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Research article

Canopy water status and photosynthesis of tropical trees are associated with trunk sapwood hydraulic properties

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ABSTRACT

Tree trunks not only provide physical support for canopy leaves but also supply and store water for transpiration. However, the relationships between trunk hydraulic properties and canopy leaf physiology in tropical trees are not well-understood. In this study we concurrently measured morning and midday canopy leaf photosynthesis (*A*), stomatal conductance (g_s), and leaf water potentials (Ψ_L) in 40 tropical trees representing 14 species at the beginning of the rainy season in Xishuangbanna, Southwest China. We also measured trunk sapwood capacitance (*C*), wood density, and sap flux density to assess their association with canopy leaf physiology. Among the 14 studied species, only three and four species did not show a significant midday reduction in *A* and g_s respectively. The diurnally maximum *A* and g_s were significantly positively related to sapwood hydraulic capacitance, maximum sap flux density (midday), and sap flux density at 11:00. Those species with lower wood density and higher *C* showed a lower reduction in Ψ_L at midday, whereas, species with high *C*, and large values of maximum sap flux density also showed high carbon assimilation at midday. Our results provide new insights into the close coordination between canopy physiology and trunk sapwood hydraulic properties in tropical trees.

1. Introduction

An understanding of canopy physiology and its diurnal dynamics is important for evaluating both whole tree performance and ecosystem carbon and water fluxes (Flanagan et al., 2012; Mizunuma et al., 2014; Lin et al., 2015; Bussotti et al., 2018; Grossiord et al., 2018). Daily maximum values carbon assimilation (*A*) and stomatal conductance (g_s) are generally observed in the morning, followed by midday declines (Koch et al., 1994; Brodribb et al., 2002; Kosugi et al., 2008; Tucci et al., 2010; Yang et al., 2012; Resco de Dios et al., 2017). However, this pattern can show marked variation depending on species and environmental conditions. The diurnal patterns of canopy *A* and g_s are not only related to changes in environmental conditions, such as light intensity, temperature (Franks and Farquhar, 1999) and air vapor pressure deficits (VPD), but are also strongly regulated by leaf water status, which is influenced by leaf and stem hydraulic properties (Cochard et al., 2004; Brodribb et al., 2007; Woodruff et al., 2007; Johnson et al., 2009; Zhang et al., 2013). In this regard, it is believed that there is a coordination between leaf stomatal regulation and stem hydraulic properties to optimize carbon gain per water loss, and also to maintain the integrity of the hydraulic system (Brodribb et al., 2002; Meinzer et al., 2009; Zhang et al., 2013). For large trees, the trunk not only represents a hydraulic pathway linking roots and canopy branches, but also provides a water storage reservoir that is closer to the canopy. Therefore, the hydraulic properties of the trunk could play an important role in determining canopy transpiration and carbon exchange, which to date has not been well-studied in tropical trees.

Photosynthetic gas exchange behavior and the water status of trees during the day could be regulated by trunk sapwood hydraulic capacitance (*C*) (Zhang et al., 2013; Richards et al., 2014). The contribution of water stored in stems to the daily transpiration of trees varies widely among species, ranging from 10% to 50% (Meinzer et al., 2003; Scholz et al. 2007, 2011). The storage of water in trunks and branches provides a closely available source of water for the canopy, particularly during the midday when the transpirational demand is high (Holtta et al., 2009; Pivovaroff et al., 2016). Previously, Meinzer et al. (2008) have

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reported the close relationships between maximum stomatal conductance, leaf and stem water potentials (Ψ), and maximum sap flux density and *C* in some tropical forest canopy trees. However, despite the significance of *C* as an important determinant of tree canopy physiology, there are few studies that have examined the role of *C* in regulating diurnal changes in canopy leaf water status and gas exchange behavior.

