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Research paper

Metrics and proxies for stringency of regulation of plant water status (iso/anisohydry): a global data set reveals coordination and trade-offs among water transport traits

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Plants operate along a continuum of stringency of regulation of plant water potential from isohydry to anisohydry. However, most metrics and proxies of plant iso/anisohydric behavior have been developed from limited sets of site-specific experiments. Understanding the underlying mechanisms that determine species' operating ranges along this continuum, independent of site and growing conditions, remains challenging. We compiled a global database to assess the global patterns of metrics and proxies of plant iso/anisohydry and then explored some of the underlying functional traits and trade-offs associated with stringency of regulation that determines where species operate along the continuum. Our results showed that arid and semi-arid biomes were associated with greater anisohydry than more mesic biomes, and angiosperms showed marginally greater anisohydry than gymnosperms. Leaf water potential at the turgor loss point (Ψ_{tlp}) and wood density were the two most powerful proxies for ranking the degree of plant iso/anisohydry for a wide range of species and biomes. Both of these simple traits can be easily and rapidly determined, and therefore show promise for a priori mapping and understanding of the global distribution pattern of the degree of plant iso/anisohydry. Generally, the most anisohydric species had the most negative values of Ψ_{tlp} and highest wood density, greatest resistance to embolism, lowest hydraulic capacitance and lowest leaf-specific hydraulic conductivity of their branches. Wood density in particular appeared to be central to a coordinated series of traits, trade-offs and behaviors along a continuum of iso/anisohydry. Quantification of species' operating ranges along a continuum of iso/anisohydry and identification of associated trade-offs among functional traits may hold promise for mechanistic modeling of species-specific responses to the anticipated more frequent and severe droughts under global climate change scenarios.

Keywords: anisohydry, drought tolerance, hydraulic architecture, hydraulic safety margin, isohydry, leaf osmotic potential, plant functional traits, stomata, wood density, xylem embolism resistance.

Introduction

Increasingly detailed knowledge of how plants cope with drought is necessary to accurately predict how species will perform and survive during the more frequent and severe droughts anticipated under current global change scenarios (Breshears et al. 2005, 2009, Carnicer et al. 2011, Anderegg et al. 2012).

Previous studies conducted during natural and experimentally imposed drought have identified numerous individual traits and complexes of traits associated with overall drought resistance (Lo Gullo and Salleo 1988, Markesteijn and Poorter 2009, Blackman et al. 2010, O'Brien et al. 2014). However, robust predictions of species-specific drought performance, particularly susceptibility to drought-induced mortality, remain elusive in part

because coordinated variation in multiple traits determines performance at the organismal level and because drought-induced mortality does not appear to be associated with a single mechanism (McDowell et al. 2008, Sala et al. 2010, Pineda-García et al. 2013, Mencuccini et al. 2015, García-Fórner et al. 2016). Efforts to model species' responses to drought are likely to be simplified by identification of single traits or small groups of coordinated traits that reliably represent coordination and integration of larger complexes of traits that ultimately govern organismal behavior (e.g., Bartlett et al. 2012a, Skelton et al. 2015, Anderegg et al. 2016, Bartlett et al. 2016, Greenwood et al. 2017).

One approach that may show promise for modeling species-specific responses to drought is classification of species' positions along a continuum of iso/anisohydric behavior (Stocker 1956, Tardieu and Simonneau 1998). Broadly, isohydric plants regulate transpiration to maintain a relatively constant midday leaf water potential (Ψ_{md}) as soil water potential and predawn leaf water potential (Ψ_{pd}) decrease. Anisohydric species, by contrast, respond to drought by allowing Ψ_{md} to decline nearly in parallel with Ψ_{pd} . Regulation of plant water potential during soil drying is likely to be a consequence of coordination and trade-offs among a series of structural and functional traits relevant to drought performance. The relatively isohydric *Pinus edulis* was reported to have much higher drought-induced mortality than the anisohydric *Juniperus monosperma* in the southwestern US (McDowell 2011, Plaut et al. 2012). However, West et al. (2012) showed that anisohydric ericoid shrubs were highly vulnerable to drought mortality, while isohydric restioids and proteoid shrubs displayed little drought mortality in South Africa. Similarly, *Liriodendron tulipifera* with a relatively constant seasonal Ψ_{md} was also found to be at lower risk of drought-induced mortality than *Viburnum rafinesquianum* with declining Ψ_{md} during soil drying in a temperate forest (Hoffmann et al. 2011). The contradictory findings in these and other studies suggest that vulnerability of woody species to drought mortality may not be monotonic along the iso/anisohydric continuum (Gu et al. 2015) or that different definitions or metrics of iso/anisohydry would lead to inconsistent rankings of the degree of iso/anisohydry for a given species (Martínez-Vilalta and García-Fórner 2017, Hochberg et al. 2018). Thus, defining suitable and consistent metrics for where species operate along this continuum is of central importance for understanding and predicting the global distribution pattern of species' performance during drought. Recently, several metrics have been developed based on data derived from the repeated measurement of leaf water potential (Ψ_{md} and Ψ_{pd}) during soil drying (Martínez-Vilalta et al. 2014, García-Fórner et al. 2016, Meinzer et al. 2016), leaf water potential thresholds corresponding to different degrees of stomatal closure (Klein 2014), or defined as the degree of stomatal regulation of xylem embolism (Skelton et al. 2015). As suggested above, these and other conceptualizations and resulting metrics of iso/anisohydry may yield inconsistent rankings of

species and therefore inconsistent predictions of their vulnerability to drought-induced mortality.

There is a growing list of traits shown to be correlated with various metrics and proxies for iso/anisohydry. At the stem level, more anisohydric species tend to have higher xylem resistance to embolism (Klein 2014, Martínez-Vilalta et al. 2014), but lower stem-level hydraulic safety margins, the difference between typical minimum xylem water potential and that causing xylem dysfunction (Skelton et al. 2015). With respect to regulation of photosynthetic gas exchange, more anisohydric species were reported to have faster kinetics of stomatal opening and activation of photosynthesis, greater stomatal conductance and photosynthetic capacity and lower intrinsic water-use efficiency (Meinzer et al. 2017). In a recent greenhouse study, species' values of leaf water potential at the turgor loss point (Ψ_{tjp}) were a robust proxy for their 'hydroscape' a metric of iso/anisohydry that describes a water potential landscape over which stomata can regulate leaf water potential prior to permanent drought-induced stomatal closure (Meinzer et al. 2016). Species with more negative values of Ψ_{tjp} had larger hydroscape areas (MPa^2) during soil drying and were therefore more anisohydric. The preceding relationship is consistent with the notion that Ψ_{tjp} is a strong predictor of overall drought tolerance across species and biomes (Bartlett et al. 2012a). However, most of the results reviewed here were obtained from a limited number of species under a limited range of growing conditions and their relationship to general patterns across global plant diversity has not been examined. Defining iso/anisohydry and its metrics, proxies and associated traits in a manner that results in consistent ranking of species globally, independent of site and growing conditions, thus remains challenging.

