

RESEARCH ARTICLE

Aridity-dependent sequence of water potentials for stomatal closure and hydraulic dysfunctions in woody plants

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Funding information

National Natural Science Foundation of China, Grant/Award Number: 31901278; the National Key Research and Development Program of the Ministry of Science and Technology of the People's Republic of China, Grant/Award Number: 2021YFD220040108

Abstract

The sequence of physiological events during drought strongly impacts plants' overall performance. Here, we synthesized the global data of stomatal and hydraulic traits in leaves and stems of 202 woody species to evaluate variations in the water potentials for key physiological events and their sequence along the climatic gradient. We found that the seasonal minimum water potential, turgor loss point, stomatal closure point, and leaf and stem xylem vulnerability to embolism were intercorrelated and decreased with aridity, indicating that water stress drives trait co-selection. In xeric regions, the seasonal minimum water potential occurred at lower water potential than turgor loss point, and the subsequent stomatal closure delayed embolism formation. In mesic regions, however, the seasonal minimum water potential did not pose a threat to the physiological functions, and stomatal closure occurred even at slightly more negative water potential than embolism. Our study demonstrates that the sequence of water potentials for physiological dysfunctions of woody plants varies with aridity, that is, xeric species adopt a more conservative sequence to prevent severe tissue damage through tighter stomatal regulation (isohydric strategy) and higher embolism resistance, while mesic species adopt a riskier sequence via looser stomatal regulation (anisohydric strategy) to maximize carbon uptake at the cost of hydraulic safety. Integrating both aridity-dependent sequence of water potentials for physiological dysfunctions and gap between these key traits into the hydraulic framework of process-based vegetation models would improve the prediction of woody plants' responses to drought under global climate change.

KEYWORDS

drought tolerance, plant hydraulics, stomatal closure, stomatal safety margin, turgor loss point, xylem vulnerability

1 | INTRODUCTION

Shifts in precipitation regimes and rising temperatures driven by global climate change increase drought frequency and intensity (Dai, 2013), which cause worldwide tree mortality even in mesic habitats (Adams et al., 2017; Allen et al., 2010; Anderegg et al., 2016). A

recent global investigation also evidenced that worldwide tree mortality events were closely linked to hotter-drought stress (Hammond et al., 2022). Plant adaptation to drought is complex, involving coordination and trade-offs of multiple traits, particularly the interactions of stomatal (controlling the rate of water loss in exchange for CO₂ uptake; Martin-StPaul et al., 2017) and hydraulic traits (maintaining the integrity of the hydraulic system; Choat et al., 2012).

These interactions provide a great number of viable morphological and physiological solutions that enable vascular plants to survive and grow under diverse climates (Bourne et al., 2017; Brodribb et al., 2014; Choat et al., 2018). Therefore, understanding the coordination and trade-offs between stomatal and hydraulic traits would reveal how multi-physiological traits interact to determine the overall drought tolerance of plants (Bartlett et al., 2016).

Drought-induced increase in the tension within the xylem leads to an increased risk of xylem embolism and ultimately leads to tree mortality (Tyree & Sperry, 1989). The maintenance of the integrity of the hydraulic system depends on the ability of a species to resist embolism, which is generally quantified as the water potential causing 50% loss of hydraulic conductivity (P50; Choat et al., 2012). Yet, the probability of reaching this critical water potential is influenced by stomatal regulation (Blackman et al., 2019; Brodribb et al., 2017; Choat et al., 2018; Martin-StPaul et al., 2017). Stomatal closure (often designated as water potential at 88% loss of stomatal conductance, Ψ_{close}) is a critical mechanism for limiting excessive decrease in water potential that will protect the xylem from extensive embolism, but at the expense of reducing net CO₂ assimilation (Nolan et al., 2017; Pivovarov et al., 2018) and losing canopy evaporative cooling through transpiration (Leigh et al., 2017). Stomatal safety margin (SSM, the difference between Ψ_{close} and P50; Skelton et al., 2015), integrating the xylem hydraulic safety and stomatal regulation, is a more comprehensive metric to characterize plant response to drought. This metric provides a direct proxy of the degree of iso/anisohydry (Skelton et al., 2015), with a more positive value being stronger isohydric (conservatively responds to dehydration by rapidly stomatal closure) and a more negative one being stronger anisohydric (risky stomatal regulation to maintain stomata open even at the occurrence of significant embolism). However, whether isohydric or anisohydric strategy favors species to occupy more drought-prone habitats is unclear (Fu & Meinzer, 2019; Martínez-Vilalta et al., 2014), which might be due to different metrics (e.g., minimum midday water potential, seasonal range of minimum midday water potential, and the slope of the relationship between leaf predawn and midday water potential) result in different species rankings across the iso/anisohydric continuum (Martínez-Vilalta & García-Forner, 2017).

The sequence of physiological events during dehydration strongly impacts overall plant function (Bartlett et al., 2016; Trueba et al., 2019). Bartlett et al. (2016) first proposed a sequence of water potentials for physiological events during dehydration, that is, the seasonal minimum water potential (Ψ_{min}) occurred at the similar water potential as leaf embolism, followed sequentially by wilting, stomatal closure, and stem embolism; but it has been challenged. For example, it has been reported that P50_{leaf} was lower than (Creek et al., 2020) or similar to Ψ_{close} (Hochberg et al., 2017); Ψ_{close} occurred at higher water potential than leaf wilting to prevent mesophyll damage (Dayer et al., 2020; Trueba et al., 2019). Hydraulic safety margin (HSM) characterizes the order of Ψ_{min} and P50 (Delzon & Cochard, 2014): $\Psi_{\text{min}} < P50$ indicates a risky strategy, whereas $\Psi_{\text{min}} > P50$ indicates a conservative strategy (Anderegg et al., 2016;

Choat et al., 2012). Plant survival and competition under different climates depend on its ability to balance the imperative to grow and the risk of hydraulic failure (Brodribb et al., 2014). Plants in xeric environments tend to adopt a conservative sequence to enhance the likelihood of survival with high SSM and HSM (Bourne et al., 2017). In contrast, plants in mesic environments may evolve a risky sequence to support high growth rates with low SSM and HSM. Therefore, the sequence of physiological responses to drought may change with climates but needs more validation along aridity gradient and among different leaf habits, life forms, and functional types.

