Stem and leaf traits as co-determinants of canopy water flux

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ABSTRACT

Transpiration through stomata in tree canopies plays an important role in terrestrial water cycles. However, the empirical relationship between leaf stomata anatomy and canopy stomatal conductance (G s) is surprisingly rare, thereby the underlying biological mechanisms of terrestrial water flux are not well elucidated. To gain further insight into these mechanisms, we reanalyzed the dataset of G s previously reported by Gao et al. (2015) using a quantile regression model. The results indicated that the reference G s (G sref, G s at 1 kPa) was negatively correlated with wood density at each quantile, which confirmed previous data; however, G sref was significantly correlated with stomatal density at the 0.6 quantile, i.e., 450 stomata mm -2. This highlighted the potential of using stomatal density as a trait to predict canopy water flux. A conceptual model of co-determinants of xylem and stomatal morphology suggests that these traits and their coordination may play a critical role in determining tree growth, physiological homeostatic response to environmental variables, water use efficiency, and drought resistance.

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1. Introduction

Tree transpiration is important to terrestrial water flux (Jasechko et al., 2013). It significantly influences carbon, water, and nutrient cycles, and thus determines biodiversity patterns and ecosystem services (Bernacchi and VanLoocke, 2015). The tree transpiration process involves water uptake by roots, after which it is transported by xylem vessels and/or tracheids to the leaf stomata, and eventually diffuses into the atmosphere through transpiration forces (vapor pressure deficit, D). This process is controlled by plants through the joint regulation of xylem and leaf traits; however, little is known about the extent to which tree transpiration is determined by these tree biological attributes (i.e., xylem and stomatal traits) (Brodribb and McAdam, 2011). Several global-scale estimates of transpiration from climate models at the ecosystem level currently exist; however, these models are potentially inaccurate because they do not consider stomatal behavior (Jasechko et al., 2013).

Water flux can be precisely modeled by compiling in situ transpiration measurements (e.g., sap flow at the forest stand level) upscaled to canopy stomatal conductance (G s) based on tree biological parameters (Granier et al., 1996). However, canopy biological attributes are rarely measured due to logistical and technical difficulties (Dial et al., 2004). In the past decades, a large body of evidence suggests that there exists empirical relationships between leaf stomatal conductance (g s), CO2 uptake, and stomatal anatomy (Araus et al., 1986; Chen et al., 1990; Dow et al., 2014a,b; Drake et al., 2013; Giday et al., 2013; McElwain et al., 2015; Raven, 2014). However, little is known about the influence of leaf stomata morphology on canopy water flux at the individual tree level. Currently, to our knowledge, no empirical studies have quantified the possible correlation between G s and stomata morphology.
In the present study, a quantile model was used to investigate the relationship between functional leaf traits and water flux at the tree level (Gao et al., 2015, 2016). Quantile regression is particularly applicable in the study of stomatal behavior, which is constantly influenced by a range of environmental/biological variables (Cade et al., 2005; Gao et al., 2016). In the current study, we compiled fine measurements of the biophysical attributes of seven tree species (Gao et al., 2015), the published $G_s$, alongside unpublished stomata data. Because stomata are regarded as hydraulically driven valves on the leaf surface, or alternatively the so-called 'Watergates' (Roelfsema and Hedrich, 2005), we hypothesized that canopy water flux and stomatal density are positively correlated, especially for the trees with denser stomata. In addition to stomata, we also hypothesized that xylem functional traits, such as wood density, would be negatively correlated with canopy water flux. A vast body of literature has shown that trees with heavier wood have lower $g_v$ and leaf-specific conductance than those with lighter wood (Gao et al., 2015; Hacke et al., 2001; Jacobsen et al., 2007).

Therefore, linking the two key components of the hydraulic continuum in trees, the "intermediate path" (i.e., xylem conduits indicated by wood density) and "export" (i.e., leaf stomata), should provide new knowledge regarding the underlying physiological mechanisms that influence tree transpiration. We thus hypothesized that stomatal density might also be a predictor of canopy water flux similar to wood density.

