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Tree-level stomatal regulation is more closely related to xylem hydraulic traits than to leaf photosynthetic traits across diverse tree species

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ABSTRACT

Understanding stomatal regulatory mechanisms across various woody species is helpful for explaining their adaptations to diverse environmental conditions. Stomatal opening and closing are driven by the requirements for maintaining water transport integrity and carbon uptake; however, distinguishing which factor plays a dominant role in the regulation of tree-level stomatal behavior has seldom been explored. To address this knowledge gap, we investigated differences in tree-level iso/anisohydric stomatal regulation among various tree species (61 and 59 species, at daily and hourly timescales, respectively) across diverse biomes, and analyzed the association of tree-level stomatal regulation with xylem hydraulic and leaf photosynthetic traits. Xylem hydraulic traits were closely related to tree-level stomatal regulation, whereas leaf photosynthetic traits showed non-significant correlations. Reduction in tree-level stomatal conductance with the same vapor pressure deficit increment (ranging from 0.6 to 2 kPa; L_{cond}), representing the degree of iso/anisohydry, was positively correlated to xylem pressure inducing 50% loss of hydraulic conductivity and vessel diameter, but negatively correlated to the hydraulic safety margin. The associations between xylem hydraulic traits and L_{cond} revealed that tree species with greater xylem hydraulic efficiency were more likely to adopt an avoidance strategy for tree-level stomatal regulation, whereas tolerance strategy occurred in species with a stronger hydraulic safety system. Furthermore, L_{cond} was positively correlated to mean annual precipitation and temperature, suggesting that species inhabiting humid and warm regions rely upon isohydric stomatal regulation. Moreover, L_{cond} displayed a phylogenetic signal, suggesting that variation in L_{cond} has been influenced by evolutionary history. Overall, tree-level stomatal regulation is more closely related to xylem hydraulic traits than to leaf photosynthetic traits, and maintaining water transport integrity rather than fulfilling requirements for carbon uptake is the major factor impacting tree-level stomatal regulation.

1. Introduction

The maintenance of root-to-leaf water transport pathway integrity is critical for sustaining the carbon assimilation and growth of terrestrial plants (Meinzer and McCulloh, 2013). Embolism disturbs whole-tree water pathway integrity, causes a dramatic loss of xylem hydraulic transport capacity, and decreases plant productivity (Choat et al., 2012; Zwieniecki and Holbrook, 2009). The ability to maintain water transport integrity is determined by the plant water use regulation strategy, which is the result of evolutionary processes, together with environmental and biophysical constraints (Flo et al., 2021; Lu et al., 2020). Therefore, understanding the hydraulic regulatory mechanisms across various woody species would be beneficial for explaining the adaptations of these plants to environmental conditions, and predicting variation in plant behavior under global climate change scenarios (Anderegg, 2015; Meinzer and McCulloh, 2013).

Vulnerability curves have been frequently used as a measure of plant susceptibility to drought (Chen et al., 2021; Venturas et al., 2019). Under natural conditions, tree-level vulnerability to embolism is not necessarily equivalent to the risk of embolism in situ, which is also

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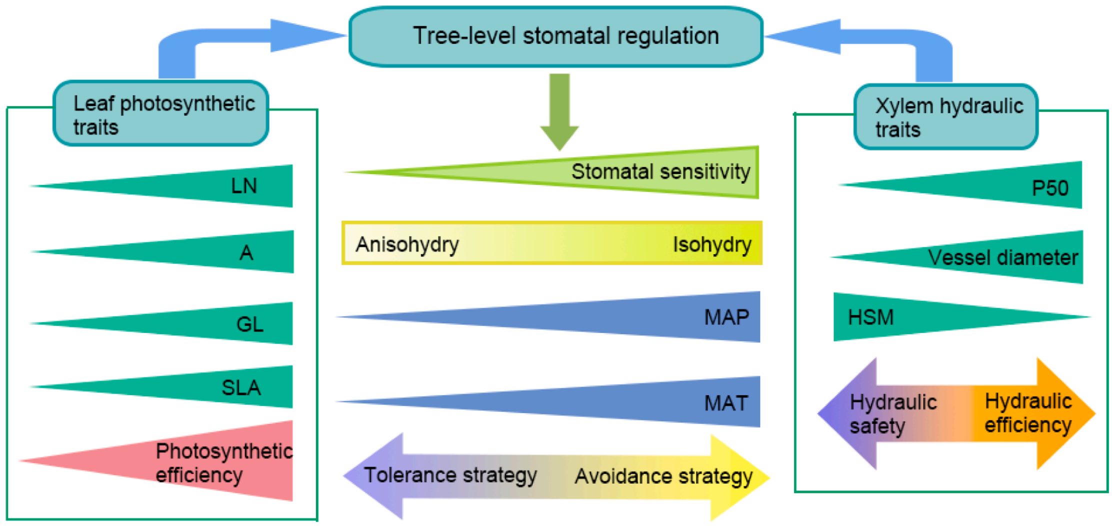

Fig. 1. Association of tree-level iso/anisohydric stomatal regulation with xylem hydraulic and leaf photosynthetic traits. LN: leaf nitrogen content; A: leaf photosynthetic rate; G_L: leaf-level stomatal conductance; SLA: specific leaf area; V_{dia}: vessel diameter; P_{50}: xylem pressure inducing 50% loss of hydraulic conductivity; HSM: hydraulic safety margin; *MAP*: mean annual precipitation; *MAT*: mean annual temperature.

determined by the influence of stomatal regulation on xylem tension (Meinzer and McCulloh, 2013). Hence, stomatal regulatory patterns may be critical factors determining the survival of tree species under adverse environmental conditions (Hochberg et al., 2018; Martínez-Vilalta and Garcia-Forner, 2017; McDowell et al., 2008). Typically, two categories of plants have been identified across the continuum of stomatal regulation of water status: those with isohydric or anisohydric regulation (McDowell et al., 2011; Meinzer and McCulloh, 2013). Isohydric species reduce stomatal conductance when soil water potential decreases or dry atmospheric conditions occur, maintaining a relatively constant midday leaf water potential. However, anisohydric species allow midday leaf water potential to decline while confronting arid environmental conditions (Franks et al., 2007; Konings and Gentine, 2017). In other words, isohydric species avoid drought-induced embolism via stomatal closure (i.e. avoidance strategy), while anisohydric species can withstand drought episodes due to their high tolerance of low water potential (i.e. tolerance strategy) (Klein, 2014; McDowell et al., 2011).

In general, plants regulate stomata to ensure the integrity of water transport system (Domec et al., 2006; Li et al., 2019), and xylem hydraulic traits are directly related to the tolerance of low water potential (Adams et al., 2017; Xu et al., 2016); thus, xylem hydraulic traits should be highly correlated to tree-level stomatal behavior. Previous studies have demonstrated a trade-off between xylem hydraulic efficiency and safety (Gleason et al., 2016; Santiago et al., 2018; Sperry et al., 2008). Nevertheless, how tree-level stomatal regulatory patterns are correlated to xylem hydraulic efficiency and safety in various tree species remains largely unknown. Generally, tree species with greater hydraulic safety exhibit lower water potential corresponding to 50% loss of conductivity (P_{50}), and higher hydraulic safety margin (HSM) given by the difference between minimum xylem water potential (ψ_{min}) and P_{50} (Oliveira et al., 2021), while tree species with higher efficiency have a larger vessel diameter (V_{dia}) (Hacke et al., 2017; Venturas et al., 2017). Furthermore, tree species with a higher V_{dia} tend to be more vulnerable to cavitation (Cai and Tyree, 2010; Chave et al., 2009), whereas those with a larger HSM or lower P_{50} exhibit higher resistance to cavitation and drought tolerance (Choat et al., 2012; Markesteijn et al., 2011). Given that tree species with a larger V_{dia}, higher P_{50}, and smaller HSM (i.e. xylem hydraulic efficiency system) are less resistant to cavitation, we hypothesize that these species usually employ isohydric stomatal regulation.