In addition to the traits described above, xylem hydraulic capacitance and non-structural carbohydrate storage are important components of plant drought resistance/avoidance strategies (Meinzer et al. 2009, Sala et al. 2012, Pratt and Jacobsen 2017). Wood density is often positively related to xylem resistance to embolism (Hacke et al. 2001), but is also negatively correlated with xylem hydraulic capacitance (Scholz et al. 2007, McCulloh et al. 2014, Jupa et al. 2016) and carbohydrate storage capacity (Johnson et al. 2012, Pratt and Jacobsen 2017). Despite the potential use of this easily measured trait for characterizing plant water-use strategies, no study to our knowledge has tested the relationship between wood density and the degree of iso/anisohydry based on a global data set, or its performance as an indicator of degree of iso/anisohydry relative to other potential proxies. However, a study conducted at one site showed that species with dense wood were strongly anisohydric, as indicated by a large decline in midday water potential during drought (Hoffmann et al. 2011).

Given the above context, the goal of this study is to apply a specific metric and potential proxies of plant iso/anisohydry to a global data set and assess the extent to which they are coordinated

across a wide range of biomes and a diverse group of species. To accomplish this, we firstly compiled a database to scale the degree of woody plant iso/anisohydry globally, based on species' 'hydrosapes', a recently developed metric of iso/anisohydry (Meinzer et al. 2016) based on the broad definition of iso/anisohydry given by Tardieu and Simonneau (1998). Then, we assessed whether potential proxies of plant iso/anisohydry obtained from additional data sets scaled consistently with global patterns of plant iso/anisohydry. Lastly, we addressed coordination and trade-offs among selected functional traits along the spectrum of iso/anisohydry and the underlying mechanisms that determine species' operating ranges along this continuum. We focused on woody plants because of the greater availability of data and the persistence of woody species in the face of climate variability, particularly with respect to drought severity.

Materials and methods

Metrics of iso/anisohydry

Martínez-Vilalta et al. (2014) assumed that the relationship between Ψ_{md} and Ψ_{pd} during soil drying was a linear function (black line, Figure 1),

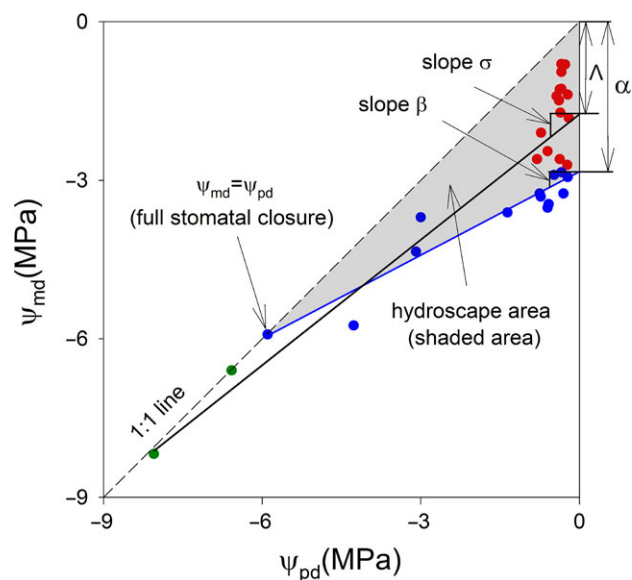


Figure 1. Illustration of two metrics of plant iso/anisohydry. Colored symbols represent the measured trajectory of predawn and midday leaf water potential (Ψ_{pd} , Ψ_{md}) of *Quercus garryana* during soil drying. Red symbols represent data collected under moist conditions when Ψ_{md} likely varied with irradiance only, independent of Ψ_{pd} . Blue symbols reflect stomatal regulation of Ψ_{md} prior to complete stomatal closure ($\Psi_{md} = \Psi_{pd}$). Green symbols represent the range over which stomata are no longer effective in mitigating the rate of decline in Ψ_{md} . The metric slope σ was obtained by fitting a linear regression (black line) to the entire trajectory of Ψ_{md} vs Ψ_{pd} (Martínez-Vilalta et al. 2014). The metric hydroscape area was obtained by determining the area of a triangle bounded by the blue regression line, the y-axis, and the 1:1 line (Meinzer et al. 2016). See text for further details.

$$\Psi_{md} = \Lambda + \sigma \Psi_{pd} \quad (1)$$

where Λ is the intercept at $\Psi_{pd} = 0$, σ is the slope and Ψ_{pd} is a proxy for soil Ψ . In this equation, the slope σ was taken as a metric of plant iso/anisohydry where $0 < \sigma < 1$ implies partial isohydry, $\sigma = 1$ implies strict anisohydry and $\sigma > 1$ implies extreme anisohydry. However, trajectories of Ψ_{md} vs Ψ_{pd} during soil drying typically consist of three distinct phases (Figure 1). The nearly vertical array of data points in the first phase (red symbols, Figure 1) reflects variation in Ψ_{md} that is likely associated with variation in irradiance and vapor pressure deficit rather than soil Ψ . Inclusion of data points in this phase will drive the regression toward a steeper slope (more anisohydric) and may result in an estimate of Ψ_{md} when $\Psi_{pd} = 0$ (Λ , Figure 1) that is substantially less negative than the true value under clear, dry atmospheric conditions. The second phase (blue symbols and line, Figure 1) occurs between the point at which the slope of the relationship between Ψ_{md} and Ψ_{pd} abruptly transitions from nearly vertical to < 1 and ends when $\Psi_{md} = \Psi_{pd}$, the point of complete stomatal closure. Inclusion of data beyond the point where further decline in Ψ_{md} is driven by declining soil Ψ rather than stomatal behavior (phase 3) would also make the regression slope steeper (green symbols, Figure 1). A regression fitted to the second phase will usually have a slope < 1 (slope β , Figure 1) and will likely provide a more robust estimate of Ψ_{md} when $\Psi_{pd} = 0$ (α , Figure 1).