The ability of trees to maintain a high leaf water potential (Ψ_L) and high carbon assimilation during active transpiration is also related to trunk water transport capacity (hydraulic conductance): the efficiency of water supply from the roots to the canopy leaves (Tyree and Zimmermann, 2002; Pickard, 1981; Zimmermann and Milburn, 1982). Provided that other biological and environmental factors, including rooting depth and, leaf area:sapwood area and root:shoot ratios, are held constant, species with high water transport efficiency would be able to replace the transpirational water loss more rapidly and therefore maintain a higher Ψ_L on daily basis. Such species would show less change in Ψ_L during the period from pre-dawn to midday. Species that can maintain a high midday Ψ_L can probably also maintain higher values of *A,* and g_s than those species with lower water transport efficiency (Pivovaroff et al., 2014), and therefore, the maximum rate of water transport in a trunk is probably important in determining canopy photosynthetic performance.

Moreover, both sapwood water transport and storage capacity are determined to a large degree by wood structure (Domec et al., 2006; Choat et al., 2008; Apgaua et al., 2015). Vessel diameter strongly affects sapwood-specific hydraulic conductivity, which scales with the vessel diameter to the fourth power (Zimmermann, 1983; Tyree and Ewers, 1991). Furthermore, a large vessel diameter is generally associated with low wood density, whereas low wood density has been found to be negatively related to water storage capacity in trees (Chave et al., 2009; Hietz et al., 2016). In this study, we aimed (1) to quantify the diurnal changes in canopy water status and photosynthesis of tropical trees in SW China by using a crane to access the canopy, and (2) to characterize the relationships between the canopy water status and photosynthesis and trunk hydraulic properties of these trees. We hypothesized that the maintenance of canopy gas exchange during a day is associated with the ability to maintain high canopy leaf water status, which in turn is determined by both trunk sapwood hydraulic capacitance and conductance.

2. Material and methods

2.1. Study site and species

The study was carried out in plantation stands in Xishuangbanna Tropical Botanical Garden (XTBG; 21° 54′ N, 101° 46 ′ E, 580 m a.s.l.), southern Yunnan Province, Southwest China. This region has a typical tropical monsoon climate and hence a pronounced dry season from November to April. The mean annual precipitation is 1560 mm, approximately 80% of which falls during the wet season (May to October). The mean annual temperature of the study site is 21.7 °C (Cao et al., 2006). For the purpose of the present study, we selected 14 broadleaf timber tree species (Table 1) growing in closely located plantation stands in the arboretum of XTBG, with three replicates per species for 12 of these species. For the remaining two species (*Pterocarpus indicus* and *Shorea assamica*), only two individuals with crane access to their canopies were available for measurements. The species names, leaf phenology, diameter at breast height (DBH), and replicates used are shown in Table 1. All canopy physiological measurements were made from the last week of April to the first week of May 2013, which coincided with the beginning of the wet season, a period characterized by continuous sunny days and thus optimal time for diurnal physiological measurements.

2.2. Canopy gas exchange and leaf water potentials

We used a canopy crane mounted on a truck to access the tree canopies, which were between 20 and 35 m in height. Daily maximum and midday gas exchange (leaf photosynthesis, stomatal conductance, and transpiration) were measured using a portable photosynthesis measurement system (LI-6400; LI-COR, Nebraska, USA) under ambient conditions on sunny days. The maximum gas exchange was between at 09:00 and 11:00, whereas midday measurements were taken between 12:00 and 14:30. The chamber temperature during the measurement time was approximately 23 °C in the morning and 30 °C at midday, whereas the leaf to air vapor pressure deficit (VPD) was approximately 0.9 kPa, and 2.5 kPa in the morning and at midday, respectively. For each species, six to eight new fully-developed mature leaves from different sun-exposed terminal branches of two to three individuals were selected to measure canopy gas exchange at two to three canopy positions. For each species, six to eight values of photosynthetic rate and stomatal conductance were logged and stored in the LI-COR LI 6400 instrument. The leaf water potential was measured on site from five to six leaves per tree using a pressure chamber (PMS, Albany, OR, USA). Predawn leaf samples were collected and measured in the field between 06:00 and 07:00, whereas midday samples were collected between 12:30 and 14:30. The midday decline in leaf water potential ($\Delta\Psi_L$) from that predawn was calculated as the difference between midday and predawn values.