Here, we synthesized the published data of wilting, stomatal, and hydraulic traits of the leaves and stems of 202 woody species worldwide (Figure S1; Text S1; Dataset S1). Our specific objectives were to: (1) explore the coordination and trade-offs between stomatal and hydraulic traits; (2) investigate how the iso/anisohydric continuum varies with aridity; and (3) discern the sequence of water potentials for stomatal closure and hydraulic dysfunctions with aridity. We hypothesized that species in xeric regions would exhibit a conservative sequence via isohydric regulation (high SSM) and low risk of experiencing xylem embolism (high HSM), while species in mesic regions would exhibit a risky sequence via anisohydric regulation (low SSM) and high risk of experiencing xylem embolism (low HSM).

2 | MATERIALS AND METHODS

2.1 | Data source

We searched the publications that had concomitant measurements of leaf stomatal conductance and water potential for the construction of stomatal response curves using the keywords of “stomatal closure” OR “stomatal conductance” AND “water potential” at the Web of Science and Google scholar. In total, 202 woody species were recorded from 51 publications (Figure S1; Text S1; Dataset S1).

Two methods were used to quantify the stomatal response curves. One is dehydrating excised branches in the laboratory. In the current data set, all the excised branches were cut in wet or growing season except one species that was measured in dry season, which prohibited our analysis on the difference in stomatal closure point between wet and dry seasons. The other method is dry down. For potted and greenhouse experiments, the whole plant experienced dehydration by stopping watering or watering a little, leaf stomatal conductance and water potential were periodically measured during such dry down process. For field experiments, the stomatal response curves were measured during natural dry down (in which one study with eight species experienced severe drought; Dataset S1). Inconsistent metrics of stomatal closure point were used in different studies. In specific, water potentials at 80%, 88%, and 90% loss of stomatal conductance were frequently reported. We defined water potential at 88% declines in stomatal conductance as the stomatal closure point (Ψ_{close}). In addition, some studies provided stomatal

response curves, while others did not. Therefore, if the publications provided the stomatal response scatter plots, we first extracted the data points from the published figures. The following four functions were used to fit the relationships between leaf stomatal conductance (g_s) and water potential (Ψ) (Henry et al., 2019): linear ($g_s = a\Psi + b$), sigmoidal ($g_s = \frac{a}{1 + e^{-\left(\frac{\Psi - \Psi_0}{b}\right)}}$), logistic ($g_s = a / \left[1 + \left(\frac{\Psi}{\Psi_0}\right)^b \right]$), and exponential function ($g_s = ae^{-b\Psi} + c$). The best function was chosen from which the model with the lowest Akaike Information Criterion value. The maximum stomatal conductance ($g_{s_{max}}$) and Ψ_{close} were finally calculated from the optimal curve. If the publications did not provide the stomatal response scatter plots, the $g_{s_{max}}$ and Ψ_{close} were extracted from the tables, figures, or text.

Meanwhile, corresponding hydraulic traits of leaves and stems were collected from the same study (Dataset S1), including the minimum seasonal water potential (Ψ_{min}), leaf turgor loss point (Ψ_{tlp}), the maximum leaf hydraulic conductance ($K_{leaf_{max}}$), the maximum sapwood area-specific stem hydraulic conductivity ($K_{stem_{max}}$), and the water potential for 50% declines in $K_{leaf_{max}}$ ($P50_{leaf}$) and $K_{stem_{max}}$ ($P50_{stem}$). Ψ_{min} in the literature was characterized as the minimum leaf water potential across monthly measurements over a year, which provides a reasonable proxy for the maximum water stress experienced by species in natural conditions (Bartlett et al., 2016). We did not record the Ψ_{min} from potted and glasshouse experiments because it cannot reflect the water stress in situ. Considering the controversy on the measurements of stem vulnerability to embolism because the exponential curve or R-shaped curve generally overestimates the actual vulnerability to cavitation (Cochard et al., 2013), we removed the stem vulnerability to embolism with the R-shaped curve (including six species; showed in Dataset S1). Stem vulnerability to embolism in our data set was measured by air injection, bench dehydration, and centrifugation methods (Dataset S1).

We also recorded the information of growing conditions (field vs. potted and greenhouse), age stages (mature vs. seedling and sapling), leaf habits (deciduous vs. evergreen), life forms (shrub vs. tree), and functional types (angiosperm vs. gymnosperm) (Dataset S1). Biomes were classified into (sub)tropical, temperate forests, Mediterranean, woodland, and desert according to the original papers. Mean annual temperature (MAT) and mean annual precipitation (MAP) were obtained from the original papers or extracted from WorldClim version 2.1 (<https://worldclim.org/>). De Martonne Aridity Index (AI) was calculated by $AI = \frac{MAP}{MAT + 10}$, with a greater AI value representing a more mesic climate (de Martonne, 1926). The AI was further classified into the xeric region (AI lower than 20) and mesic region (AI greater than 35) according to Baltas (2008).

2.2 | Data analysis

Leaf (SSM_{leaf}) and stem (SSM_{stem}) SSMs were calculated as Ψ_{close} minus leaf and stem P50, respectively. Leaf (HSM_{leaf}) and stem (HSM_{stem}) hydraulic safety margins were calculated as Ψ_{min} minus leaf and stem P50, respectively. The covariance analyses (AI as the covariate) were used to test the potential effects of measuring

methods on Ψ_{close} , and no significant effect was found (Figure S2). This was in accordance with most previous studies, which suggested that Ψ_{close} measured by dehydrating excised branches in laboratory agreed well with that measured by dry down on living plants (Henry et al., 2019; Skelton et al., 2015). $P50_{stem}$ quantified using air injection, bench dehydration, and centrifugation methods showed no significant difference (Figure S3). In addition, covariance analysis was also used to test the effects of growing conditions, age stages, leaf habits, life forms, and functional types on stomatal and hydraulic traits.