Stomatal opening and closing are affected by carbon demand, in addition to the maintenance of plant water status (Manzoni et al., 2011; Medlyn et al., 2011; Resco de Dios et al., 2016); thus, leaf photosynthetic traits may affect stomatal regulation. Generally, tree species with higher photosynthetic ability exhibit greater hydraulic efficiency (Campanello et al., 2008; Oliveira et al., 2021; Scoffoni et al., 2016); thus, these species are expected to take avoidance strategy of stomatal regulation based on the association between hydraulic traits and stomatal regulation. However, tree species with higher leaf photosynthetic ability, which is associated with a higher leaf N content and respiration rate (Atkin et al., 2015; Reich et al., 2008; Scoffoni et al., 2016), also have a higher carbon demand which may decrease stomatal sensitivity. Thus, how leaf photosynthetic traits are related to stomatal regulation, and whether xylem hydraulic or leaf photosynthetic traits are more closely related to tree-level stomatal regulation warrant further investigation.

The hydraulic structures of tree species vary across diverse climatic regions (Liang et al., 2019; Schuldt et al., 2016). A meta-analysis of xylem-specific hydraulic conductivity of 1,186 species under diverse environmental conditions showed that tree species in humid regions exhibited higher hydraulic conductivity and efficiency (He et al., 2020). In contrast, tree species in arid regions have developed a xylem hydraulic safety system; in other words, these species have a lower P_{50} and V_{dia} (Larter et al., 2017; Oliveira et al., 2021). As trees in humid regions exhibit higher hydraulic efficiency and lower cavitation resistance, there is a high possibility that these species would adopt isohydric stomatal regulation to avoid cavitation. Moreover, a previous study focusing on the association between stomatal parameters and climatic factors at the leaf level showed that the stomata of desert plants were relatively less sensitive to vapor pressure deficit (Hoshika et al., 2018). Hence, based on these differences in xylem hydraulic traits, we hypothesize that tree species in humid regions are more likely to adopt isohydric stomatal regulation (i.e. avoidance strategy), whereas anisohydric stomatal regulation occurs in tree species growing in arid regions.

In addition to climatic conditions, there may be genetic controls on tree-level stomatal regulation, i.e. phylogeny may constrain the flexibility in water-use strategies independent of the environment (Flo et al., 2021). Previous studies have demonstrated that tree hydraulic traits, e.g., V_{dia}, P_{50}, HSM and leaf-level stomatal conductance, show significant phylogenetic signals (Hietz et al., 2017; Sanchez-Martinez et al., 2020; Yu et al., 2019). However, whether tree-level stomatal regulatory patterns exhibit phylogenetic signals has seldom been investigated. Given its link to xylem hydraulic traits (e.g., V_{dia}, P_{50} and HSM), tree-level stomatal regulation is anticipated to exhibit phylogenetic signal and thus be influenced by evolutionary history.

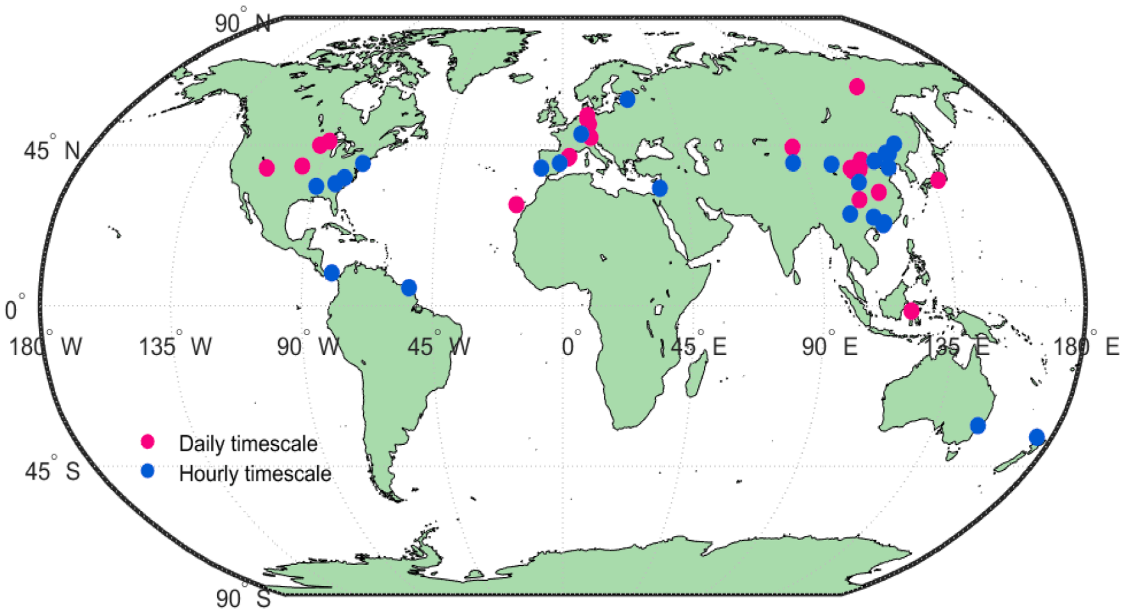

Fig. 2. Geographical locations of tree species studied at the daily (solid red circle) and hourly (solid blue circle) timescale.

To this end, understanding tree-level stomatal regulation across various woody species could be beneficial for explaining the adaptations of these plants to diverse environmental conditions. Therefore, in the present study, we analyzed variation in stomatal regulatory patterns of diverse tree species using data collected from the literature and the TRY Plant Trait Database (https://www.try-db.org/TryWeb/Home.php). We aim at: (1) exploring the association of tree-level stomatal regulation with xylem hydraulic and leaf photosynthetic traits; and (2) examining the effects of climatic conditions and phylogeny on tree-level stomatal regulation (Fig. 1). Our objectives were to test four hypotheses: (1) tree species with higher xylem hydraulic efficiency are more likely to adopt an avoidance strategy of tree-level stomatal regulation; (2) tree-level stomatal regulation is more closely related to xylem hydraulic traits than to leaf photosynthetic traits; (3) tree species inhabiting humid regions are more likely to adopt an avoidance strategy of tree-level stomatal regulation, whereas tolerance strategy occurs in tree species growing in arid region; and (4) tree-level stomatal regulation is affected by evolutionary history.