2.3. Sapwood capacitance and wood density

In order to estimate sapwood capacitance, two cores were from each tree obtained at 1.3 m above ground level using a 5-mm increment corer. These cores were sealed in plastic vials, and immediately transported to the laboratory for fresh weight and volume measurements. The wood volume was determined using the water displacement method. The cores were subsequently allowed to hydrate overnight in distilled water, and in the following morning, they were rapidly blotted to remove excess water prior to determining their saturated weight. Thereafter, the cores were cut into 10-mm segments and placed into a small plastic sample cup for sapwood pressure-volume measurements using a WP-4T Dew Point Potential Meter (Decagon Devices, Inc. USA). The equipment was allowed to stabilize for 30 min prior to placing the samples into the chamber of the device, which was run in continuous mode. Having made three consecutive measurements of water potential, the sample was weighed on a digital balance. Thereafter, the sample cup was taken out from the WP-4T device to release moisture for approximately 20–30 min, after which the water potential and weight were re-measured. This procedure was repeated until the sapwood water potential had reached a value of approximately to −5 to −10 MPa, depending upon tree species. Sapwood capacitance (*C*, kg m^{-3} MPa^{-1}) was calculated from the slope of the linear portion of a moisture release curve (Meinzer et al., 2003). The capacitance was normalized by sapwood volume to facilitate a comparison of the absolute amounts of water released per unit decline in water potential across species (Scholz et al., 2007). The relative water content (RWC) was determined using the following formula:

$$RWC = \frac{W\text{f}-Wd}{Ws-Wd}$$

where *Ws* is the saturated weight, W_f is the fresh weight, and W_d is the dry weight. The dry weight of a wood core was determined by placing the samples in an oven at 70 °C for 48 h. Although when using small stem segments and potentially causing an initial release of xylem water, this method may overestimate hydraulic capacitance (Wolfe and Kursar, 2015), we believe that this systematic artifact could apply to all the species analyzed, and thus would not affect the comparison among species.

Trunk sapwood wood density was measured for the individual trees

Table 1
List of the fourteen species studied, species abbreviation, range of diameters at 1.3 m height (DBH) and replicates.

Sr no.	Scientific Name	Code	Family	DBH range (cm)	No. of trees
Evergreen Trees					
1.	*Anisoptera laevis* Ridl.	Al	Dipterocarpaceae	31–37	3
2.	*Dipterocarpus alatus* Roxb. Ex G.Don	Da	Dipterocarpaceae	30–58	3
3.	*Hopea hainaniensis* Merr. & Chun	Hh	Dipterocarpaceae	19–32	3
4.	*Mesua ferrea* L.	Mf	Calophyllaceae	16–22	3
5.	*Phoebe puwenensis* W.C. Cheng	Pb	Lauraceae	18–29	3
6.	*Shorea assamica* Dyer	Sa	Dipterocarpaceae	17–20	2
7.	*Shorea chinensis* Merr.	Sc	Dipterocarpaceae	16–25	3
8.	*Vatica magachapai* Blanco	Vm	Dipterocarpaceae	20–22	3
Deciduous Trees					
9.	*Anogeisus acuminata* (Roxb. Ex Dc.) Guillaum & Perr.	Aa	Combretaceae	19–35	3
10.	*Dalbergia fusca* Prain	Df	Fabaceae	19–41	3
11.	*Dalbergia odorifera* T.C.Chen	Do	Fabaceae	18–23	3
12.	*Dipterocarpus tuberculatus* Roxb.	Dt	Dipterocarpaceae	19–40	3
13.	*Pterocarpus indicus* Willd.	Pi	Fabaceae	20–31	2
14.	*Swietenia mahogany* (L.) Jacq.	Sm	Meliaceae	31–55	3

of each species using a 5-mm increment corer. The cores were sealed in plastic vials, and immediately transported to the laboratory. After removing the bark and pith with a razor blade, the cores were weighed, placed in water in a small graduated cylinder to determine their volume, and then oven-dried to a constant weight and re-weighed to obtain the dry mass. Density was then determined by dividing the dry mass by the volume of the sample.

