

The correlations and sequence of plant stomatal, hydraulic, and wilting responses to drought

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Climate change is expected to exacerbate drought for many plants, making drought tolerance a key driver of species and ecosystem responses. Plant drought tolerance is determined by multiple traits, but the relationships among traits, either within individual plants or across species, have not been evaluated for general patterns across plant diversity. We synthesized the published data for stomatal closure, wilting, declines in hydraulic conductivity in the leaves, stems, and roots, and plant mortality for 262 woody angiosperm and 48 gymnosperm species. We evaluated the correlations among the drought tolerance traits across species, and the general sequence of water potential thresholds for these traits within individual plants. The trait correlations across species provide a framework for predicting plant responses to a wide range of water stress from one or two sampled traits, increasing the ability to rapidly characterize drought tolerance across diverse species. Analyzing these correlations also identified correlations among the leaf and stem hydraulic traits and the wilting point, or turgor loss point, beyond those expected from shared ancestry or independent associations with water stress alone. Further, on average, the angiosperm species generally exhibited a sequence of drought tolerance traits that is expected to limit severe tissue damage during drought, such as wilting and substantial stem embolism. This synthesis of the relationships among the drought tolerance traits provides crucial, empirically supported insight into representing variation in multiple traits in models of plant and ecosystem responses to drought.

drought tolerance | stem hydraulics | leaf hydraulics | stomatal closure | turgor loss point

Plants worldwide are expected to face more frequent and severe droughts under climate change (1). Characterizing drought tolerance for diverse species is key to improved predictions of ecosystem responses to global change (2), and ecological and phylogenetic patterns have been established across many species for individual drought tolerance traits (3–7). However, plant drought tolerance is determined by multiple traits. The relationships among traits within plants and across species have not been evaluated for general patterns across global plant diversity. We synthesized the published data to elucidate global patterns in the relationships among stomatal, hydraulic, and leaf mesophyll drought tolerance traits. We evaluated the roles of functional coordination, covariance with water stress, and shared ancestry in driving trait correlations across species. Additionally, we focused on clarifying relationships among drought tolerance traits within plants of given species, i.e., determining the sequence of their water potential thresholds.

Classical drought tolerance traits quantify the water potentials that induce declines in key physiological processes, such as stomatal conductance, hydraulic conductivity, and cell turgor pressure. Previous studies have shown that these water potential thresholds are intercorrelated for small species sets (8–12). We tested these correlations for a large dataset to produce a framework for extrapolating plant responses to a wide range of water stress from one or two traits. Evaluating these correlations across a global dataset can provide additional insights into their drivers. Drought tolerance traits can be correlated across species because of (i) functional

coordination, such as mechanistic linkages; (ii) concerted convergence (13), i.e., coselection by the environment, wherein traits are directionally but independently selected by water supply to optimize overall plant function; and/or (iii) shared ancestry. We compiled hypotheses from the literature for the drivers of each trait correlation, and evaluated these hypotheses by testing for greater coordination among traits than explained by water stress and relatedness. Water stress was measured as the minimum leaf water potential observed over the course of a year or during the dry season, at predawn ($\Psi_{\min, PD}$) and midday ($\Psi_{\min, MD}$). $\Psi_{\min, PD}$ is taken when transpiration is at its minimum and the water potential of the plant is closest to equilibration with that of the soil, whereas $\Psi_{\min, MD}$ is affected by any cuticular or stomatal transpiration and, thus, broadly captures the integrated effects of plant traits and the environment on the minimum water potential a plant reaches in natural conditions (14).

The sequence of water potential thresholds for drought tolerance traits within a plant is expected to strongly impact overall plant function under water stress (8, 15–17). Previous studies have compared values for some traits (e.g., refs. 9, 10, and 18), but have not included enough traits or species to characterize their overall sequence. We tested the degree to which plants exhibit a trait sequence that is expected to limit severe drought damage. Plants are expected to undergo stomatal closure at sufficiently high water potentials to prevent wilting and/or substantial (i.e., $\geq 50\%$) declines in stem hydraulic conductivity (6, 19, 20). Additionally, the vulnerability segmentation hypothesis predicts that plants limit stem embolism by exhibiting less negative thresholds for declines

Significance

Many plant species face increasing drought under climate change, making plant drought tolerance integral to predicting species and ecosystem responses. Many physiology traits interact to determine overall drought tolerance, but trait relationships have not been assessed for general patterns across global plant diversity. We analyzed stomatal, hydraulic, and mesophyll drought tolerance traits for 310 species from ecosystems worldwide. We evaluated the sequence of drought responses for plants under increasing water stress, and showed that coselection with environmental water stress drives most trait correlations across species, with functional coordination additionally important for some relationships. These results provide insight into how variation in multiple traits should be represented within plants and across species in models of plant responses to drought.

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in hydraulic conductivity in the leaves and roots, thereby sequestering hydraulic damage in those organs (17). Plants that do not exhibit this trait sequence are expected to avoid drought damage by limiting water stress (i.e., maintaining a high $\Psi_{\min, MD}$ relative to thresholds for damage) through deep roots, capacitance from stored water, drought deciduousness, or a preference for mesic environments (21, 22), or to experience significant damage at $\Psi_{\min, MD}$ and survive through recovery processes (23).

We compiled species means from the published literature for 262 woody angiosperm and 48 gymnosperm species from 174 studies for the water potential thresholds for wilting, plant death, and declines in stomatal conductance (g_s) and hydraulic conductivity (K) of leaves, stems, and roots (trait symbols and definitions in Table 1, references in *SI Appendix, Table S1*, and ranges in *SI Appendix, Fig. S1*). Controversy has recently arisen regarding measurements of stem and root hydraulic traits (24), in particular about whether nonsigmoidal vulnerability relationships (i.e., of K vs. Ψ) are caused by methodological artifacts that overestimate vulnerability. We tested the correlations across species by using all available data (*SI Appendix, SI Methods*), but confirmed our conclusions for the smaller dataset derived from sigmoidal relationships ($n = 285$) and present these results in the main text (*Dataset S1*). We evaluated the drivers of the correlations and the trait sequence for the subset of species for which all traits were measured at the same site during the same ≤ 6 mo sampling period, to minimize intraspecific variation ($n = 238$) (*Dataset S2*). Both analyses used hydraulic traits derived from sigmoidal relationships, and the sequence analyses focused on woody dicots, because there was insufficient data to test other curve shapes or plant functional types.

Results and Discussion

Correlations Across Species in Drought Tolerance Traits. We found significant correlations among most of the drought tolerance traits, with r values ranging from 0.21 to 0.87 (Fig. 1 and *SI Appendix, Table S2*; $n = 11$ –151). The nonsignificant correlations were between $K_{\text{stem}} \Psi_{12}$ and $g_s \Psi_{50}$, and $K_{\text{leaf}} \Psi_{50}$ and $g_s \Psi_{50}$, $g_s \Psi_{95}$ and $K_{\text{stem}} \Psi_{88}$ ($P > 0.1$, $n = 11$ –52). These correlations were robust to vulnerability curve shape, except that $K_{\text{leaf}} \Psi_{50}$ and $K_{\text{stem}} \Psi_{88}$ were correlated when including data for all curves ($P = 0.03$, $n = 61$; *SI Appendix, Table S3*). The stomatal and leaf hydraulic trait correlations represent particularly small species sets, indicating a need for more measurements of these traits. Nearly all traits were correlated with $\Psi_{\min, MD}$ and $\Psi_{\min, PD}$, with r values ranging from 0.21 to 0.86 (*SI Appendix, Figs. S2 and S3 and Table S2*). $\Psi_{\min, PD}$ and $K_{\text{leaf}} \Psi_{50}$ were not significantly correlated ($P = 0.07$, $n = 44$), and there were insufficient data to test correlations between $\Psi_{\min, PD}$ and the stomatal traits. Six of the 19 correlations with sufficient data to test ($n \geq 10$ for each functional type) were significantly different between the angiosperms and gymnosperms. $K_{\text{stem}} \Psi_{12}$ was significantly correlated with $K_{\text{leaf}} \Psi_{50}$ and $\Psi_{\min, MD}$ in the gymnosperms but not the angiosperms (*SI Appendix, Table S4 and Fig. S2E*), whereas the two functional types showed significantly different slopes for the correlations of $K_{\text{stem}} \Psi_{50}$ with π_{tlp} and $K_{\text{stem}} \Psi_{12}$ (Fig. 1D), and of $\Psi_{\min, MD}$ with $K_{\text{stem}} \Psi_{50}$ and $K_{\text{root}} \Psi_{50}$ (*SI Appendix, Fig. S2 F and H*).

Applying the Framework To Predict Drought Tolerance Traits. These correlations provide a framework representative of many species for extrapolating plant responses to a wide range of water stress from a small number of measured traits. Extrapolating from the correlations with $K_{\text{stem}} \Psi_{50}$, which has been measured for the most species (4), or π_{tlp} , which can be assessed rapidly (25), provides a reasonable estimate for less commonly measured

Table 1. The symbol, definition, and functional significance of the drought tolerance traits and the environmental water supply and general plant water status variables

Symbol	Definition	n	Significance
Ψ_w	Water potential		Potential energy of water; a thermodynamically explicit and scalable index of water status
$\Psi_{\text{leaf}}, \Psi_{\text{stem}}, \Psi_{\text{root}}$	Ψ_w of the leaf, stem, and root		Index of hydration and the demand for water of each organ
π_{tlp}	Bulk leaf turgor loss point, the Ψ_{leaf} where turgor potential = 0	285	Point at which, on average, leaf cells lose turgor and the leaf wilts (7)
$g_s \Psi_{50}$	Ψ_{leaf} at 50% loss of stomatal conductance	49	Ψ_w at 50% loss is a standard and, thus, comparable measure of drought tolerance across physiological processes (6)
$g_s \Psi_{95}$	Ψ_{leaf} at 95% loss of stomatal conductance	49	Approximates the maximum leaf water stress a plant can tolerate while maintaining gas exchange and C uptake
$K_{\text{leaf}} \Psi_{50}$	Ψ_{leaf} at 50% loss of leaf conductivity	117	Hydraulic traits measure drought impacts on the water supply for transpiration, which limits gas exchange and C uptake (17). Leaf water supply is hypothesized to be the most direct hydraulic constraint on transpiration (8)
$K_{\text{stem}} \Psi_{12}$	Ψ_{stem} at 12% loss of stem conductivity	208	Early declines in stem water supply are expected to impact gas exchange and C uptake more directly than later declines (10)
$K_{\text{stem}} \Psi_{50}$	Ψ_{stem} at 50% loss of stem conductivity	286	Hypothesized to correspond closely to the maximum water stress plants tolerate in natural conditions (4)
$K_{\text{stem}} \Psi_{88}$	Ψ_{stem} at 88% loss of stem conductivity	204	Hypothesized to be the point of irreversible xylem damage (18)
$K_{\text{root}} \Psi_{50}$	Ψ_{root} at 50% loss of root conductivity	44	Roots are hypothesized to be the “weakest link” (least tolerant organ), limiting tolerance of the entire hydraulic system (45)
Plant Ψ_{lethal}	Ψ_{leaf} at plant death; here, the Ψ_{leaf} at which all leaves show tissue damage	15	Integrates physiological and metabolic drought responses and recovery and directly links drought to performance (11)
$\Psi_{\min, MD}, \Psi_{\min, PD}$	Seasonal minimum water potential (Ψ_{\min}), the most negative Ψ_{leaf} measured in the growing season at predawn (PD) or midday (MD)	174	Midday measurements quantify the strongest water stress the leaves experience in a typical year, whereas predawn measurements characterize the most negative soil water potential (13)

n is the number of species compiled for each trait. All units are MPa.

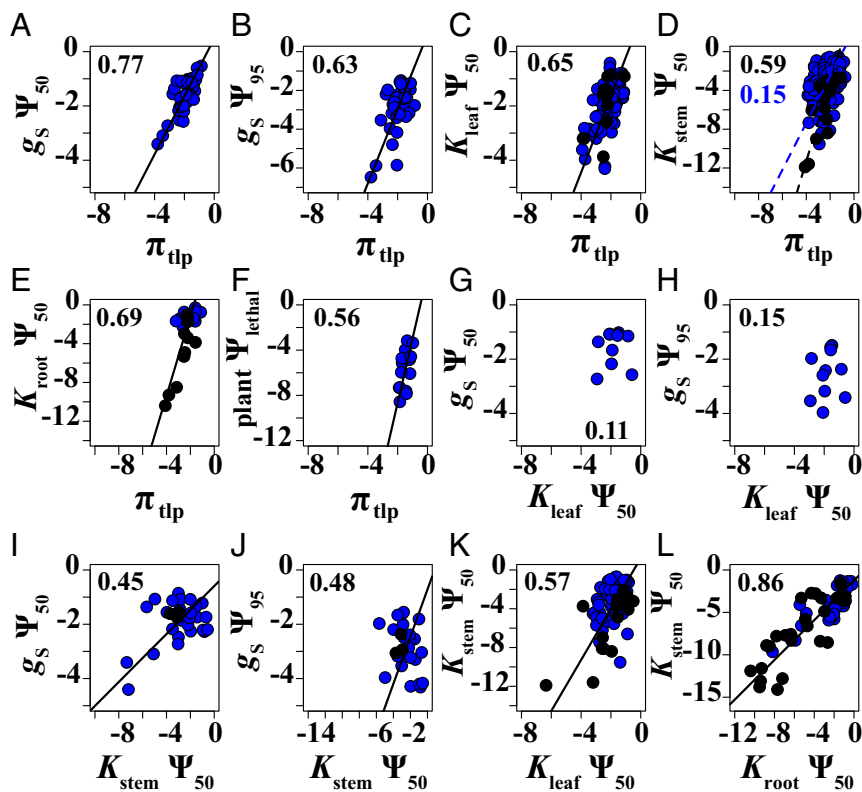


Fig. 1. Correlations among drought tolerance traits across species. Symbols follow Table 1. Blue points represent angiosperms, and black points represent gymnosperms. Solid black lines are standard major axis relationships that are significant across all species. Dashed lines are correlations that are significantly different between the gymnosperms (black lines) and angiosperms (blue lines). All significant correlations remained significant after correcting for multiple tests (46). The r values are shown on each graph, and P values and sample sizes are in *SI Appendix, Table S2*. All of the traits were significantly correlated (A–F and I–L), except for $K_{\text{leaf}} \Psi_{50}$ and $g_s \Psi_{50}$ (G) and $g_s \Psi_{95}$ (H). For graphical clarity, correlations with $K_{\text{stem}} \Psi_{12}$ and Ψ_{88} are not shown. All of the stem hydraulic traits showed the same correlations, except that $K_{\text{stem}} \Psi_{12}$ was not significantly correlated with $g_s \Psi_{50}$ and $K_{\text{leaf}} \Psi_{50}$ was not significantly correlated with $K_{\text{stem}} \Psi_{88}$ (*SI Appendix, Table S2*). $K_{\text{stem}} \Psi_{12}$ was significantly correlated with $K_{\text{leaf}} \Psi_{50}$ in the gymnosperms but not the angiosperms, whereas the two functional types showed significantly different slopes for the correlations of $K_{\text{stem}} \Psi_{50}$ with π_{tlp} (D) and with $K_{\text{stem}} \Psi_{12}$ (*SI Appendix, Table S4*). We did not compile variation in plant Ψ_{lethal} from the literature, because most published studies use different definitions for plant death, but instead show this correlation from the largest study of these traits (11) for comparison with the other correlations with π_{tlp} (F).

traits, until such data become available in the literature for more species (see *Dataset S3* for estimating traits from these correlations). The correlations strongly support predicting $K_{\text{leaf}} \Psi_{50}$ and, for the angiosperms, the stomatal traits from π_{tlp} ($r^2 = 0.40$ – 0.59), and π_{tlp} enabled trait estimation with considerably smaller prediction intervals than $K_{\text{stem}} \Psi_{50}$. π_{tlp} also enabled estimation of $\Psi_{\text{min, MD}}$ with smaller prediction intervals than $K_{\text{stem}} \Psi_{50}$ in both the angiosperms and gymnosperms. These “first pass” estimates lend expediency to assessing drought tolerance for many species, and potentially enable more detailed modeling of plant drought responses, given that few species have been studied relative to the worldwide diversity of plant species, and even these have only been assessed for a few traits.

Trait Correlations with Environmental Water Supply. The significant correlations with $\Psi_{\text{min, MD}}$ support the selective pressure of plant water stress on all of the traits (*SI Appendix, Fig. S2*). Further, the correlations with $\Psi_{\text{min, PD}}$ supported the use of any of the traits but $K_{\text{leaf}} \Psi_{50}$ to predict species distributions relative to soil water supply (*SI Appendix, Fig. S3*), although previous studies of smaller species sets have shown significant correlations between $K_{\text{leaf}} \Psi_{50}$ and precipitation (5, 26), indicating a need to test this relationship across yet-larger species sets. Notably, $\Psi_{\text{min, MD}}$ was especially strongly correlated with $g_s \Psi_{50}$ and $g_s \Psi_{95}$ ($r = 0.76$ – 0.86), suggesting that these stomatal traits may be especially important influences on the maximum water stress the leaves experience (*SI Appendix, Fig. S2 B and C*), whereas $K_{\text{root}} \Psi_{50}$ had the strongest association with minimum soil water potential ($r = 0.72$) (*SI Appendix, Fig. S3F and Table S2*). Testing these hypotheses requires measuring more traits for the same species, and, especially, focusing on closely related species within clades that have diversified across habitats ranging widely in water availability.