Using only slopes σ or β (slope of the second phase) as quantitative metrics of iso/anisohydry could yield ambiguous and inconsistent results (see Figure S1 available as Supplementary Data at *Tree Physiology Online*). Two species with very different trajectories of Ψ_{md} vs Ψ_{pd} (see Figure S1a available as Supplementary Data at *Tree Physiology Online*) could have similar values of σ (see Figure S1b available as Supplementary Data at *Tree Physiology Online*) or β (see Figure S1c available as Supplementary Data at *Tree Physiology Online*), yet have very different values of Ψ_{md} when $\Psi_{pd} = 0$ and therefore very different values of Ψ_{md} at complete stomatal closure ($\Psi_{md} = \Psi_{pd}$; see Figure S1c available as Supplementary Data at *Tree Physiology Online*). In view of the preceding considerations, Meinzer et al. (2016) developed a new metric of plant iso/anisohydry:

$$HA = \frac{\alpha^2}{2(1 - \beta)} \quad (2)$$

where HA is the hydroscape area and α and β are the intercept and slope of the regression fitted to phase 2 of the trajectory of Ψ_{md} vs Ψ_{pd} during soil drying (Figure 1). The versatility of the hydroscape is that it integrates the impacts of multiple mechanisms that regulate plant water potential and stomatal behavior during soil drying and thus is a comprehensive metric of overall iso/anisohydry. First, the hydroscape encompasses the entire range of soil water availability over which stomata exert effective

control over transpiration, and therefore Ψ_{md} , prior to complete stomatal closure at $\Psi_{\text{pd}} = \Psi_{\text{md}}$. The hydroscape also incorporates the influence of drought-induced osmotic adjustment on Ψ_{tip} and therefore on the Ψ_{leaf} corresponding to complete stomatal closure (Meinzer et al. 2016). Additionally, drought-induced partial leaf shedding that serves to buffer declines in whole-plant leaf-specific hydraulic conductance (Bucci et al. 2005) should affect the slope of the trajectory of Ψ_{pd} vs Ψ_{md} that defines the lower boundary of the hydroscape (Figure 1). In view of the above, we used hydroscape area as the metric of iso/anisohydry in the present study. Larger hydroscales would be indicative of a greater degree of anisohydry.

Datasets

Hydroscape areas were derived from published datasets containing repeated measurements of Ψ_{md} and Ψ_{pd} during soil drying. To compile a global database for this metric, a literature search was conducted using Google Scholar and the terms: leaf + midday + predawn water potential. Additional data were obtained from references in our personal collections of published literature. The raw data for Ψ_{md} and Ψ_{pd} were extracted mainly by digitizing graphs using the GetData Graph Digitizer (version 2.24, S. Federow, Moscow, Russia). The detailed approach for fitting the linear regression that defines the lower boundary of the hydroscape (Figure 1) is described in Meinzer et al. (2016). This linear regression was accepted when the correlation was significant at $P < 0.05$, with the exception of *Acacia xanthophloea*, *Fagus sylvatica*, *Populus deltoides* and *Quercus suber*. Although the linear regressions were not statistically significant for these four species, they were still included in this analysis because of the clearly linear but horizontal trends in Ψ_{md} vs Ψ_{pd} over the range where stomata have control over Ψ_{md} (see Figure S2 available as Supplementary Data at *Tree Physiology* Online). For some species with raw data mainly distributed in the first phase of the trajectory of Ψ_{md} vs Ψ_{pd} (red symbols, Figure 1), it was not possible to generate hydroscales. When comparing the hydroscape areas for the same species grown under different environmental conditions (e.g., field- vs container-grown in a greenhouse or outdoors), we found that some species showed substantial plasticity in their hydroscape area (see Table S1 available as Supplementary Data at *Tree Physiology* Online). For example, the coefficient of variation within species across environmental gradients for *Arbutus unedo*, *Heteromeles arbutifolia*, *Quercus ilex*, *Rhamnus ilicifolia* and *Vitis vinifera* ranged from 7% to 46%. In order to focus on the effect of species on the degree of plant iso/anisohydry and rank them along the iso/anisohydry continuum globally, plant water potential data were combined across treatments at the species level for studies involving multiple treatments. When more than one published report for the same species grown under different environmental conditions was available, water potential data sets were also combined. Ultimately, raw data collected for 128

species yielded sufficiently complete trajectories of Ψ_{md} vs Ψ_{pd} to generate hydroscape areas for 74 species using the criteria described above (see Table S2 available as Supplementary Data at *Tree Physiology* Online). These 16 gymnosperm and 58 angiosperm species represented multiple biomes (24 temperate species, 35 Mediterranean species, 11 desert species and four tropical species). Among these 74 species, hydroscales for 54 species (73%) were generated by combining data from multiple studies carried out under different environmental conditions to obtain an adequate range of Ψ_{md} vs Ψ_{pd} . The resulting combined trajectories of leaf Ψ were reasonably consistent despite being obtained from plants of different sizes and ages growing in different types of soil (e.g., *Olea europaea*; see Figure S3 available as Supplementary Data at *Tree Physiology* Online). The hydroscales for the remaining 20 species were generated from data collected in individual studies.

The plant functional traits Ψ_{tip} , wood density, Ψ_{50} (the water potential causing 50% loss in xylem hydraulic conductivity), Ψ_{88} (the water potential causing 88% loss in xylem hydraulic conductivity), the Ψ_{50} safety margin (difference between minimum midday water potential (Ψ_{min}) and Ψ_{50}), the Ψ_{88} safety margin (difference between Ψ_{min} and Ψ_{88}), native leaf-specific hydraulic conductivity of branches (measured without using a high-pressure flush to remove embolism in the stem segment) and stem wood saturated water content (a proxy for stem hydraulic capacitance) were evaluated as potential proxies for the degree of plant iso/anisohydry as measured by species' hydroscape areas. Of these, Ψ_{tip} was previously shown to be a robust proxy for hydroscape area in a greenhouse study of eight woody species (Meinzer et al. 2016). All of these potential proxies were collected directly from peer-reviewed publications (see Table S3 available as Supplementary Data at *Tree Physiology* Online), with the exception of stem wood saturated water content, which we calculated based on wood density (Simpson 1993). In 60% of our samples Ψ_{tip} and leaf water potential trajectories for hydroscape area generation were collected from the same population of plants in the same study. Wood density, Ψ_{50} and Ψ_{88} were mainly obtained from three previously compiled datasets (Zanne et al. 2009, Choat et al. 2012, Bartlett et al. 2016). In these three datasets, averaged values were used when more than one value was available for a given species. Values of the Ψ_{50} and Ψ_{88} safety margins were obtained from the Supplementary Data in Choat et al. (2012). We note that 86% of the Ψ_{min} values used for safety margin calculation in our study were measured as xylem or stem water potential. The remaining 14% of Ψ_{min} values were measured as leaf water potential (*A. unedo*, *Q. ilex*, *J. monosperma*, *Pinus halepensis*, *Pinus sylvestris*). Because leaf Ψ is typically more negative than xylem Ψ , it is possible that safety margins were underestimated in these cases (Choat et al. 2012).