2. Materials and methods

2.1. Site description and tree species

Three research plots with different tree species were used in this study. All three research sites were located in lower sub-tropical China, where there is a moist climate type. The first plot, in the Huangmian State Forest Farm (109° 54'E, 24° 46'N), was mainly used for the plantation of Eucalyptus grandis Hill × Eucalyptus urophylla S. T. Blake over the last 5 years. We selected five trees for measurement of sap flux during the period from 1 October to 31 October 2012. The second research plot was located in Heshan National Field Research Station of Forest Ecosystem, Chinese Academy of Sciences, Guangdong Province (112° 54'E, 22° 41'N). This plot contained mostly native species, with trees approximately 25 years old. The sap flux measurements were performed in a secondary broadleaf forest that contained Schima superba Gardn. et Champ, Michelia macclurei Dandy, Castanopsis fissa (Champ. ex Benth.) Rehd. et Wils., and Castanopsis hystrix Miq. as the dominant tree species. We selected 3–5 individual trees of each species for sap flux measurement from 1 October to 31 October 2012, which was a period where there was no apparent soil water deficit. The third research plot was located in an Australian Garden of the South China Botanical Garden (113° 22'E, 23° 11'N). In this garden, species from Australia were introduced, with trees approximately 50 years old. Acacia auriculiformis A. Cunn. ex Bentham and Eucalyptus citriodora Hook. f. were planted in this garden in the 1960s, mainly for appreciation. We selected five individual trees of each species for sap flux measurement from 1 October to 31 October 2013. The characteristics of the biometrics of the studied trees and climate variables are summarized in Table 1 (Gao et al., 2015).

2.2. Sap flux and vapor pressure deficit

Granier thermal dissipation probes (TDP) were directly inserted into the xylem of the studied trees to measure the sap flux ($J_s$) (Granier, 1987). Each TDP sensor consisted of a pair of 20-mm long, 2-mm diameter stainless steel probes installed approximately 10–15 cm apart along the axis of the hydroactive xylem. The upper probe was heated by a constant power of 0.2 W with a DC supply of 120 mA, whereas the lower probe remained unheated. An instantaneous temperature difference between the probes could be converted into a voltage value and recorded using a data collection instrument (Gao et al., 2017). The data were measured every 30 s and stored as 10-min averages using a Delta-T logger (DL2e, UK). Finally, the $J_s$ (g H$_2$O m$^{-2}$ s$^{-1}$) was calculated according to the following formula:

$$J_s = 119 \times \left(\frac{\Delta T_m - \Delta T}{\Delta T}\right)^{1.231}$$

(1)

where $\Delta T_m$ is the temperature difference obtained under zero flux conditions and $\Delta T$ is the instantaneous temperature (Granier, 1987).

Data on photosynthetically active radiation (PAR), air temperature (T) and relative humidity (RH), and wind speed (m·s$^{-1}$) were obtained from a meteorological station of the Heshan National Field Research Station, which was approximately 100 m away from the experimental plot. For Huangmian Forest Farm and Botanical Garden, the meteorological data were directly collected from the observation tower (18–20 m) in the forest. The radiation (LI-COR, Lincoln, USA), temperature, and humidity (Delta-T Devices Ltd. Cambridge, UK) sensors were deployed on the top of the towers. We calculated vapor pressure deficit ($D$, kPa) by combining the air temperature and RH:

$$D = a \times \exp\left[b \times (T + c)\right] \times (1 - RH)$$

(2)

where $a$, $b$, and $c$ are fixed parameters, which are 0.611 kPa, 17.502 (unitless), and 240.97 °C, respectively.

