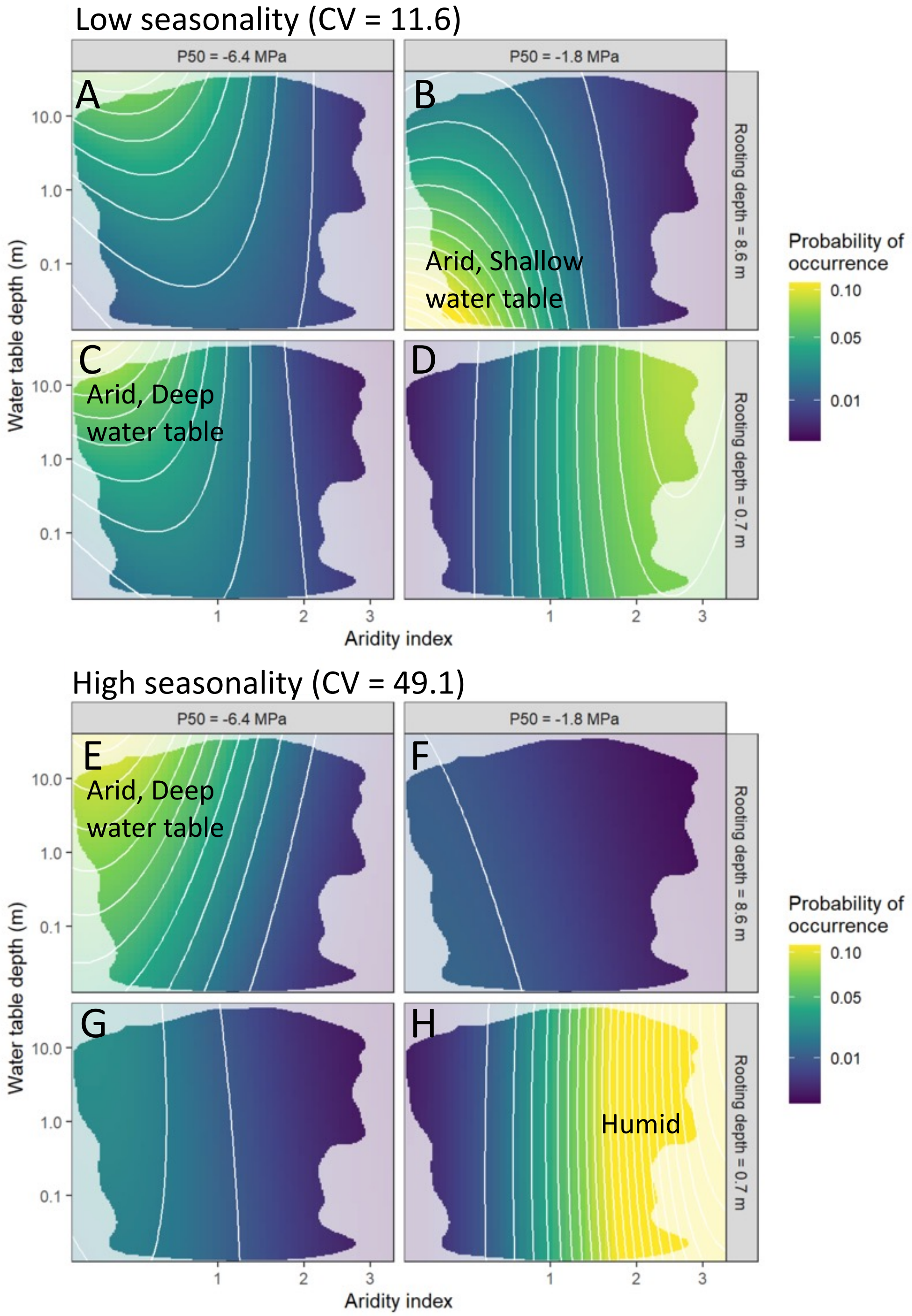


Figure 5. Occurrence probability landscapes illustrating changes in the probability of woody species occurrence for each of the four plant strategies (i.e., set as the 5th and 95th percentiles of P_{50} and maximum rooting depth) along continuous gradients of the aridity index and water table depth at the 5th and 95th percentiles of precipitation seasonality. Warm colors indicate higher probability of occurrence and cool colors indicate lower probability of occurrence. The environmental space is masked to emphasize the 99th percentile of observed environmental variation. Contour interval = 0.01.