Data analysis An independent samples *t*-test was used to compare hydroscape areas between gymnosperms and

angiosperms after arctan transformation of the data. Comparisons of hydroscape areas between biomes were made with an ANOVA followed by Tukey's HSD after log-transformation of the data. Linear (Pearson) or non-linear (Spearman) correlations were used to examine the relationships between the hydroscape area and the potential proxies for the degree of plant iso/anisohydry. All analyses above were performed using SPSS 17.0 (SPSS Inc., Chicago, IL, USA). Ψ_{50} and Ψ_{88} were treated as two independent parameters, even though they were derived from the same curve. Relationships among the traits used as proxies for iso/anisohydry were determined to test for potential trade-offs among the traits and explore the underlying mechanisms that determine species' operating ranges along this continuum. To achieve this, we used reduced major axis (RMA) regression to evaluate the relationships between traits using the SMATR package in R (Warton et al. 2012). Heterogeneity of slopes between gymnosperms and angiosperms was tested via a permutation test (Anderson 2001). When regressions fitted to gymnosperm and angiosperm data were not significantly different, data for all species were pooled.

Results

Global variation in plant iso/anisohydry

Using a data set representing a broad range of species and biomes mostly from field studies, hydroscape area captured a wide range of the global interspecific variation in iso/anisohydry (Figure 2). The relative range of hydroscape areas among species was ~13-fold. On average, the hydroscape areas of desert and Mediterranean species were comparable but significantly higher than that of temperate and tropical species (Figure 2a). Although much overlap occurred in the distributions of hydroscape areas between gymnosperms and angiosperms, the mean hydroscape area of gymnosperms was marginally lower than that of angiosperms (Figure 2b).

Correlations between hydroscape area and plant functional traits

Across all species, hydroscape area was significantly correlated with Ψ_{tip} , wood density and Ψ_{88} , and marginally correlated with the Ψ_{50} safety margin, but not significantly correlated with Ψ_{50} itself or with the Ψ_{88} safety margin (Figure 3, see Table S4 available as Supplementary Data at Tree Physiology Online). The trajectories of the relationships between hydroscape area and the Ψ_{50} safety margin were significantly different between the angiosperms and gymnosperms based on the permutation test (Figure 3d, $P = 0.038$). The hydroscape area was more strongly correlated with Ψ_{tip} and wood density than with Ψ_{88} and the Ψ_{50} safety margin. Both Ψ_{tip} and wood density were thus robust proxies for species' degree of iso/anisohydry. The hydroscape area also decreased exponentially with increasing stem wood

saturated water content, a proxy for stem hydraulic capacitance (Figure 4).

We used Ψ_{tip} as a proxy for species' degree of iso/anisohydry to examine relationships of Ψ_{tip} with other functional traits in species for which insufficient data on Ψ_{pd} vs Ψ_{md} during soil drying were available to calculate hydroscape areas. To account for the uncertainty associated with using Ψ_{tip} as a proxy for species' degree of iso/anisohydry, the hydroscape area for species with insufficient Ψ data was generated from the Ψ_{tip} , based on the relationship between Ψ_{tip} and hydroscape area in Figure 3a. There was a linear decline in diurnal minimum leaf water potential with increasing anisohydry over a range of Ψ_{tip} from ca -1.5 MPa to -6 MPa (Figure 5a and c). However, the slope of the regression was significantly >1 in Figure 5c, resulting in an increasing offset between diurnal minimum leaf water potential and Ψ_{tip} with increasing anisohydry, implying an increasing 'turgor safety margin'. The trajectory slopes of gymnosperms and angiosperms in Figure 5a were not significantly different ($P = 0.525$) based on the permutation test, however, a larger sampling of gymnosperms might reveal significantly different trajectories. Leaf-specific conductivity of branches appeared to decline exponentially with decreasing Ψ_{tip} and therefore increasing anisohydry among 59 angiosperm species sampled (Figure 5b and d).

Correlations among proxies for the degree of iso/anisohydry

Several significant relationships among the four proxies in Figure 3 were observed when the data were pooled across all species or divided into angiosperm and gymnosperm groups (Figure 6, see Table S5 available as Supplementary Data at Tree Physiology Online). A highly significant negative relationship between Ψ_{tip} and wood density was found when the data were pooled across all species (Figure 6a). Species with higher wood density and more negative Ψ_{tip} had more negative values of Ψ_{88} (Figure 6b and c). For the gymnosperms, the Ψ_{50} safety margin increased with increasing wood density and decreasing Ψ_{tip} , whereas in the angiosperms the opposite pattern was observed with the Ψ_{50} safety margin becoming negative with increasing wood density and decreasing Ψ_{tip} (Figure 6d and e). Species with lower Ψ_{50} safety margins had less negative Ψ_{88} , but the Ψ_{50} safety margin decreased more steeply with increasing Ψ_{88} in the gymnosperms (Figure 6f).

Discussion

Metrics and proxies for global variation in iso/anisohydry

We found that a recently proposed metric for woody species' degree of iso/anisohydry, a water potential landscape (hydroscape) over which they operate prior to complete drought-induced stomatal closure (Meinzer et al. 2016), ranked species along a continuum of iso/anisohydry in a global data set representative of a wide range of species and biomes (Figure 2). The

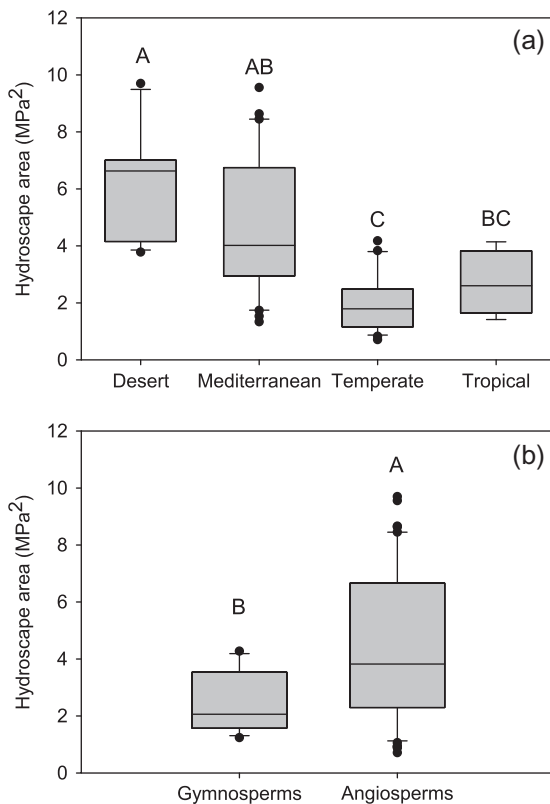


Figure 2. Boxplot of species-specific hydroscape area across (a) biomes and (b) plant functional groups. Boxes show the 25th, 50th (median) and 75th percentiles, error bars above and below each box show 90th and 10th percentiles, and filled symbols show outliers. Differences between biomes were significant ($P < 0.001$, $F = 19.503$). Differences between plant functional groups were marginally significant ($P = 0.063$, $F = 3.556$). Differences between means are indicated by letters above boxes. Larger hydroscape areas reflect increasingly anisohydric behavior.

larger variation in hydroscape areas among desert and Mediterranean species is consistent with a broader array of adaptive solutions for achieving adequate photosynthetic gas exchange in drought-prone environments. The finding that species from desert and Mediterranean climates had larger hydroscape areas than species from temperate and tropical regions is consistent with the expectation that anisohydric species tend to occupy more drought-prone habitats compared with isohydric species (McDowell et al. 2008).