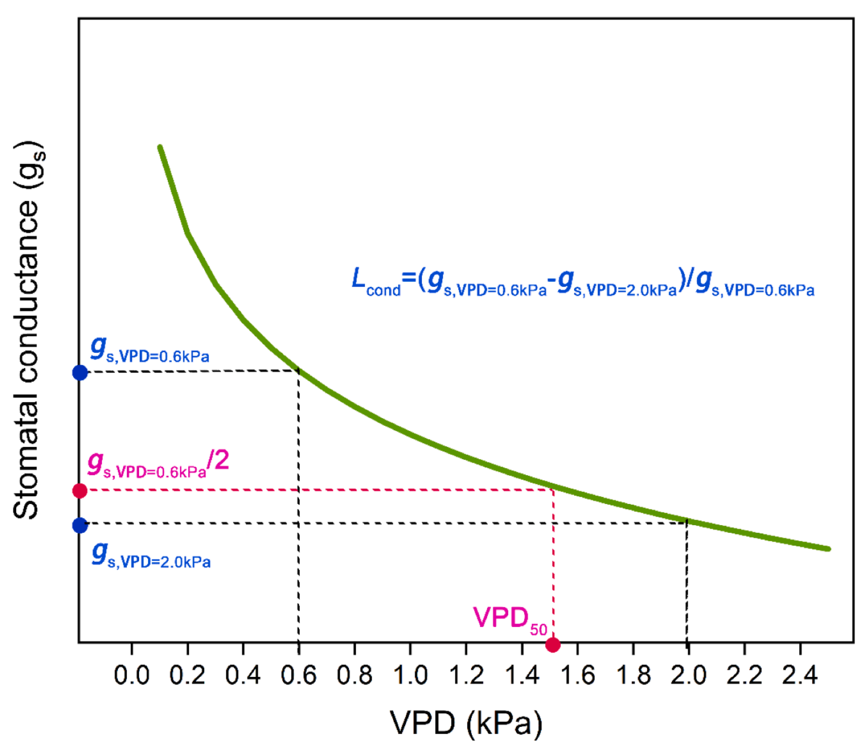

Fig. 3. Schematic diagram for the estimation of tree-level stomatal sensitivity to vapor pressure deficit (*VPD*). L_{cond}: stomatal conductance loss upon increase in *VPD* from 0.6 to 2 kPa (%); VPD_{50}: vapor pressure deficit at which 50% stomatal conductance loss occurred (kPa); $\mathbf{g}_{s,\ VPD=0.6kpa}$: stomatal conductance at *VPD* = 0.6 kPa; $\mathbf{g}_{s,\ VPD=2.0kpa}$: stomatal conductance at *VPD* = 2.0 kPa.

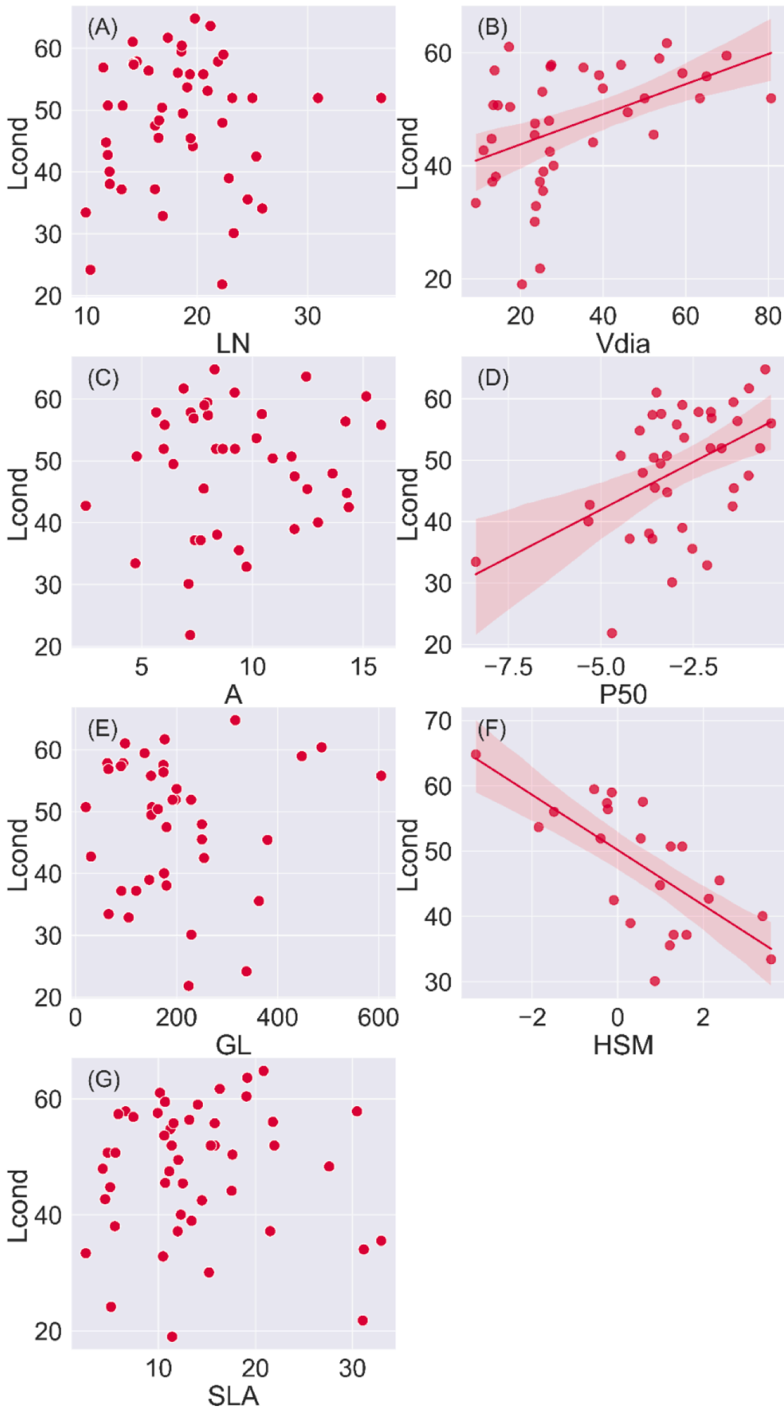

Fig. 4. Correlations between functional traits and stomatal conductance loss upon increase in vapor pressure deficit from 0.6 to 2 kPa (L_{cond}). LN: leaf nitrogen content ($mg{\cdot}g^{-1}$); *A*: leaf photosynthetic rate ($\mu mol{\cdot}m^{-2}{\cdot}s^{-1}$); G_L: leaf-level stomatal conductance ($mmol{\cdot}m^{-2}{\cdot}s^{-1}$); SLA: specific leaf area ($m^2{\cdot}g^{-1}$); V_{dia}: vessel diameter (μm); P_{50}: xylem pressure inducing 50% loss of hydraulic conductivity (MPa); HSM: hydraulic safety margin (MPa).

2. Methods

2.1. Data collection

The following data were collected: (1) tree species; (2) mean annual temperature (*MAT*,°C) and total precipitation (*MAP*, mm) at the study sites; (3) equations describing the association between vapor pressure deficit (*VPD*, kPa) and tree transpiration (*E*) or the formula describing the correlation between *VPD* and stomatal conductance (g_s), as obtained from sap flow measurements; (4) xylem hydraulic traits, namely, xylem pressure inducing 50% loss of hydraulic conductivity (P_{50}, MPa), vessel diameter (V_{dia}, μm) and hydraulic safety margin (HSM, MPa) (tree species with a lower P_{50} were considered hydraulic safety species, while those with a higher V_{dia} were considered hydraulic efficiency species); and (5) leaf functional traits, including leaf nitrogen content (LN, $mg{\cdot}g^{-1}$), leaf maximum photosynthetic rate (*A*, $\mu mol{\cdot}m^{-2}{\cdot}s^{-1}$), leaf-level maximum stomatal conductance (G_L, $mmol{\cdot}m^{-2}{\cdot}s^{-1}$), and specific leaf area (SLA, $m^2{\cdot}g^{-1}$). The numbers of tree species which had collected data on LN, *A*, G_L, SLA, V_{dia}, P_{50}, and HSM were 47, 41, 39, 48, 40, 39, and 23, respectively.