To examine the degree of hydricity of species under drought using leaf or stem SSMs as the proxy (more positive values being defined as more isohydric and more negative values being defined as more anisohydric, Skelton et al., 2015), we collected 39 species from the data set that reported the slope of the linear relationship between predawn and midday leaf water potential (lower slope implies more isohydric, whereas greater slope implies more anisohydric; Dataset S1), and regressed the slope against leaf or stem SSMs using the simple linear regression procedure. The Spearman correlations were used to quantify relationships among stomatal and hydraulic traits. The one-way ANOVA was used to test the difference in the traits among biomes. All the statistical analyses were conducted with R-4.2.2 (R Core Team, 2022).

3 | RESULTS

The 202 woody species synthesized were distributed across a wide range of climate conditions, that is, MAT varied from 1 to 28°C, MAP varied from 110 to 1850 mm, and AI varied from 6 to 94. Such large climatic gradients resulted in great variations in drought tolerance traits, that is, Ψ_{close} ranged from -7.5 to -0.7 MPa, Ψ_{tlp} ranged from -3.5 to -0.6 MPa, Ψ_{min} ranged from -5.2 to -0.2 MPa, $P50_{leaf}$ ranged from -8.9 to -0.3 MPa, $P50_{stem}$ ranged from -8.5 to -0.5 MPa (Dataset S1). These traits were positively correlated with each other (Figure 1). Both $K_{leaf_{max}}$ and $K_{stem_{max}}$ were positively related to all the five drought tolerance traits ($p < .05$), while $g_{s_{max}}$ was only positively related to Ψ_{tlp} ($p = .035$). $K_{leaf_{max}}$ was positively related to $K_{stem_{max}}$ ($R^2 = .41$, $p = .004$), but both of them were unrelated to $g_{s_{max}}$ (Figure S4).

Ψ_{close} , Ψ_{tlp} , Ψ_{min} , $P50_{leaf}$ and $P50_{stem}$ were all positively correlated with AI and MAP ($p < .001$), while stomatal and hydraulic safety margins were negatively correlated with AI and MAP ($p < .05$) excepting the relationship between HSM_{stem} and AI (Figures 2 and 3 and Figures S5 and S7). Both $K_{leaf_{max}}$ ($R^2 = .15$, $p = .006$) and $K_{stem_{max}}$ ($R^2 = .14$, $p < .001$) were positively correlated with AI, while $g_{s_{max}}$ was decoupled with AI (Figure 2). The traits examined except for HSM_{stem} ($R^2 = .10$, $p = .009$) and $g_{s_{max}}$ ($R^2 = .13$, $p < .001$) were not significantly correlated with MAT (Figure S6).

The covariance analysis showed that there were significant effects of growing conditions on Ψ_{close} ($p = .011$) and SSM_{stem} ($p = .003$), age stages on the Ψ_{min} ($p = .002$) and SSM_{leaf} ($p = .024$), life forms on $P50_{stem}$ ($p = .002$) and SSM_{stem} ($p = .012$), functional types on the $P50_{stem}$ ($p = .009$), and SSM_{stem} ($p < .001$), and HSM_{stem} ($p = .009$),

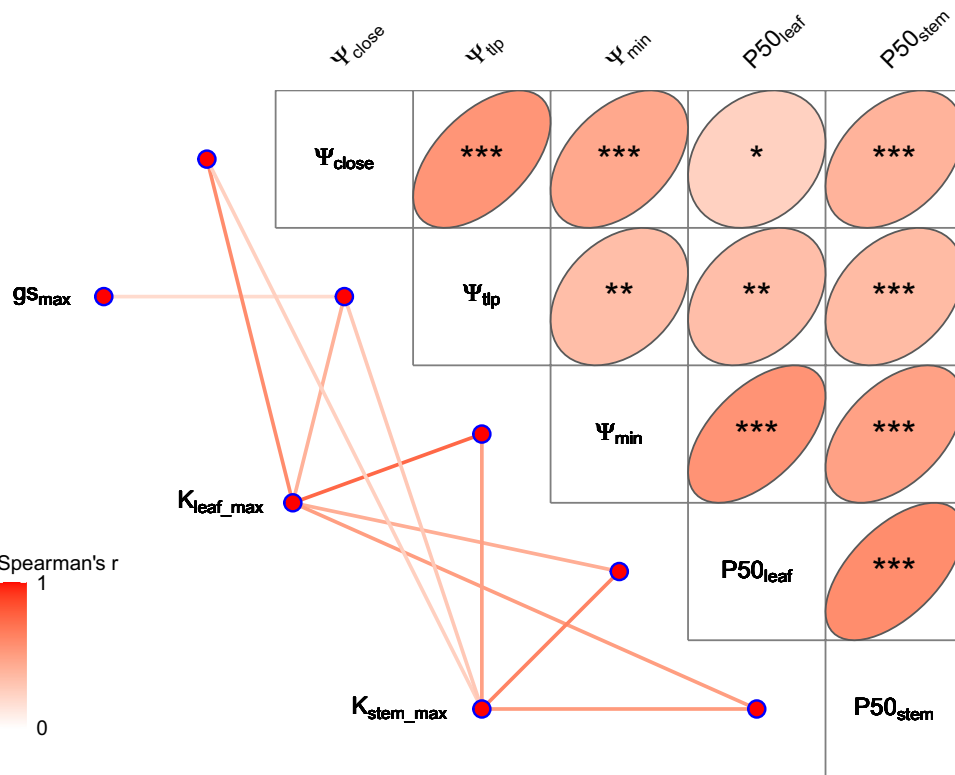


FIGURE 1 Correlations among stomatal and hydraulic traits. Ψ_{close} , water potential at 88% loss of stomatal conductance (stomatal closure point); Ψ_{tlp} , turgor loss point; Ψ_{min} , minimum seasonal water potential; $P50_{leaf}$, water potential at 50% loss of leaf hydraulic conductance; $P50_{stem}$, water potential at 50% loss of stem hydraulic conductivity; $g_{s_{max}}$, maximum stomatal conductance; $K_{leaf_{max}}$, maximum leaf hydraulic conductance; $K_{stem_{max}}$, maximum sapwood area-specific stem hydraulic conductivity. *, $p < .05$; **, $p < .01$; ***, $p < .001$. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/gcb.16605)]