Species' values of Ψ_{tip} were a robust proxy for their hydroscape areas (Figure 3a). These findings are consistent with those of Meinzer et al. (2016) based on a greenhouse study of eight species and suggest that this approach may be broadly applicable for characterizing hydraulic strategies of field-grown woody plants. A major advantage of using species' Ψ_{tip} as a proxy for their degree of iso/anisohydry is that it may obviate the need to conduct labor-intensive, species-specific studies of regulation of water potential during prolonged periods of soil drying. Estimating Ψ_{tip} by osmometry (Bartlett et al. 2012b)

would be even less time-consuming than obtaining estimates from leaf pressure–volume curves. We note that this approach characterizes inherent coordination between leaf osmotic properties and stringency of stomatal control of plant water status (Meinzer et al. 2017). We expect that the plasticity of species' hydroscales and therefore the breadth of their operating ranges along a continuum of iso- to anisohydry to be partly determined by species-specific differences in the plasticity of Ψ_{tip} and its coordination with other plant traits and site conditions. Consistent with this, transitions between iso- and anisohydric behavior within species have been attributed to osmotic adjustment (Domec and Johnson 2012, Rogiers et al. 2012).

The integrative trait, wood density, proved to be an equally strong proxy for positioning species along a continuum of iso/anisohydry in our global data set (cf. Figure 3a and b). Compared with Ψ_{tip} , which can vary considerably over fairly short time scales as a result of osmotic adjustment during soil drying (Bartlett et al. 2014), wood density is an inherently more conservative trait that shows relatively small short-term variations (Bouriaud et al. 2005). Moreover, wood density is perhaps the most commonly and easily assessed wood property. One compiled database of wood density encompasses 8412 taxa, 1683 genera and 191 families (Chave et al. 2009). This database is several times larger than global Ψ_{tip} databases (e.g., Bartlett et al. 2012b, 2014), suggesting that wood density may have an advantage over Ψ_{tip} for quantifying or calibrating global geographic variations in vegetation iso/anisohydry.

Our analysis showed that the hydroscape area was negatively correlated with Ψ_{88} and the Ψ_{50} safety margin across all species sampled globally (Figure 3c, see Table S4 available as Supplementary Data at *Tree Physiology Online*). This is in line with two recent metrics introduced for the degree of iso/anisohydry at the species level, showing similar correlations with Ψ_{88} across plant groups (gymnosperms vs angiosperms) and biomes (Martínez-Vilalta et al. 2014) and with the Ψ_{50} safety margins within a specific ecosystem of South Africa's Cape Floristic Region (Skelton et al. 2015). Our results provide further evidence to support the finding that the degree of iso/anisohydry was more tightly correlated with Ψ_{88} than with Ψ_{50} (Martínez-Vilalta et al. 2014).

Trade-offs along a spectrum of iso/anisohydry at the stem level

We found that the more anisohydric angiosperm species tended to have lower leaf-specific hydraulic conductivity (Figure 5b), which may be compensated for by their greater embolism resistance with increasing anisohydry (Figure 3c). In line with previous findings that more dense wood tends to confer greater embolism resistance (Hacke et al. 2001, Pratt et al. 2007, Hoffmann et al. 2011), we found that the more anisohydric species tended to have higher wood density (Figure 3b) and thus greater embolism resistance (Figure 6b). The link between

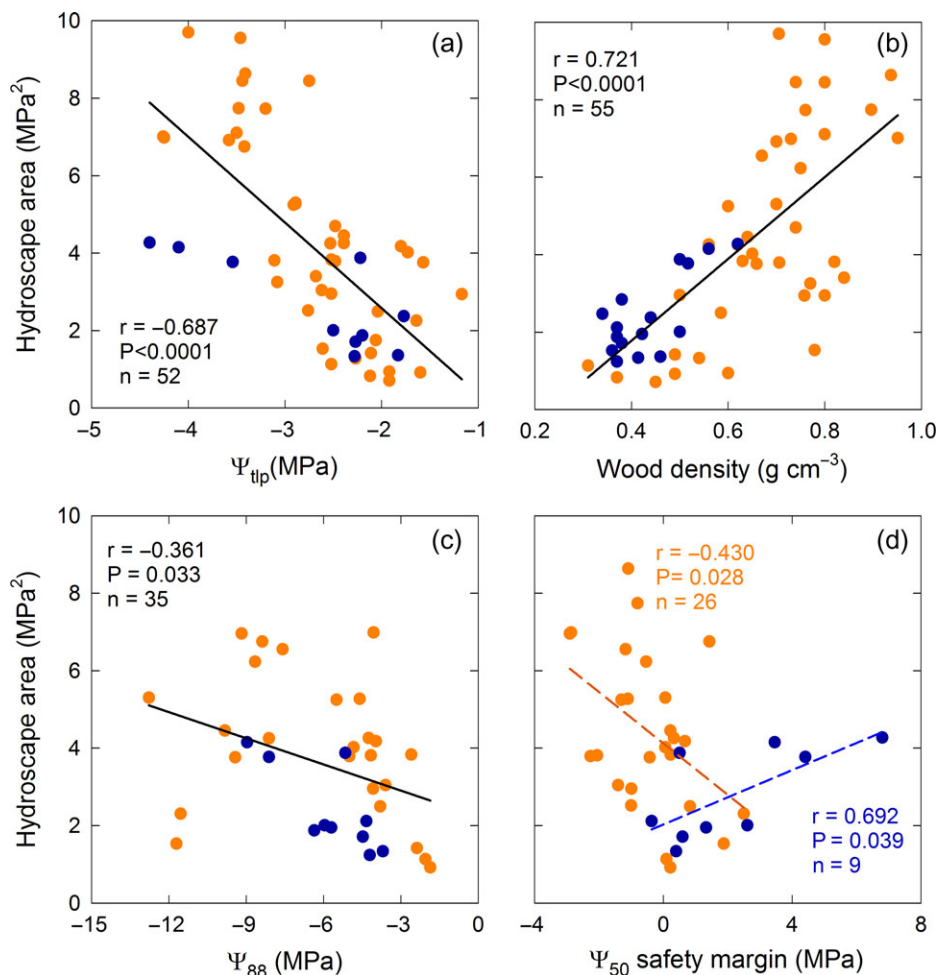


Figure 3. Hydroscape area in relation to (a) leaf water potential at the turgor loss point (Ψ_{tlp}), (b) wood density, (c) the water potential causing 88% loss in branch xylem hydraulic conductivity (Ψ_{88}) and (d) the difference between the minimum diurnal leaf water potential the water potential causing 50% loss in branch xylem hydraulic conductivity (Ψ_{50} safety margin). Solid lines represent significant regressions across all species. Dashed lines represent significantly different regressions between the angiosperms (orange symbols) and gymnosperms (blue symbols).