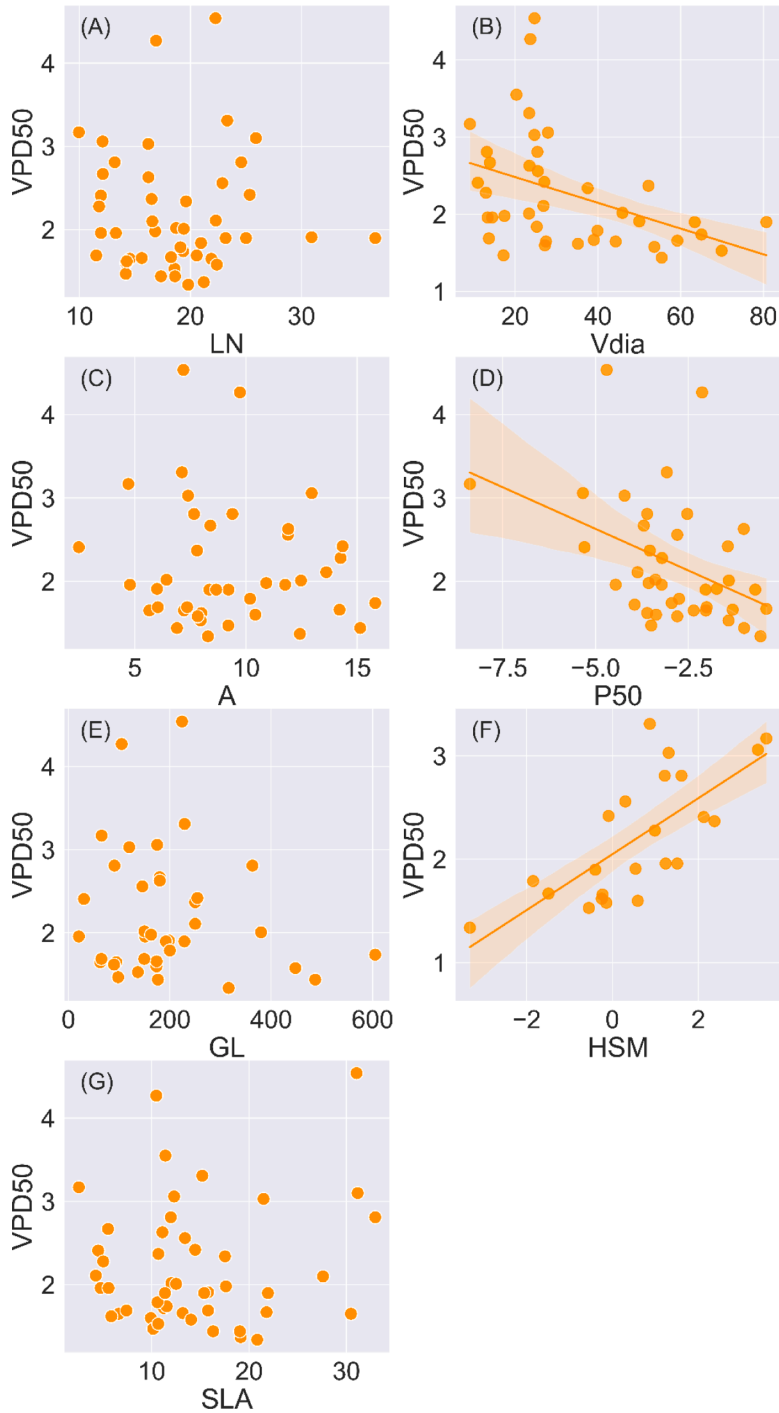

Fig. 5. Correlations between functional traits and vapor pressure deficit at which 50% stomatal conductance loss occurred (VPD_{50}). LN: leaf nitrogen content (mg·g^{-1}); A: leaf photosynthetic rate (μmol·m^{-2}·s^{-1}); G_L: leaf-level stomatal conductance (mmol·m^{-2}·s^{-1}); SLA: specific leaf area (m^2·g^{-1}); V_{dia}: vessel diameter (μm); P_{50}: xylem pressure inducing 50% loss of hydraulic conductivity (MPa); HSM: hydraulic safety margin (MPa).

In this study, the data of respectively 80 and 21 angiosperm and gymnosperm tree species were collected, whose individuals grew within a latitudinal range of 37°S to 63°N and a longitudinal range of 110°W to 175°E (Fig. 2). *MAP* at the field sites ranged from 123 to 3500 mm. Forest sites with a *MAP* of 0-500 mm, 500-800 mm, and >800 mm were considered dry, semi-humid, and humid regions, respectively (Wang et al., 2011).

Considering the plasticity of functional traits, a published dataset which contains the hydraulic traits of interest but measured at other sites was used to compile the P_{50}, HSM, and V_{dia} data for each species (Liu et al., 2019). The average values for each hydraulic trait calculated from a published dataset (Liu et al., 2019) were used as representative values for the studied species. Leaf functional traits (LN, A, G_L, and SLA) were obtained from the Plant Trait Database (https://www.try-db.org/TryWeb/Home.php) (Kattge et al., 2020), and their species-specific average values were derived and used as the representative values for the studied species. Leaf and xylem functional traits were collected from separate references for tree species not included in the TRY database. The full dataset (including site characteristics, hydraulic traits, and leaf functional traits), along with their corresponding references, is provided in Supplementary Materials.

2.2. Data analysis

To determine the stomatal regulation characteristics of different tree species growing in diverse climatic regions, two indices were analyzed: (1) the decline proportion of stomatal conductance from sap flow measurements upon increase in *VPD* from 0.6 to 2 kPa (hereafter called L_{cond}; Fig. 3), which represents the magnitude of stomatal regulation when confronting atmospheric water deficit, and (2) *VPD* at which 50% maximum stomatal conductance loss occurred (hereafter called VPD_{50}; Fig. 3); g_s at *VPD* 0.6 kPa was used to represent the maximum value. A lower L_{cond} implies that the species is more likely to adopt anisohydric regulation, whereas a higher L_{cond} implies that species is more likely to adopt isohydric regulation (Oren et al., 1999; Siddiq et al., 2017). Previous studies have used the quotient between the sensitivity of canopy stomatal conductance to *VPD* and the reference g_s at $VPD = 1$ kPa (i.e. $\frac{g_{s,VPD=1kPa} - g_{s,VPD=2kPa}}{\ln(2) \times g_{s,VPD=1kPa}}$) to represent the degree of iso/anisohydry (Fan et al., 2020; Kropp et al., 2017; Siddiq et al., 2017; Song et al., 2020). Here, we used the decline proportion of g_s at the same *VPD* increment from 0.6 to 2 kPa (i.e. $\frac{g_{s,VPD=0.6kPa} - g_{s,VPD=2kPa}}{g_{s,VPD=0.6kPa}}$) as a substitute, because tree species estimated at the daily timescale showed a lower daily mean *VPD* than hourly mean *VPD*. The lowest value of the *VPD* range was set to 0.6 kPa, because the estimation of g_s from sap flow measurements is limited to conditions with $VPD \geq 0.6$ kPa (Ewers and Oren, 2000); the highest value of the *VPD* range was set to 2.0 kPa, because transpiration remains stable or decreases in most species when *VPD* exceeds 2 kPa (Cernusak et al., 2019; Grossiord et al., 2020).