Disentangling the Basis for Trait Correlations. We found support for hypotheses from the literature (Fig. 2) that attributed drought tolerance trait correlations to functional coordination, concerted

convergence (wherein water stress selects for each trait independently), and/or shared ancestry. Of the 14 correlations with sufficient data to test ($n = 19$ – 64), 4 correlations were improved beyond the correlation of each trait with $\Psi_{\text{min, MD}}$ alone by accounting for a trait predictor (29%), 1 by accounting for phylogeny (7%), and 1 by accounting for both (7%) (*SI Appendix, Table S5*). Thus, for a total of 43% of trait correlations, we could resolve linkages beyond simply a correlation arising from independent associations with water stress. As hypothesized, π_{tlp} improved prediction of $K_{\text{leaf}} \Psi_{50}$, and vice versa, whereas the stem hydraulic traits $K_{\text{stem}} \Psi_{12}$ and Ψ_{88} were not correlated with π_{tlp} after accounting for water stress. However, contrary to prediction, $K_{\text{stem}} \Psi_{50}$ and $K_{\text{leaf}} \Psi_{50}$ were more related than expected from correlations with water stress alone. Further, the π_{tlp} improved prediction of $K_{\text{stem}} \Psi_{50}$, and $K_{\text{stem}} \Psi_{12}$ improved prediction of $K_{\text{leaf}} \Psi_{50}$, but not vice versa.

It is well recognized that $\Psi_{\text{min, MD}}$ can be affected by plant traits in addition to soil dryness (14), so we verified these findings for $\Psi_{\text{min, PD}}$ ($n = 18$ – 40 ; *SI Appendix, Table S6*). The water stress variables were strongly correlated ($r^2 = 0.85$, $P < 0.001$, $n = 71$). The coordination analyses showed largely similar results, with the exceptions that $K_{\text{leaf}} \Psi_{50}$ and $K_{\text{stem}} \Psi_{12}$ were both more strongly related than expected from associations with $\Psi_{\text{min, PD}}$, whereas $K_{\text{stem}} \Psi_{50}$ and π_{tlp} were not correlated after accounting for $\Psi_{\text{min, PD}}$.

Several mechanisms could potentially drive the observed trait coordination. The coordination between $K_{\text{leaf}} \Psi_{50}$ and π_{tlp} supports the hypothesized mechanistic effect of turgor loss in the mesophyll on declines in K_{leaf} via the extraxylary pathway (20). As a leaf dries, and the mesophyll cells lose turgor, the cells shrink, and aquaporin activity and abscisic acid levels can shift rapidly, affecting water transport (20). The extraxylary pathway accounts for a significant proportion of overall leaf hydraulic resistance (~ 25 – 70%) (27), and the vulnerability of this pathway strongly impacts $K_{\text{leaf}} \Psi_{50}$ (20). Indeed, species with more negative π_{tlp} values undergo less cell shrinkage under dehydration and have slower declines in K_{leaf} with leaf water potential (20). The coordination between $K_{\text{leaf}} \Psi_{50}$ and $K_{\text{stem}} \Psi_{50}$,

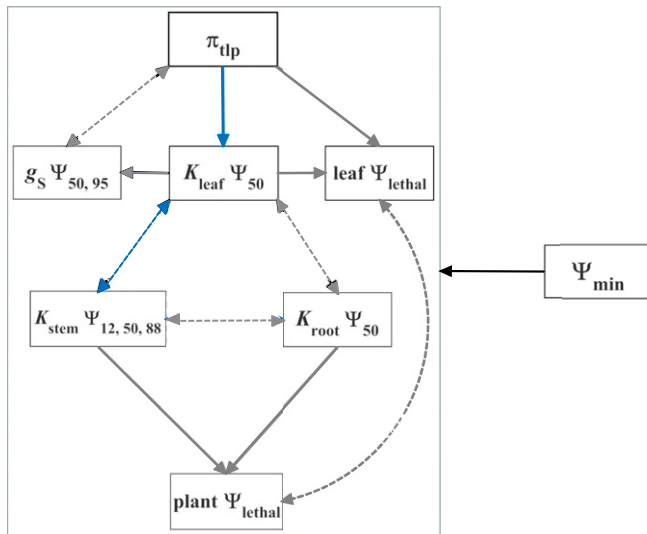


Fig. 2. Testing hypotheses for the drivers of the correlations among the drought tolerance traits. Most of the trait correlations are predicted to be driven by concerted convergence, wherein the selective pressure of water stress ($\Psi_{\min, MD}$ or $\Psi_{\min, PD}$) acts independently on each trait to optimize overall plant function during drought (10, 17, 28). These hypotheses are indicated with dashed lines. Additionally, π_{tlp} was hypothesized to influence $K_{leaf} \Psi_{50}$ mechanistically (20). $K_{leaf} \Psi_{50}$, in turn, would influence $g_s \Psi_{50}$ and Ψ_{95} and the threshold Ψ_{lethal} for leaf death (leaf Ψ_{lethal}) (30, 31), and the stem and root hydraulic traits would influence the plant mortality threshold (plant Ψ_{lethal}) (19). These hypotheses are indicated with solid lines. As predicted, π_{tlp} and $K_{leaf} \Psi_{50}$ were more correlated than expected from water stress and relatedness alone. Functionally coordinated traits are indicated with blue lines. Other correlations were best explained by the independent relationship of each trait with water stress. Concerted convergence is indicated with black lines. Conversely, $K_{stem} \Psi_{50}$ was also more strongly correlated with $K_{leaf} \Psi_{50}$ and, when characterizing water stress with $\Psi_{\min, MD}$, with π_{tlp} than expected from concerted convergence, consistent with strong functional coordination within the hydraulic system across organs (SI Appendix, Tables S5 and S6). The remaining hypotheses had insufficient data to test (indicated with gray lines).

and potentially, $K_{stem} \Psi_{12}$, might arise because hydraulic function in these organs is closely linked. At a given transpiration rate, K_{stem} influences Ψ_{leaf} , and K_{leaf} impacts the gradient between Ψ_{leaf} and Ψ_{stem} (17, 27). Further, many other extrinsic factors beyond Ψ_{\min} (e.g., vapor pressure deficit, light exposure) may directionally select for stem and leaf hydraulic traits, producing correlations among these traits within habitats with similar soil water supply. Conversely, independent linkages with $K_{leaf} \Psi_{50}$ may partly drive the correlation between $K_{stem} \Psi_{50}$ and π_{tlp} . Sampling these traits across a wider range of species and environments has the potential to resolve the coordination between π_{tlp} and $K_{stem} \Psi_{50}$ after accounting for their linkages with $K_{leaf} \Psi_{50}$ and water stress.

Linkages Between the Stomatal and Hydraulic Traits. The correlations of stomatal and hydraulic traits can provide insight into their functional linkages. Whereas the drivers of stomatal closure are not fully resolved, the hydromechanical model predicts that guard cells regulate their aperture in response to the water status at the stomatal evaporation site; this water status, in turn, is influenced by the hydraulic conductivity of the stems, leaves, and roots (8, 28, 29). Further, declines in stomatal conductance have been hypothesized to respond more directly to K_{leaf} than K_{stem} (30, 31). Our analyses instead showed that across species, the stomatal traits were significantly correlated with stem but not leaf vulnerability. The statistical independence of $g_s \Psi_{50}$ and Ψ_{95} and $K_{leaf} \Psi_{50}$ is consistent with previous studies, showing wide species variation in the safety margins between stomatal closure

and leaf hydraulic dysfunction (32), wherein species vary between “isohdry,” which maintains high Ψ_{leaf} and K_{leaf} via early stomatal closure, and “anisohdry,” which maintains gas exchange to low Ψ_{leaf} at the expense of hydraulic function. The correlation between the stomatal traits and $K_{stem} \Psi_{50}$ and Ψ_{88} corroborates a previous metaanalysis of species from ecosystems worldwide (6), but contradicts two studies within specific ecosystems (10, 33). Thus, the coordination of stomatal sensitivity with stem vulnerability across species appears to be related to their independent roles in drought tolerance rather than to coordinated function, with stomatal responses affecting carbon uptake during mild and moderate drought, and vulnerability affecting the ability of stems to survive strong drought (2, 15).

Sequence of Drought Response Traits. On average, the woody dicots exhibited a typical trait sequence that is expected to limit severe tissue damage during drought, such as wilting and substantial stem embolism (Fig. 3). The 12% declines in stem conductivity ($K_{stem} \Psi_{12}$) occurred at the least negative water potentials, followed sequentially by $K_{leaf} \Psi_{50}$, wilting (π_{tlp}), and 50% and 88% declines in stem conductivity ($K_{stem} \Psi_{50}$ and Ψ_{88}) (Fig. 3B). The positions of these traits in the sequence were clearly resolved by mixed effects models, which showed significant differences between all of these traits (SI Appendix, Table S7). Wilting (π_{tlp}) occurred after $g_s \Psi_{50}$, as predicted, but before $g_s \Psi_{95}$, contrary to the expectation that plants would undergo stomatal closure at sufficiently high water potentials to prevent wilting. Placing $\Psi_{\min, MD}$ in this sequence indicated the drought responses that plants experience under seasonal water stress in natural conditions. $\Psi_{\min, MD}$ occurred at similar water potentials as $K_{leaf} \Psi_{50}$, and significantly before wilting and $K_{stem} \Psi_{50}$, but after $K_{stem} \Psi_{12}$ (SI Appendix, Table S7). The water potential at plant death (plant Ψ_{lethal}) was the most negative trait. There were insufficient data to compare $g_s \Psi_{50}$ and $g_s \Psi_{95}$ to traits besides π_{tlp} , or to place $K_{root} \Psi_{50}$ in the sequence.

Phenology significantly affected one comparison (SI Appendix, Table S8). $K_{leaf} \Psi_{50}$ occurred after $\Psi_{\min, MD}$ in evergreen but not deciduous species, consistent with previous studies of smaller species sets showing that deciduous species undergo greater leaf hydraulic dysfunction to maximize carbon uptake, because the leaves are replaced annually (16). More studies are needed to characterize the variation in the sequence across leaf functional types within ecosystems and across ecosystems relative to water supply.

We applied additional statistics to confirm that the mean trait differences are robust to measurement uncertainty, and to evaluate the degree to which plants conform to the average trait sequence. We compared the 95% confidence intervals around mean trait values for each species for all traits for which SEs were provided (i.e., $g_s \Psi_{50}$, $K_{leaf} \Psi_{50}$, $K_{stem} \Psi_{50}$, π_{tlp} , and $\Psi_{\min, MD}$). Across all comparisons, 42–82% of the species significantly supported the findings for the mean trait differences shown in the general sequence (SI Appendix, Figs. S4–S6), confirming that these results were largely robust to measurement uncertainty. Vulnerability segmentation was strongly supported, with $K_{stem} \Psi_{50}$ significantly more negative than $K_{leaf} \Psi_{50}$ for 82% of the species, and no species significantly showing the opposite pattern (SI Appendix, Fig. S4). Plants showed the most variation in the order of π_{tlp} and $K_{stem} \Psi_{50}$, with the finding that π_{tlp} occurs at a less negative water potential significantly supported by 33% of the species and opposed by 21% (SI Appendix, Fig. S5). Notably, the low sample size at the ends of the stomatal response and hydraulic vulnerability curves and the nonlinear curve shapes suggest that $g_s \Psi_{95}$, $K_{stem} \Psi_{12}$, and $K_{stem} \Psi_{88}$ will tend to have much larger errors. Further, these traits are typically estimated from nonlinear regressions with organ water potential as the independent variable and extrapolated as x values from the regression at given y values. This convention precludes estimating SEs for these traits. Thus, strongly resolving the certainty of the position of these traits in

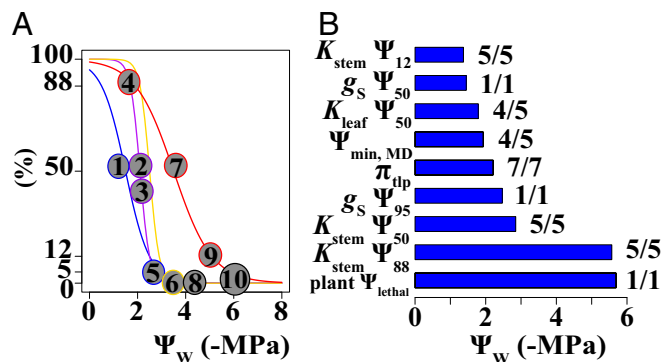


Fig. 3. The hypothesized (A) and observed (B) sequence of water potential values for the drought tolerance traits within individual plants. A shows the relationship between organ water potential (Ψ_w) and the percent decline in stomatal conductance (g_s , blue), hydraulic conductivity in the leaves, roots and stems (K_{leaf} and K_{root} , purple; K_{stem} , red), and turgor pressure (Ψ_p , yellow). The numbered circles show the order in which given declines in function will occur if plants generally follow a trait sequence that is expected to limit tissue damage during drought. In this sequence, 50% declines in stomatal conductance (g_s Ψ_{50} , #1) are expected to occur at the least negative water potentials to slow transpiration (37), followed by moderate (50%) declines in K_{leaf} and K_{root} (K_{leaf} and K_{root} Ψ_{50}) and minor (12%) declines in K_{stem} (K_{stem} Ψ_{12}), if leaf and root dysfunction protects the stem from embolism, as predicted by vulnerability segmentation (17). (These traits are labeled #2-4 but shown in the same position, because their order is not hypothesized). Stomatal closure, or g_s Ψ_{95} (#5), would occur before potentially major damage, including loss of turgor pressure in the leaf cells, or wilting (π_{tip} , #6), and 50% declines in K_{stem} (K_{stem} Ψ_{50} , #7) (6, 10). K_{stem} Ψ_{50} is hypothesized to limit the water stress that plants tolerate, and thus, we expected the most negative Ψ_{leaf} values plants reach under natural growing conditions ($\Psi_{min, MD}$, #8) to be near K_{stem} Ψ_{50} (4). Eighty-eight percent declines in K_{stem} (K_{stem} Ψ_{88} , #9) have been hypothesized to induce irreversible xylem damage and, thus, to occur somewhat before plant death (plant Ψ_{lethal} , #10) (19), which we estimated as the Ψ_{leaf} at which all leaves showed tissue damage (11). The sequence is determined from pairwise comparisons between all of the traits (SI Appendix, Table S7), but, for clarity, B shows the mean of each trait from its pairwise comparison with the trait immediately after (i.e., more negative than) it in the sequence. The traits generally followed this sequence, with the order of K_{stem} $\Psi_{12} > K_{leaf}$ Ψ_{50} & $\Psi_{min, MD} > \pi_{tip} > K_{stem}$ $\Psi_{50} > K_{stem}$ Ψ_{88} supporting the hypothesized sequence, with the exception that K_{leaf} Ψ_{50} and $\Psi_{min, MD}$ were not significantly different. π_{tip} occurred after g_s Ψ_{50} , as hypothesized, but before g_s Ψ_{95} , contrary to prediction. There were insufficient data to test K_{root} Ψ_{50} , or to compare the stomatal traits to any other trait. For each trait, the number to the left is the number of other traits it was significantly different from, and the number to the right is the total number of trait comparisons with sufficient data to test. Notably, the sequence is shown with respect to organ-specific water potentials; in the transpiring plant, the high resistance of the hydraulic pathway produces a gradient of increasingly negative water potentials from the root to the leaf. Thus, the stem may undergo less embolism than suggested by this sequence.

the sequence will require the further development of statistical and computational methods to estimate these uncertainties (34).

The sequence provides several key insights into plant responses to drought. First, the occurrence of K_{stem} Ψ_{50} at lower water potentials than $\Psi_{min, MD}$ is generally consistent with the “high embolism resistance” paradigm, wherein plants are predicted to prevent substantial (i.e., 50%) declines in K_{stem} over the course of typical variation in water supply, and contrary to the “high embolism repair” paradigm, which expects plants to typically reach such declines and maintain function through recovery mechanisms (15, 23, 35). However, $\Psi_{min, MD}$ was more negative than K_{stem} Ψ_{50} for nearly one-fifth of the species (SI Appendix, Fig. S4), consistent with a previous metaanalysis of data for stem hydraulic dysfunction that were also included in this study (4). These species may experience substantial embolism during drought and depend strongly on recovery mechanisms to survive, such as refilling embolisms from stored water and/or growing new xylem in branching patterns that circumvent embolized conduits (36). However, when inferring K_{stem}

responses to drought, it is important to note that, during transpiration, the leaf experiences more negative water potentials than the stem, given the high resistance of the leaf hydraulic pathway (27). This water potential difference protects the stem and, especially, the roots from extreme tension that would drive embolism during dehydration; thus, for a plant experiencing a Ψ_{leaf} equal to $\Psi_{min, MD}$, the actual Ψ_{stem} should be less negative. Therefore, these species could potentially experience less severe embolism than expected from this sequence of organ-scale water potential thresholds. Under drought, the water potentials across organs are expected to be highly variable, depending on hydraulic conductivity and influx from water storage. Thus, either in situ psychrometer measurements or a modeling approach is needed to quantify the impact of the trait sequence on the actual organ water potentials and conductivities that the plant experiences at a given soil water potential and transpiration rate.

The strong support for vulnerability segmentation and for leaf hydraulic decline under mild drought indicates that hydraulic redundancy (i.e., excess hydraulic capacity) and/or the capacity for hydraulic recovery in the leaf is crucial to drought tolerance for many plants (12, 16, 37). These findings point to the importance of elucidating the leaf traits that determine this capacity (20). Although contrary to our hypotheses, the occurrence of g_s Ψ_{95} at more negative water potentials than π_{tip} is consistent with previous findings that the guard cells that control stomatal aperture (38) are largely isolated from bulk leaf turgor (28). Notably, many species are known to adjust π_{tip} under water stress to improve drought tolerance (39), but only a few species were assessed for drought response traits during the dry season. Although moderate plastic shifts would tend to be toward the direction of greater tolerance and, thus, unlikely to affect the sequence of traits, further studies are needed to evaluate the degree to which plasticity in π_{tip} , or in other traits, impacts this sequence. Greater sampling is also required to characterize the role of stomatal closure in preventing damage to the hydraulic system.