2.3. Canopy water flux ($G_s$ and $G_{stref}$)

Owing to the difficulty in obtaining the leaf area data of studied trees, canopy stomatal conductance ($G_s$) was determined by using sap flux and $D$ in the following equation:

$$G_s = \frac{J_s}{D}$$

(3)

which assumes that sap flux is equal to canopy transpiration, and stem sap flux is not affected by hydraulic capacitance (Gao et al., 2015). $D$ was standardized by standard atmospheric pressure. Analyses were only conducted on clear days (10:00–16:00) with high PAR and high $D$ (>1 kPa) to minimize the effects of stem water storage; this procedure also minimized the impact of low irradiance on $G_s$. The three research plots were open and void of canopy closure, thus satisfying our assumption that $T_{canopy} = T_{air}$. The calculations of sensitivity and reference $G_s$ were based on the model of Oren et al. (1999) as follows:

$$G_s = G_{stref} - m \ln D$$

(4)

where $m$ ($-\frac{dG_s}{dln D}$) is the sensitivity of $G_s$ to $D$, and $G_{stref}$ is reference $G_s$ when $D = 1$ kPa.

In this study, canopy water flux was characterized by $G_{stref}$. $G_{stref}$ was a good modeling scalar that could be used to compare among different tree species from different sites (Gao et al., 2015).

2.4. Wood and stomatal density

Two cores ($\Phi = 5.15$ mm) from 6–7 trees per species were sampled using an increment borer (Haglöf, Sweden) in September 2012 wrapped with a wet towel immediately after sampling, and placed in sealed plastic bags. Sampled cores were then transported...
to the laboratory and weighed on an electronic balance (Shinko, Japan) to an accuracy of 0.0001 g. The wood cores were dried until weights were constant at 80 °C to obtain a dry weight value. The wood density was calculated as the ratio of the dry weight to fresh volume.

Three mature, sun-exposed leaves in three trees of each species were selected for the measurement of stomata density in June 2013, which was determined using nail-polish imprints following a modiﬁed version of the method of Li and Xing (2007) and Xiong et al. (2014). The number of stomata ( # mm$^{-2}$) was recorded using a light microscopy (Zeiss, Jena, Germany). At least ﬁve ﬁelds of view on the abaxial surface of leaves were randomly selected for counting. Most of the trees selected were chosen from or at least around the research plots. The leaves were sampled in those shorter trees as surrogates due to the diﬃculties in sampling very tall trees, e.g., A. auriculiformis and E. citriodora.

2.5. Statistical analysis

In this study, to test the correlations between canopy water flux and wood, stomatal density, we ﬁtted linear models using both ordinary least-squares (OLS) and quantile regressions. Quantile regression seeks to complement classical linear regression analysis to estimate all parts of the response distribution conditional to the predictor variable, thus providing a more comprehensive characterization of the effects than those provided by estimates of the conditional mean made with OLS regression (Cade et al., 2005).

Quantile regression is a non-parametric test that makes no assumptions regarding normality of distribution or variance homogeneity. Thus, quantile regression overcomes various limitations of using OLS regression. For instance, by focusing on the mean, information about the tails of distribution is lost. Additionally, OLS regression is particularly sensitive to extreme outliers, which can signiﬁcantly distort the results. By contrast, quantile regression reduces outlier effects because it is based on absolute values rather than on squared deviations. We estimated the quantile regression functions of 0.2, 0.4, and 0.6 quantiles using the R package ‘quantreg’ (Koenker, 2013).

Statistical analysis of stomatal and wood density was performed using one-way ANOVA in the predictive analysis software (PASW, IBM, USA). When the one-way ANOVA results were signiﬁcant at alpha = 0.05, the differences among the means were then explored using Duncan multiple range test.

3. Results

Sap ﬂux of the seven tree species was measured during the late wet season of October 2012 and 2013. During this period, there was no apparent soil water deﬁcit, thereby aiding the comparison of data collected from three diﬀerent sites in these lower subtropical forests.