respectively, while no significant effect of leaf habits was found on all the examined traits (Figure 3 and Figure S7). Gymnosperms had more negative $P50_{stem}$ than angiosperms, but they had no significant difference in Ψ_{close} ; thus, the former had higher SSM_{stem} than the latter (Figure 3 and Figure S7). All the traits examined (except for $g_{s_{max}}$) were significantly affected by biomes ($p < .05$; Figures S8 and S9). The species from relatively xeric biomes (Mediterranean, woodland, and desert) tended to have more negative Ψ_{tlp} , Ψ_{min} , Ψ_{close} , $P50_{leaf}$, and $P50_{stem}$ than those from relatively mesic biomes ((sub)tropical and temperate forests) ($p < .01$). The former biomes also had greater stomatal and hydraulic safety margins than the later biomes ($p < .05$), but an opposite pattern occurred for $K_{leaf_{max}}$ ($p < .001$) and $K_{stem_{max}}$ ($p = .001$).

The sequence of water potentials for physiological events in xeric regions ($AI < 20$) was $\Psi_{tlp} > \Psi_{min} > \Psi_{close} > P50_{leaf} > P50_{stem}$, whereas that in mesic regions ($AI > 35$) was $\Psi_{min} > P50_{leaf} > \Psi_{tlp} > P50_{stem} > \Psi_{close}$ (Figure 4). The slope of the linear relationship between predawn and midday water potential was negatively correlated with both stem ($R^2 = .27$, $p = .010$) and leaf ($R^2 = .27$, $p = .034$) SSMs (Figure 5).

4 | DISCUSSION

We quantified stomatal and hydraulic traits of 202 woody species with different ages, leaf habits, life forms and functional types

across a wide range of climatic conditions and biomes. The results showed that the drought tolerance traits (Ψ_{close} , Ψ_{tlp} , Ψ_{min} , $P50_{leaf}$ and $P50_{stem}$) were intercorrelated and decreased with AI decreasing, indicating that water stress drives trait co-selection. Species from xeric regions tended to show a conservative sequence that prevented species from severe tissue damage during drought through a tight stomatal regulation (isohydric strategy) and high mesophyll and embolism resistance. Conversely, species from mesic regions tended to exhibit a risky sequence that allowed species to maximize carbon uptake by loose stomatal regulation (anisohydric strategy) and highly efficient hydraulic system at the cost of hydraulic safety. These findings suggest that both aridity-dependent sequence of physiological dysfunctions and gaps between these key traits should be integrated into the hydraulic framework and modeling of tree growth and distribution in future climate.

4.1 | Coordination and trade-offs between stomatal and hydraulic traits

We found that Ψ_{min} was correlated with all the traits examined (except $g_{s_{max}}$; Figure 1), supporting the selective pressure of plant water stress on stomatal and hydraulic traits (Bartlett et al., 2016). It is reasonable to expect that species experiencing more negative Ψ_{min} could close stomata at lower water potential to maximize