Future Directions To Improve the Predictive Capacity of Drought Tolerance Traits. This synthesis provides insight into the roles of trait coordination, coselection with water stress, and shared ancestry in the correlations of stomatal, hydraulic, and mesophyll drought tolerance traits, as well as the average trait sequence within plants.

This perspective also points to key developments needed to improve the predictive capacity of trait-based approaches for plant drought tolerance. More measurements are needed for the stomatal and root hydraulic traits, especially because these traits were the strongest correlates of environmental water stress. More data are also needed for gymnosperms, which have a lower capacity for recovery and may thus depend more strongly on the trait sequence (4, 40). Further, 70% of the species were represented in more than one comparison in the sequence analysis, but most of this overlap is accounted for by $\Psi_{min, MD}$, with only 30% of species assessed for more than two plant traits. It is thus critical that the general sequence be verified by sampling more traits within given species, with this sequence serving as a “first-pass” approximation until such data are more widely available. In addition, many physiological processes contribute to growth and survival during drought. Capacitance, embolism recovery, and metabolic synthesis of abscisic acid and nonstructural carbon reserves have all been predicted to influence drought survival, but the roles of these traits and their interactions with the classical drought tolerance traits, or their influence on plant Ψ_{lethal} , are not well understood (15, 23). Indeed, measurements of plant Ψ_{lethal} are sparse in the literature, and most studies use different definitions for plant death (11, 41). These values correlate with π_{tip} (11), as shown here, and with leaf and stem hydraulic traits across small species sets ($n \leq 5$) (19, 37, 41), and it is increasingly critical for further studies to determine how these traits interact to influence plant mortality during drought.

Methods

To compile the drought tolerance trait dataset, we drew on references from several recent metaanalyses of variation in individual drought tolerance traits (4, 6, 7, 26) and conducted Web of Science and Google Scholar searches by using the keywords “turgor loss point,” “wilting point,” “stomatal closure,” “stomatal conductance,” “lethal leaf water potential,” and “hydraulic vulnerability” or “cavitation” paired with “leaf,” “stem,” or “root.” These studies measured traits with standard methods (detailed in the *SI Appendix, SI Methods*). To minimize ontogenetic and methodological variation, we included only studies that met the following criteria. For all traits, we included only studies that sampled (i) mature plant organs from (ii) sapling or adult plants, and not seedlings, growing in (iii) natural ecosystems or urban conditions for wild species, or typical agricultural conditions for crop species. For π_{tip} values, we selected only studies that measured (iv) leaves that were rehydrated ≥ 6 h before measurement, unless the study reported no significant effect of a shorter rehydration time. We included g_5 , Ψ_{50} and Ψ_{95} values only from studies that (v) measured Ψ_L and g_5 for leaves collected at the same time and (vi) included Ψ_L values that were less negative than -1.5 MPa to capture early declines in g_5 .

We evaluated the correlations among traits with standard major axis regressions by using the *smatr* package for R software (version 3.3.0) (42). We present the correlations for untransformed data and confirmed these findings for log-transformed values. We identified the drivers of the trait correlations

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1 **Supplementary Methods**

2 The compiled drought tolerance traits and water stress indices were measured according to
 3 standard methods. The turgor loss point (π_{tlp}) was interpolated from pressure-volume curves,
 4 which relate the relative water content, a measure of cell volume, to the leaf water potential
 5 (Ψ_{leaf}) in a dehydrating leaf (1). This value is a bulk leaf trait, representing the volume-weighted
 6 average π_{tlp} of all of the leaf cells. The water potential thresholds for 50% declines in leaf, stem,
 7 and root hydraulic conductivity (K_{leaf} , K_{stem} , and K_{root} Ψ_{50}), and for 12% and 88% declines in
 8 stem conductivity (K_{stem} Ψ_{12} and Ψ_{88}) were interpolated from curves relating the percent loss of
 9 hydraulic conductivity to the water potential of dehydrating leaves, stems, or roots (2, 3). The
 10 water potential thresholds for 50% and 95% declines in stomatal conductance (g_s Ψ_{50} and Ψ_{95})
 11 were interpolated from curves relating g_s to Ψ_{leaf} for a dehydrating plant or excised branch (4).
 12 Water stress at pre-dawn ($\Psi_{min, PD}$) and midday ($\Psi_{min, MD}$) was characterized as the minimum
 13 Ψ_{leaf} for each time observed across multiple measurements during the dry season (e.g. 5), across
 14 monthly measurements over the course of a year (e.g. 6), or, less often, as the Ψ_{leaf} observed in a
 15 single measurement during the dry season (e.g. 7). The water potential at plant death (plant
 16 Ψ_{lethal}) was measured as the Ψ_{leaf} of a plant dehydrated to the point of all leaves showing at least
 17 some tissue damage (8).

18 The trait differences in the sequence analysis were tested with the mixed effects model
 19 (9):

$$20 \quad Y_{ijk} = \mu + \alpha_k + \varepsilon_{ijk} \quad \text{Eqn S1}$$

21 where Y_{ijk} is the trait difference for species j from study k , α_k is the random effect of study, ε_{ijk} is
 22 the residual error, and μ is the overall fixed intercept. 95% confidence intervals for μ were
 23 calculated from 1000 nonparametric bootstraps, since some of the trait differences were non-

24 normal after standard transformations (10). We focused these analyses on the subset of species
 25 for which all traits were measured at the same site during the same ≤ 6 month period by the same
 26 researchers ($n = 234$). For some of the species the trait values were published in different papers,
 27 but we considered these data to come from the same ‘study’ in fitting the random intercepts.

28 To ensure that the trait comparisons in the angiosperm sequence were robust to
 29 uncertainty in trait measurements, we calculated 95% confidence intervals (CI) around the mean
 30 trait values for each species for which sufficient information was reported ($n = 182$). For π_{tip} and
 31 $\Psi_{\text{min, MD}}$, we calculated 95% CI from the mean (\bar{x}), standard error (s_e), and sample size (n) of the
 32 trait measurements across individuals within each species, according to the equation (11):

$$33 \quad 95\% \text{ CI} = \bar{x} \pm s_e * t_{n-1, \alpha/2} \quad \text{Eqn S2}$$

34 This method was also applicable to $K_{\text{stem}} \Psi_{50}$ values determined with the air injection method, for
 35 which species means for $K_{\text{stem}} \Psi_{50}$ are averaged from $K_{\text{stem}} \Psi_{50}$ values measured for multiple
 36 individual stems. The $K_{\text{stem}} \Psi_{50}$ values of the individual stems are interpolated from repeated
 37 measurements of K_{stem} and Ψ_{stem} on each stem as it dehydrates, similar to the pressure-volume
 38 curve method for π_{tip} (12).

39 The stomatal and hydraulic traits are typically estimated from non-linear regressions
 40 fitting data compiled across all measured individuals, with organ water potential as the
 41 independent variable. This convention generally precludes estimating standard errors for these
 42 trait values, since these regressions assume the independent variable is measured without error
 43 (11), and all individuals are analyzed with one regression relationship. However, Ψ_{50} values are
 44 estimated as regression parameters for logistic and sigmoidal relationships, allowing us to
 45 determine standard errors and, thus, 95% confidence intervals for trait values estimated from
 46 these regression relationships. We first extracted the data from plots of the $g_s - \Psi_{\text{leaf}}$ or $K - \Psi$

47 curves using ImageJ software. We then fitted a sigmoidal relationship to the $K_{\text{stem}} - \Psi_{\text{stem}}$ curve
48 for each species to calculate $K_{\text{stem}} \Psi_{50}$ and its standard error, using the *optim* function in R
49 software (v. 3.3.0) (13, 14). K_{leaf} and g_s responses to Ψ_{leaf} have been shown to vary in shape
50 across species, due to the influence of both mesophyll and xylem processes (15). To determine
51 whether logistic and sigmoidal regressions could accurately characterize these responses, we
52 used the *optim* function to compare Aikake Information Criteria values corrected for small
53 sample sizes (AICc) for exponential, sigmoidal, logistic, and linear models for each curve (15).
54 We then used *optim* to calculate $g_s \Psi_{50}$, $K_{\text{leaf}} \Psi_{50}$, and their standard errors for each curve for
55 which a logistic or sigmoidal relationship was the most strongly supported (i.e., exhibited the
56 lowest AICc value). We then calculated 95% confidence intervals from the standard errors using
57 Eqn S2, but with t_{df} instead of t_{n-1} , where df is the degrees of freedom of the best-fit regression.
58 We confirmed that the Ψ_{50} values estimated from these relationships corresponded to the values
59 reported in the original studies ($r^2 = 0.90 - 0.98$). Because more studies reported $g_s \Psi_{50}$ and K_{stem}
60 Ψ_{50} than $g_s \Psi_{95}$ and $K_{\text{stem}} \Psi_{12}$ and Ψ_{88} , we also used the fitted $K_{\text{stem}} - \Psi_{\text{stem}}$ curves the best-fit
61 relationship determined from the AICc comparisons for the $g_s - \Psi_{\text{leaf}}$ curves to interpolate these
62 trait values for each species for which these trait values were not reported. None of the root
63 hydraulic vulnerability studies reported the full $K - \Psi$ curve.

64 These analyses were unable to determine 95% confidence intervals for $g_s \Psi_{95}$ and K_{stem}
65 Ψ_{12} and Ψ_{88} , which would require fitting the data with Ψ as the dependent variable. However,
66 non-linear regressions are potentially highly asymmetric when reversing the x and y variables,
67 which could potentially produce very different trait values from those reported in the original
68 studies. At the same time, the low sample size at the ends of the curves and the non-linear curve
69 shape suggests that these traits will have much larger errors than g_s and $K_{\text{stem}} \Psi_{50}$. Thus,

70 determining the uncertainty in the distances between these traits and others in the sequence will
71 require the further development of statistical and computational methods that can estimate these
72 uncertainties (16).

73 **Supplementary Figure Captions**

74 **Fig. S1.** Trait distributions for all values compiled from the literature for the leaf water potential
 75 (Ψ_L) at 50% stomatal closure ($g_s \Psi_{50}$, panel **A**), 50% declines in leaf hydraulic conductivity (K_{leaf}
 76 Ψ_{50} , **B**), the turgor loss point (π_{tlp} , **C**), and 95% stomatal closure ($g_s \Psi_{95}$, **D**), the stem water
 77 potential at 12% declines in stem hydraulic conductivity ($K_{stem} \Psi_{12}$, **E**), 50% declines in stem
 78 conductivity ($K_{stem} \Psi_{50}$, **F**), and 88% declines in stem conductivity ($K_{stem} \Psi_{88}$, **G**), the root water
 79 potential at 50% declines in root hydraulic conductivity ($K_{root} \Psi_{50}$, **H**), the leaf water potential at
 80 plant death (plant Ψ_{lethal} , **I**), and the minimum seasonal leaf water potential at midday, an index
 81 of plant water stress ($\Psi_{min, MD}$, **K**). Blue dashed lines indicate trait means. The gray bars in **E-H**
 82 show trait values calculated from sigmoidally shaped stem and root hydraulic vulnerability
 83 curves, and the white bars show trait values calculated from the other vulnerability curve shapes.

84 **Fig. S2.** Standardized major axis (SMA) relationships across species between the drought
 85 tolerance traits and the minimum seasonal water potential at midday ($\Psi_{min, MD}$), an index of
 86 maximum plant water stress. Blue points represent angiosperms, and black points are
 87 gymnosperms. The r values are shown in each panel. Lines indicate significant correlations.
 88 Solid lines are correlations across all species, and dashed lines are correlations that were
 89 significantly different between the gymnosperms (black lines) and angiosperms (blue lines). All
 90 of these correlations were significant after correcting for multiple comparisons. P-values and
 91 sample sizes are in Table S2. All of the traits were significantly correlated with $\Psi_{min, MD}$,
 92 indicating that all of these traits can predict the maximum water stress that a plant experiences in
 93 natural conditions, and that no trait emerges as a primary driver of ecological drought tolerance.
 94 $K_{stem} \Psi_{12}$ was significantly correlated with $\Psi_{min, MD}$ in the gymnosperms but not the angiosperms

95 (E), while the angiosperms and gymnosperms showed significantly different slopes for the
 96 correlations of $\Psi_{\min, MD}$ with $K_{\text{stem}} \Psi_{50}$ and with $K_{\text{root}} \Psi_{50}$ (F, H) (Table S4).

97 **Fig. S3.** Standardized major axis (SMA) relationships across species between traits and the
 98 minimum seasonal leaf water potential measured pre-dawn ($\Psi_{\min, PD}$), which reflects the
 99 minimum water potential of the soil. Symbols follow Fig S2. Nearly all of the traits were
 100 significantly correlated with both the seasonal maximum for environmental water stress ($\Psi_{\min, PD}$)
 101 and for water stress experienced by the plant ($\Psi_{\min, MD}$) (Fig. S2), which further supports the
 102 ability of any of these traits to predict ecological drought tolerance. $K_{\text{leaf}} \Psi_{50}$ was significantly
 103 correlated with $\Psi_{\min, MD}$ but not $\Psi_{\min, PD}$ (Table S2).

104 **Fig. S4.** Means and 95% confidence intervals for traits for which sufficient information was
 105 available to determine the standard error. Each pair of red and blue points represents one
 106 angiosperm species. There were insufficient data to test the trait sequence for the gymnosperms.
 107 Red indicates mean values of $K_{\text{leaf}} \Psi_{50}$, and blue indicates means for π_{tlp} (A), $\Psi_{\min, MD}$ (B), and
 108 $K_{\text{stem}} \Psi_{50}$ (C). Species with non-overlapping confidence intervals exhibit significantly different
 109 trait values. The species are ordered by trait differences (i.e., the distance between the red and
 110 blue points), with the value of π_{tlp} – the second trait (the trait indicated in blue) increasing from
 111 right to left. The vertical dashed lines separate the species with significant and non-significant
 112 trait differences. The species for which $K_{\text{leaf}} \Psi_{50}$ is significantly more negative than the second
 113 trait are on the right, species with non-significant trait differences are in the middle, and species
 114 for which $K_{\text{leaf}} \Psi_{50}$ is significantly less negative than the second trait are on the left. These trait
 115 comparisons accounting for measurement uncertainty support the findings from the mean trait
 116 differences (Fig. 3; Table S7), with the confidence intervals able to resolve significant trait
 117 differences in 55 – 82% of species. The π_{tlp} was significantly more negative than $K_{\text{leaf}} \Psi_{50}$ in

118 47% of the species, with only 8% of species showing the opposite pattern ($n = 62$) (**A**). $\Psi_{\min, MD}$
 119 was significantly more negative than $K_{\text{leaf}} \Psi_{50}$ for 15% of species and less negative for 42%, but
 120 these traits did not show a significant difference across species when accounting for random
 121 study effects ($n = 52$) (**B**). $K_{\text{stem}} \Psi_{50}$ was significantly more negative than $K_{\text{leaf}} \Psi_{50}$ for 82% of
 122 species, with no species showing the opposite pattern ($n = 22$) (**C**).

123 **Fig. S5.** Means and 95% confidence intervals for traits for which sufficient information was
 124 available to determine the standard error. Symbols follow Fig. S4, except that red indicates mean
 125 values of π_{tlp} , and blue indicates means for $g_s \Psi_{50}$ (**A**), $\Psi_{\min, MD}$ (**B**), and $K_{\text{stem}} \Psi_{50}$ (**C**). These
 126 comparisons strongly supported the findings across species (Fig. 3; Table S7), with the
 127 confidence intervals able to resolve significant trait differences in 55 – 57% of the species. The
 128 π_{tlp} was significantly more negative than $g_s \Psi_{50}$ in 43% of the species, with only 14% showing
 129 the opposite pattern ($n = 14$) (**A**). The π_{tlp} was also significantly more negative than $\Psi_{\min, MD}$ for
 130 42% of species and less negative for only 10% ($n = 67$) (**B**), and more negative than $K_{\text{stem}} \Psi_{50}$ for
 131 33% of species, with 21% showing the opposite pattern ($n = 38$) (**C**).

132 **Fig. S6.** Means and 95% confidence intervals for values of $\Psi_{\min, MD}$ (blue) and $K_{\text{stem}} \Psi_{50}$ (red) for
 133 each species with sufficient information to determine the standard error. $K_{\text{stem}} \Psi_{50}$ was
 134 significantly less negative than $\Psi_{\min, MD}$ in 43% of species and less negative in 17% of species,
 135 supporting the findings across species ($n = 46$).