Both stomatal density (Figs. 1 and 2A, $F_{6, 14} = 10.127$, $P < 0.00001$) and wood density (Fig. 2B, $F_{6, 36} = 27.145$, $P < 0.00001$) varied signiﬁcantly between species. We also found that stomatal density was signiﬁcantly positively correlated with $G_{\text{ref}}$ at the 0.6 quantile (Fig. 3A and Table 2); however, there was no correlation with $G_{\text{ref}}$ at lower quantiles, i.e., the 0.2 and 0.4 quantiles, which suggests that stomatal density likely has a “threshold eﬀect” on $G_{\text{ref}}$. We also found that wood density was negatively correlated with $G_{\text{ref}}$ regardless of quantile, but displayed signiﬁcant correlation at the 0.2 and 0.4 quantiles (Fig. 3B and Table 2).

We constructed a conceptual model (Fig. 4) illustrating the correlation between stem, leaf traits, and water ﬂux. This model is based on our empirical study and describes four scenarios. Scenario I denotes “lighter wood, denser stomata,” indicating a higher sap ﬂow ($G_0$), and higher sensitivity to $D$, i.e., higher slope. Scenario II denotes “heavier wood, less stomata,” indicating a lower sap ﬂow ($G_0$), and lesser sensitivity to $D$, i.e., lower slope. “Light wood, less stomata ($G_0$)” (scenario III) and “heavy wood, denser stomata (higher $G_0$)” (scenario IV) in addition to further intermediate states or scenarios are between the two extremes, i.e., scenarios I and II (Fig. 4).
4. Discussion

In the current study, wood density correlated with \( G_{\text{ref}} \) at each of the analyzed quantiles, suggesting that there was an inhibited impact of xylem biophysical attributes on canopy water flux, which agrees with other studies (Hacke et al., 2001; Jacobsen et al., 2007). We also found that stomatal density positively correlated with \( G_{\text{ref}} \) at a high quantile. Xylem and stomata are two key components of a plant's hydraulic system; their co-ordination or tradeoff determines tree growth, function, and survival (Brodribb et al., 2014; Carlson et al., 2016; Skelton et al., 2015). As is the case for wood density, which is a good predictor of \( G_{\text{ref}} \), this study highlights the potential of using stomatal density as a trait to predict canopy water flux.

Plant biomass, vegetation productivity, carbon and water exchange, and water use efficiency are mainly determined by stomatal morphology and physiology, i.e., \( g_s \) and \( G_{\text{ref}} \), which are widely used scalars for modeling water and carbon balance (Drake et al., 2013; Lawson and Blatt, 2014; McElwain et al., 2015; Wang et al., 2015). Many studies have reported that smaller, denser stomata lead to a greater maximum \( g_s \) and are more sensitive to environmental variables (Drake et al., 2013; Giday et al., 2013; Raven, 2014), indicating that stomata directly influence water flow. The relationship between \( g_s \) (transpiration) and stomatal attributes at the leaf level are well characterized (Dow et al., 2014a,b; McElwain et al., 2015). However, the empirical correlation between leaf stomatal traits and water flux at the whole-tree level has been surprisingly rarely investigated.

![Optical images of stomata in the seven studied tree species. Black scale bar = 30 µm.](image_url)
et al., 2015). By contrast, possessing heavier wood (Fig. 2B), exhibit more resistance to embolism in order to avoid hydraulic failure (Gao et al., 2015). The $G_I$ of these trees is not very sensitive to environmental variables, and thus are classified as anisohydric (Domec and Johnson, 2012; Gao et al., 2015; McCulloh and Woodruff, 2012). The co-ordination between stem and leaf is important for tree growth and drought survival (Skelton et al., 2015).