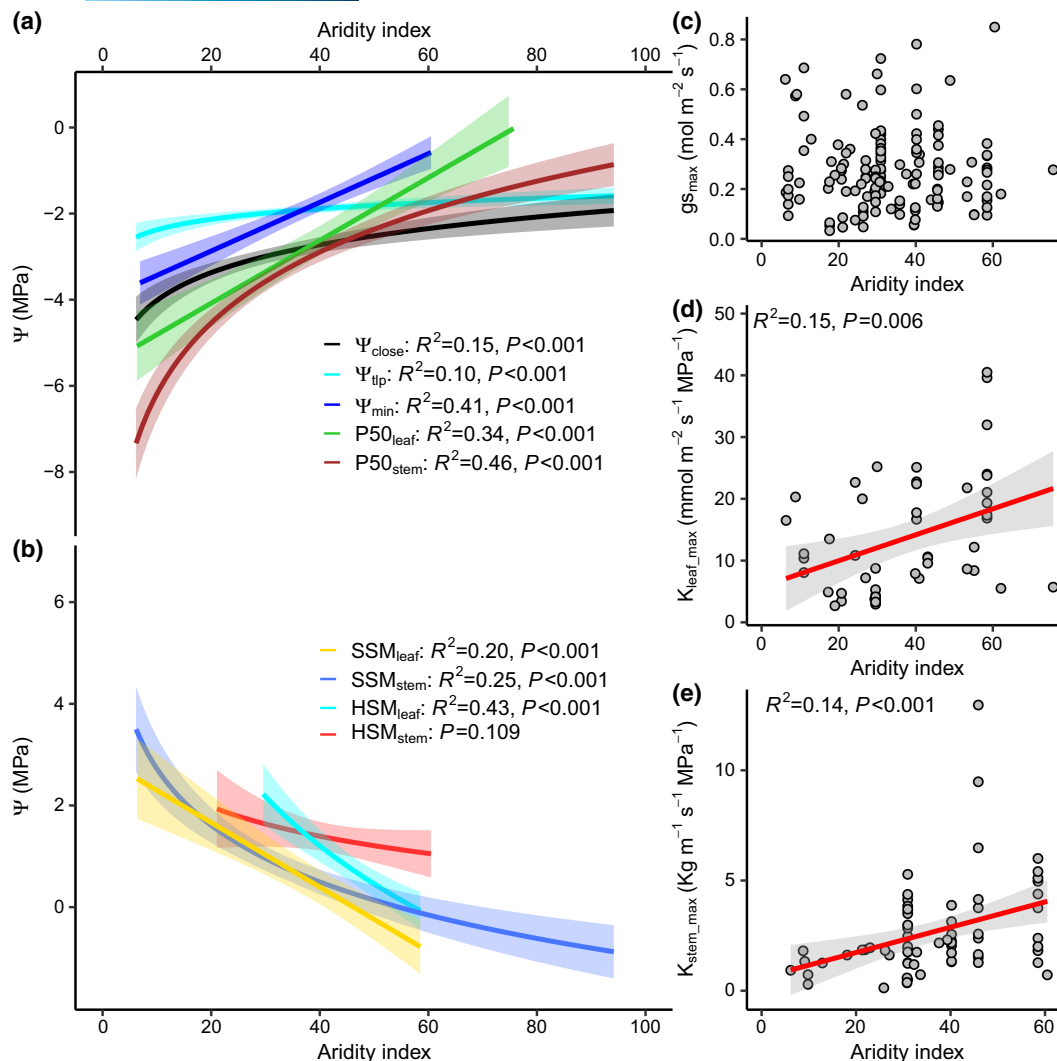


FIGURE 2 Relationships between aridity index and (a) drought tolerance traits, (b) hydraulic and stomatal safety margins, (c) maximum stomatal conductance, (d) maximum leaf hydraulic conductance, and (e) maximum sapwood area-specific stem hydraulic conductivity. A smaller value of Aridity Index indicates a drier climate. The shadings around the regression lines are the 95% confidence intervals. Ψ_{close} , water potential at 88% loss of stomatal conductance (stomatal closure point); Ψ_{tip} , turgor loss point; Ψ_{min} , minimum seasonal water potential; $P50_{leaf}$, water potential at 50% loss of leaf hydraulic conductance; $P50_{stem}$, water potential at 50% loss of stem hydraulic conductivity; SSM_{leaf} , leaf stomatal safety margin; SSM_{stem} , stem stomatal safety margin; HSM_{leaf} , leaf hydraulic safety margin; HSM_{stem} , stem hydraulic safety margin; $g_{S_{max}}$, maximum stomatal conductance; $K_{leaf_{max}}$, maximum leaf hydraulic conductance; $K_{stem_{max}}$, maximum sapwood area-specific stem hydraulic conductivity. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

carbon uptake, but require embolism-resistant xylem to maintain hydraulic safety. The positive association between Ψ_{tip} and $P50_{leaf}$ (Figure 1) supported a mechanistic effect of cell turgor loss on declines in leaf hydraulic conductance via extra-xylary pathway (Scoffoni et al., 2014), due to cell shrinkage or decreased membrane permeability induced by aquaporin deactivation during dehydration (Kim & Steudle, 2007; Scoffoni et al., 2017). The decline in extra-xylary leaf hydraulic conductance would have a great impact on overall leaf hydraulic conductance because extra-xylary pathway accounts for up to 70% of the total leaf hydraulic resistance (Sack & Holbrook, 2006; Scoffoni et al., 2012). Therefore, species with more negative Ψ_{tip} confer higher resistance to the declines in leaf hydraulic conductance by maintaining cell turgor to prevent cell shrinkage

through accumulating solutes and/or allowing aquaporins to remain activated, which consequently contribute to higher leaf embolism resistance (Kim & Steudle, 2007; Scoffoni et al., 2014).

High resistance to xylem embolism is typically associated with narrow conduits and thick conduit walls (Hacke et al., 2001, 2006), while narrow conduits tend to have small pores, and thick and less porous pit membranes (Wheeler et al., 2005). These anatomical features are directly linked to reduced water transport efficiency, supporting the hydraulic safety-efficiency trade-offs in leaves and stems (Figure 1; Gleason et al., 2016; Li et al., 2018; Pratt et al., 2021). However, the exception was that we did not find a stomatal safety-efficiency trade-off. Small stomata are supposed to have a greater value of $g_{S_{max}}$ through reducing the pore depth and,