Among all collected published papers, some focused on the correlation between transpiration and *VPD*, without reporting the association between stomatal conductance and *VPD*. In those studies that provided the regression function between *E* and *VPD*, g_s was obtained by dividing *E* by *VPD* (Köstner et al., 1992; Zhu et al., 2015). Although *E* in various studies was estimated on different area bases (i.e. some studies analyzed *E* on a sapwood area basis, while the others investigated *E* on a leaf area basis), L_{cond} and VPD_{50} would not be affected because there were only coefficient differences in the process of unit transformation. Moreover, as the analyzed timescale varied among studies, data collected at two different timescales (i.e. daily and hourly) were investigated separately. In addition, studies conducted at the half-hour timescale were assigned to the hourly timescale category. Overall, data of respectively 61 and 59 tree species were estimated on the daily and hourly timescales.

2.3. Statistical analysis

The associations of functional traits (namely LN, *A*, SLA, G_L, P_{50}, V_{dia} and HSM) with L_{cond} (or VPD_{50}) at the daily timescale were estimated using correlation analysis. A multiple regression analysis was applied to examine the association of functional traits with L_{cond} and VPD_{50}. All variables were standardized before the multiple regression analysis. To remove multicollinear variables, only those variables with a variance inflation factor (VIF) of < 5 were selected (Akinwande et al., 2015). One-way analysis of variance (ANOVA), followed by the least significant difference (LSD) test, was used to examine differences in L_{cond} or VPD_{50} (α=0.05) among tree species growing in diverse climatic regions. The independent-sample t-test was used to examine the differences in L_{cond} or VPD_{50} between gymnosperms and angiosperms. A linear model was used to examine the association between *MAP* (or *MAT*) and L_{cond} (or VPD_{50}) at both daily and hourly timescales. All analyses were performed using Python (version 3.8, Python Software Foundation, USA).

A phylogenetic tree of species studied on the daily timescale was constructed using the *R* package 'V.PhyloMaker' (Jin and Qian, 2019), and drawn using the *R* package 'ggtree'. Blomberg's *K* statistic on phylogenetic tree was calculated using the 'phylosignal' function of the *R* package 'PICANTE' (Kembel et al., 2010). Blomberg's *K* assumes a Brownian motion model for the evolutionary process. $K < 1$ indicates a low phylogenetic signal, implying that closely related species are more different from each other than expected. $K > 1$ indicates a high degree of phylogenetic signal, implying that closely related species are more similar than expected (Ackerly, 2009).

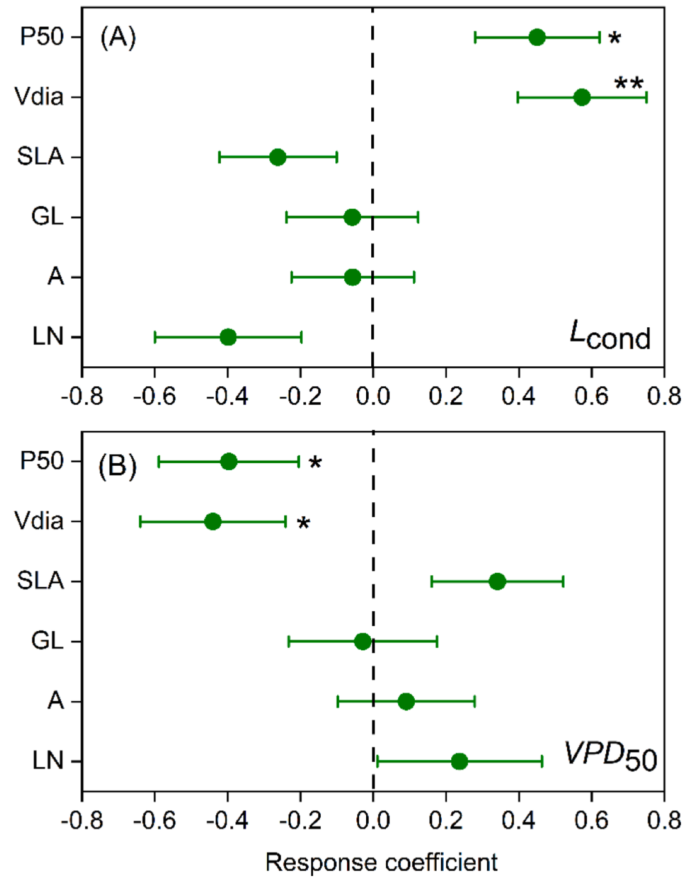

Fig. 6. Effects of functional traits on stomatal conductance loss upon increase in vapor pressure deficit (*VPD*) from 0.6 to 2 kPa (L_{cond}; panel A) and *VPD* at which 50% stomatal conductance loss occurred (VPD_{50}; panel B). LN: leaf nitrogen content (mg·g^{-1}); *A*: leaf photosynthetic rate (μmol·m^{-2}·s^{-1}); G_L: leaf-level stomatal conductance (mmol·m^{-2}·s^{-1}); SLA: specific leaf area (m^2·g^{-1}); V_{dia}: vessel diameter (μm); P_{50}: xylem pressure inducing 50% loss of hydraulic conductivity (MPa). Circles indicate the response coefficients between functional traits and L_{cond} (or VPD_{50}) obtained in the multiple regression analysis. Statistically significant levels: * $P < 0.05$; ** $P < 0.01$.

3. Results

3.1. Association between stomatal regulation and functional traits

Xylem hydraulic traits were strongly correlated to tree-level stomatal regulation. L_{cond} was positively correlated to P_{50} and V_{dia}, but negatively correlated with HSM (Fig. 4). VPD_{50} was negatively correlated to P_{50} and V_{dia}, while positively correlated to HSM (Fig. 5). Nevertheless, leaf functional traits (i.e. LN, *A*, G_L, and SLA) showed no significant correlations with P_{50} and V_{dia} (Figs. 4 and 5, $P > 0.05$). The scatter plots and correlation coefficients of the association between functional traits and tree-level stomatal regulation are presented in Figs. S1 and S2 in Appendix S1. Multiple regression analysis showed that P_{50} and V_{dia} were positively correlated to L_{cond} but negatively correlated to VPD_{50}; meanwhile, leaf functional traits (i.e. LN, *A*, G_L, and SLA) were not significantly correlated with either L_{cond} or VPD_{50} (Fig. 6).