Species	Biome	$g_s \Psi_{50}$	$g_s \Psi_{95}$	$K_{leaf} \Psi_{50}$	τ_{tip}	$K_{stem} \Psi_{50}$	$K_{stem} \Psi_{88}$	$K_{root} \Psi_{50}$	Plant Ψ_{lethal}	$g_s \Psi_{50, 95}$ Ref	$K_{leaf} \Psi_{50}$ Ref	τ_{tip} Ref	$K_{stem} \Psi_{12, 50, 88}$ Ref	$K_{root} \Psi_{50}$ Ref	Plant Ψ_{lethal} Ref
Angiosperms															
<i>Acacia greggii</i>	Semidesert				-4.25	-0.88	-4.06					(17)	(18)		
<i>Acer campestre</i>	Temperate			-1.32	-1.9	-3.87	-4.60				(19)	(19)	*, (20)		
<i>Acer grandidentatum</i>	Temperate				-2.45	-3.66	-7.14	-0.86				(21)	(21)		
<i>Acer monspessulanum</i>	Med./ Dry Temperate			-1.89	-2.2	-3.31	-4.61	-1.6			(19)	(19)	(22)	(22)	
<i>Acer negundo</i>	Temperate				-1.59	-1.34	-2.74	-0.3				(23)	(24)	(25)	
<i>Acer pseudoplatanus</i>	Temperate			-1.19	-1.4	-2.37	-2.71				(19)	(19)	*, (20)		
<i>Acer rubrum</i>	Temperate				-1.59	-3.9	-6.00	-1.69				(26)	(26)	(27)	
<i>Acer saccharum</i>	Temperate	-1.6	-2.02		-2.78	-3.97	-3.97	-1.5		(28)		(28)	(29, 30)	(31) (32)	
<i>Acmena acuminatissima</i>	Tropical Dry				-1.47	-1.94	-3.85					(33)	(33)		
<i>Acronychia pedunculata</i>	Tropical Dry				-1.73	-1.86	-4.12					(33)	(33)		
<i>Adansonia rubrostipa</i>	Tropical Dry				-1.12	-1.1	-2.82					(34)	(34)		
<i>Adansonia za</i>	Tropical Dry				-1.26	-1.7	-3.49					(34)	(34)		
<i>Adenostoma fasciculatum</i>	Med./ Dry Temperate				-3.79	-7.98	-12.0					(35)	(36)		
<i>Adesmia boronioides</i>	Semidesert			-2.74	-2.44	-4.42	-7.58				(12)	(37)	(12)		
<i>Aegiphila lhotskiana</i>	Tropical Dry			-0.8	-1.25						(38)	(38)			
<i>Aegiphila sellowiana</i>	Tropical Dry			-1.7	-1.33						(38)	(38)			
<i>Aidia canthioides</i>	Tropical Dry				-1.31	-1.95	-4.55					(33)	(33)		
<i>Alberta magna</i>	Med./ Dry Temperate	-1.76	-2.56		-1.97					(15)		(15)			
<i>Alchornea trewioides</i>	Tropical Dry				-1.32	-0.9	-1.96					(33)	(33)		
<i>Aleurites moluccana</i>	Tropical Dry			-1.11	-1.97	-2.17	-3.74				(39)	(40)	(39)		
<i>Allocasuarina campestris</i>	Med./ Dry Temperate				-2.99	-2.96	-8.50					(41)	(41)		
<i>Alnus glutinosa</i>	Temperate					-1.91	-2.77	-2.25					*, (42)	(42)	
<i>Alnus incana</i>	Temperate					-1.7	-2.15	-0.2					(43)	(25)	
<i>Alphonsea mollis</i>	Tropical Dry				-2.2	-1.82	-3.31					(5)	(5)		
<i>Amborella trichopoda</i>	Tropical Moist				-1.1	-3	-4.07					(44)	(45)		
<i>Anacardium excelsum</i>	Tropical Dry				-1.13	-1.45	-2.50	-0.76				(46)	(46)	(46)	
<i>Aporosa dioica</i>	Tropical Dry				-0.97	-1.43	-2.52					(33)	(33)		
<i>Aporosa globifera</i>	Tropical Dry				-1.49				-3.96			(8)			(8)
<i>Aporosa microstachya</i>	Tropical Dry				-1.7				-5.13			(8)			(8)
<i>Aporosa symplocoides</i>	Tropical Dry				-1.25				-4.83			(8)			(8)
<i>Arbutus menziesii</i>	Med./ Dry Temperate			-5.18	-2.74						(47)				
<i>Arbutus unedo</i>	Med./ Dry Temperate				-1.68	-3.09	-4.84	-1.2				(48)	(22)	(22)	
<i>Arctostaphylos</i>	Med./ Dry Temperate		-3.09	-5.88	-3.45	-5.09				(49)		(50)	(49)		

<i>glandulosa</i>													
<i>Ardisia quinquegona</i>	Tropical Dry				-1.93	-2.88	-6.54				(33)	(33)	
<i>Ascarina rubricaulis</i>	Tropical Moist				-1.4	-2.8	-3.39				(44)	(51)	
<i>Ascarina solmsiana</i>	Tropical Moist				-0.75	-2.63	-3.63				(44)	(51)	
<i>Atherosperma moschatum</i>	Temperate	-1.01	-1.36	-1.48	-1.78				(52)	(7)	(7)		
<i>Atriplex confertifolia</i>	Semidesert					-4.25	-7.10	-1.53				(53)	(53, 54)
<i>Austrobaileya scandens</i>	Tropical Moist				-1.3	-0.5	-1.97				(44)	(51)	
<i>Baccaurea ramiflora</i>	Tropical Dry				-1.28	-2	-4.11				(55)	(55)	
<i>Balfourodendron riedelianum</i>	Tropical Moist		-2.19	-2.27	-1.13	-2.57				(56)	(56, 57)	(56, 57)	
<i>Banksia attenuata</i>	Med./ Dry Temperate				-2.73	-2.69	-6.00				(58)	(59)	
<i>Banksia sphaerocarpa</i>	Med./ Dry Temperate				-3.12	-3.7	-5.30				(41)	(41)	
<i>Bauhinia variegata</i>	Tropical Dry				-1.15	-1.55	-5.98				(55)	(55)	
<i>Berberis microphylla</i>	Med./ Dry Temperate		-3.2	-3.87	-4.5	-6.91				(12)	(37)	(12)	
<i>Betula occidentalis</i>	Temperate				-2.27	-1.6	-2.01	-0.69			(1)	(60)	(25, 60, 61)
<i>Betula papyrifera</i>	Temperate				-1.65	-2.34	-3.12				(62)	(43)	
<i>Bischofia javanica</i>	Tropical Dry		-0.81		-1.27	-2.40				(39)		(39, 63)	
<i>Blastus cochinchinensis</i>	Tropical Dry				-1.25	-4.26	-6.40				(33)	(33)	
<i>Blepharocalyx salicifolius</i>	Tropical Dry				-2.52	-1.72	-4.08	-1.4			(64)	(64)	(65)
<i>Bursaria spinosa</i>	Tropical Dry		-3.2	-2.99						(7)	(7)		
<i>Bursera simaruba</i>	Tropical Dry	-1.33	-1.68		-1.39	-0.95	-1.80			(4)	(4)	(4)	
<i>Calycophyllum candidissimum</i>	Tropical Dry	-1.55	-1.96		-1.3	-2.87	-4.30			(4)	(4)	(4)	
<i>Camelia sasanqua</i>	Temperate		-1.78	-2.12						(15)	(15)		
<i>Canella winterana</i>	Tropical Dry				-3	-0.23	-1.01				(66)	(51)	
<i>Caryocar brasiliense</i>	Tropical Dry				-1.45	-1.48	-4.02				(64)	(64)	
<i>Castanopsis chinensis</i>	Tropical Dry				-2.33	-3.04	-9.27				(33)	(33)	
<i>Castanopsis chrysophylla</i>	Temperate		-2.4	-2.68						(47)	(47)		
<i>Castanopsis fissa</i>	Tropical Dry				-2.35	-1.37	-3.14				(33)	(33)	
<i>Casuarina obesa</i>	Wetland/Mangrove				-4.59	-1.39					(58)	(67)	
<i>Ceanothus crassifolius</i>	Med./ Dry Temperate					-8.8	-11.8	-6.24				(68, 69) (70)	(69, 71, 72)
<i>Ceanothus cuneatus</i>	Med./ Dry Temperate	-4.41	-8.37			-7.19				(49)		(49)	
<i>Ceanothus leucodermis</i>	Med./ Dry Temperate					-3.56	-7.86	-2.79				(69, 70)	(69,

<i>Cedrela fissilis</i>	Tropical Moist	-1.7	-1.28	-0.73		(56)	(56, 57)	(56, 57)	71)
<i>Celtis philippensis</i>	Tropical Dry		-2.98	-1.5	-2.90		(5)	(5)	
<i>Ceratonia siliqua</i>	Med./ Dry Temperate	-2.55	-2.02	-8.12	-9.05	(73)	(73)	(74)	
<i>Cercis canadensis</i>	Temperate			-2.52	-6.50	-0.9		(27)	(27)
<i>Cercis siliquastrum</i>	Temperate	-2.7		-1.8	-3.20	(75)		(75)	
<i>Cercocarpus betuloides</i>	Med./ Dry Temperate	-2.76	-2.59	-7.46		(15)	(15)	(6)	
<i>Chrysothamnus nauseosus</i>	Semidesert			-2.9	-3.90	-1.2		(53)	(53, 54)
<i>Chrysothamnus viscidiflorus</i>	Semidesert			-4.25	-6.70	-1.31		(53)	(54); (53)
<i>Cipadessa baccifera</i>	Tropical Dry		-1.78	-2.45	-4.70		(5)	(5)	
<i>Cistus albidus</i>	Med./ Dry Temperate			-5.78	-8.86	-2		(22)	(22)
<i>Cistus laurifolius</i>	Med./ Dry Temperate			-3.65	-6.36	-0.9		(22)	(22)
<i>Cleistanthus sumatranus</i>	Tropical Dry		-1.72	-3.19			(5)	(5)	
<i>Clerodendrum fortunatum</i>	Tropical Dry		-1.54	-1.89	-3.99		(33)	(33)	
<i>Codiaeum variegatum</i>	Tropical Dry	-0.92		-2.23	-3.27	(39)		(39, 63)	
<i>Colliguaja integerrima</i>	Semidesert	-3.1	-3.71	-4.4	-5.98	(12)	(37)	(12)	
<i>Comarostaphylis diversifolia</i>	Med./ Dry Temperate	-2.85	-3.45	-5.61		(15)	(15)	(6)	
<i>Combretum latifolium</i>	Tropical Dry		-1.29	-1.12	-3.76		(55)	(55)	
<i>Cordia alliodora</i>	Tropical Moist		-1.97	-3.27	-5.59		(76)	(76)	
<i>Cordia americana</i>	Tropical Dry	-1.63	-1.58	-1.37		(56)	(56, 57)	(56, 57)	
<i>Cordia cymosa</i>	Tropical Moist		-1.5	-1.2	-2.55		(76)	(76)	
<i>Cordia dentata</i>	Tropical Moist		-2.14	-3.6	-6.25		(76)	(76)	
<i>Cordia lasiocalyx</i>	Tropical Moist		-1.63	-2.57	-4.27		(76)	(76)	
<i>Cordia lucidula</i>	Tropical Moist		-1.4	-1.58	-2.97		(76)	(76)	
<i>Cordia panamensis</i>	Tropical Moist		-2	-2.33	-3.61		(76)	(76)	
<i>Cornus florida</i>	Temperate		-2.28	-3.9	-7.10	-1.6		(77)	(78)
<i>Corylus cornuta</i>	Temperate	-2.51	-1.93			(79)	(79)		(27, 78)
<i>Corymbia callophylla</i>	Med./ Dry Temperate		-2.62	-1.5			(80)	(80)	
<i>Croton yanhuii</i>	Tropical Dry		-1.82	-1.48	-2.60		(5)	(5)	
<i>Cryptocarya chinensis</i>	Tropical Dry		-1.52	-3.78	-6.75		(33)	(33)	
<i>Cryptocarya concinna</i>	Tropical Dry		-1.77	-1.74	-4.44		(33)	(33)	
<i>Curatella americana</i>	Tropical Dry	-1.17	-1.91	-1.48	-2.17	(81)	(81)	(82)	
<i>Cyathodes straminea</i>	Temperate	-2	-2.02			(7)	(7)		

<i>Diospyros morrisiana</i>	Tropical Dry			-1.79	-0.89	-1.22			(33)	(33)		
<i>Diplospora dubia</i>	Tropical Dry			-1.93	-2.21	-4.75			(33)	(33)		
<i>Dryandra sessilis</i>	Med./ Dry Temperate			-2.82	-1.93	-3.40			(41)	(41)		
<i>Dryandra vestita</i>	Med./ Dry Temperate			-2.97	-3.19	-7.05			(41)	(41)		
<i>Drypetes indica</i>	Tropical Dry		-1.68		-2.32	-4.00		(39)		(39, 63)		
<i>Dysoxylum papuanum</i>	Tropical Moist		-2.24	-2.12	-2.63	-4.24			(83)	(83)		
<i>Elaeocarpus grandis</i>	Tropical Moist		-1.66	-2.16	-3.06				(83)	(83)		
<i>Encelia californica</i>	Med./ Dry Temperate	-2.27	-4.32			-0.82		(49)		(49)		
<i>Encelia farinosa</i>	Semidesert				-2.63	-6.13			(17)	(18)		
<i>Enterolobium cyclocarpum</i>	Tropical Dry	-1.84	-2.36		-1.82	-2.73	-3.50		(4)	(4)	(4)	
<i>Ericameria nauseosus</i>	Semidesert					-2.90	-3.90	-1.20			(53)	(54)
<i>Eriogonum cinereum</i>	Med./ Dry Temperate	-2.26	-4.29			-1.97			(49)		(49)	
<i>Eucalyptus accedens</i>	Med./ Dry Temperate				-3.48	-3.2				(80)	(80)	
<i>Eucalyptus albidia</i>	Med./ Dry Temperate				-3.14	-0.92	-2.80			(41)	(41)	
<i>Eucalyptus capillosa</i>	Med./ Dry Temperate				-3.69	-3.08	-5.70			(41)	(41)	
<i>Eucalyptus coccifera</i>	Med./ Dry Temperate		-2.65		-2.36				(7)	(7)		
<i>Eucalyptus globoidea</i>	Med./ Dry Temperate				-1.22	-1.20				(84)	(84)	
<i>Eucalyptus marginata</i>	Med./ Dry Temperate				-2.48	-2.39	-5.00			(80)	(80)	
<i>Eucalyptus pauciflora</i>	Med./ Dry Temperate	-1.34	-1.82	-1.56	-1.6	-1.61	-2.90		(85)	(85)	(85)	(85)
<i>Eucalyptus pulchella</i>	Med./ Dry Temperate				-4.31	-2.41			(7)	(7)		
<i>Eucalyptus piperita</i>	Med./ Dry Temperate				-1.27	-0.99				(84)	(84)	
<i>Eucalyptus sclerophylla</i>	Med./ Dry Temperate				-1.50	-1.15				(84)	(84)	
<i>Eucalyptus sieberi</i>	Med./ Dry Temperate				-1.51	-1.02				(84)	(84)	
<i>Eucalyptus tetradonta</i>	Med./ Dry Temperate	-2.3		-2.13					(86)	(86)		
<i>Eucalyptus wandoo</i>	Med./ Dry Temperate				-3.41	-3.41				(80)	(80)	
<i>Fagus sylvatica</i>	Temperate				-2.04	-3.08	-3.90	-0.4		(87)	(88-90)	(91)
<i>Ficus pisocarpa</i>	Tropical Dry				-1.38	-0.81	-1.37			(5)	(5)	
<i>Ficus auriculata</i>	Tropical Dry	-0.73	-3.14		-0.86				(92)	(92)		
<i>Ficus benjamina</i>	Tropical Dry	-1.2	-2.40		-1.65				(92)	(92)		
<i>Ficus concinna</i>	Tropical Dry	-1.99	-2.27		-2.32				(92)	(92)		
<i>Ficus curtipes</i>	Tropical Dry	-1.11	-1.44		-1.47				(92)	(92)		
<i>Ficus esquiroliana</i>	Tropical Dry	-0.91	-1.93		-1.15				(92)	(92)		
<i>Ficus hispida</i>	Tropical Dry	-1.23	-1.85		-1.23				(92)	(92)		
<i>Ficus racemosa</i>	Tropical Dry	-1.17	-3.02		-1.44				(92)	(92)		
<i>Ficus religiosa</i>	Tropical Dry	-1.49	-1.80		-1.69				(92)	(92)		
<i>Ficus semicordata</i>	Tropical Dry	-0.5	-2.15		-1.52				(92)	(92)		
<i>Ficus tinctoria</i>	Tropical Dry	-1.37	-2.16		-1.82				(92)	(92)		
<i>Fraxinus americana</i>	Temperate				-2.14	-1.92				(23)	(93)	
<i>Fraxinus ornus</i>	Temperate				-2.84	-2.2	-4.20			(75)	(94)	