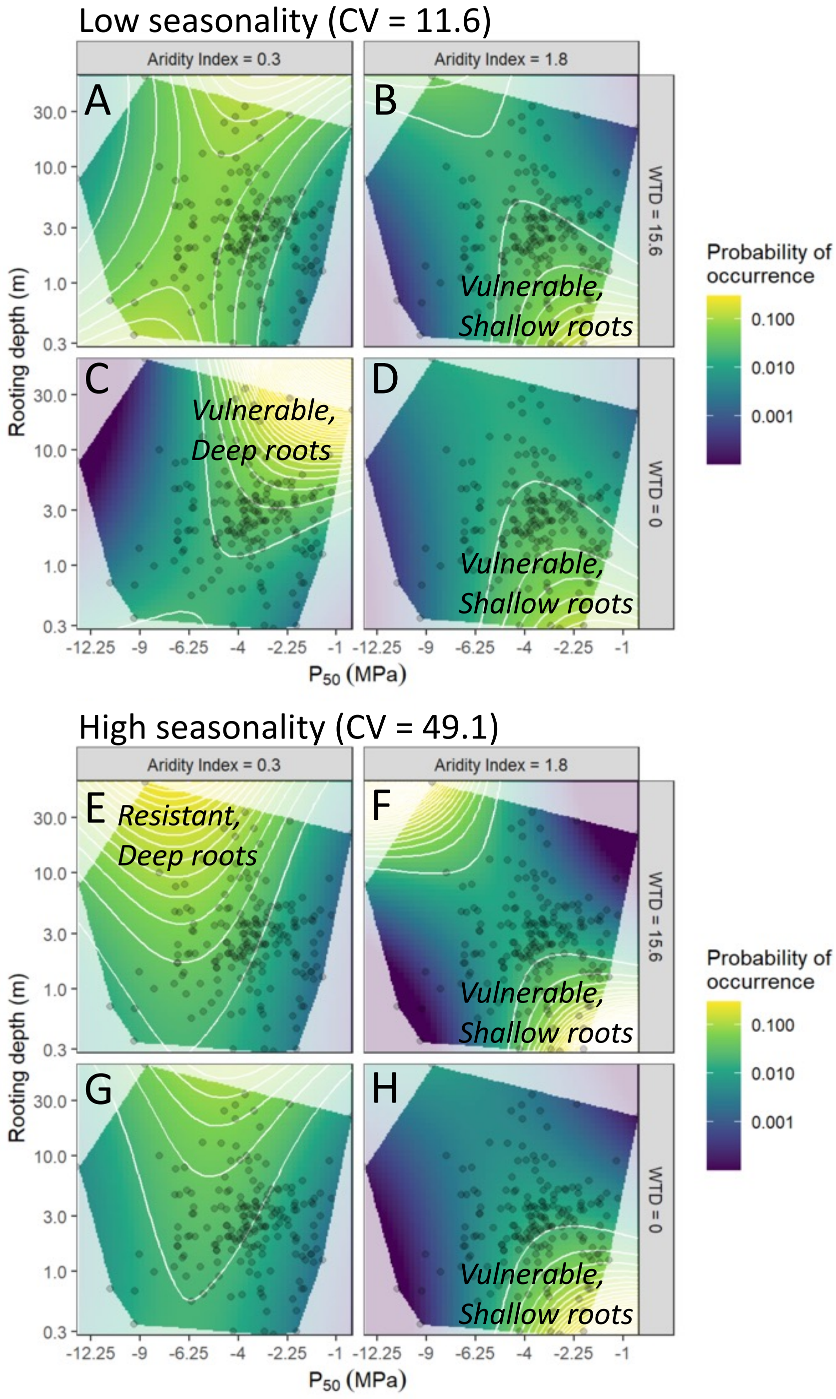


Figure 6. Occurrence probability landscapes illustrating changes in the probability of woody species occurrence in different environments (i.e., set as the 5th and 95th percentiles of the aridity index and water table depth (WTD) at the 5th and 95th percentiles of precipitation seasonality along continuous gradients of P_{50} and maximum rooting depth. Warm colors indicate higher probability of occurrence and cool colors indicate lower probability of occurrence. The trait space is masked to illustrate the convex hull of observed trait values. Contour interval = 0.01.

