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Global change biology

Leaf hydraulic safety margin and safety–efficiency trade-off across angiosperm woody species

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Leaf hydraulic conductance and the vulnerability to water deficits have profound effects on plant distribution and mortality. In this study, we compiled a leaf hydraulic trait dataset with 311 species-at-site combinations from biomes worldwide. These traits included maximum leaf hydraulic conductance (K_{leaf}), water potential at 50% loss of K_{leaf} ($P_{50\text{leaf}}$), and minimum leaf water potential (Ψ_{min}). Leaf hydraulic safety margin (HSM_{leaf}) was calculated as the difference between Ψ_{min} and $P_{50\text{leaf}}$. Our results indicated that 70% of the studied species had a narrow HSM_{leaf} (less than 1 MPa), which was consistent with the global pattern of stem hydraulic safety margin. There was a positive relationship between HSM_{leaf} and aridity index (the ratio of mean annual precipitation to potential evapotranspiration), as species from humid sites tended to have larger HSM_{leaf} . We found a significant relationship between K_{leaf} and $P_{50\text{leaf}}$ across global angiosperm woody species and within each of the different plant groups. This global analysis of leaf hydraulic traits improves our understanding of plant hydraulic response to environmental change.

1. Introduction

Plant hydraulics plays an important role in forest functioning [1,2]. The leaves contribute more than 30% (up to 80%) of the hydraulic resistance to water flow in whole plants, regarded as a hydraulic bottleneck that underlies plants' hydraulic mechanism for dealing with drought [3]. The maximum leaf hydraulic conductance (K_{leaf}) is correlated with gas exchange [3,4], and thus affects tree growth and forest productivity [2]. Leaves dehydrate owing to insufficient water supply during droughts, leading to a decline in leaf hydraulic conductance from mesophyll turgor loss, vein xylem cavitation and/or reversible collapse of minor-vein conduits [5–8]. Once the water status drops below a critical threshold, the leaves would be damaged or senesce owing to hydraulic dysfunction [9,10]. Therefore, to cope with drought, plants should maintain their leaf water status above the hydraulic threshold by stomatal regulation of the minimum water potential [11], and/or enhance their leaf cavitation resistance [12].

Leaf water potential at 50% loss of K_{leaf} ($P_{50\text{leaf}}$) is a commonly used trait to estimate leaf vulnerability to hydraulic conductance decline, and this trait has been investigated to explain species distributions across water availability gradients [13,14]. Leaf hydraulic safety margin (HSM_{leaf}) is calculated as the difference between minimum water potential under natural drought conditions (Ψ_{min}) and $P_{50\text{leaf}}$ [15,16]. Narrow or negative HSM_{leaf} indicates a high risk of leaf hydraulic failure under drought [10,17]. The vulnerability segmentation hypothesis suggests that leaves are more vulnerable to cavitation than stems,

and early decline in leaf hydraulic conductance could prevent water loss and protect the main stems from hydraulic dysfunction [15,18–20]. Indeed, species with narrower HSM_{leaf} values tend to have stronger leaf-to-stem vulnerability segmentation [20,21]. Moreover, a recent study from seasonally dry tropical forests reports a significant relationship between HSM_{leaf} and mortality rates during an extreme drought episode, indicating that HSM_{leaf} may play a role in predicting tree demographic rates under climate change [22].

The trade-off between hydraulic safety and efficiency in leaves has been widely investigated in the past decade [12,14,23,24], but there are conflicting results about leaf hydraulic trade-off. Some studies have reported that there is no significant relationship between K_{leaf} and $P50_{leaf}$ [12,14,24]. One possible reason is that K_{leaf} and $P50_{leaf}$ are influenced by both xylem [12,25] and outside-xylem pathways [6,9,26], thus obscuring such a trade-off. Conversely, other studies have found a significant leaf hydraulic trade-off in Mediterranean-type forest [27] and across angiosperm species from different biomes [5]. Therefore, a global meta-analysis incorporating a broad range of plant functional groups and water environments would provide a more complete understanding of such a trade-off [28].

In this study, we compiled a dataset of leaf hydraulic traits (including K_{leaf} , $P50_{leaf}$, Ψ_{min} and HSM_{leaf}) of global angiosperm woody species from published literature and our unpublished data (S.-D. Zhu, P.-C. He 2020, unpublished data). Our main objectives were: (1) to investigate the variation in HSM_{leaf} across habitats with a broad range of water availability, and (2) to test the leaf hydraulic safety–efficiency trade-off across global woody species, and within different phenology (evergreen and deciduous), growth forms (lianas, shrubs and trees) and water habitats (arid and humid).