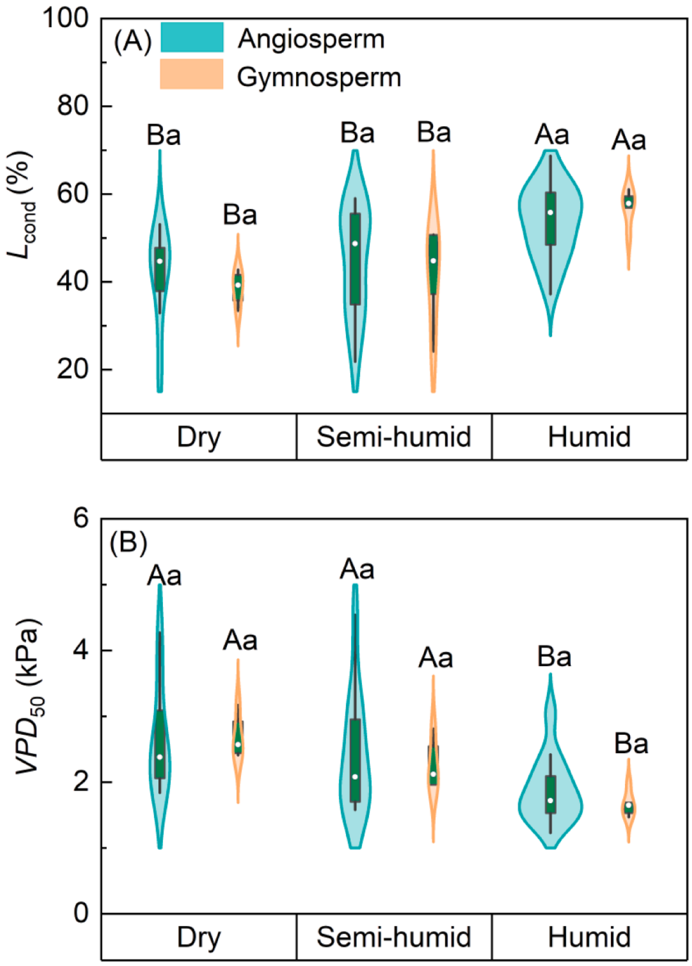

Fig. 7. Differences in the decline proportion of stomatal conductance upon increase in vapor pressure deficit (*VPD*) from 0.6 to 2 kPa (L_{cond}, panel A) and the *VPD* at which 50% stomatal conductance loss occurred (VPD_{50}, panel B) between gymnosperm and angiosperm species growing in humid, semi-humid, and dry regions. Boxes represent the 25th to 75th percentiles; the dot represents the median; and error bars represent ±1.5 SD (standard deviation). Different uppercase letters indicate significant differences in L_{cond} or VPD_{50} among tree species located in different climate regions, and different lowercase letters indicate significant differences in L_{cond} or VPD_{50} between angiosperms and gymnosperms (α=0.05).

3.2. Comparison of stomatal regulation between gymnosperms and angiosperms

There were no significant differences in L_{cond} between gymnosperms and angiosperms growing in dry, semi-humid, and humid regions ($P > 0.05$; Fig. 7A). In both gymnosperms and angiosperms, the L_{cond} of species growing in humid regions was significantly higher than that of species growing in arid and semi-humid regions ($P < 0.05$; Fig. 7A). Similar to L_{cond}, the VPD_{50} was similar between gymnosperms and angiosperms ($P > 0.05$; Fig. 7B). Likewise, in gymnosperms and angiosperms, VPD_{50} of species growing in humid regions was significantly lower than that of species growing in arid and semi-humid regions ($P < 0.05$; Fig. 7B).

3.3. Variation in tree-level stomatal regulation across climatic conditions

L_{cond} ranged from 19% to 68% on the daily timescale, and was in range of 11-70% on the hourly timescale (Fig. 8). L_{cond} and *MAP* were positively correlated on both daily and hourly timescales (Fig. 8A). Tree species growing in dry regions had lower L_{cond}, suggesting that a smaller percentage of stomata would close given the same *VPD* increment. Similar to the correlation between L_{cond} and *MAP*, L_{cond} and *MAT* were positively correlated on both daily and hourly timescales (Fig. 8B).

Meanwhile, contrary to the correlation between L_{cond} and *MAP*, VPD_{50} and *MAP* were negatively correlated on both daily and hourly timescales (Fig. 8C). VPD_{50} of woody species growing in arid regions was higher, suggesting that these species would lose 50% of their stomatal conductance at a higher *VPD* and exhibit less stringent control of stomatal closure. Furthermore, VPD_{50} was negatively correlated with *MAT* on both daily and hourly timescales (Fig. 8D).

3.4. Phylogenetic signals for tree stomatal regulation and xylem hydraulic traits

A phylogenetic tree was constructed for the species studied on the daily timescale (Fig. 9). Based on Blomberg's *K* statistics, L_{cond}, P_{50}, HSM, LN, and SLA showed significant phylogenetic signals ($P < 0.05$), whereas VPD_{50}, V_{dia}, *A*, and G_L did not display clear phylogenetic signals ($P > 0.05$; Fig. 9). In addition, Blomberg's *K* for L_{cond}, P_{50}, HSM, LN, and SLA was below 1 (Fig. 9), suggesting these traits showed low phylogenetic signals and that closely related species were more different from one another than expected from a Brownian motion model.

4. Discussion

4.1. Association between stomatal regulatory patterns and functional traits

Isohydric and anisohydric behavior represent two extremes of the continuum of regulation of xylem tension (Meinzer and McCulloh, 2013). A common paradigm is that isohydric species avoid conduit embolism through stomatal closure when exposed to water deficit, whereas anisohydric species are more tolerant of low water potential (Martínez-Vilalta and Garcia-Forner, 2017; McDowell et al., 2008). The observed positive correlation between L_{cond} and P_{50}, along with the negative correlation between L_{cond} and HSM, indicates that tree species with greater xylem hydraulic efficiency are more likely to adopt isohydric stomatal regulation, whereas anisohydric stomatal regulation

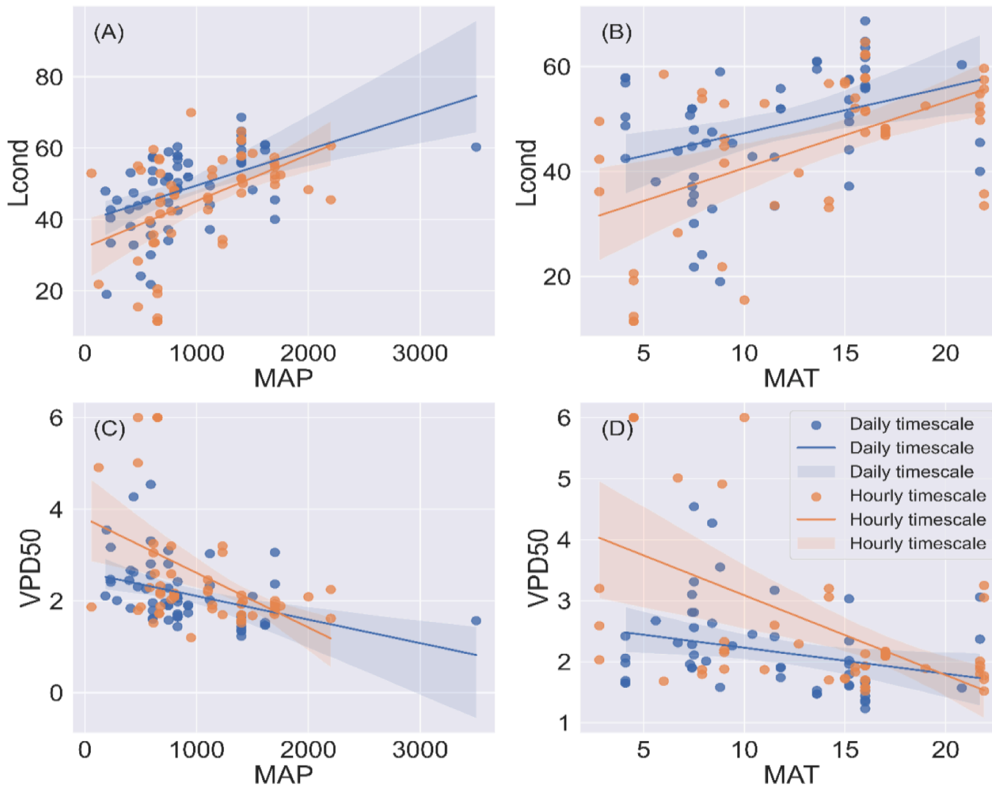

Fig. 8. Correlations between mean annual precipitation (*MAP*, mm) or temperature (*MAT*, °C) at the study site and tree-level stomatal regulation. L_{cond}: stomatal conductance loss upon increase in vapor pressure deficit (*VPD*) from 0.6 to 2 kPa (%); VPD_{50}: *VPD* at which 50% stomatal conductance loss occurred (kPa).

occurs in species with a stronger hydraulic safety system. Tree species with a lower P_{50} and higher HSM would be more tolerant of more negative xylem pressure (Laughlin et al., 2020; Oliveira et al., 2021; Powell et al., 2017), consequently adopting anisohydric stomatal regulation to maximize carbon gain. Meanwhile, tree species with a higher P_{50} and lower HSM have a greater risk of cavitation under the same xylem pressure (Choat et al., 2012; Delzon and Cochard, 2014; Oliveira et al., 2021), and are therefore more likely to adopt the avoidance strategy of stomatal regulation (i.e. isohydric stomatal regulation) to protect their hydraulic pathways from dysfunction.