A conceptual model was established to describe the xylem, stomatal traits, and transpiration based on the empirical and theoretical relationships between wood density, stomatal density, and $G_{sref}$ (Fig. 4). The model demonstrated how $G_s$ was regulated by wood and stomatal traits. The co-ordination between wood and stomata promoted water flux in scenario I (“lighter wood, denser stomata”). Trees with these characteristics were more competitive in mesic environments, similarly to those $E. grandis \times urophylla$ trees in this study. However, the trees of scenario II (“heavier wood, less stomata”) displayed slower water flux, which allowed higher drought resistance. Scenario III (“Lighter wood, less stomata”) and scenario IV (“heavier wood, denser stomata”), in addition to further intermediate scenarios, should also be included in natural forest ecosystems. The co-ordination between leaf and stem is determined by functional groups, genotypes, ontogenic development and environmental conditions (Apgaua et al., 2015; Arango-Velez et al., 2011; Carlson et al., 2016; Franks et al., 2009; Locosselli and Ceccantini, 2012). For example, the vulnerability segmentation hypothesis that characterized by the co-ordination by xylem and leaves, as well as the maintenance of hydraulic continuum, is determined by the aridity level (Zhu et al., 2016). This indicates that the relationships between xylem and stomata would be diverse.
Stomata pores of plants respond to the environment by facilitating transpirative cooling for mesophyll enzyme activity, CO₂ uptake, and transpirational water loss. On the other hand, for tree stems, which underlie tree height growth, a higher density results in lower hydraulic efficiency during drought-resistance, which is a tradeoff between “efficiency” and “safety” (Brodrribb et al., 2014; Meinzer and McCulloch, 2013). Moreover, hydraulic efficiency is determined by stomatal density and size. A recent study by de Boer et al. (2016) revealed a highly negative correlation between stomatal size and density, indicating a tradeoff between stomata size and density. This indicates that there is higher leaf hydraulic conductance, leading to more stringent control of transpiration (Charun et al., 2015).

Existing theory and models suggest that stomatal density has a significant positive influence on gs (Brown and Escombe, 1900; Franks and Beering, 2009; Sack and Buckley, 2016). However, in the present study, higher wood density lead to a lower Gsref at each quantile, whereas stomatal density was positively correlated with water flux only after surmounting a high level “threshold,” which was inconsistent with the law of “diminishing returns” applied in plants’ water use (Cowan and Farquhar, 1977; Eagleson, 2002; Niklas et al., 2007; Schulze et al., 1994). The observed correlations may be attributed to (1) possible hormonal regulations or heterogeneous canopy nutrients (e.g., nitrogen) in those trees at lower quantiles, i.e., τ = 0.2 and 0.4 (less stomata but higher Gs); (2) low sample size was acknowledged for this kind study of tree physiology. The significant correlation between stomatal density and Gsref at τ = 0.6 was consistent with the study in Eucalyptus globulus, indicating higher gs observed in those trees with higher stomatal density in more favorable environments (Franks et al., 2009). This result indicated that stem and leaf hydraulics are finely tuned to avoid embolism in the xylem (Locosselli and Ceccantini, 2012; Méndez-Alonzo et al., 2012; Nolf et al., 2015). The co-ordination between wood density and stomatal morphology could potentially also be explained by the tradeoff between “efficiency” and “safety.” Trees with heavier wood, for example, exhibit low density and lower stomatal density, indicating a lower sap flow and denser stomata, and higher sensitivity to vapor pressure deficit (D), i.e., lower slope (scenario I). The right panel denotes “heavy wood, lower Gs,” indicating a lower sap flow and less stomata, and lesser sensitivity to D, i.e., lower slope (scenario II). This figure depicts the two extreme scenarios describing the impacts of wood and stomatal density on tree transpiration. “Light wood, lower Gs” (lesser stomata) (scenario III) and “heavy wood, higher Gs” (denser stomata)” (scenario IV), in addition to further intermediate states or scenarios, are not fully depicted. $\text{Ln} D$ is the natural logarithm of D.

### Table 2

Linear regression models, summarizing the relationships between stomatal density, wood density and reference canopy stomatal conductance ($G_{\text{sref}}$) in Fig. 3. For OLS regression, the coefficient of determination, $R^2$, is also shown.

| Regression type | Stomatal density vs $G_{\text{sref}}$ | Wood density vs $G_{\text{sref}}$ |
|----------------|--------------------------------------|----------------------------------|
| OLS            | 0.12 ($R^2 = 0.006$)                  | $-0.00095^{**}$ ($R^2 = 0.237$)  |
| Quantile       | $\tau = 0.2$ 0.000                    | $-0.00094^*$                     |
|                | $\tau = 0.4$ 0.000                    | $-0.0014^{**}$                   |
|                | $\tau = 0.6$ 0.753**                  | $-0.00074$                       |

OLS, ordinary least-squares regression; $\tau$, quantile value; *$P < 0.05$; **$P < 0.01$.  