2.4. Sap flow

Data for the morning and midday sap flow were obtained from the ongoing sap flow measurements for trees that were measured for gas exchange. Sap flow was measured at DBH, with each tree being equipped with two sets of 2-cm long lab-made thermal dissipation sap flow measuring sensors (Granier, 1987), which were installed at 90° angles to the stem and positioned directionally opposite to one another along the same compass direction. The sap flow sensors consisted of a thermocouple surrounded by a heating coil and a reference sensor, and the sensors of all the sample trees were connected to four data loggers (CR-1000; Campbell Scientific, Inc., Utah, USA) via a multiplexer (AM 16/32; Campbell Scientific, Inc.,Utah, USA) and supplied with a constant power of 0.2 W to heat the sensors. Aluminum foil was used to protect the sensors from mechanical damage and solar radiation. Data were logged every 30 s and averaged over 30-min intervals. The original Granier equation was calibrated to calculate the sap flux density, as the original Granier equation can substantially underestimate the sap flux density of tropical trees (Siddiq et al., 2017).

2.5. Data analysis

Differences between morning and midday canopy photosynthesis and stomatal conductance and between pre-dawn and midday leaf water potentials across the species were analyzed using two-way ANOVA. The statistical analyses were carried out using R software (R Core Team, 2013). The generation of graphics and regression analyses were carried out using Sigma plot (version-12.5; Systat Software Inc. USA).

3. Results

3.1. Trait and physiological variation across species

High variations in canopy maximum photosynthetic rate (A) and stomatal conductance (g_s) were detected among the 14 tropical trees, with most species showing significant decline in A and g_s at midday. $A_{\max}$ values ranged from 5.01 to 15.43 μ mol m^{-2} s^{-1} across species, whereas g_{smax} ranged from 0.11 to 0.59 mol m^{-2} s^{-1} (Fig. 1a). The percentage midday decline in A ranged from 12% to 48% whereas the midday decrease in g_s ranged from 19% to 76% across the study species. Three species (Sc, Hh and Mf) and four species (Sc, Hh,Mf and Pi) showed no significant midday decrease in A and g_s respectively (Fig. 1a and b). The leaf water potential (Ψ_L) values measured at midday ranged from −0.47 MPa to −2.02 MPa across species (Fig. 1c).

The ANOVA type III SS, showed that C had the significant effect on photosynthetic rate and stomatal conductance ($P > 0.0001$). Two way ANOVA revealed overall significant differences in photosynthetic rate and stomatal conductance between maximum and midday values, as well as between pre-dawn and midday leaf water potentials across all the species. There was also a significant effect of species on all of the afore mentioned variables.

3.2. Relationships between canopy physiology and stem hydraulic traits

Both $A_{\max}$, g_{smax} and A_{mid}, g_{smid} were significantly positively associated with trunk sapwood capacitance across the 14 tropical tree species (Fig. 2a–d).

The sapwood capacitance was significantly negatively associated with wood density, and positively associated with DBH (Fig. 3a and b), whereas wood density was significantly positively associated with the midday decline in leaf water potential ($\Delta\Psi_L$) (Fig. 4).

A significantly positive relationship between maximum photosynthetic rate, maximum stomatal conductance, and maximum sap flux density observed at midday was also found across species (Fig. 5a and b). Additionally, maximum photosynthetic rate and maximum stomatal conductance were also related with sap flux density at 11:00, but the relationships are weaker compared to those with maximum sap flux density (Fig. 5c and d).