Further, tree species with a larger V_{dia} would adopt an isohydric stomatal regulation strategy, indicating that these species exhibit more stringent stomatal regulation. Previous studies have shown that V_{dia} is positively correlated with P_{50} (Cai and Tyree, 2010; Hacke et al., 2017); thus, the less negative P_{50} of species with a larger V_{dia} resulted in a higher L_{cond}. Furthermore, xylem V_{dia} is negatively correlated to wood density, which protects the xylem pipeline from collapsing under a large negative pressure (Greenwood et al., 2017; Preston et al., 2006). Accordingly, species with a larger V_{dia} exhibit lower wood density and are more likely to adopt isohydric stomatal regulation to avoid drought-induced embolism through stomatal closure.

Tree species with higher photosynthetic ability generally exhibit greater hydraulic efficiency, and these species are expected to have higher L_{cond}. However, leaf functional traits (i.e. LN, *A*, G_L, and SLA) showed non-significant correlations with tree-level stomatal regulation. There may be two reasons for the non-significant association between L_{cond} and leaf functional traits. First, a few tree species with a higher *A* or G_L exhibited a relatively lower V_{dia} (Fig. S3 in Appendix S1), indicating that these species showed a lower L_{cond} based on the association between L_{cond} and V_{dia} discussed above; consequently, some species with a higher *A* or G_L but lower V_{dia} did not show a larger L_{cond}. Second, tree species with a larger LN (or *A*) also had a higher carbon demand, which may decrease stomatal sensitivity and L_{cond}, and consequently weakened the expected positive correlation between L_{cond} and leaf photosynthetic traits. Moreover, LN was negatively correlated with L_{cond} after accounting for V_{dia} as a controlled variable (Fig. S4 in Appendix S1), proving that species with a higher LN exhibited lower stomatal sensitivity for species with similar xylem hydraulic traits.

Angiosperm and gymnosperm species present different hydraulic structural characteristics. Specifically, xylem tissue of angiosperms largely constitutes dead tracheids and vessels, whereas that of gymnosperms is composed essentially of tracheids without vessels (Pallardy, 2008). Differences in hydraulic structures between angiosperm and gymnosperm species would consequently result in different stomatal regulation pattern (Hacke et al., 2005; Roddy, 2019). Indeed, V_{dia} and P_{50} of angiosperms were significantly higher than those of gymnosperms in this study ($P < 0.05$), and thus gymnosperms were expected to have a lower L_{cond}. However, there were no significant differences in L_{cond} between angiosperms and gymnosperms growing in humid, semi-humid, or dry regions (Fig. 7). A previous analysis of HSM in a plant's hydraulic strategy across 226 forest species revealed that gymnosperms showed a greater HSM than angiosperms, suggesting angiosperms adopt a higher-risk strategy for hydraulic failure (Choat et al., 2012). A higher HSM may result from a greater ψ_{min} or lower P_{50}. When the higher HSM of gymnosperms results from greater ψ_{min}, gymnosperms would adopt the conservative strategy and close the stomata at higher leaf water potential, which compensated for the lower L_{cond} induced by smaller V_{dia} and P_{50}, resulting in a similar L_{cond} between angiosperms and gymnosperms.

Furthermore, gymnosperms featured a lower V_{dia} and P_{50} but equal L_{cond} compared to angiosperms, implying the weakening of the association between L_{cond} and V_{dia} (or P_{50}). The positive relationships between L_{cond} and V_{dia} (or P_{50}) were still observed in this study (Fig. 4). The conservative strategy of stomatal regulation led to a slightly increased or equal L_{cond} in gymnosperms compared with that in angiosperms with similar xylem hydraulic traits (Fig. S5 in Appendix S1). Nevertheless, gymnosperms with a smaller V_{dia} (or P_{50}) still exhibited a lower L_{cond} than angiosperms with a larger V_{dia} (or P_{50}). Thus, a positive correlation