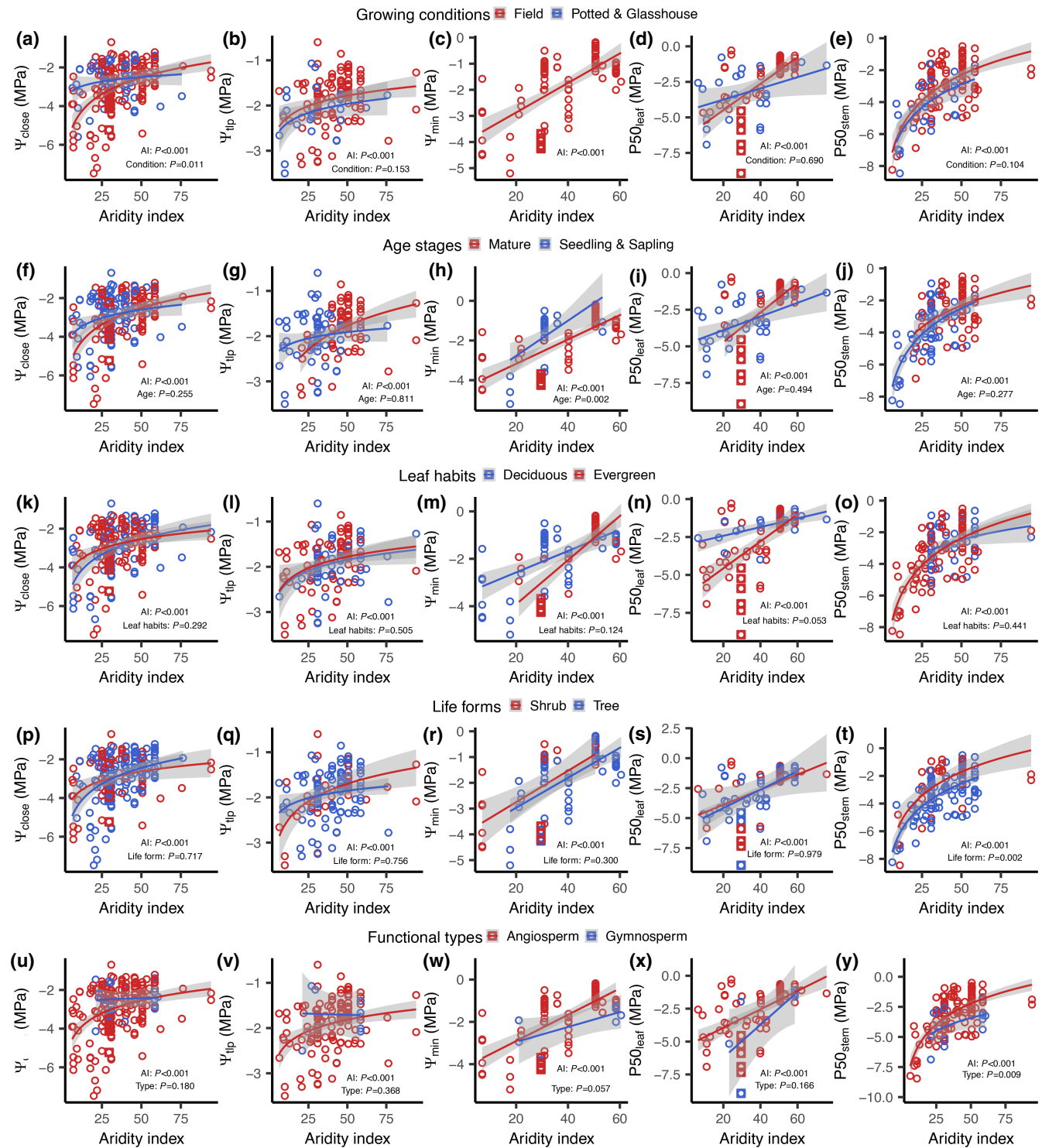


FIGURE 3 Effects of (a–e) growing conditions, (f–j) age stages, (k–o) leaf habits, (p–t) life forms, and (u–y) functional types on the relationships between drought tolerance traits and aridity index (AI). Ψ_{close} , water potential at 88% loss of stomatal conductance (stomatal closure point); Ψ_{tip} , turgor loss point; Ψ_{min} , minimum seasonal water potential; $P50_{leaf}$, water potential at 50% loss of leaf hydraulic conductance; $P50_{stem}$, water potential at 50% loss of stem hydraulic conductivity. The p values are from the covariance analyses with AI as the covariate. The squares for Ψ_{close} , Ψ_{min} , and $P50_{leaf}$ are eight species suffering from extreme drought events. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

thus, decreasing the diffusion distance through the stomatal pore (Franks & Beerling, 2009; Franks & Farquhar, 2007), and also have a greater sensitivity to closure because such stomata have greater membrane surface-to-volume ratios that confer stronger and faster

ion movements (Henry et al., 2019). The decoupling between $g_{s,max}$ and Ψ_{close} provided more possible trait combinations for selections, which may promote more diverse strategies for species under drought.

The covariation of stomatal, embolism resistance, and osmotic adjustment traits with AI influences the adaptation of woody plants to habitats (Figure 2). Woody plants in xeric conditions are exposed to higher evaporative demand and lower soil water availability and, thus, experience lower Ψ_{\min} than those in mesic conditions (Klein, 2014).

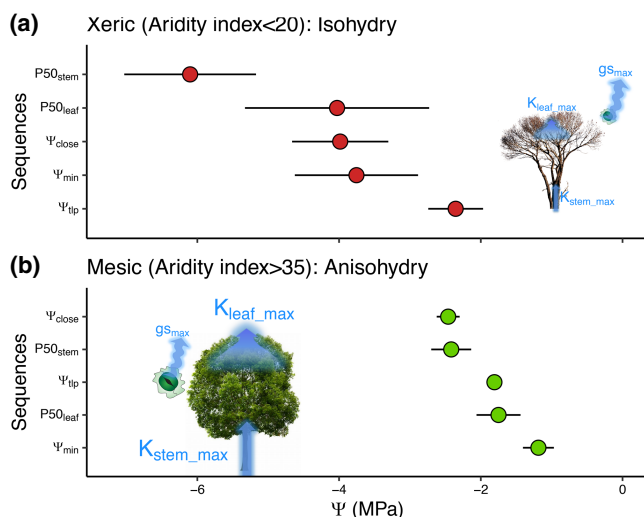


FIGURE 4 Diagram showing the sequences of water potentials for stomatal closure and hydraulic dysfunctions in (a) xeric versus (b) mesic regions. The dots and their corresponding error bars are the means and 95% confidence intervals. The sizes of arrows represent the relative magnitude of the maximum stomatal conductance (g_{smax}), maximum leaf hydraulic conductance (K_{leaf_max}), and maximum sapwood area-specific stem hydraulic conductivity (K_{stem_max}). Ψ_{close} , water potential at 88% loss of stomatal conductance (stomatal closure point); Ψ_{tip} , turgor loss point; Ψ_{min} , minimum seasonal water potential; $P50_{leaf}$, water potential at 50% loss of leaf hydraulic conductance; $P50_{stem}$, water potential at 50% loss of stem hydraulic conductivity. [Colour figure can be viewed at wileyonlinelibrary.com]

Our results suggested that, compared with mesic species, higher drought tolerance via higher leaf and stem embolism resistance (more negative $P50_{leaf}$ and $P50_{stem}$) and stronger osmoregulation to prevent leaf wilting (more negative Ψ_{tip}) for xeric species favor them to adapt to drought-prone climates (Bartlett et al., 2012; Choat et al., 2012; Nardini & Luglio, 2014). The higher cavitation resistance for species in xeric regions might be promoted by narrower, shorter, more frequent xylem vessels and/or thicker, less porous pit membranes in the hydraulic system (Jansen et al., 2009; Sperry et al., 2006, 2008). These anatomical adaptations also compromise hydraulic efficiency, contributing to the decreased K_{leaf_max} and K_{stem_max} with aridity increasing (Bourne et al., 2017; Gleason et al., 2016; Nardini & Luglio, 2014). Moreover, the higher xylary and extra-xylary drought resistances in xeric habitats might allow species to close their stomata at lower water potentials (more negative Ψ_{close}), compensating for their lower photosynthetic rate caused by lower hydraulic conductivity. In summary, this coordination and trade-offs between stomatal and hydraulic traits and their changes with climatic conditions suggest that water stress drives trait co-selection of woody species.