<i>Gaultheria hispida</i>	Temperate			-1.32	-2.08					(7)	(7)		
<i>Genipa americana</i>	Tropical Dry			-1.27	-2.55					(95)	(95)		
<i>Gironniera subaequalis</i>	Tropical Dry				-1.07	-2.98	-3.65					(33)	(33)
<i>Glyricidia sepium</i>	Tropical Dry	-1.69	-2.15	-1.91	-1.61					(95)	(95)	(95)	
<i>Grayia spinosa</i>	Semidesert					-5.25	-9.00	-2.24					(53) (53, 54)
<i>Hakea lissosperma</i>	Temperate	-1.35	-1.92	-2.85	-2.67	-5.66	-6.41			(52)	(7)	(7)	**
<i>Hakea microcarpa</i>	Med./ Dry Temperate			-3.96	-3.73						(7)	(7)	
<i>Hazardia squarrosa</i>	Med./ Dry Temperate	-1.74	-3.30		-1.42					(49)			(49)
<i>Hedera canariensis</i>	Temperate	-1.10	-1.57	-0.85	-2.06					(14)	(14)	(14)	
<i>Heteromeles arbutifolia</i>	Med./ Dry Temperate			-2.57	-2.53	-6.2	-8.12				(15)	(15)	(96)
<i>Hevea brasiliensis</i>	Tropical Dry			-1.06		-1.27	-2.38				(39)		(39, 63)
<i>Hybanthus prunifolius</i>	Tropical Dry				-1.74	-2.6	-6.00					(97)	(98)
<i>Hymenaea courbaril</i>	Tropical Dry	-2.44	-3.07		-2.17	-3	-3.90			(4)		(4)	(4)
<i>Hymenaea martiana</i>	Tropical Dry			-1.4	-2.32	-2.8	-0.66				(38)	(38)	(38)
<i>Hymenaea stignocarpa</i>	Tropical Dry			-1.6	-2.64	-3.17					(38)	(38)	(38)
<i>Ilex aquifolium</i>	Temperate			-0.89	-1.68	-6.6	-9.70				(99)	(99)	(22) (22)
<i>Illicium anisatum</i>	Temperate				-1.35	-3.66	-4.70					(44)	(51)
<i>Illicium floridanum</i>	Temperate				-1.1	-3.28	-4.25					(44)	(51)
<i>Irvingia malayana</i>	Tropical Dry				-1.85			-8.57				(8)	(8)
<i>Isopogon gardneri</i>	Med./ Dry Temperate				-2.93	-3.75	-7.00					(41)	(41)
<i>Juglans regia nigra</i>	Temperate	-0.23	-0.96		-1.53					(100)		(100)	
<i>Khaya senegalensis</i>	Med./ Dry Temperate			-1.5	-2.77						(86)	(86)	
<i>Kielmeyera coriacea</i>	Tropical Dry					-1.91		-0.8					(101) (65)
<i>Lagerstroemia tomentosa</i>	Tropical Dry				-1.94	-1.29	-2.80					(5)	(5)
<i>Lantana camara</i>	Tropical Dry			-0.8	-1.37						(15)	(15)	
<i>Lasiococca comberi</i>	Tropical Dry				-2.73	-1.66	-3.43					(5)	(5)
<i>Liquidambar styraciflua</i>	Temperate				-2.34	-3.12	-5.30	-0.78				(102)	(27) (27, 78)
<i>Liriodendron tulipifera</i>	Temperate				-1.13	-3						(26)	(26)
<i>Lomatia polymorpha</i>	Med./ Dry Temperate			-1.57	-2.47						(7)	(7)	
<i>Lomatia tinctoria</i>	Med./ Dry Temperate	-0.74	-3.17	-2.08	-2.51	-4.97	-5.57			(52)	(7)	(7)	(74), **
<i>Lycium chilense</i>	Semidesert			-2.97	-1.96	-4.9					(12)	(37)	(12)
<i>Macaranga denticulata</i>	Tropical Dry			-1.27		-1.14	-1.86				(39)		(39, 63)
<i>Machilus chinensis</i>	Tropical Dry				-1.98	-2.52	-5.78					(33)	(33)
<i>Maclura tinctoria</i>	Tropical Moist			-1.61	-1.85	-0.71	-2.25				(56)	(56, 57)	(56, 57)
<i>Magnolia grandiflora</i>	Temperate			-0.42	-2.06	-2.02					(15)	(15)	(67)
<i>Malacothamnus fasciculatus</i>	Med./ Dry Temperate	-2.21	-4.20			-0.94				(49)			(49)

<i>Mallotus paniculatus</i>	Tropical Dry			-1.48	-1.32	-2.80			(33)	(33)		
<i>Mallotus penangensis</i>	Tropical Dry			-1.19			-4.83		(8)		(8)	
<i>Mallotus wrayi</i>	Tropical Moist			-2.19	-0.53				(103)	(104)		
<i>Malosma laurina</i>	Med./ Dry Temperate	-1.74	-3.04	-2.27	-0.68		(49)		(49)	(49)		
<i>Melastoma sanguineum</i>	Tropical Dry			-1.4	-1.2	-2.67			(33)	(33)		
<i>Melicope pteleifolia</i>	Tropical Dry			-1.65	-2.7	-5.02			(33)	(33)		
<i>Memecylon ligustrifolium</i>	Tropical Dry			-1.13	-1.03	-2.11			(33)	(33)		
<i>Miconia cuspidata</i>	Tropical Dry			-2.66	-3.4				(38)	(38)		
<i>Miconia pohliana</i>	Tropical Dry			-1.75	-3.1				(38)	(38)		
<i>Microdesmis caseariifolia</i>	Tropical Dry			-1.96	-2.6	-6.06			(33)	(33)		
<i>Milletia atropurpurea</i>	Tropical Dry			-1.17			-6.08		(8)		(8)	
<i>Millettia cubittii</i>	Tropical Dry			-1.6	-0.74	-1.38			(5)	(5)		
<i>Millettia pachycarpa</i>	Tropical Dry			-1.52	-1.32	-2.65			(55)	(55)		
<i>Mischocarpus pentapetalus</i>	Tropical Dry			-1.54	-1.79	-2.98			(33)	(33)		
<i>Mulinum spinosum</i>	Semidesert	-2.97		-2.66	-5.7	-11.0			(12)	(37)	(12)	
<i>Myrsine ferruginea</i>	Tropical Dry	-1		-1.79	-3.08				(38)	(38)	(38)	
<i>Myrsine guianensis</i>	Tropical Dry	-1.1		-1.76	-2.12				(38)	(38)	(38)	
<i>Neoscortechenia kingii</i>	Tropical Dry			-1.72			-4.72		(8)		(8)	
<i>Nothofagus alessandri</i>	Temperate	-1.7		-1.79	-4.3	-6.56			(105)	(105)	(105)	
<i>Nothofagus antarctica</i>	Temperate	-2.21		-1.73	-5.3	-6.79			(105)	(105)	(105)	
<i>Nothofagus cunninghamii</i>	Temperate	-1.7		-2.09	-2.31	-2.70			(7)	(7)	**	
<i>Nothofagus dombeyi</i>	Temperate	-1.47		-1.63	-3.8	-7.25			(105)	(105)	(105)	
<i>Nothofagus glauca</i>	Temperate	-0.94		-1.95	-3.2	-7.89			(105)	(105)	(105)	
<i>Nothofagus gunnii</i>	Temperate	-1.53		-1.82					(7)	(7)	(105)	
<i>Nothofagus obliqua</i>	Temperate	-1.2		-1.68	-4.5				(105)	(105)	(105)	
<i>Nothofagus pumilio</i>	Temperate	-1.97		-1.68	-3.8	-6.70			(105)	(105)	(105)	
<i>Nyssa sylvatica</i>	Temperate				-1.82	-2.20	-1.7				(27)	(27)
<i>Ochroma pyramidale</i>	Tropical Dry			-1.6	-1	-1.40				(106)	(106)	
<i>Olea europaea</i>	Med./ Dry Temperate			-2.93	-7.1					(107)	(108)	
<i>Olearia hookeri</i>	Med./ Dry Temperate	-2.36		-2.27					(7)	(7)		
<i>Olearia pinifolia</i>	Temperate	-1.71		-2.09					(7)	(7)		
<i>Orites diversifolia</i>	Temperate	-1.25		-1.84					(7)	(7)		
<i>Ouratea hexasperma</i>	Tropical Dry			-2.34	-1.48	-4.60				(64)	(64)	
<i>Ouratea lucens</i>	Tropical Dry			-1.87	-1.8	-4.50				(97)	(98)	
<i>Oxydendrum arboreum</i>	Med./ Dry Temperate				-4.54	-5.70	-1.95			(56)	(27)	(27)
<i>Palaquim sumatrana</i>	Tropical Dry			-1.9			-7.32			(8)		(8)

<i>Parashorea densiflora</i>	Tropical Dry																		(8)	(8)									
<i>Peltophorum dubium</i>	Tropical Moist																		(56)	(56, 57)									
<i>Phillyrea angustifolia</i>	Med./ Dry Temperate																		(99)	(99)	(74)								
<i>Phillyrea latifolia</i>	Med./ Dry Temperate																			(109)	(22)	(22)							
<i>Pieris japonica</i>	Temperate																			(47)	(47)								
<i>Pistacia terebinthus</i>	Med./ Dry Temperate																				(107)	(74)							
<i>Pistacia weinmannifolia</i>	Tropical Dry																				(5)	(5)							
<i>Pittosporum bicolor</i>	Temperate																			(7)	(7)								
<i>Plachonia careya</i>	Med./ Dry Temperate																			(110)	(7)								
<i>Platanus racemosa</i>	Temperate																				(15)	(67)							
<i>Populus balsamifera</i>	Temperate																				(1)	(42)	(42)						
<i>Populus euphratica</i>	Med./ Dry Temperate	-2.52	-4.80																		(111)	(112)							
<i>Populus trichocarpa</i>	Temperate																					(113)	(114)	(115)					
<i>Prionostemma aspera</i>	Tropical Dry																					(46)	(46)	(46)					
<i>Prosopis velutina</i>	Med./ Dry Temperate																						(18, 116)	(116)					
<i>Protium panamense</i>	Tropical Moist																					(47)	(47)	(117)					
<i>Prunus armeniaca</i>	Crop																						(118)	(119)					
<i>Prunus mahaleb</i>	Temperate																					(99)	(99)	(119)					
<i>Prunus virginiana</i>	Temperate																						(1)	(31)					
<i>Prunus serotina</i>	Temperate																						(23)						
<i>Pseudobombax septenatum</i>	Tropical Dry																						(106)	(106)					
<i>Psychotria horizontalis</i>	Tropical Dry																							(120)	(98)				
<i>Pygeum topengii</i>	Tropical Dry																							(33)	(33)				
<i>Pyrus amygdaliformis</i>	Temperate																							(107)	(121)				
<i>Qualea parviflora</i>	Tropical Dry																							(64)	(64)	(65)			
<i>Quercus agrifolia</i>	Med./ Dry Temperate																							(15)	(15)	(6)			
<i>Quercus alba</i>	Temperate																								(122)	(27)	(27)		
<i>Quercus berberidifolia</i>	Med./ Dry Temperate	-1.34	-2.54																						(49)	(49)			
<i>Quercus falcata</i>	Temperate																									(27)	(27)		
<i>Quercus fusiformis</i>	Med./ Dry Temperate																									(123)	(123)		
<i>Quercus garryana</i>	Temperate																								(79)	(47)			
<i>Quercus ilex</i>	Med./ Dry Temperate																								(19)	(124)	(125)	(22, 126)	
<i>Quercus nigra</i>	Temperate																									(27)	(27)		
<i>Quercus oleoides</i>	Tropical Dry	-2.75	-3.73	-2.93	-3.12	-3.03	-3.90																	(4)	(95)	(95)	(4)		
<i>Quercus petraea</i>	Med./ Dry Temperate	-2.16	-3.04	-1.96	-2.39	-3.5	-4.25	-0.53																	(127)	(19)	(19)	(128)	(91)
<i>Quercus phellos</i>	Temperate																										(27)	(27)	
<i>Quercus pubescens</i>	Med./ Dry Temperate	-3.37	-4.10	-2.84	-2.91	-3.3	-5.50																		(73)	(19)	(19)	(125)	
<i>Quercus robur</i>	Temperate																										(129)	(128)	

<i>Quercus rubra</i>	Temperate			-1.98	-2.92	-2.06	-3.32	-1.15		(79)	(79)	(27, 130)	(27)
<i>Quercus semiserrata</i>	Tropical Moist				-1.44				-7.62		(8)		(8)
<i>Quercus wislizeni</i>	Med./ Dry Temperate					-2.49		-0.83				(6)	(131)
<i>Quisqualis indica</i>	Tropical Dry				-1.37	-1.43	-3.69				(55)	(55)	
<i>Raphiolepis indica</i>	Temperate	-2.24	-4.06	-2.08	-2.07					(15)	(14)	(15)	
<i>Rhamnus californica</i>	Med./ Dry Temperate				-2.52	-2.51	-4.09	-0.74				(35)	(69, 70)
<i>Rhamnus crocea</i>	Med./ Dry Temperate					-5.17	-8.66	-2.03					(69, 70)
<i>Rhamnus ilicifolia</i>	Med./ Dry Temperate					-5.92	-9.83	-2.55					(69, 70)
<i>Rhedera trinervis</i>	Tropical Dry	-1.16	-1.47	-1.57	-1.85	-2.8	-4.70			(4)	(95)	(4)	(4)
<i>Rhododendron macrophyllum</i>	Temperate			-1.95		-2.96	-5.00				(79)		(132)
<i>Rhodomyrtus tomentosa</i>	Tropical Dry				-1.29	-1.1	-3.16					(33)	(33)
<i>Rhus ovata</i>	Med./ Dry Temperate	-2.19	-4.17		-2.04	-0.56				(49)		(133)	(49)
<i>Richea scoparia</i>	Temperate			-1.41	-1.53						(7)	(7)	
<i>Rinorea anguifera</i>	Tropical Dry				-1.76				-5.96			(8)	(8)
<i>Sapium sebiferum</i>	Tropical Dry				-2.05	-1.01	-1.56					(33)	(33)
<i>Sarcosperma laurinum</i>	Tropical Dry				-1.75	-3.14	-7.86					(33)	(33)
<i>Schefflera heptaphylla</i>	Tropical Dry				-1.56	-2.59	-4.53					(33)	(33)
<i>Schefflera macrocarpa</i>	Tropical Dry				-1.67	-1.72	-3.95					(64)	(64)
<i>Schima superba</i>	Tropical Dry				-1.54	-5.19	-8.99					(33)	(33)
<i>Schinus johnstonii</i>	Semidesert			-2.82	-3.78	-3.6					(12)	(37)	(12)
<i>Schinus terebinthifolius</i>	Tropical Dry				-2.5	-1.68	-5.33					(134)	(24)
<i>Schisandra glabra</i>	Temperate				-0.85	-1.06	-1.97					(44)	(51)
<i>Senecio filaginoides</i>	Semidesert			-2.6	-1.98	-5	-7.33				(12)	(37)	(12)
<i>Shorea guiso</i>	Tropical Dry				-1.41				-7.85			(8)	(8)
<i>Shorea lepidota</i>	Tropical Dry				-1.36				-3.17			(8)	(8)
<i>Shorea macroptera</i>	Tropical Dry				-0.98				-3.36			(8)	(8)
<i>Shorea parvifolia</i>	Tropical Dry				-1.12				-4.57			(8)	(8)
<i>Sideroxylon lanuginosum</i>	Med./ Dry Temperate					-2.6		-0.42					(123)
<i>Simarouba glauca</i>	Tropical Dry	-1.38	-1.79	-2.09	-2.21	-2	-2.70			(4)	(95)	(4)	(4)
<i>Sorbus torminalis</i>	Med./ Dry Temperate					-3.18	-4.86	-0.9					(22)
<i>Styrax ferrugineus</i>	Tropical Dry			-1.2	-2.49	-3.35					(38)	(38)	(38)
<i>Styrax pohlii</i>	Tropical Dry			-1.4	-2.46	-2					(38)	(38)	(38)
<i>Sweitenia macrophylla</i>	Tropical Dry	-1.79	-2.60		-2.21					(4)		(4)	
<i>Symplocos lanceolata</i>	Tropical Dry			-1.3	-1.45	-1.5					(38)	(38)	(38)
<i>Symplocos mosenii</i>	Tropical Dry			-1.3	-1.95	-1.6					(38)	(38)	(38)
<i>Syzygium cumini</i>	Tropical Dry			-2.03	-1.69	-0.97					(135)	(135)	(135)

<i>Syzygium latilimbium</i>	Tropical Dry			-1.54	-1.17	-2.08				(135)	(135)	(135)	
<i>Syzygium levinei</i>	Tropical Dry				-1.75	-1.37					(33)	(33)	
<i>Syzygium rehderianum</i>	Tropical Dry				-1.85	-1.71					(33)	(33)	
<i>Syzygium sayeri</i>	Tropical Dry			-1.72	-1.86	-2.1				(83)	(83)	(83)	
<i>Syzygium szemaoense</i>	Tropical Dry				-1.52	-1.95					(55)	(55)	
<i>Tachigalia versicolor</i>	Tropical Moist			-1.41	-2.39	-1.6				(47)	(47)	(117)	
<i>Tamarix ramosissima</i>	Semidesert				-2.05	-0.65	-1.42	-2.99			(112)	(24)	(136)
<i>Tasmannia lanceolata</i>	Temperate	-1.13	-1.56	-1.56	-1.79	-3.49	-3.99		(52)	(7)	(7)	**	
<i>Telopea truncata</i>	Temperate			-1.58	-2.07					(7)	(7)		
<i>Tetradymia glabrata</i>	Semidesert					-5.5	-11.0	-2.56				(53)	(31, 53, 54)
<i>Toxicodendron succedaneum</i>	Tropical Moist				-1.59	-1.51	-3.07				(33)	(33)	
<i>Trichostigma octandrum</i>	Tropical Dry				-1.49	-2.9	-6.50				(46)	(46)	(46)
<i>Trimenia neocaledonica</i>	Tropical Moist				-1.15	-1.25	-3.68				(44)	(51)	
<i>Turpinia pomifera</i>	Tropical Dry				-1.4	-2.05	-3.62				(5)	(5)	
<i>Ulmus alata</i>	Temperate					-0.4	-2.50	-0.13				(78)	(78)
<i>Vaccinium myrtillus</i>	Temperate	-1.72	-2.44		-1.38	-2.08			(137)		(137)	(137)	
<i>Vaccinium vitis-idaea</i>	Temperate	-1.64	-2.67		-1.88	-1.97			(137)		(137)	(137)	
<i>Viburnum tinus</i>	Med./ Dry Temperate				-1.3	-2				(138)	(99)	(139)	
<i>Vitis vinifera</i>	Crop		-1.89	-1.13	-1.51				(140)		(140)		
<i>Vochysia ferruginea</i>	Tropical Dry			-2.03	-2.25	-1				(47)	(47)	(117)	
<i>Xanthophyllum hainanense</i>	Tropical Dry				-1.73	-1.5	-3.76				(33)	(33)	
Gymnosperms													
<i>Abies alba</i>	Temperate	-1.61	-3.06			-3.71	-3.31		(141)			(142)	
<i>Abies balsamea</i>	Temperate				-1.57	-2.79	-3.34	-3.87			(62)	(143)	(143)
<i>Abies concolor</i>	Temperate			-1.95	-2.22	-5.15	-6.36	-3.4		(144)	(145)	(146)	(31)
<i>Abies grandis</i>	Temperate				-2.27	-3.65	-4.07				(145)	(147)	
<i>Abies lasiocarpa</i>	Temperate					-3.3		-3.3			(148)	(148)	(149)
<i>Austrocedrus chilensis</i>	Temperate			-0.91	-1.1	-2.7	-4.4			(150)	(150)	(150)	
<i>Ginkgo biloba</i>	Temperate				-2.22	-3.1					(1)	(148)	
<i>Juniperus arizonica</i>	Temperate					-13.8		-9.5				(151)	(151)
<i>Juniperus ashei</i>	Temperate					-13.1		-9.4				(151)	(151)
<i>Juniperus barbadensis</i>	Temperate					-12.8		-7.2				(151)	(151)
<i>Juniperus communis</i>	Temperate				-3.54	-6.05	-8.12				(152)	(142, 147,	