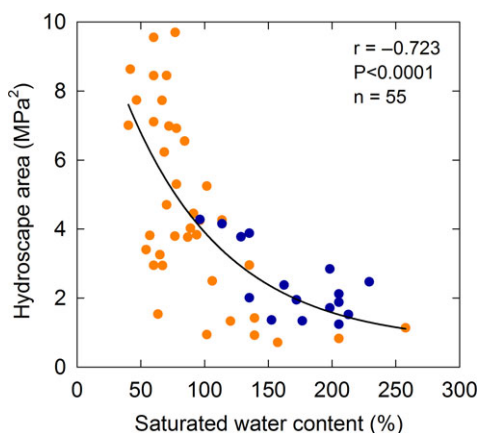


Figure 4. Correlation between hydroscape area and wood saturated water content, a proxy for hydraulic capacitance. Symbols as in Figure 3.

wood density and embolism resistance has been attributed to the thicker xylem conduit walls needed to avoid wall collapse

and withstand the lower operating pressures that plants experience during drought (Hacke et al. 2001, Lens et al. 2011). Combined with the finding that because of their higher wood density, the more anisohydric species tended to have lower stem water storage capacity (Figure 4), it seems that along a continuum of iso/anisohydry, there is decreasing reliance on capacitance to buffer changes in xylem tension to avoid embolism and an increase in reliance on structural reinforcement of xylem to resist embolism.

We further found that more negative values of Ψ_{88} were associated with larger Ψ_{50} safety margins (Figure 6f). This pattern may be related to observations that species with higher embolism resistance showed lower capacity to recover hydraulic function once conductivity had been lost (Ogasa et al. 2013, Trifilò et al. 2015). Combined with the observation that the higher wood density was associated with more negative values of Ψ_{88} (Figure 6b), it is not surprising that higher wood density resulted in larger Ψ_{50} safety margins in gymnosperms (Figure 6d).

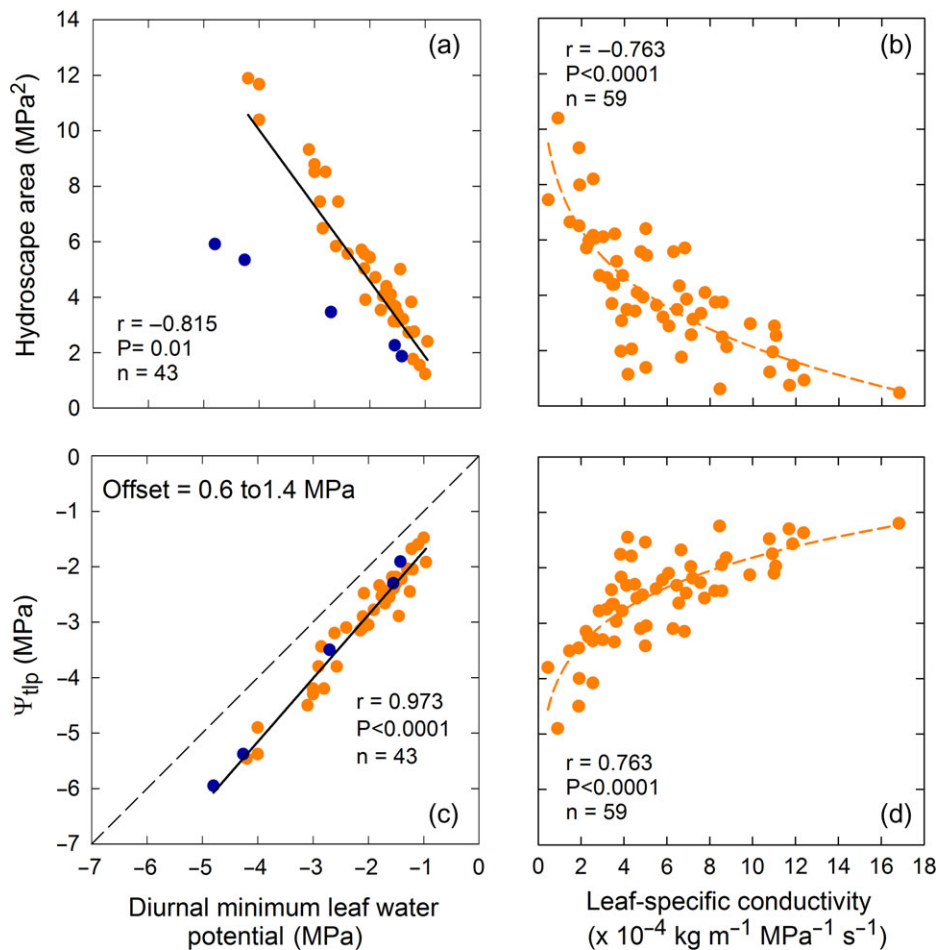


Figure 5. Relationships between hydroscape area, leaf turgor loss point (Ψ_{tlp}), diurnal minimum leaf water potential and leaf-specific conductivity. The hydroscape area in (a) and (b) was generated from the Ψ_{tlp} in (c) and (d), based on the relationship between Ψ_{tlp} and hydroscape area in Figure 3a. Orange symbols represent angiosperms and blue symbols gymnosperms.

In one study, the Ψ_{50} safety margin was positively correlated with wood density only for the more isohydric species (Trifilò et al. 2015). Our global pattern is partially consistent with this finding because the gymnosperm species in our dataset were clustered closer to the more isohydric end of the spectrum (Figure 2b). It is interesting that in the context of iso/anisohydry, the relationship between wood density and the Ψ_{50} hydraulic safety margin was negative for the angiosperms (Figure 6d). These results indicate that a negative correlation between wood density and stem safety margins exists in the angiosperms, or that other variables are influencing this relationship, which may differ between angiosperms and gymnosperms.