4.2 | The sequence of water potentials for physiological dysfunctions depends on aridity

The water potential values of stomatal, wilting, and embolism decreased at different rates with aridity increasing (Figure 2), indicating that species from xeric to mesic environments displayed different sequences of physiological events during dehydration. In xeric regions ($AI < 20$), Ψ_{min} was lower than Ψ_{tip} but higher than Ψ_{close} , suggesting that the seasonal water stress experienced by xeric species in natural conditions resulted in turgor loss but not complete stomatal closure. However, in mesic regions ($AI > 35$), higher leaf and stem hydraulic conductivities allowed more efficient water transport

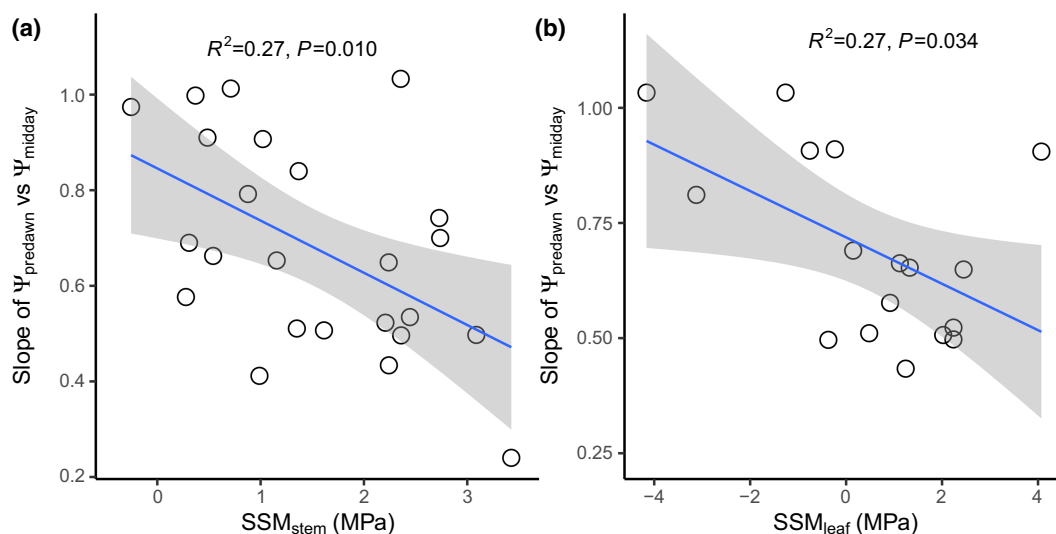


FIGURE 5 Relationships between stomatal safety margins and the slope of the linear relationship between leaf predawn and midday water potential. SSM_{leaf} , leaf stomatal safety margin; SSM_{stem} , stem stomatal safety margin; $\Psi_{predawn}$, predawn water potential; Ψ_{midday} , midday water potential. The lower slope implies more isohydric. The shaded areas represent the 95% confidence intervals. [Colour figure can be viewed at wileyonlinelibrary.com]

from roots to leaves; this led to higher Ψ_{\min} (Sack & Holbrook, 2006), which posed little threat to tree physiological functions.

The plants in xeric climates close stomata at higher water potential than $P50_{\text{leaf}}$ and $P50_{\text{stem}}$, markedly slowing the rate of decrease in water potential and delaying catastrophic hydraulic dysfunction at the cost of CO_2 assimilation (Bartlett et al., 2016; Choat et al., 2018; Creek et al., 2020; Martin-StPaul et al., 2017). If drought persists, the water potential would continue decreasing at a low rate via permeable leaf cuticles and stomatal leakiness after stomatal closure, and ultimately reach a critical embolism level (Blackman et al., 2016; Choat et al., 2018). On the contrary, the plants in mesic climates keep their stomata open at the water potential lower than leaf embolism and slightly lower than stem embolism (Choat et al., 2018; Skelton et al., 2015). This result suggests that they adopt a riskier strategy of prioritizing carbon gain over hydraulic safety (Trifilò et al., 2015; Zufferey et al., 2011), while may restore their hydraulic capacity through refilling embolisms and/or growing new xylem (Brodersen & McElrone, 2013). The stem and leaf SSMs, describing the sequence of embolism resistance and stomatal closure, increased with aridity increasing, suggesting that the greater buffer from stomatal closure to embolism resistance in xeric habitats allow xeric species to tolerate water loss after stomatal closure for longer time and, thus, extend the operational range of water potentials. Therefore, the species in xeric habitats display a conservative strategy in which maintaining the hydraulic integrity to survive drought may be more important than achieving high growth rates (Choat et al., 2018; Nardini & Luglio, 2014).

Our findings supported that using SSM as a proxy for the degree of hydricity of a species (more positive values being defined as more isohydric and more negative values being defined as more anisohydric, Skelton et al., 2015). The significant negative relationship between SSMs and AI suggested that isohydric species tend to dominate in xeric regions, whereas anisohydric species tend to dominate in mesic regions. This is in agreement with global synthesis using the slope of the linear relationship between predawn and midday water potential as a metric of the degree of isohydric-anisohydric (Martínez-Vilalta et al., 2014). However, it is contrary to the global synthesis by Fu and Meinzer (2019) who used hydroscape area as the metric. Species with high $P50$ are assumed to have strict isohydric regulation to rapidly close stomata before xylem embolism at the local scale with same water availability (Chen et al., 2021; Johnson et al., 2018; Quero et al., 2011). However, at a large scale, species in xeric climates need more negative Ψ_{close} for carbon assimilation and more negative $P50$ for improving hydraulic safety, while a wider safety margin of xeric species also tends to be more isohydric, this stomatal strategy would be more successful under extreme drought conditions (Martin-StPaul et al., 2017; Pivovarov et al., 2018). In addition, one recent local study also confirmed that anisohydric *Quercus alba* L. is more vulnerable to embolism than isohydric co-dominants (Benson et al., 2022). Overall, SSM provides a comprehensive isohydric-anisohydric framework to characterize plant response to drought.