2. Material and methods

(a) Data collection

We compiled a dataset of leaf hydraulic traits (i.e. K_{leaf} , $P50_{leaf}$, Ψ_{min} and HSM_{leaf}) of 311 species-at-site combinations (302 angiosperm woody species) from published papers and our own unpublished data (97 species; (S.-D. Zhu, P.-C. He 2020, unpublished data)). The dataset was collected according to the following criteria: (1) all the measurements were made from mature individuals in the field; (2) the Ψ_{min} values were obtained as the most negative leaf water potential observed for a plant species [29]. In our dataset of Ψ_{min} (220 observations), 42% of the observations were collected during serious drought events, and the rest of the observations were collected during seasonal drought periods of a year. It should be noted that the estimation of leaf hydraulic safety margin ($\Psi_{min} - P50_{leaf}$) for some species in this study was coarse because of lacking long-term monitoring of water potential. The values of K_{leaf} and $P50_{leaf}$ were determined from leaf hydraulic vulnerability curves. It should also be noted that the leaf vulnerability curves were measured by using different methods, including the rehydration kinetics method (89% of the 311 observations), optical visualization method (6%), evaporative flux method (3.5%) and others (less than 1%). Although previous studies have shown consistent results between different methods for several tree species [30,31], this should be still taken with caution for the global meta-analysis.

Based on information in source papers and online floras (e.g. <http://www.iplant.cn/>), woody species were divided into different functional groups by phenology (i.e. evergreen and deciduous), or plant growth forms (i.e. lianas, shrubs and trees). Biomes were classified as tropical rainforest, tropical

seasonal forest, temperate rainforest, temperate seasonal forest, Mediterranean forest and woodland and desert shrubland. The aridity index could estimate the degree of drought stress for each study site (electronic supplementary material, table S1), which was obtained from the literature (the climatic data are concomitant with hydraulic traits in several publications used for the dataset), adjacent meteorological stations and the Geospatial Database (<http://www.cgiar-csi.org>). This index is calculated as the ratio of mean annual precipitation to potential evapotranspiration, as smaller values indicate more arid climate [32]. Aridity index greater than 0.65 and less than or equal to 0.65 were classified as humid and arid climate, respectively [32,33].

(b) Data analysis

To analyse the relationship between HSM_{leaf} and aridity index and to compare mean HSM_{leaf} among biomes, we used the mean values of each species at each site. Data were $\log_{10}$ -transformed prior to analysis of the relationship between K_{leaf} and $P50_{leaf}$. Linear regression analysis was used to test the correlations between HSM_{leaf} and aridity index, and between K_{leaf} and $P50_{leaf}$ across species. The difference in HSM_{leaf} among biomes was examined by one-way analysis of variance (ANOVA), followed by *post hoc* pairwise comparisons based on the Games–Howell test. All the analyses were performed in SPSS 16.0 (SPSS, Chicago, IL, USA).

3. Results

The mean HSM_{leaf} of the angiosperm woody species was 0.55 MPa, ranging from -4.12 to 3.53 MPa. About 70% of the studied species exhibited HSM_{leaf} narrower than 1 MPa, and 30% of them showed negative values. Across species from different sites, HSM_{leaf} was positively correlated with aridity index ($r = 0.40$, $p < 0.001$; figure 1). Mean HSM_{leaf} was significantly higher in the biomes from humid climate (i.e. tropical rainforest and temperate rainforest) compared to other biomes ($p < 0.05$; figure 1).

There was a significant relationship between $P50_{leaf}$ and K_{leaf} across global angiosperm woody species ($r = 0.49$, $p < 0.001$; figure 2). This relationship was also significant within deciduous species ($r = 0.30$, $p < 0.01$) and evergreen species ($r = 0.50$, $p < 0.001$), or within each growth form, such as the lianas ($r = 0.65$, $p < 0.05$), trees ($r = 0.50$, $p < 0.001$) and shrubs ($r = 0.24$, $p < 0.05$), or for species from arid ($r = 0.56$, $p < 0.001$) and humid habitats ($r = 0.47$, $p < 0.001$).

4. Discussion

Most angiosperm woody species in this study operated with narrow HSM_{leaf} (less than 1 MPa; figure 1). This result was consistent with a previous meta-analysis of stem hydraulic safety margin [29] and indicated that leaves could also be hydraulically vulnerable to drought conditions across global angiosperm woody species [22]. Additionally, a large proportion of species showed negative HSM_{leaf} , as found in both humid and arid biomes. It is likely that these species may rely largely on leaves acting as safety valves (early loss of hydraulic conductance) to maintain the hydraulic functioning of the stem during drought periods [15,20]. Further study on the hydraulic safety margins of the leaves and stems simultaneously would enable accurate assessments of the plant hydraulic risk during drought and improve our understanding of vulnerability segmentation [15,20,34].

We found a weak positive relationship between HSM_{leaf} and aridity index across global angiosperm woody species

Figure 1. Relationship between the aridity index and leaf hydraulic safety margin (HSM_{leaf}). The aridity index is calculated as the ratio of mean annual precipitation to potential evapotranspiration, and smaller values indicate a more arid climate. Each point denotes one species in each site. Linear function: $y = 0.834x - 0.393$ ($r = 0.40$, $p < 0.001$, $n = 220$). Inset: mean HSM_{leaf} of six major biomes. Boxes show the 25th to 75th percentiles, solid lines within boxes represent median values, dashed lines within boxes represent mean values, bars represent 10th and 90th percentiles, and circles represent extreme values. The horizontal dotted line indicates that HSM_{leaf} equals zero. Different letters indicate statistically significant differences at $p < 0.05$. Biome abbreviations: TRRF, tropical rainforest ($n = 95$); TERF, temperate rainforest ($n = 15$); MED, Mediterranean forest and woodland ($n = 31$); TESF, temperate seasonal forest ($n = 15$); DES, desert shrubland ($n = 9$); TRSF, tropical seasonal forest ($n = 55$).