(Méndez-Alonzo et al., 2012). Further research is required to elucidate these correlations (Martínez-Vilalta et al., 2014).

Our previous research showed there was no significant correlation between Gsref and tree structure factors (Gao et al., 2015). This indicated that tree biometric parameters exert trivial effects on Gs, although they play a dominant role in whole tree water transport. This was attributed to the following: (1) Gs is mainly the function of environmental variables, i.e., D, radiation, and maximum daily temperature (Asamaa and Söber, 2011), and results from passive water transport; and (2) Gs is influenced by biological attributes to a greater extent (e.g., stomatal density in this study). The stomatal density of the seven tree species studied varied significantly (Figs. 1 and 2A), and was positively correlated with Gsref above 450 mm², suggesting that there were intrinsic associations between stomatal morphology and tree water use. Recently, a study on three Eucalyptus species showed that there was no significant relationship between stomatal anatomy and whole tree transpiration (Charun et al., 2015). Similarly, Locosselli and Ceccantini (2012) reported that leaf stomatal distribution and tracheid dimensions in the wood of Podocarpus lambertii were only weakly correlated. However, these studies were qualitative in nature and did not quantify the extent to which whole tree water use, or transpiration, was determined by stomatal density.

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**Fig. 4.** A conceptual model illustrating the relationship between wood, leaves, and canopy water flux (reference canopy stomatal conductance, $G_{\text{sref}}$). The left panel denotes “light wood, higher canopy stomatal conductance ($G_s$),” indicating a higher sap flow and denser stomata, and higher sensitivity to vapor pressure deficit (D), i.e., higher slope (scenario I). The right panel denotes “heavy wood, lower Gs,” indicating a lower sap flow and less stomata, and lesser sensitivity to D, i.e., lower slope (scenario II). This figure depicts the two extreme scenarios describing the impacts of wood and stomatal density on tree transpiration. “Light wood, lower Gs (less stomata)” (scenario III) and “heavy wood, higher Gs (denser stomata)” (scenario IV), in addition to further intermediate states or scenarios, are not fully depicted. $\text{Ln} D$ is the natural logarithm of D.
sensitivity to environmental variables (low sap flow); in these trees, the stem and canopy are well-tuned if the leaves atop have denser stomata to relieve the relatively weak transpirative force (Wu et al., 2015). However, if the leaves atop have sparser stomata, the trees are at a growth disadvantage (e.g., scenario II of Fig. 4), but may be more drought tolerant, similar to A. auriculiformis in this study (Figs. 2 and 4). Xylem and stomata are two adjoining parts of the hydraulic system, their relationship determines homeostasis in the hydraulic continuum. The antagonistic effects of xylem and stomata on water flux most likely form the basis of the trees’ homeostatic responses to environmental variables (Brodribb et al., 2014).

5. Conclusions

We demonstrated that the co-determinants of $G_{\text{ext}}$ are wood and stomatal density, i.e., stomata above 450 mm$^{-2}$ promoted water flux, whereas canopy water flux was decreased with increasing wood density. The conceptual model demonstrated the significance of the hydraulic continuum to tree growth and drought tolerance. Scenario I (“lighter wood, denser stomata”) emphasized the significance of rapid growth, whereas scenario II (“heavier wood, less stomata”) emphasized drought resistance. Scenarios III (“Lighter wood, less stomata”) and IV (“heavier wood, denser stomata”), and further intermediate scenarios, were essentially determined by environmental variables, functional groups, and genotypes among others. Understanding the plant–water coordination between stem and canopy may be useful in predicting the impacts of climate change on woody plants. We believe that the contributions of stems and leaves to canopy water flux would be clarified following the collection of data describing in situ whole tree transpiration and tree stomata.

Conflict of interest

The authors declare that they have no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pld.2019.06.003.

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