Discussion

Xylem vulnerability to drought-induced embolism and maximum rooting depth have each been separately investigated as drivers of drought resistance and avoidance in woody species (Canadell *et al.*, 1996; Choat *et al.*, 2012), yet their phylogenetic correlation and the joint effect of these traits on species distributions were unknown until now. Here we have shown that 1) drought resistance and avoidance are orthogonal woody plant strategies, and 2) P_{50} and rooting depth jointly improve predictions of species occurrence probabilities along gradients of aridity, seasonality, and water table depth.

First, it has been suggested that drought resistance trades-off with drought avoidance because species in a tropical forest were either shallow-rooted trees that built resistant xylem or were deep-rooted trees that built vulnerable xylem (Brum *et al.*, 2019). This proposed trade-off assumed that investment in deep root systems comes at a cost of constructing vulnerable xylem. However, our large sample across the phylogeny of woody plants provides strong evidence that P_{50} and rooting depth are phylogenetically uncorrelated. The many species that "show deviations from statistical correlations" (Carlquist, 1975, p. 1) provide insight into the adaptive value of these traits. The large carbon investment into growth and maintenance of deep roots and resistant xylem must be offset by the large carbon gains that are made possible by deep roots and resistant xylem in dry environments, otherwise these phenotypes could not persist in these environments. Moreover, many plant species construct shallow root systems and vulnerable xylem to maximize carbon gain in wetter environments. Drought resistance and avoidance do not exhibit a trade-off and species representing most major clades of woody seed plants have been able to explore the full range of combinations of these two traits to occupy a broad range of environments.

Second, P_{50} and rooting depth jointly explain species occurrence probabilities, thereby advancing our conceptual understanding of how species may respond to changing water availability under climate change. Our modeling results suggest that forecasting woody species range shifts in response to changing climate must also consider topographically mediated hydrologic regimes. While both xylem vulnerability and rooting depth were more strongly related to aridity, they interacted with water table depth to determine species occurrence probabilities. Given that water table depth is relatively independent of regional climate (Fan *et al.*, 2017), if evaporative demand changes faster than water table depth under climate change, then deeply-rooted vegetation responses may be buffered in the near-term by stable water table depths.

To facilitate the interpretation of model results based on a complex five-way interaction of continuous traits and environments, we discuss each of the four strategies that represent low and high values of each trait in turn (Fig. 1B, Fig. 3, Fig. 5). First, resistant avoiders (low P_{50} and deep roots) exhibit, in theory, the most drought-tolerant strategy because they can withstand substantial negative pressures in their xylem and at the same time are also able to avoid these strongly negative pressures when accessing deep soil water reservoirs (Hammond *et al.*, 2019; Tumber-Dávila *et al.*, 2022). This strategy is most likely to occur in arid, seasonal climates with deep water tables (Figs. 5E and 6E). This result was consistent for deciduous and evergreen species, but most resistant avoiders were evergreen. For example, the evergreen angiosperm *Arbutus unedo*, a small tree that grows in Mediterranean chaparral on dry slopes and ridges, and the evergreen gymnosperm *Juniperus monosperma*, a small tree that grows in arid deserts, illustrate how resistant xylem and deep roots optimize growth and survival in arid uplands. In order to survive in some of the driest environments on earth, constructing deep roots and resistant xylem is the optimal strategy for maintaining a positive carbon balance.