Figure 2. Relationships between maximum leaf hydraulic conductance (K_{leaf}) and leaf water potential at 50% loss of K_{leaf} ($P50_{leaf}$) across angiosperm woody species. Inset plot shows log-transformed relationship for all species. Inset table shows the relationships within each plant group: all species, $n = 279$; evergreen, $n = 201$; deciduous, $n = 78$; liana, $n = 12$; shrub, $n = 74$; tree, $n = 193$; arid habitat, $n = 76$; humid habitat, $n = 189$. Aridity index (AI) > 0.65 and ≤ 0.65 indicate humid and arid climate, respectively [32,33]. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

(figure 1). On average, HSM_{leaf} of the tropical rainforest showed the largest value across biomes in this study. This result was supported by recent studies showing that tree species from tropical moist forests experience low risks of leaf hydraulic failure because they exhibit high (less negative)

Ψ_{min} during drought seasons and great resistance to cavitation [16,35]. The 'weak' relationship might be partially owing to the large variations of HSM_{leaf} within biomes, e.g. tropical rainforest, tropical seasonal forest and Mediterranean forest and woodland (figure 1). Several previous studies

conducted in those biomes have revealed that co-occurring woody species could operate diverse hydraulic strategies (e.g. isohydric–aniso-hydric behaviour, leaf shedding, internal water storage and deep root system) to deal with drought [10,17,36–38], which are associated with different degrees of potential hydraulic risks at leaf level [10,17,37].

Our results supported the leaf hydraulic safety–efficiency trade-off across global angiosperm woody species. In addition, such a hydraulic trade-off was also evident within each of the different plant functional groups (figure 2). Accumulated findings of the impact of leaf structure on leaf hydraulic function may explain such a trade-off, as both leaf hydraulic efficiency and safety are linked with the same xylem and outside-xylem characteristics, e.g. vein density [25,39], conduit size [7,40], mesophyll cell wall volume and thickness [6,26]. Furthermore, we found that intercepts of the trade-off lines differed significantly between arid and humid habitats (electronic supplementary material, figure S1). Species from arid habitats tended to exhibit more negative $P_{50_{\text{leaf}}}$ at a given K_{leaf} relative to species from humid habitats, which supported previous studies that plants growing in arid habitats show great drought resistance in leaves [13,14]. Interestingly, our result also showed that arid species had higher K_{leaf} at a given $P_{50_{\text{leaf}}}$ than humid species. This result partially supported a recent study about interspecific variations in leaf hydraulic traits of 10 *Caragana* species from a range of rainfall environments, which indicates that high K_{leaf} plays a role for species adapted to low rainfall habitats because high leaf hydraulic efficiency may match the requirement of high transpiration caused by high vapour pressure deficit and protect leaves from overheating during drought conditions [41]. Therefore, shifts of the hydraulic safety–efficiency trade-off across different water environments may provide a way to elucidate plants' hydraulic adaptation to drought.

Phylogenetic analyses are widely used to control for the lack of statistical independence among species and to test the evolutionary integration between traits [42]. We analysed phylogenetic correlation between K_{leaf} and $P_{50_{\text{leaf}}}$ in this study, and the result indicated that there was an evolutionary

integration between leaf hydraulic efficiency and safety (electronic supplementary material, figure S2). A recent global phylogenetic analysis of stem hydraulic traits did not find a significant evolutionary trade-off between hydraulic conductivity and cavitation resistance at the genus level of phylogeny, because the two stem hydraulic traits depend on several anatomical properties that might not necessarily co-evolve [43]. Therefore, the evolutionary correlation between hydraulic efficiency and safety needs to be further clarified.

In conclusion, this study expands our knowledge of leaf hydraulics. Our results reveal that across global angiosperm woody species there is a significant relationship between leaf hydraulic safety margin and aridity index, and a significant trade-off between leaf hydraulic efficiency and safety. We recommend future studies conducting a comprehensive investigation of leaf structural characteristics (including both xylem and outside-xylem) and hydraulic function (with reliable and consistent methods) across plant groups and habitats, for a better understanding of correlations among leaf hydraulic traits and their contributions to ecological performance.

Data accessibility. Data are available as the electronic supplementary material.

Authors' contributions. C.-L.Y. conceived the idea, compiled and analysed data, drafted the manuscript and revised the manuscript; M.-Y.N. compiled and analysed data and help to draft the manuscript; S.-D.Z. conceived the idea, coordinated the study and revised the manuscript; K.-F.C. conceived the idea and gave the important comments for the revision. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

Competing interests. We declare we have no competing interests.

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