												153, 154)	
<i>Juniperus deppeana</i>	Temperate				-8.9	-12.4	-8.8					(151)	(151)
<i>Juniperus flaccida</i>	Temperate				-7.8	-12.7	-7.8					(151)	(151)
<i>Juniperus lucayana</i>	Temperate				-8.3		-6.3					(151)	(151)
<i>Juniperus maritima</i>	Temperate				-7.58	-7.81	-6.35					(16)	(16)
<i>Juniperus monosperma</i>	Temperate		-3.2	-3.8	-11.6		-9.3		(155)	(156)	(151)	(151)	(151)
<i>Juniperus occidentalis</i>	Temperate			-3.15	-9	-12	-8.5				(140, 157)	(151)	(151)
<i>Juniperus osteosperma</i>	Temperate		-6.35	-4.1	-11.9		-10.4		(144)	(158)	(151)	(151)	(151)
<i>Juniperus pinchotii</i>	Temperate				-14.1		-7.7				(151)	(151)	(151)
<i>Juniperus scopulorum</i>	Temperate				-7.7	-14	-6.9				(151)	(151)	(151)
<i>Juniperus sillicicola</i>	Temperate				-6.6		-4.7				(151)	(151)	(151)
<i>Juniperus virginiana</i>	Temperate			-2.47	-6.2	-9.79	-4.9			(122)	(151)	(151)	(151)
<i>Larix decidua</i>	Temperate			-2.26	-3.53	-4.44				(159)	(154)		
<i>Picea abies</i>	Temperate		-3.87	-2.51	-3.74	-4.33			(144)	(160)	(89, 142, 147, 161-164)		
<i>Picea engelmannii</i>	Temperate		-4.22		-4.18	-5			(144)		(142)		
<i>Picea glauca</i>	Temperate				-2.73		-4.3				(143)	(143)	(143)
<i>Picea mariana</i>	Temperate			-2.53	-3.31		-5.3			(165)	(143)	(143)	(143)
<i>Picea rubens</i>	Temperate			-1.94	-3.48					(166)	(167)		
<i>Pinus cembra</i>	Temperate			-2.34	-3.39	-3.85				(159)	(142, 154, 163)		
<i>Pinus echinata</i>	Temperate				-3.21		-1.47				(27)		(27)
<i>Pinus edulis</i>	Temperate		-1.54	-2.5	-4.88	-5.96	-2.97		(155)	(156)	(168)	(168)	(168)
<i>Pinus elliotii</i>	Temperate				-1.52		-1.33				(169)	(169)	(169)
<i>Pinus flexilis</i>	Temperate			-1.6	-3.71	-4.21			(144)		(147)		
<i>Pinus halepensis</i>	Temperate		-1.75	-2.37	-3.11		-0.88		(141)		(170)	(170)	(170)
<i>Pinus nigra</i>	Temperate		-1.52	-2.28	-3.2	-4.79			(171)	(171)	(22)		
<i>Pinus palustris</i>	Temperate				-1.81		-1.31				(169)	(169)	(169)
<i>Pinus pinaster</i>	Temperate		-0.5		-3.22	-4.79			(172)		(172)		
<i>Pinus pinea</i>	Temperate				-3.65		-1.01				(170)	(170)	(170)
<i>Pinus ponderosa</i>	Temperate		-1.57	-2.23	-3.01	-4.48	-1.2		(47)	(47)	(114, 142, 147, 149, 173, 174)	(175)	(175)
<i>Pinus sylvestris</i>	Temperate		-1.55	-2.94	-2.96	-4.34			(141)		(176)		
<i>Pinus taeda</i>	Temperate		-0.91	-2.22	-3.33	-4.4	-1.74		(177)	(177)	(27, 53, 78)	(27)	(27)
<i>Pinus virginiana</i>	Temperate		-0.84	-1.98	-4.07	-5.32			(26)	(26)	(26)		
<i>Pseudotsuga menziesii</i>	Temperate		-1.39	-2.3	-3.41	-4.25	-1		(47)	(47)	(146, 147, 149, 178-180)	(175)	(175)
<i>Sequoia sempervirens</i>	Temperate			-1.97	-3.4					(181)			
<i>Sequoiadendron</i>	Temperate		-2.59		-8.1				(144)		(148, 182)		

<i>giganteum</i>									
<i>Taxodium distichum</i>	Temperate	-1.15		-2.1				(144)	
<i>Taxus baccata</i>	Temperate	-2.56	-2.26	-6.97	-9.05			(183)	(183) (142, 148)
<i>Tetraclinis articulata</i>	Temperate			-8.55		-2.65			(170) (170)
<i>Thuja occidentalis</i>	Temperate		-2.88	-3.57	-4.71			(184)	(30)

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137 **Table S1.** All values for the water potential at 50% and 95% stomatal closure ($g_s \Psi_{50}$ and $g_s \Psi_{95}$, respectively), 50% declines in leaf,
138 stem, and root hydraulic conductivity (K_{leaf} , K_{stem} , and $K_{\text{root}} \Psi_{50}$, respectively), 12% and 88% declines in K_{stem} ($K_{\text{stem}} \Psi_{12}$ and Ψ_{88}), the
139 turgor loss point (π_{tlp}), and plant death (plant Ψ_{lethal}) collected from the literature for 262 woody angiosperm and 48 gymnosperm
140 species assessed for at least two traits. The references for these data are shown below. Asterisks indicate data published for the first
141 time in this study; data indicated by * were contributed by Hervé Cochard, and data indicated by ** were contributed by Hervé
142 Cochard, Chris Blackman, and Tim Brodribb. Minimum seasonal water potential values at predawn and midday ($\Psi_{\text{min, PD}}$ and $\Psi_{\text{min, MD}}$,
143 respectively) and, for the stem and root hydraulic traits, the shape of the hydraulic vulnerability curves, are included in the
144 supplementary data spreadsheets.

	K_{root} Ψ_{50}	K_{stem} Ψ_{12}	K_{leaf} Ψ_{50}	π_{tlp}	gS Ψ_{95}	$\Psi_{\text{min, MD}}$	$\Psi_{\text{min, PD}}$	K_{stem} Ψ_{50}	K_{stem} Ψ_{88}	Ψ_{lethal}
gS Ψ_{50}	-	0.19 0.5 (18)	0.11 0.8 (11)	0.77 *** (39)	0.82 *** (48)	0.86 *** (28)	-	0.63 * (23)	0.54 * (17)	-
K_{root} Ψ_{50}		0.82 *** (28)	0.87 *** (11)	0.76 *** (20)	-	0.49 ** (27)	0.72 ** (17)	0.86 *** (46)	0.83 *** (22)	-
K_{stem} Ψ_{12}			0.37 ** (56)	0.36 *** (120)	0.48 * (18)	0.24 *** (103)	0.21 * (63)	0.81 *** (147)	0.52 *** (134)	-
K_{leaf} Ψ_{50}				0.65 *** (109)	0.15 0.7 (11)	0.49 *** (81)	0.27 0.1 (44)	0.55 *** (71)	0.25 0.1 (52)	-
π_{tlp}					0.63 *** (39)	0.58 *** (150)	0.39 ** (88)	0.47 *** (151)	0.42 *** (118)	0.56 * (15)
gS Ψ_{95}						0.76 *** (28)	-	0.74 ** (23)	0.72 *** (17)	-
$\Psi_{\text{min, MD}}$							0.91 *** (103)	0.53 *** (139)	0.52 *** (103)	-
$\Psi_{\text{min, PD}}$								0.59 *** (90)	0.58 ** (64)	-
K_{stem} Ψ_{50}									0.89 *** (142)	-

145 **Table S2.** Univariate correlations between each pair of traits measured for at least 10 species.
146 These are the trait correlations shown in Fig. 1 and S2 - S3. In each cell, the top number is the r
147 value, and the bottom numbers are the p-value (the p-value number is shown for $p > 0.05$, and
148 for significant correlations, * indicates $p < 0.05$, ** indicates $p < 0.01$, and *** indicates $p <$
149 0.001) and the number of species (in parentheses). Data are untransformed. Significant
150 correlations are bolded. All correlations remained significant after correction for multiple tests
151 (185). The cell colors indicate the strength of the significant correlations, with dark red for $r \geq$

152 0.75, medium red for $r \geq 0.50$, pink for $r \geq 0.25$, and no color for $r \leq 0.25$. Only stem and root
153 hydraulic trait values estimated from sigmoidally-shaped vulnerability curves were included in
154 these tests.

	$K_{\text{root}} \Psi_{50}$	$K_{\text{stem}} \Psi_{12}$	$K_{\text{leaf}} \Psi_{50}$	π_{tlp}	$g_S \Psi_{95}$	$\Psi_{\text{min, MD}}$	$\Psi_{\text{min, PD}}$	$K_{\text{stem}} \Psi_{50}$	$K_{\text{stem}} \Psi_{88}$	Ψ_{lethal}
$g_S \Psi_{50}$	-	0.19 0.5 (18)	0.11 0.8 (11)	0.77 *** (39)	0.82 *** (48)	0.86 *** (28)	-	0.45 * (29)	0.54 * (17)	-
$K_{\text{root}} \Psi_{50}$		0.85 *** (41)	0.87 *** (13)	0.69 *** (28)	-	0.20 ** (43)	0.42 ** (31)	0.86 *** (63)	0.75 *** (36)	-
$K_{\text{stem}} \Psi_{12}$			0.43 ** (65)	0.39 *** (134)	0.48 * (18)	0.27 *** (113)	0.25 * (70)	0.83 *** (172)	0.55 *** (159)	-
$K_{\text{leaf}} \Psi_{50}$				0.65 *** (109)	0.15 0.7 (11)	0.49 *** (81)	0.27 0.1 (44)	0.57 *** (83)	0.31 * (61)	-
π_{tlp}					0.63 *** (39)	0.58 *** (150)	0.39 ** (88)	0.48 *** (173)	0.44 *** (134)	0.56 * (15)
$g_S \Psi_{95}$						0.76 *** (28)	-	0.48 ** (29)	0.73 *** (17)	-
$\Psi_{\text{min, MD}}$							0.91 *** (103)	0.50 *** (161)	0.53 *** (114)	-
$\Psi_{\text{min, PD}}$								0.59 *** (98)	0.59 ** (71)	-
$K_{\text{stem}} \Psi_{50}$									0.88 *** (169)	-

155 **Table S3.** The univariate correlations between each pair of traits measured for at least 10
156 species, including the stem and root hydraulic trait values interpolated from non-sigmoidally
157 shaped vulnerability curves. Symbols follow Table S2. Only the correlation between $K_{\text{leaf}} \Psi_{50}$ and
158 $K_{\text{stem}} \Psi_{88}$ was changed by the inclusion of these data, indicating that the trait correlations across
159 species are largely robust to the methodological differences in this compiled dataset.

160

Response	Predictor	P	Slope	Angiosperm			Gymnosperm			
				r ²	P	N	Slope	r ²	P	N
$K_{\text{leaf}} \Psi_{50}$	π_{tlp}	0.03	1.27	0.37	***	97	2.04	0.66	**	12
$K_{\text{leaf}} \Psi_{50}$	$K_{\text{stem}} \Psi_{12}$	0.01	0.36	0.39	*	45	0.76	0.53	*	11
$K_{\text{leaf}} \Psi_{50}$	$K_{\text{stem}} \Psi_{50}$	0.25	0.36	0.13	**	55	0.46	0.56	**	16
$K_{\text{leaf}} \Psi_{50}$	$K_{\text{stem}} \Psi_{88}$	0.02	0.28	0.11	0.06	41	0.66	0.06	0.5	11
$K_{\text{leaf}} \Psi_{50}$	$\Psi_{\text{min, MD}}$	0.02	0.76	0.19	***	70	1.46	0.51	*	11
π_{tlp}	$K_{\text{stem}} \Psi_{12}$	0.17	0.47	0.05	*	102	0.36	0.65	***	18
π_{tlp}	$K_{\text{stem}} \Psi_{50}$	0.001	0.42	0.15	***	127	0.24	0.59	***	24
π_{tlp}	$K_{\text{stem}} \Psi_{88}$	0.35	0.31	0.16	***	102	0.33	0.24	*	16
π_{tlp}	$\Psi_{\text{min, MD}}$	0.13	0.54	0.29	***	136	0.69	0.79	***	14
$K_{\text{stem}} \Psi_{50}$	$K_{\text{stem}} \Psi_{12}$	0.002	1.18	0.63	***	118	1.90	0.53	***	29
$K_{\text{stem}} \Psi_{50}$	$K_{\text{stem}} \Psi_{88}$	0.20	0.71	0.76	***	118	0.63	0.88	***	24
$K_{\text{stem}} \Psi_{50}$	$\Psi_{\text{min, MD}}$	0.0001	1.04	0.28	***	117	2.35	0.58	***	22
$K_{\text{stem}} \Psi_{50}$	$K_{\text{root}} \Psi_{50}$	0.22	1.04	0.77	***	17	1.27	0.71	***	29
$K_{\text{stem}} \Psi_{88}$	$K_{\text{stem}} \Psi_{12}$	0.16	1.73	0.22	***	112	2.29	0.36	**	22
$K_{\text{stem}} \Psi_{88}$	$\Psi_{\text{min, MD}}$	0.13	1.53	0.28	***	88	2.35	0.14	0.2	15
$K_{\text{stem}} \Psi_{88}$	$K_{\text{root}} \Psi_{50}$	0.15	2.11	0.40	*	12	1.36	0.80	***	10
$K_{\text{stem}} \Psi_{12}$	$\Psi_{\text{min, MD}}$	0.002	0.86	0.03	0.12	88	1.67	0.66	***	15
$K_{\text{stem}} \Psi_{12}$	$K_{\text{root}} \Psi_{50}$	0.38	0.96	0.31	0.06	12	0.72	0.59	***	16
$\Psi_{\text{min, MD}}$	$K_{\text{root}} \Psi_{50}$	0.004	1.02	0.46	**	15	0.37	0.39	*	12

161 **Table S4.** Tests for significant differences in the slope of the trait relationships between the
162 angiosperm and gymnosperm species. Relationships are standardized major axes (SMA). The
163 left-most P column is the p-value of the test for different slopes. Six of the 19 relationships with
164 sufficient data to test ($n \geq 10$ for each functional type) were significantly different after
165 correcting for multiple tests (185). $K_{\text{stem}} \Psi_{12}$ was significantly correlated with $K_{\text{leaf}} \Psi_{50}$ and $\Psi_{\text{min, MD}}$
166 in the gymnosperms but not the angiosperms, while the two functional types showed
167 significantly different slopes for the relationships of $K_{\text{stem}} \Psi_{50}$ with π_{tlp} and $K_{\text{stem}} \Psi_{12}$, and of
168 $\Psi_{\text{min, MD}}$ with $K_{\text{stem}} \Psi_{50}$ and $K_{\text{root}} \Psi_{50}$. Only stem and root hydraulic trait values estimated from
169 sigmoidally-shaped vulnerability curves were included in these tests, to reduce the influence of
170 methodological differences on the functional type comparisons.