Although plants have many mechanisms to avoid embolism formation and propagation, the capacity for embolism refilling varies markedly among species (Brodrribb et al. 2010, Ogasa et al. 2013, Uri et al. 2013, Trifilò et al. 2015). The contrasting correlations between wood density and stem safety margin in gymnosperms and angiosperms are likely to be related to differences across the two major plant lineages in the capacity to recover from embolism. The transport of sugars from non-

structural carbohydrate depolymerization in nearby parenchyma cells into empty conduits is proposed to be involved in embolism refilling (Secchi and Zwieniecki 2011, 2016, Johnson et al. 2012). Across the range of wood density observed in the two groups, gymnosperms have a lower xylem parenchyma fraction than angiosperms (Morris et al. 2016), consistent with their lower woody tissue non-structural carbohydrate concentration (Johnson et al. 2012) and apparently negligible capacity for reversal of massive embolism (Brodrribb et al. 2010). This is consistent with the positive relationship between the Ψ_{50} safety margin and wood density in gymnosperms (Figure 6d). In contrast, a number of woody angiosperm species have been observed to readily recover from high levels of experimentally induced embolism (Ogasa et al. 2013, Uri et al. 2013, Trifilò et al. 2015). However, the validity of these observations, especially in species with long xylem vessels, has been questioned (Cochard and Delzon 2013). Thus, the apparently negative hydraulic safety margins in angiosperms with the highest wood density do not necessarily imply that they are at greater risk of irreversible hydraulic failure than gymnosperms with larger

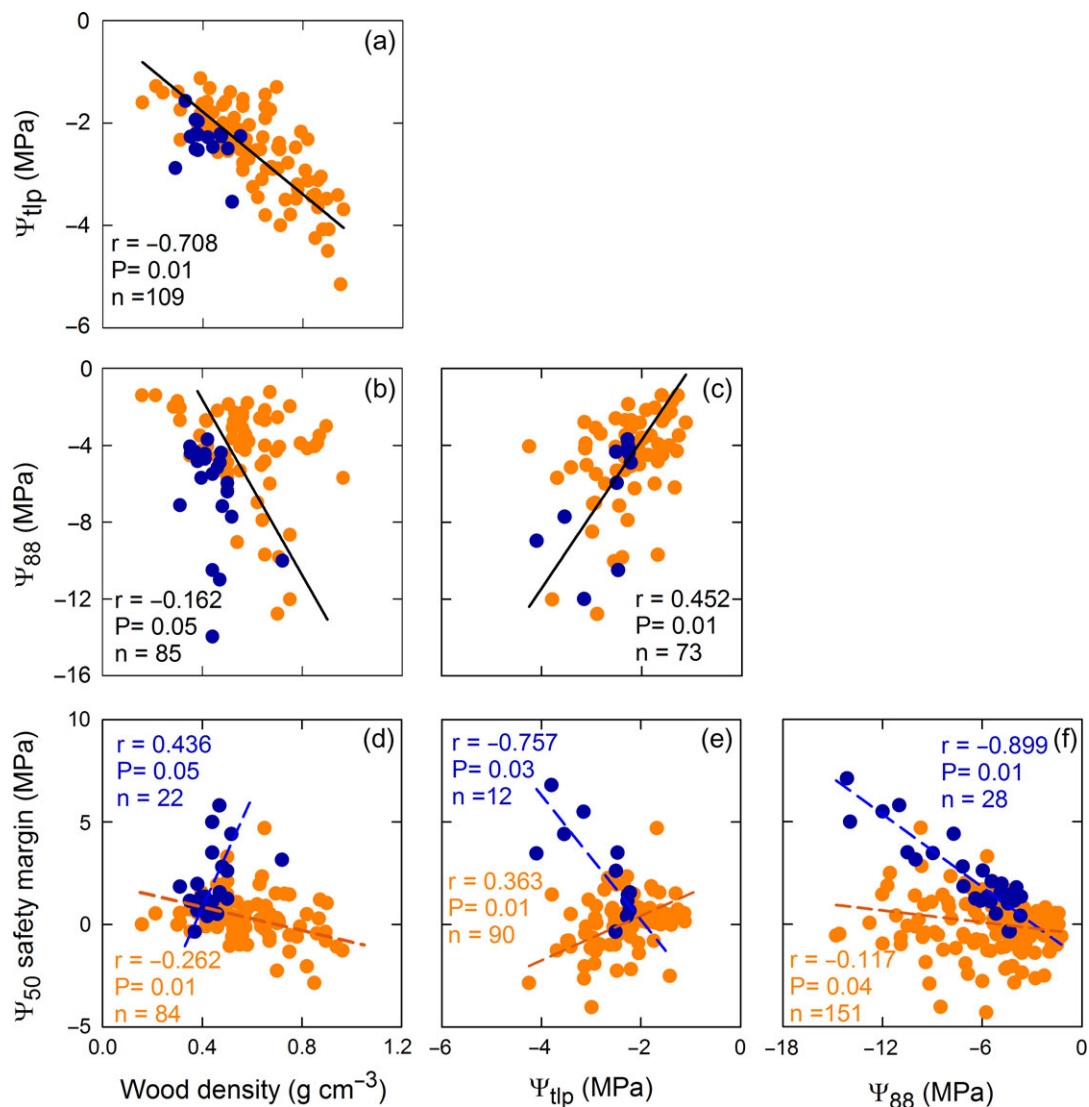


Figure 6. Relationships among functional traits serving as proxies for iso/anisohydry. Symbols and lines as in Figure 3. Note that artefacts during xylem vulnerability curve measurement in long-vesseled angiosperm species may have contributed to the generally greater scatter in the angiosperm data in (b)–(f). However, this was likely not an issue for the gymnosperms, which have tracheids rather than vessels.

safety margins. Moreover, the absolute value of the slope of the relationship between wood density and the Ψ_{50} safety margin in angiosperms is much smaller than that of gymnosperms, suggesting a greater relative importance of stem hydraulic safety margins in gymnosperms than in angiosperms. This is consistent with the notion that stem safety margins of gymnosperms but not angiosperms influenced the species-specific mortality rate deviations from the mean community averaged tree mortality rate (Anderegg et al. 2016).

Trade-offs along a spectrum of iso/anisohydry at the leaf level

In greenhouse experiments, water-use efficiency decreased with increasing anisohydry (Attia et al. 2015, Meinzer et al. 2017). However, the lower leaf level intrinsic water-use efficiency of

anisohydric species might be compensated for by faster stomatal responses to rapid fluctuations in environmental variables and higher rates of photosynthesis per unit leaf area under non-drought conditions (Meinzer et al. 2017). The increase in the 'turgor safety margin' with increasing anisohydry implies an additional trade-off of increasing energy costs for solute uptake and maintenance with increasing anisohydry (Figure 5a and c). In addition to the overall energy cost for maintaining higher bulk leaf solute concentrations, the marginal energy costs increase as indicated by the steeper decline in Ψ_{tlp} than in diurnal minimum leaf water potential across and within species. The consistency of the relationship between Ψ_{tlp} and diurnal minimum leaf water potential among species growing in a range of habitats from deserts to tropical forests and savannas, as well as greenhouse-grown plants, suggests that the trade-off of increasing energy costs for solute uptake and maintenance against increasing

anisohydry may be largely independent of growth environment. Therefore, there may be a universal scaling relationship among woody species in terms of how stomata regulate transpiration and daily minimum leaf water potential in relation to bulk leaf osmotic properties.