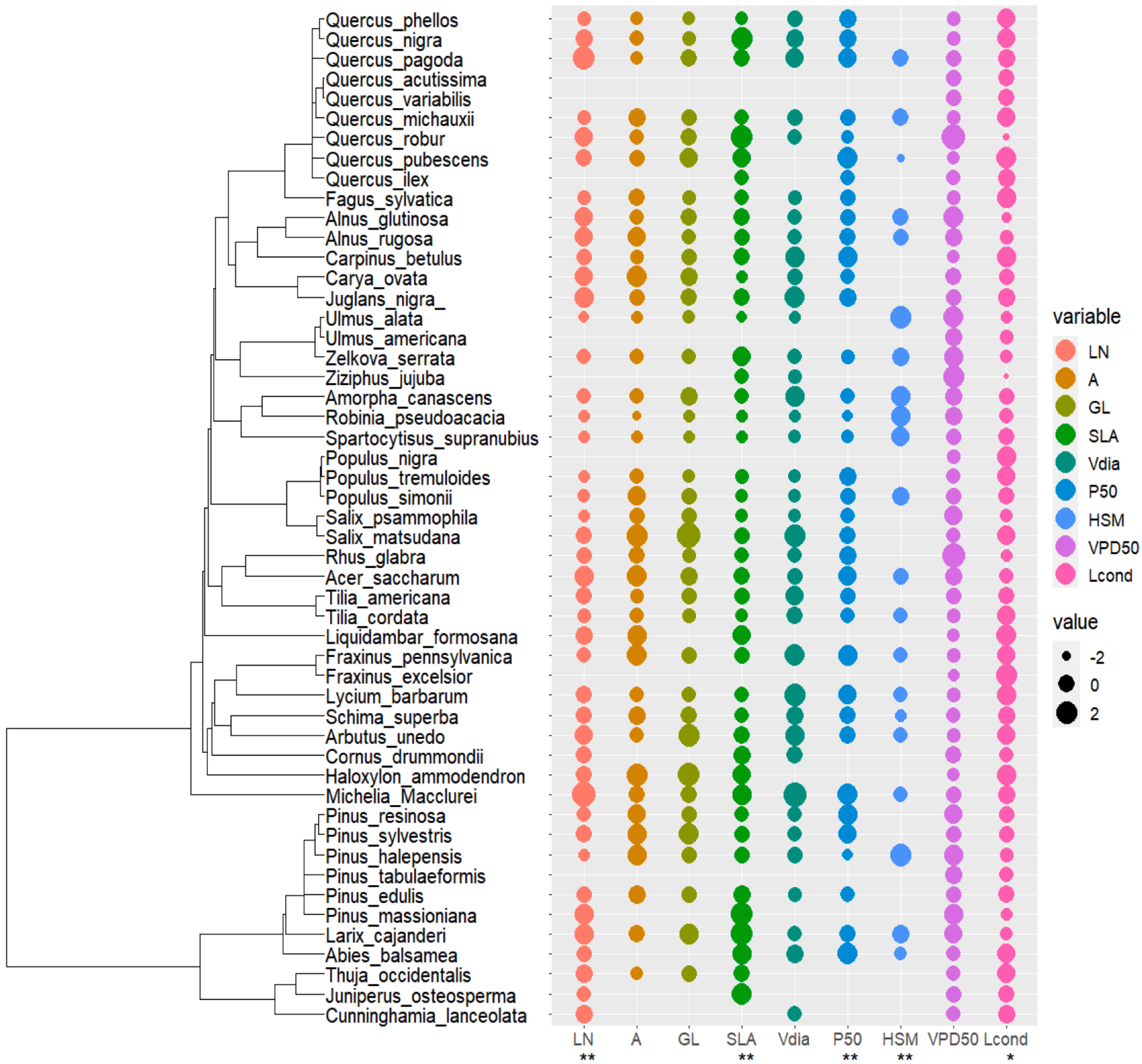

Fig. 9. Phylogenetic tree and functional traits of the studied species on a daily timescale. LN: leaf nitrogen content (mg·g^{-1}); A: leaf photosynthetic rate (μmol·m^{-2}·s^{-1}); G_L: leaf-level stomatal conductance (mmol·m^{-2}·s^{-1}); SLA: specific leaf area (m^2·g^{-1}); V_{dia}: vessel diameter (μm); P_{50}: xylem pressure inducing 50% loss of hydraulic conductivity (MPa); HSM: hydraulic safety margin (MPa); L_{cond}: stomatal conductance loss upon increase in vapor pressure deficit (*VPD*) from 0.6 to 2 kPa (%); VPD_{50}: the *VPD* at which 50% stomatal conductance loss occurred (kPa). Plant trait values were standardized and in proportion to the circle size of each species. *$P < 0.05$; ** $P < 0.01$.

was still observed between L_{cond} and V_{dia} (or P_{50}) including both gymnosperms and angiosperms.

In addition to atmospheric water deficit, soil water content can affect L_{cond}. To minimize that effect, we avoided choosing the raw data on the response of stomatal conductance to *VPD* during the dry season or under drought stress conditions. Moreover, because trees exhibit more stringent stomatal regulation (i.e. larger L_{cond}) under drought stress, the studied trees growing in arid regions may exhibit a lower or equal L_{cond} if those trees grew under water-sufficient conditions. Thus, if all studied trees were growing in soil water-sufficient conditions, those species inhabiting the arid regions or those with a higher hydraulic safety system would also have a high possibility to exhibit a lower L_{cond}, which is consistent with the conclusions of the present study. In this context, experimental analysis of tree-level stomatal regulation across diverse species growing at the same site would be a more precise approach to explain the association between functional traits and tree-level stomatal regulation.

For most tree species, the average values of functional traits from the database were used as representative values. As functional traits in the database were collected from diverse literature sources, the measurement approach may have affected the estimation of functional traits. For LN, *A*, G_L, SLA, and V_{dia} traits, well-established uniform approaches are usually used. However, approaches for estimating P_{50} and HSM can vary widely (Martin-StPaul et al., 2014), which would lead to large variations in the estimates of these two indicators. Hence, further investigations with more rigorous experiments measuring functional traits using consistent approaches are warranted to precisely elucidate the accurate association between stomatal regulation and functional traits.

4.2. Influences of climatic conditions and phylogeny on tree-level stomatal regulation

Annual precipitation, which cannot be manipulated, may affect xylem hydraulic traits and may therefore be related to tree-level stomatal regulation. L_{cond} was positively correlated with *MAP* and *MAT* on the daily and hourly timescales in our study (Fig. 8). The higher L_{cond} of trees growing in humid regions indicates that these species adopted isohydric stomatal regulation, whereas anisohydric stomatal regulation occurred in tree species growing in dry regions. Given the association between xylem hydraulic traits (i.e. P_{50} and V_{dia}) and stomatal regulation, variation in xylem hydraulic traits is likely responsible for differences in stomatal regulation among tree species distributed across diverse climatic regions. Other studies have shown that precipitation contributes considerably to the variation in plant hydraulics (Martínez-Vilalta et al., 2009; Schreiber et al., 2015). In general, species growing in dry regions show a smaller V_{dia} and more negative P_{50} (Dória et al., 2019; Hacke et al., 2017; Larter et al., 2017), indicating that these species close the stomata at a lower water potential and are more likely to adopt anisohydric stomatal regulation. Consistently, tree species growing in dry regions had smaller V_{dia} ($P < 0.01$) and lower P_{50} with marginal significance ($P < 0.1$) in this study, indicating that these species have developed a hydraulic safety system rather than a hydraulic efficiency system. Consequently, the hydraulic safety system of species growing in dry regions leads to anisohydric stomatal regulation.

The VPD_{50} was higher for woody species distributed in arid regions (Fig. 7), suggesting that these species would lose 50% stomatal conductance at a higher *VPD* and exhibit less stringent control of stomata closure. Based on our analysis of L_{cond}, most tree species in arid regions used the anisohydric strategy and were more tolerant of low leaf water potential; consequently, these species presented a higher VPD_{50}. The individual leaf area of woody species in dry regions is smaller to reduce excessive transpiration (Peppe et al., 2011; Wright et al., 2017); their larger *VPD* range allowing for stomatal opening within the tolerance limit of the hydraulic system may thus be a form of compensation to generate carbohydrate products required for daily consumption.

Phylogeny may affect tree-level stomatal regulation independent of environmental conditions. The significant phylogenetic signals for L_{cond}, P_{50}, HSM, LN, and SLA confirmed that the variation in these traits has been influenced by evolutionary history. Blomberg's K for L_{cond}, P_{50}, HSM, LN, and SLA was below 1 (Fig. 9), suggesting that the effect of phylogeny on trait evolution was weaker than that expected from a Brownian motion model. Nevertheless, VPD_{50}, V_{dia}, A, and G_L did not display clear phylogenetic signals in the present study (Fig. 9). Previous research has shown that convergent evolution is the antithesis of phylogenetic signals (Losos, 2008), and the predominance of plasticity over evolutionary legacies usually results from evolutionary lability or high rates of trait evolution, which lead to pronounced differences among close relatives (Blomberg et al., 2003; Kamilar and Cooper, 2013). Hence, the observed phylogenetic independence of the above four traits could be due to their rapid responses and convergent evolution to environmental changes (Blomberg et al., 2003; Edwards Erika et al., 2010). Additionally, since L_{cond} and VPD_{50} were strongly correlated, VPD_{50} was expected to show a significant phylogenetic signal. However, VPD_{50} did not display a clear phylogenetic signal in the present study. This might be due to the presence of two species (i.e. *Carpinus betulus* and *Populus simonii*) whose VPD_{50} values slightly deviated from the regression line between L_{cond} and VPD_{50}. If these two species were excluded, the remaining species showed a significant phylogenetic signal for VPD_{50}.

5. Conclusions

Xylem hydraulic traits, but not leaf functional traits, are closely correlated with tree-level stomatal regulation. Tree species with higher xylem hydraulic efficiency are more likely to adopt the avoidance strategy of stomatal regulation, whereas the tolerance strategy occurs in tree species with a stronger hydraulic safety system. Variation in hydraulic traits leads to differences in the stomatal regulatory patterns among tree species distributed in diverse climatic regions. In particular, trees in humid regions generally adopt the avoidance hydraulic strategy and are more likely to become isohydric for avoiding drought-induced embolism. By contrast, anisohydric stomatal regulation occurs in tree species growing in arid regions. Finally, the stomatal regulatory pattern shows a significant phylogenetic signal and is affected by evolutionary history. Overall, maintaining water transport integrity rather than fulfilling the requirements for carbon uptake is the major factor governing tree-level stomatal regulation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2022.109291.

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