4. Discussion

Our analysis of the hydraulic traits of tropical trees in SW China revealed high variations in canopy water status, maximum photosynthetic performance, and their diurnal changes. We further identified that the canopy water status and photosynthetic performance of the studied tropical trees were closely associated with trunk hydraulic properties. As hypothesized, canopy leaf water status and photosynthetic performance were strongly coordinated with both trunk sapwood hydraulic capacitance *(C)* and maximum sap flux density across the study species. Our results accordingly indicate the significance of both water storage and vertical water transport in determining canopy photosynthesis and water status.

The maintenance of canopy leaf water status during the day is strongly related to trunk structure and sapwood hydraulic *C*. Among the tree species studied, we found that wood density and vessel diameter

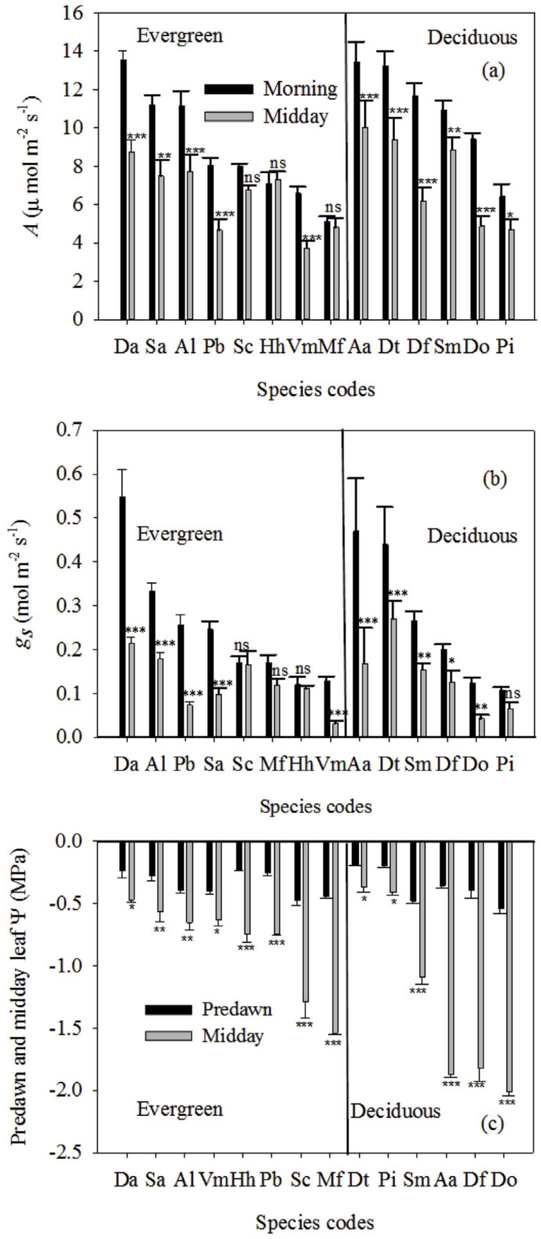

Fig. 1. Morning and midday canopy photosynthesis and stomatal conductance (a–b), pre-dawn, and midday leaf water potential ($\Psi_{L,}$ c) across eight evergreen and six deciduous species. Species codes are listed in Table 1. Bars and whiskers indicate means and SE. ***$P < 0.0001$, **$P < 0.001$, *$P < 0.01$, ns indicates non-significance.