Trade-offs along a spectrum of iso/anisohydry between leaf and stem

The Ψ_{tip} is a trait quantifying the ability to 'tolerate' drought and is determined by the inherent basal osmotic potential at full leaf hydration (Bartlett et al. 2012a). Generally, a more negative Ψ_{tip} is thought to imply greater drought tolerance (Bartlett et al. 2012a, 2014). According to the 'fast-slow' plant economics spectrum, slow strategy species with high tissue density have a long tissue life span and low rates of resource acquisition and flux, and have a greater chance of survival when resources are scarce (Reich 2014). Wood density is inversely correlated with Ψ_{88} (Figure 6b), and thus a high wood density could reflect a high ability to 'tolerate' drought to some extent by building conduits with high hydraulic safety. Based on the preceding relationships, slow strategy species with higher wood density and lower Ψ_{tip} may have a greater chance of survival during drought events. In addition to the results from our global data set, negative correlations between wood density and Ψ_{tip} are supported by previous studies with fewer species (Meinzer et al. 2008, Savage and Cavender-Bares 2012). This notion is further consistent with several studies where negative correlations between wood density and drought-induced mortality were found (Chave et al. 2009, Greenwood et al. 2017).

However, one study in a temperate deciduous forest in central North Carolina found that species with high wood density did not cope well with drought (Hoffmann et al. 2011), consistent with niche partitioning, but inconsistent with the 'fast-slow' trade-off theory. Desiccation tolerance and avoidance are two major mechanisms of drought resistance in woody plants. The relative importance of these two mechanisms can change within species across different habitats (Picon et al. 1996). Wood density is inversely correlated with stem wood saturated water content (a proxy for stem hydraulic capacitance) and thus high wood density is also a trait reflecting the low ability to 'avoid' drought to some extent through buffering transient fluctuations in xylem pressure (Meinzer et al. 2009). Moreover, the unexpected result from Hoffmann et al. (2011) also may be attributable to other drought avoidance traits such as rooting depth and morphology and drought-induced leaf shedding. These drought avoidance strategies are clearly more complex than simpler traits such as wood density and Ψ_{tip} , suggesting that wood density and Ψ_{tip} may not be adequate proxies for predicting susceptibility to drought-induced mortality. Instead, the safety margin, for example, integrates the inherent xylem resistance to embolism and some elements of stomatal response to leaf water potential regulated by multiple physiological processes, and thus

performed better in predicting tree mortality across species within individual ecosystems (Anderegg et al. 2016).

The utility of iso/anisohydry in predicting drought mortality

Using Ψ_{tip} as a surrogate for Ψ at stomatal closure, Martin-StPaul et al. (2017) found that the difference between species-specific values of Ψ_{tip} and stem Ψ_{50} increased with decreasing Ψ_{50} in both gymnosperms and angiosperms, leading them to conclude that timely stomatal closure to maintain an adequate hydraulic safety margin is necessary for avoiding drought-induced mortality. For the gymnosperms sampled in our study, the relationship between Ψ_{tip} and the Ψ_{50} safety margin (Figure 6e) was consistent with that reported by Martin-StPaul et al. (2017). However, the angiosperms we sampled showed the opposite pattern. Data for additional species are needed to test the generality of the relationship between Ψ at stomatal closure and hydraulic safety margins across gymnosperms and angiosperms. The use of Ψ at $\Psi_{\text{pd}} = \Psi_{\text{md}}$ offers a quantitative alternative to Ψ_{tip} as a surrogate for the level of plant water deficit causing stomatal closure. Species that close their stomata later during soil drying likely, but not necessarily, have much larger HAs than species that close their stomata early. However, it should be noted that Ψ at $\Psi_{\text{pd}} = \Psi_{\text{md}}$ alone cannot be used as an indicator of the risk of drought-induced mortality from hydraulic failure, since it merely shows how fast stomata close during soil drying rather than how fast stomata close relative to stem embolism resistance (Martin-StPaul et al. 2017).

The reliability of metrics of iso/anisohydry as predictors of species' vulnerability to drought-induced mortality has not been systematically evaluated. In an evaluation of three potential definitions of the degree of iso/anisohydry: minimal seasonal Ψ_{md} , seasonal variability of Ψ_{md} and the slope σ , Martínez-Vilalta and García-Forner (2017) found that they yielded little information by themselves about leaf gas exchange dynamics during soil drying and thus were not useful predictors of plant vulnerability to drought. However, Gu et al. (2015) conducted decade-long continuous observations of tree mortality and predawn leaf water potential, and found that vulnerability of woody species to drought-induced mortality may not vary monotonically, with species occupying middle positions along the continuum being less vulnerable than those operating toward either extreme. This non-monotonic relationship might be explained by considering relationships between embolism resistance and rooting depth. Although resistance to xylem embolism has been observed to increase with rooting depth, there is also evidence that the opposite relationship between these two traits can also occur (Martínez-Vilalta and García-Forner 2017). Therefore, lower embolism resistance in strongly isohydric species with smaller hydroscape areas (Figure 3c) could be compensated by deeper root systems reducing the rate and magnitude of decline Ψ_{md} during soil drying and potentially increasing survival during drought (Pivovarov et al. 2018). However, the potential

advantage of higher embolism resistance in strongly anisohydric species with larger hydroscape areas (Figure 3c) could be offset by shallower rooting depth.

Conclusions

A continuum of coordination and trade-offs among co-evolved traits gives rise to a continuum of stringency of regulation of plant water status that can be characterized and quantified as spanning relative isohydry to anisohydry. Mapping the global distribution pattern of the degree of plant iso/anisohydry still remains challenging because the existing metrics, whether based on the trajectories of Ψ_{md} and Ψ_{pd} during soil drying (Martinez-Vilalta et al. 2014, Garcia-Forner et al. 2016, Meinzer et al. 2016), stomatal conductance in relation to various levels of leaf Ψ (Klein 2014) or maximum stomatal conductance and stem xylem vulnerability curves (Skelton et al. 2015), all require labor-intensive measurements. In our analysis, we detected two powerful proxies for ranking the degree of plant isohydry for a wide range of species and biomes: Ψ_{tip} and wood density. More importantly, both of these traits can be easily and rapidly determined, and therefore show promise for a priori mapping and understanding of the global distribution pattern of the degree of plant iso/anisohydry.

The coordination and trade-offs described here pertain to aboveground traits. However, plant root traits, including morphology (Comas and Eissenstat 2009, Liu et al. 2015), architecture (Lynch 1995) and phenology (McCormack et al. 2014, Fu et al. 2016) show considerable variation among and within species. The highly diverse and plastic traits of roots are essential components of overall species' strategies for acquisition of water and coping with drought (Nord and Lynch 2009, Comas et al. 2013, Pierik and Testerink 2014, Brunner et al. 2015). Expanding exploration of the potential trade-offs among above- vs belowground traits along the continuum of iso/anisohydric regulation of plant water status is a critical area for future research.

Supplementary Data

Supplementary Data for this article are available at *Tree Physiology* Online.

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Conflict of interest

None declared.

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