Response	Predictors: full model	r^2	λ	Predictors: w/o trait	$\Delta AICc$	r^2	λ	N
π_{tlp}	$K_{leaf} \Psi_{50}, \Psi_{min, MD}$	0.42	0.6	$\Psi_{min, MD}$	4.6	0.34	0.85*	64
π_{tlp}	$K_{stem} \Psi_{12}, \Psi_{min, MD}$	0.48	1×10^{-6}	$\Psi_{min, MD}$	-2.6	0.50	1×10^{-6}	41
π_{tlp}	$K_{stem} \Psi_{50}, \Psi_{min, MD}$	0.51	1×10^{-6}	$\Psi_{min, MD}$	-0.7	0.50	0.34	62
π_{tlp}	$K_{stem} \Psi_{88}, \Psi_{min, MD}$	0.48	1×10^{-6}	$\Psi_{min, MD}$	-2.2	0.49	0.66	44
$K_{leaf} \Psi_{50}$	$\pi_{tlp}, \Psi_{min, MD}$	0.33	1×10^{-6}	$\Psi_{min, MD}$	9.3	0.21	0.53*	64
$K_{leaf} \Psi_{50}$	$K_{stem} \Psi_{12}, \Psi_{min, MD}$	0.48	0.76	$\Psi_{min, MD}$	3.0	0.25	0.82	20
$K_{leaf} \Psi_{50}$	$K_{stem} \Psi_{50}, \Psi_{min, MD}$	0.45	0.76	$\Psi_{min, MD}$	6.0	0.30	0.95	31
$K_{leaf} \Psi_{50}$	$K_{stem} \Psi_{88}, \Psi_{min, MD}$	0.27	1×10^{-6}	$\Psi_{min, MD}$	-3.7	0.31	0.85	32
$K_{stem} \Psi_{12}$	$K_{leaf} \Psi_{50}, \Psi_{min, MD}$	0.13	1×10^{-6}	$\Psi_{min, MD}$	1.2	0.01	1×10^{-6}	20
$K_{stem} \Psi_{12}$	$\pi_{tlp}, \Psi_{min, MD}$	0	1×10^{-6}	$\Psi_{min, MD}$	-2.6	0.01	1×10^{-6}	41
$K_{stem} \Psi_{50}$	$K_{leaf} \Psi_{50}, \Psi_{min, MD}$	0.30	0.41	$\Psi_{min, MD}$	3.2	0.15	1×10^{-6}	31
$K_{stem} \Psi_{50}$	$\pi_{tlp}, \Psi_{min, MD}$	0.09	0.85*	$\Psi_{min, MD}$	2.9	0.02	0.8*	62
$K_{stem} \Psi_{88}$	$K_{leaf} \Psi_{50}, \Psi_{min, MD}$	0	1	$\Psi_{min, MD}$	-3.7	0.01	1	19
$K_{stem} \Psi_{88}$	$\pi_{tlp}, \Psi_{min, MD}$	0.17	0.9*	$\Psi_{min, MD}$	-0.5	0.14	0.83*	44

171
172 **Table S5.** The r^2 , Aikake Information Criterion corrected for small sample size (AICc) values,
173 and sample size (N) for models predicting each trait as a function of 1) $\Psi_{min, MD}$ (minimum
174 seasonal leaf water potential at midday, a measure of maximum plant water stress), and 2) $\Psi_{min,}$
175 MD and one other trait. These analyses produce the trait coordination results shown in Fig. 2. We
176 used phylogenetic least-squares regression to simultaneously estimate the regression parameters
177 and the branch-length transformation parameter Pagel's λ , which characterizes the phylogenetic
178 non-independence of the trait data. λ values significantly greater than 0 are shown with an *.
179 Comparing the AICc values of the models determines whether two traits are more correlated than
180 expected from concerted convergence with water stress and relatedness. The model containing
181 the trait predictor was supported if $\Delta AICc$ ($AICc_{nested} - AICc_{full}$) ≥ 2 . The supported model is
182 shown in bold. Incorporating π_{tlp} improved prediction of $K_{leaf} \Psi_{50}$, and vice versa, as expected.
183 Contrary to prediction, accounting for $K_{leaf} \Psi_{50}$ also improved prediction of $K_{stem} \Psi_{50}$ and vice
184 versa. The π_{tlp} improved prediction of $K_{stem} \Psi_{50}$, and $K_{stem} \Psi_{12}$ improved prediction of $K_{leaf} \Psi_{50}$,

185 but not vice versa. There was insufficient data to test the hypotheses for the linkage between K_{leaf}
186 Ψ_{50} and the stomatal traits and leaf Ψ_{lethal} , and among the stem and root hydraulic traits and plant
187 Ψ_{lethal} . As predicted, none of the other trait correlations showed stronger coordination between
188 traits than expected from co-selection with $\Psi_{\text{min, MD}}$ and shared ancestry.

Response	Predictors: full model	r^2	λ	Predictors: w/o trait	$\Delta AICc$	r^2	λ	N
π_{tlp}	$K_{leaf} \Psi_{50}, \Psi_{min, PD}$	0.33	1×10^{-6}	$\Psi_{min, PD}$	7.3	0	0.9*	33
π_{tlp}	$K_{stem} \Psi_{12}, \Psi_{min, PD}$	0.09	0.78*	$\Psi_{min, PD}$	-3.2	0.13	0.79*	23
π_{tlp}	$K_{stem} \Psi_{50}, \Psi_{min, PD}$	0.16	0.95*	$\Psi_{min, PD}$	-0.1	0.14	0.93	40
π_{tlp}	$K_{stem} \Psi_{88}, \Psi_{min, PD}$	0.08	0.79*	$\Psi_{min, PD}$	-3.2	0.12	0.78*	22
$K_{leaf} \Psi_{50}$	$\pi_{tlp}, \Psi_{min, PD}$	0.34	1×10^{-6}	$\Psi_{min, PD}$	11.3	0	0.75	33
$K_{leaf} \Psi_{50}$	$K_{stem} \Psi_{12}, \Psi_{min, PD}$	0.41	0.86	$\Psi_{min, PD}$	3.1	0.10	1×10^{-6}	19
$K_{leaf} \Psi_{50}$	$K_{stem} \Psi_{50}, \Psi_{min, PD}$	0.35	0.63	$\Psi_{min, PD}$	4.0	0.22	0.48	30
$K_{leaf} \Psi_{50}$	$K_{stem} \Psi_{88}, \Psi_{min, PD}$	0.08	1×10^{-6}	$\Psi_{min, PD}$	-3.9	0.14	1×10^{-6}	18
$K_{stem} \Psi_{12}$	$K_{leaf} \Psi_{50}, \Psi_{min, PD}$	0.29	1×10^{-6}	$\Psi_{min, PD}$	2.3	0.09	1×10^{-6}	19
$K_{stem} \Psi_{12}$	$\pi_{tlp}, \Psi_{min, PD}$	0	1×10^{-6}	$\Psi_{min, PD}$	-2.9	0.02	1×10^{-6}	23
$K_{stem} \Psi_{50}$	$K_{leaf} \Psi_{50}, \Psi_{min, PD}$	0.32	1×10^{-6}	$\Psi_{min, PD}$	3.7	0.18	1×10^{-6}	30
$K_{stem} \Psi_{50}$	$\pi_{tlp}, \Psi_{min, PD}$	0.01	0.76*	$\Psi_{min, PD}$	-0.6	0	0.96*	40
$K_{stem} \Psi_{88}$	$K_{leaf} \Psi_{50}, \Psi_{min, PD}$	0	1	$\Psi_{min, PD}$	-3.5	0.17	1	18
$K_{stem} \Psi_{88}$	$\pi_{tlp}, \Psi_{min, PD}$	0.17	0.98*	$\Psi_{min, PD}$	-3.2	0.21	0.99*	22

189 **Table S6.** The analyses from Table S5 testing the drivers of the trait correlations, repeated for
190 the subset of species for which $\Psi_{min, PD}$ values were available. $\Psi_{min, PD}$ reflects the water
191 potential of the soil while plant traits have additional influence on $\Psi_{min, MD}$, which could
192 potentially impact the trait coordination results. Symbols follow Table S5. These data showed
193 the same results as in Table S5, with the exceptions that $K_{leaf} \Psi_{50}$ and $K_{stem} \Psi_{12}$ were both more
194 strongly related than expected from associations with $\Psi_{min, PD}$, while $K_{stem} \Psi_{50}$ and π_{tlp} were not
195 correlated after accounting for $\Psi_{min, PD}$. This confirms that $\Psi_{min, MD}$ can be used to robustly
196 identify trait coordination. Indeed, both measures of $\Psi_{min,}$ were strongly correlated ($r^2 = 0.85$, $p <$
197 0.001).

Trait 1	Trait 2	μ	95% CI	Sig.	N
$K_{\text{leaf}} \Psi_{50}$	π_{tlp}	0.32	[0.19, 0.46]	*	86
	$K_{\text{stem}} \Psi_{12}$	-0.52	[-0.09, -0.92]	*	29
	$K_{\text{stem}} \Psi_{50}$	1.07	[0.63, 1.52]	*	38
	$\Psi_{\text{min, MD}}$	-0.22	[-0.44, 0.01]		66
	$K_{\text{stem}} \Psi_{88}$	3.10	[2.17, 4.00]	*	27
π_{tlp}	$g_S \Psi_{50}$	-0.31	[-0.16, -0.56]	*	28
	$K_{\text{stem}} \Psi_{12}$	-0.83	[-0.45, -1.13]	*	58
	$\Psi_{\text{min, MD}}$	-0.28	[-0.06, -0.51]	*	97
	$g_S \Psi_{95}$	0.68	[0.36, 0.96]	*	28
	$K_{\text{stem}} \Psi_{50}$	0.34	[0.02, 0.65]	*	84
	$K_{\text{stem}} \Psi_{88}$	2.46	[1.91, 3.08]	*	61
$K_{\text{stem}} \Psi_{50}$	$K_{\text{stem}} \Psi_{12}$	-1.66	[-1.90, -1.39]	*	87
	$\Psi_{\text{min, MD}}$	-0.53	[-0.06, -0.99]	*	86
	$K_{\text{stem}} \Psi_{88}$	2.22	[1.91, 2.52]	*	83
$K_{\text{stem}} \Psi_{12}$	$\Psi_{\text{min, MD}}$	1.19	[0.60, 1.66]	*	63
	$K_{\text{stem}} \Psi_{88}$	3.91	[3.37, 4.42]	*	89
$K_{\text{stem}} \Psi_{88}$	$\Psi_{\text{min, MD}}$	-3.05	[-2.34, -3.78]	*	65

198 **Table S7.** The mixed effects models testing whether the trait differences are significantly
199 different from 0 for each trait combination measured in ≥ 5 studies. These results establish the
200 sequence shown in Fig. 3. The trait differences were calculated as trait 1 – trait 2, and the mean
201 trait difference (μ) was calculated as the overall fixed-effect intercept after accounting for the
202 random effect of each study (186). 95% confidence intervals for μ were determined from 1000
203 nonparametric bootstraps (10). Trait differences that are significantly different from 0 are
204 indicated with an *. Positive values of μ indicate that trait 2 is more negative than trait 1. N is the
205 number of species. There were only sufficient data to analyze angiosperm species with stem
206 hydraulic trait values interpolated from sigmoidally shaped hydraulic vulnerability curves.
207 Almost all traits showed significant differences. Trait water potential thresholds followed the
208 sequence: $K_{\text{stem}} \Psi_{12} > K_{\text{leaf}} \Psi_{50}$, $\Psi_{\text{min, MD}} > \pi_{\text{tlp}} > K_{\text{stem}} \Psi_{50} > K_{\text{stem}} \Psi_{88}$. Wilting (π_{tlp}) occurred

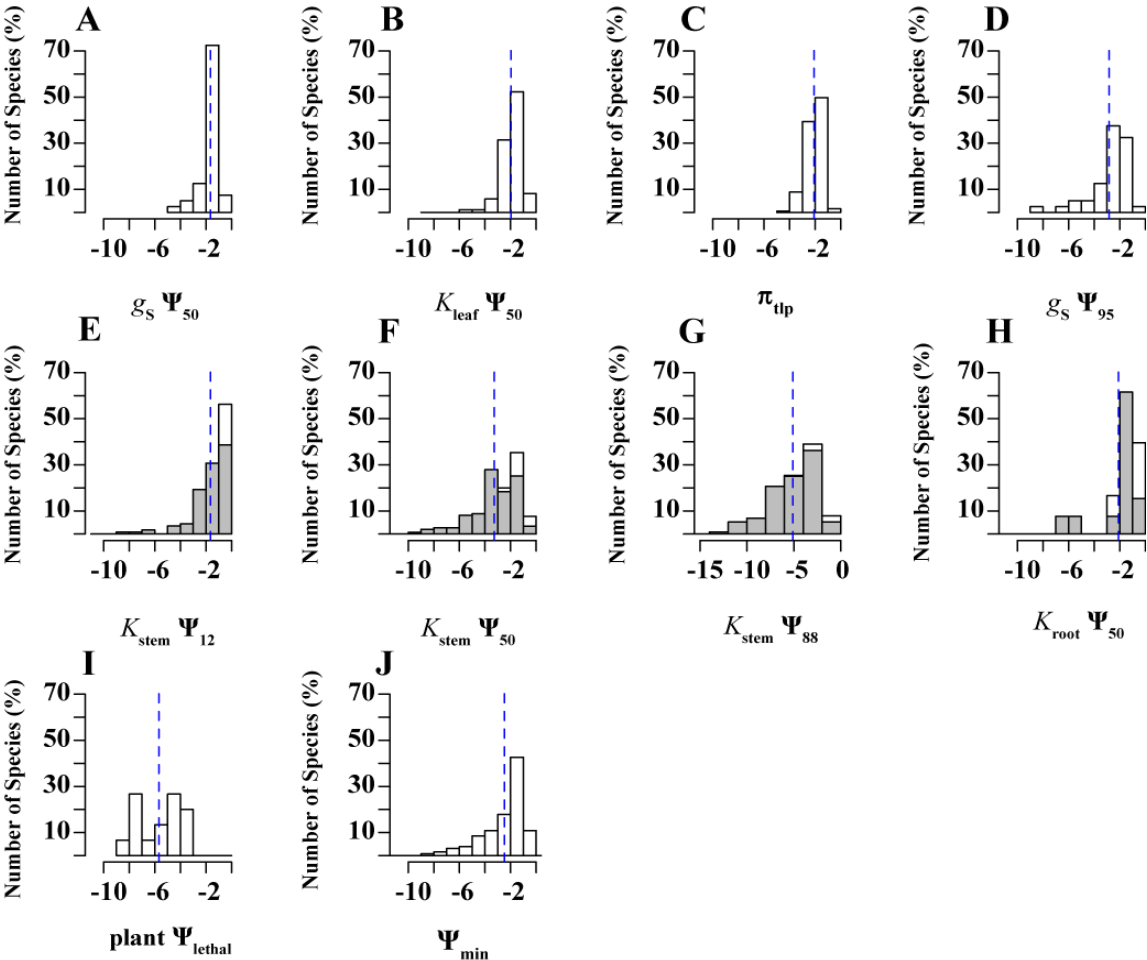
209 after $g_s \Psi_{50}$ and before $g_s \Psi_{95}$, but there were insufficient data to compare $g_s \Psi_{50}$ and Ψ_{95} to the
210 other traits.

Trait 1	Trait 2	μ	95% CI	Phenology Effect	95% CI	Sig.	N (D)	N (E)
$K_{\text{leaf}} \Psi_{50}$	π_{tlp}	0.25	[0.05, 0.54]	0.10	[-0.19, 0.30]		22	64
	$K_{\text{stem}} \Psi_{12}$	-0.33	[-1.25, 0.63]	-0.30	[-1.16, 0.48]		12	17
	$K_{\text{stem}} \Psi_{50}$	1.39	[0.50, 2.46]	-0.48	[-1.32, 0.36]		13	25
	$\Psi_{\text{min, MD}}$	0.05	[-0.18, 0.26]	-0.39	[-0.65, -0.11]	*	18	48
	$K_{\text{stem}} \Psi_{88}$	4.09	[4.08, 5.74]	-1.65	[-2.70, 0.30]		12	15
π_{tlp}	$g_s \Psi_{50}$	-0.29	[-0.85, 0.04]	-0.02	[-0.45, 0.71]		10	18
	$K_{\text{stem}} \Psi_{12}$	-0.65	[-1.09, -0.19]	-0.34	[-0.67, 0.12]		26	32
	$\Psi_{\text{min, MD}}$	-0.26	[-0.55, -0.01]	-0.02	[-0.28, 0.24]		29	68
	$g_s \Psi_{95}$	0.45	[-0.06, 0.79]	0.41	[-0.04, 1.049]		10	18
	$K_{\text{stem}} \Psi_{50}$	0.47	[-0.04, 0.97]	-0.23	[-0.65, 0.25]		31	53
	$K_{\text{stem}} \Psi_{88}$	2.67	[1.70, 3.63]	-0.40	[-1.46, 0.57]		27	34
$K_{\text{stem}} \Psi_{50}$	$\Psi_{\text{min, MD}}$	-0.56	[-1.07, 0.02]	0.05	[-0.48, 0.39]		30	58
$K_{\text{stem}} \Psi_{12}$	$\Psi_{\text{min, MD}}$	1.07	[0.19, 1.82]	0.19	[-0.54, 0.74]		26	37
$K_{\text{stem}} \Psi_{88}$	$\Psi_{\text{min, MD}}$	-3.05	[-4.21, -1.98]	-0.01	[-1.03, 1.08]		27	38

211 **Table S8.** The mixed effect models showing that the angiosperm sequence of trait water
212 potential thresholds (Fig 3, Table S7) is largely robust to leaf phenology. Trait differences are
213 calculated as trait 1 – trait 2, and the trait differences for species j from study k are modeled as:
214
$$Y_{ijk} = \mu + \alpha_k + P_j + \varepsilon_{ijk}$$

215 where P_j is the fixed effect of phenology, α_k is the random effect of study, ε_{ijk} is the residual
216 error, and μ is the overall fixed intercept. 95% confidence intervals for each parameter were
217 calculated from 1000 nonparametric bootstraps (10). An * indicates the trait comparisons with a
218 significant effect of leaf phenology. N shows the number of deciduous (D) and evergreen (E)
219 species. Leaf phenology only significantly affected two trait comparisons. $K_{\text{leaf}} \Psi_{50}$ occurred at a
220 more negative water potential than $\Psi_{\text{min, MD}}$ in the evergreen but not the deciduous species,
221 consistent with the well recognized benefit of deciduousness in maximizing carbon uptake at the
222 expense of leaf longevity, given that leaves could undergo greater hydraulic dysfunction as they
223 are replaced annually (26).