Besides the order among traits, aridity-dependent gaps among traits in the sequence also impact the overall plant function during

dehydration (Figures 2 and 4). The gap between Ψ_{close} and Ψ_{tip} increased with aridity increasing, despite that Ψ_{close} consistently occurred at more negative water potential than Ψ_{tip} . This result did not support using Ψ_{tip} as the proxy of stomatal closure point (Hochberg et al., 2018; Martin-StPaul et al., 2017; Meinzer et al., 2016). The Ψ_{tip} calculated from the pressure–volume curve represents the mean of turgor loss points of the mesophyll, bundle sheath, epidermal, and guard cells (Bartlett et al., 2012). Stomatal aperture, however, is controlled by a balance between guard cell turgor (open the pore) and epidermal turgor (close the pore); and the latter is more effective in controlling stomatal aperture due to its mechanical advantage (Buckley, 2005; Buckley & Mott, 2002). Therefore, a greater rate of increase in solute accumulation of epidermal cells, compared with guard cells, as aridity increases would allow stomata to close at more negative water potential and, thus, prolong the carbon uptake. Moreover, Ψ_{\min} was consistently higher than $P50_{\text{leaf}}$ and $P50_{\text{stem}}$ regardless of climates, which suggested that seasonal water stress did not cause a substantial decrease in hydraulic conductivities in both leaves and stems (Cochard & Delzon, 2013; Wheeler et al., 2013). Hydraulic safety margins increased with aridity increasing, and higher hydraulic safety margins in xeric climates implied that the risk of reaching a water potential for hydraulic failure was minimal during drought. Indeed, species growing in dry environments showed a more positive hydraulic safety margins by being more resistant to drought-induced cavitation, although they experience a more negative Ψ_{\min} than those growing in wet environments (Benito Garzón et al., 2018; Martin-StPaul et al., 2017; Peters et al., 2021).

4.3 | Limitations of the sequence of stomatal closure and hydraulic dysfunctions

It is noticed that plant growing conditions, age stages, life forms, functional types, and extreme drought events could alter the sequence of drought tolerance traits (Figure 3; Blackman et al., 2019). Gymnosperms had tighter stomatal regulation (higher SSM_{stem}) than angiosperms (Figure 3 and Figure S7). The looser stomatal regulation of angiosperms makes them more susceptible to drought than gymnosperms, however, this might be compensated by a greater ability to recover from drought because of higher amount of parenchyma in angiosperm wood that drives embolism repair (Anderegg et al., 2016; Jin et al., 2016, 2019; Johnson et al., 2012). Despite a low sample size, species suffering from extreme drought events showed lower Ψ_{\min} and $P50_{\text{leaf}}$ than species without experiencing extreme drought (Figure 3), which could alter the original sequence. However, our current data set was unbalanced in terms of the distributions of growing conditions, age stages, life forms, functional types, and extreme drought events, which may limit the power of our synthesis. Furthermore, even though we did not find a significant effect of methods on $P50_{\text{stem}}$, stem vulnerability curves obtained from invasive methods may overestimate the xylem vulnerability as a consequence of artifacts during sample preparation and measurement (Brodersen et al., 2013; Torres-Ruiz et al., 2014,

2015). Therefore, a better understanding of the predictivity of the sequence for drought-adaptivity and representation of stomatal and hydraulic sequences in vegetation models need much field work synchronously reporting multiple hydraulic and stomatal traits across diverse climates and species using robust and convincing methods.

Additionally, plants could also adapt to drought by drought-avoidance mechanisms besides stomatal closure, including thicker cuticles, high capacitance, drought deciduousness, and deep roots (Oliveira et al., 2021). For example, trees with access to water from deep soil layers are associated with lower xylem resistance to embolism, while coexisting trees with shallow roots may be selected for more resistant xylem (Brum et al., 2019). Late drought-deciduous species may be more embolism resistant than early drought-deciduous (Lima et al., 2018). In addition, some species may also experience significant functional damage with dehydration and survive through recovery processes (Klein et al., 2014). Therefore, plants may deviate from the aridity-dependent sequence through these mechanisms. A comprehensive understanding of coordination in all drought avoidance and drought tolerance traits should be considered in future research.

5 | CONCLUSIONS

Our global synthesis demonstrated that the water potentials for wilting, stomatal closure, and declines in hydraulic conductivity of leaves and stems were intercorrelated and decreased with aridity increasing. SSM provides a comprehensive isohydric-anisohydric framework to characterize plant response to drought. Isohydric species dominated in xeric regions tend to have a trait sequence of highly embolism-resistant systems to function safely under drought, whereas anisohydric species dominated in mesic regions tend to exhibit a trait sequence of highly efficient hydraulic systems to support high productivity at the cost of hydraulic safety. Integrating both aridity-dependent sequence of water potentials for physiological dysfunctions and gap between these key traits into the hydraulic framework of process-based vegetation models would improve the prediction of drought responses of trees under global climate change. Given the unbalanced data distribution and multiple processes involved in responses of plants to drought stress, more field-work that synchronously measures hydraulic architecture, stomatal regulation, water storage, embolism recovery, drought deciduousness, rooting depth across diverse climates and species using robust and convincing methods should be considered in future research.

AUTHOR CONTRIBUTIONS

Y.J. and C.W.—Conceptualization; Z.Z., K.Y., and X.L.—methodology; Y.J. and C.W.—funding acquisition; Y.J.—writing—original draft; G.H., K.Y., W.M.H., X.L., and Q.Y.—writing—review and editing.

ACKNOWLEDGMENTS

We thank all the researchers whose data were used in this synthesis and the reviewers for their valuable comments. This work was

supported by the National Natural Science Foundation of China (31901278) and the National Key Research and Development Program of the Ministry of Science and Technology of the People's Republic of China (2021YFD220040108).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available at <http://doi.org/10.5281/zenodo.7503012>.

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SUPPORTING INFORMATION

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

How to cite this article: Jin, Y., Hao, G., Hammond, W. M., Yu, K., Liu, X., Ye, Q., Zhou, Z., & Wang, C. (2023). Aridity-dependent sequence of water potentials for stomatal closure and hydraulic dysfunctions in woody plants. *Global Change Biology*, 29, 2030–2040. <https://doi.org/10.1111/gcb.16605>