Second, resistant confronters (low P_{50} and shallow roots) are most likely to occur in arid, non-seasonal climates over deep water tables. This agrees with previous empirical work that arid environments contain both deep and shallow-rooted species (Fan *et al.*, 2017) yet clarifies that shallow roots are more adaptive in non-seasonal arid climates where more consistent precipitation (albeit still modest amounts) wets the top soil layers throughout the year. This result appeared to be driven by deciduous species, such as *Amelanchier ovalis*, which grows in open sites in dry climates, but evergreen species, such as *Encelia farinosa* and *Juniperus scopulorum,* also grow in dry habitats with well-drained soil (Ehleringer, 1993).

Third, vulnerable avoiders (high P_{50} and deep roots) are most likely to occur in arid, non-seasonal climates over shallow water tables. This result was also most evident in deciduous species. For example, the deciduous *Populus euphratica* grows in central Asian river flood plains in arid regions (Bruelheide *et al.*, 2010). This strategy may be emblematic of deep-rooted, phraetophytic species that occur in desert riparian zones (Loheide *et al.*, 2005).

Fourth, vulnerable confronters (high P_{50} and shallow roots) present, in theory, the least drought-tolerant strategy because root-to-shoot conductance can decline under even weak negative xylem pressure that cannot be overcome by access to deep soil water (Hammond *et al.*, 2019; Tumber-Dávila *et al.*, 2022). This strategy is most likely to occur in humid climates, regardless of water table depth. This result was consistent for deciduous and evergreen species. For example, the deciduous angiosperm *Salix cinerea* is a medium-sized shrub that grows in wetlands in humid climates. *Juglans cinerea*, on the other hand, is a deciduous angiosperm tree that grows in humid climates ranging from streambanks to well-drained slopes. Other drought-related traits that were not measured here, such as leaf turgor loss point, could further explain how species that are vulnerable confronters such as *Juglans cinerea* can survive in well-drained dry soil, yet turgor loss point was not available for most of the 188 species in this dataset.

Our work represents the first systematic analysis of the combined effect of drought resistance and avoidance on the global distribution of woody species. Yet, some limitations of the study deserve attention. First, maximum rooting depth data is underestimated due to the logisitical difficulty of measuring this trait, and rooting depth within species responds plastically to variation in soil water depth (Schenk & Jackson, 2005; Fan *et al.*, 2017). Given the low number of replicated trait observations within species (Table S1, Figure S1), our analysis was unable to evaluate the phenotypic plasticity of each trait and whether individual species could acclimate to changing vapor pressure deficits and soil water availability. We urge researchers to develop methods to simultaneously measure xylem vulnerability and rooting depth on individual plants in their environments. Second, our analysis does not predict the growth, survival, and reproduction of different ontogenetic stages of trees, and these are the fitness components that are important to population dynamics that lead to range shifts (Merow *et al.*, 2017). Our analysis is an important first step to determine the joint effect of these critical traits on species responses to changing aridity, seasonality, and water table depth, but future work should link these trait-by-environment interactions to demographic rates and population growth rates to improve forecasting generality (Laughlin *et al.*, 2020b). Third, the limited data availability for drought-deciduous species prevented us from understanding how the drought escape strategy relates to drought resistance and avoidance. Future work should address these limitations.

The earliest plants to colonize the land emerged in humid tropical environments and likely did not stray too far from shorelines and streambanks where evaporative demand was moderated by humid atmospheres and shallow water tables (Willis & McElwain, 2014; Bouda *et al.*, 2022). The evolution of increasing resistance to embolism and extension of roots deep into the soil profile permitted species to occupy increasingly drier environments, and these traits have retained their adaptive advantages to this day. Simultaneous understanding of drought resistance and avoidance strategies that have evolved across the phylogeny of woody plants will enhance our predictions of vegetation response to changing water availability and guide species selection in ecological restoration projects (Laughlin *et al.*, 2017; McDowell *et al.*, 2022).

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Author Contributions

DL designed the study. AS, JF, and DL conducted the data analyses. DL and AS wrote the first draft, and all authors contributed substantially to revisions.

Competing Interests

None declared.

Data Availability

All code and data will be archived on Dryad upon acceptance and the data DOI will be included at the end of the article. Code is available for review at Andrew Siefert's GitHub repository https://github.com/andrewsiefert/xylem_root3.

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Supporting Information

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