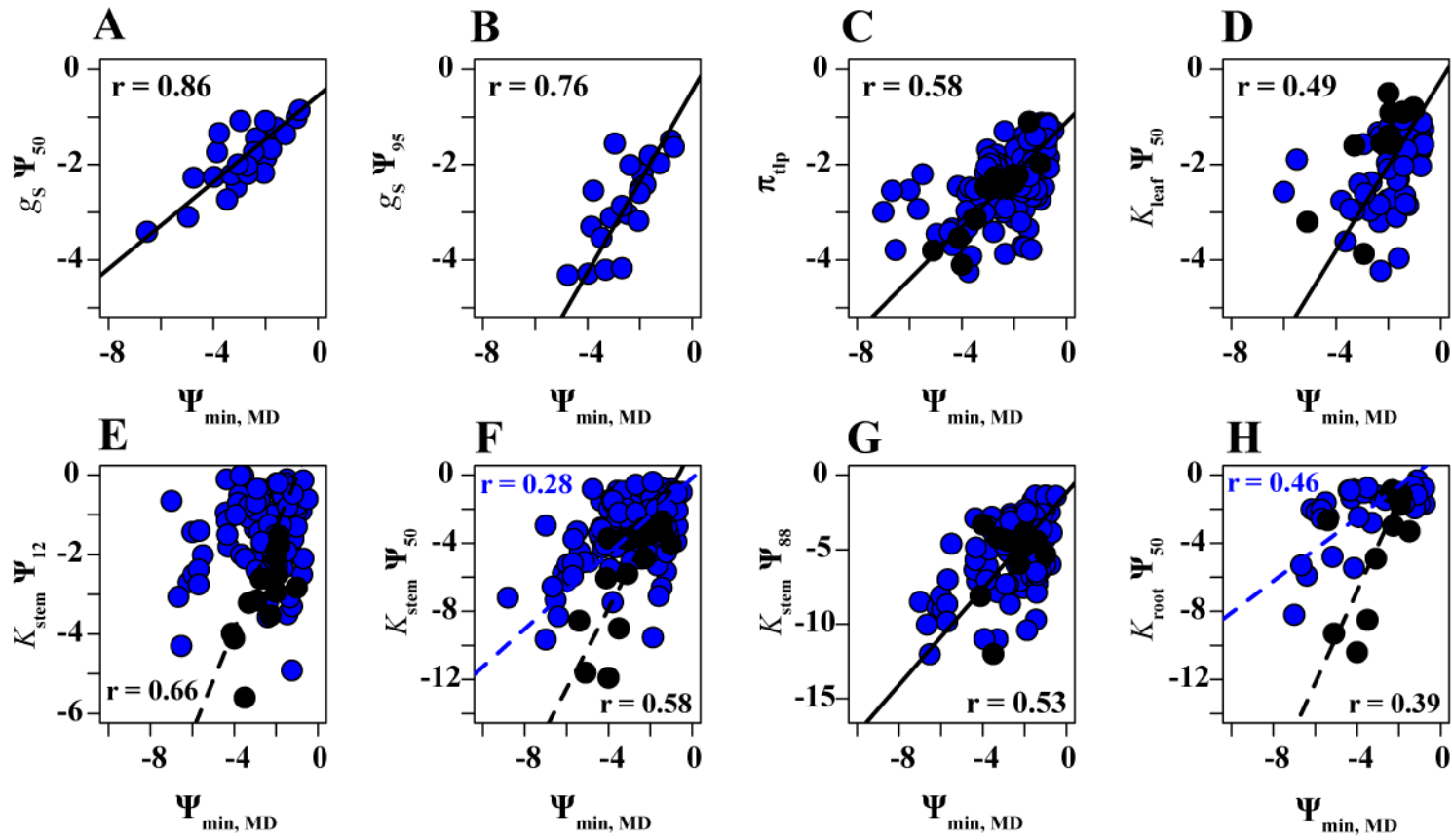
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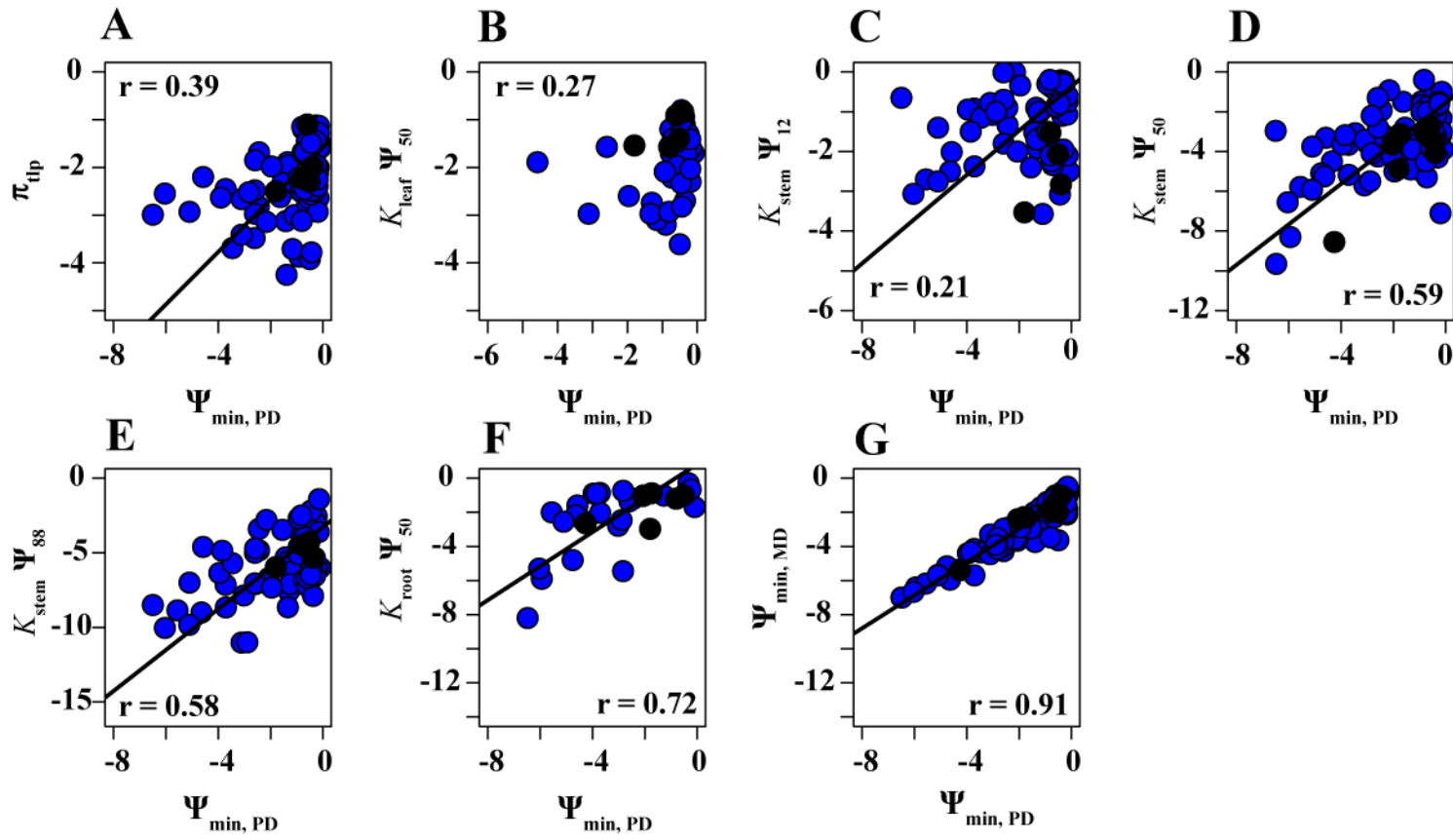
Fig. S1.



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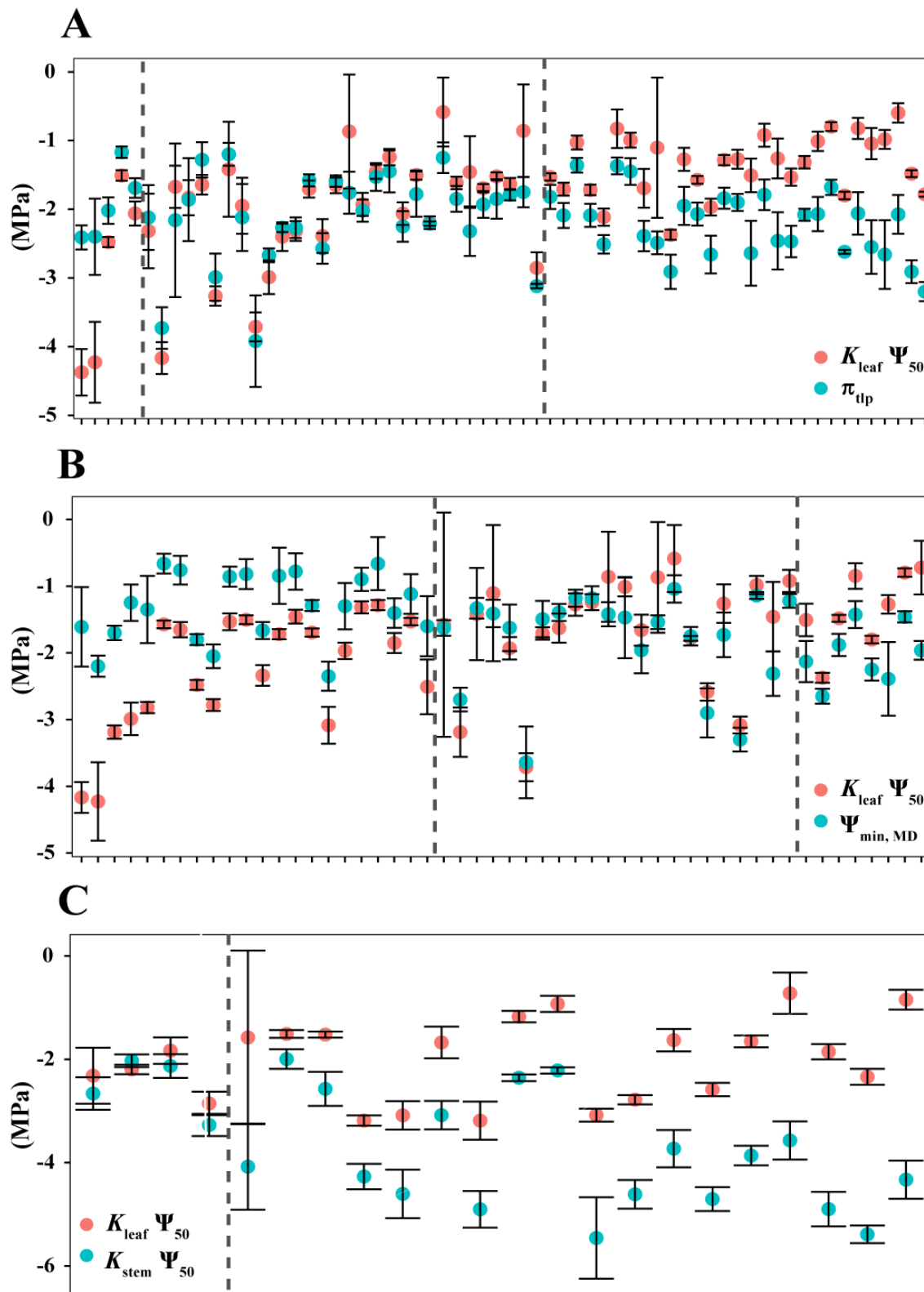
228 **Fig. S2.**

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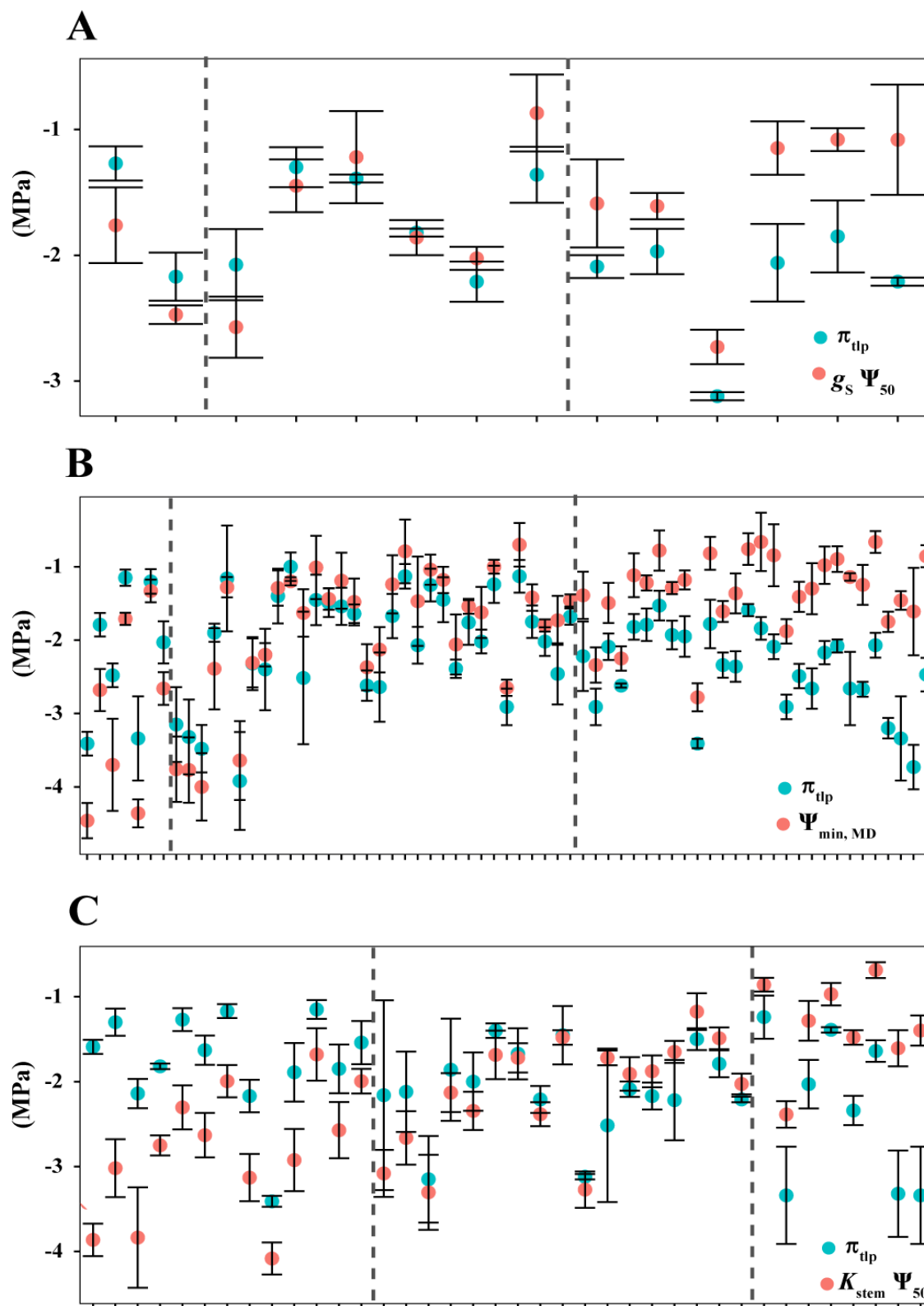
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231 **Fig. S3.**



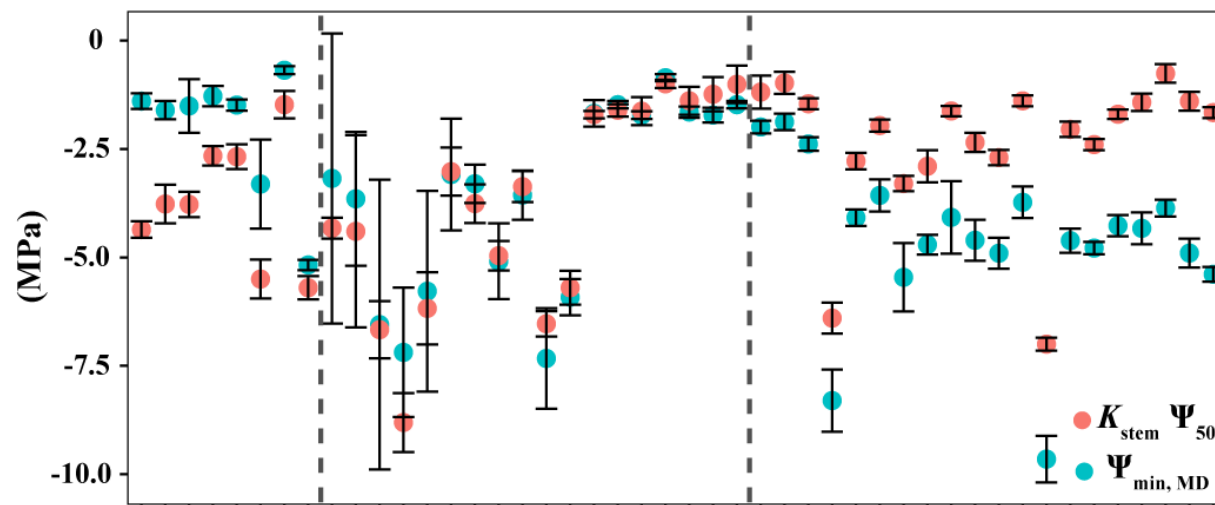
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233 Fig. S4.



234

235 **Fig. S5.**



236

237 **Fig. S6.**

238

Supplementary Methods and Data Sources References

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