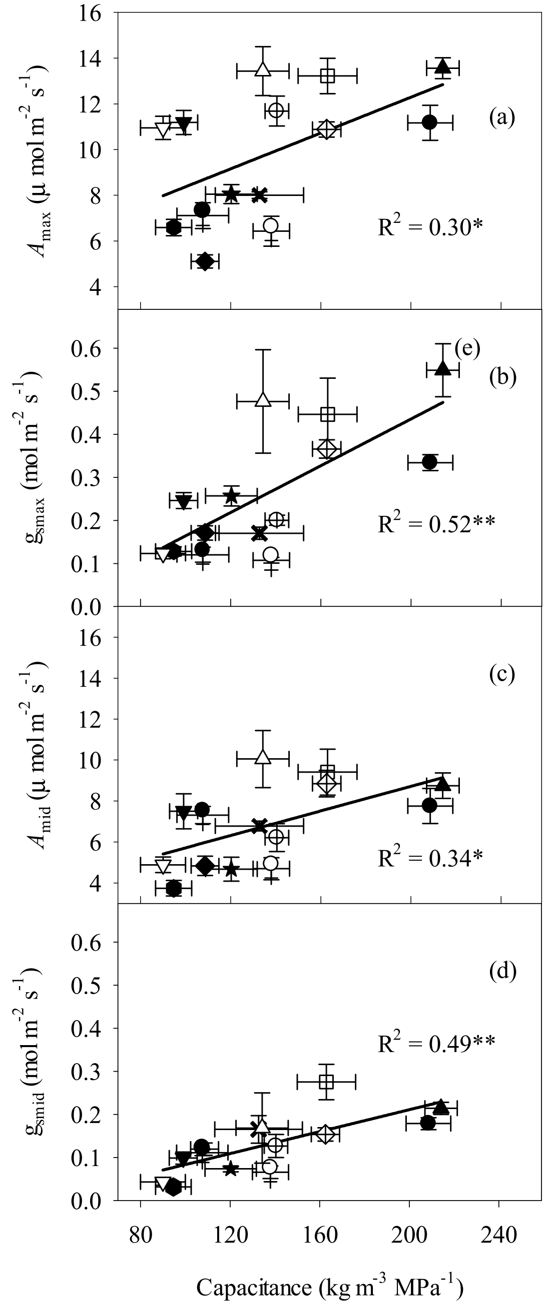

Fig. 2. The maximum (during the morning hours) and midday photosynthetic rate ($A_{\max}$, A_{mid} and stomatal conductance ($g_{\max}$, g_{smid}) in relation to sapwood capacitance. Species codes are mentioned in Table 1. Open symbols indicate deciduous while filled symbols indicate evergreen species. Symbols and whiskers are species means ± SEs. Linear regressions are fitted to the data. **$P < 0.001$, *$P < 0.01$.

strongly determined C, which reinforces the findings of previous studies on tropical savanna trees (Scholz et al., 2007; Meinzer et al., 2008). Large trunk vessels can also function as a reservoir of water storage and can play an important role in trunk water status. Whereas, midday Ψ_L is mainly determined by the transpiration in the morning (E) and whole plant hydraulic conductance (Kplant), as $\Psi_L = \Psi_{soil} - (E/K\text{plant})$, trunk and stem water storage could possibly serve as a water source for canopy leaves. Although, the accessibility of stored trunk water for daily transpiration and the hydraulic resistance from water storage pools to the xylem conduits require further mechanistic studies, significant declines in tree stem sapwood water content at midday (Zhang et al., 2013) and higher sap flux density in the upper portions of trunk than in trunk base in most of tropical rainforest woody plants (Chen et al., 2016) indicate that stored trunk water is accessible for diurnal transpiration. Moreover, the close association between wood density and $\Delta\Psi_L$, which has also been reported in other studies (Santiago et al., 2004; Maréchaux et al., 2015), also indicate a differentiation in strategies for maintaining diurnal canopy water balance among tree species. Species with high (less negative) midday water potentials may mainly rely on their high C (low wood density) for buffering transpirational water loss, whereas species with a low C and a high wood density probably, rely to a greater extent on their high resistance to cavitation to tolerate low water potentials (Woodruff et al., 2007; Johnson et al., 2009, 2011). In this regard, species with high wood density tend to have small and thick vessels to protect xylem from water deficit-induced hydraulic dysfunction (Hacke et al., 2001; Bucci et al., 2004; McCulloh et al., 2012; Brodersen and McElrone, 2013).

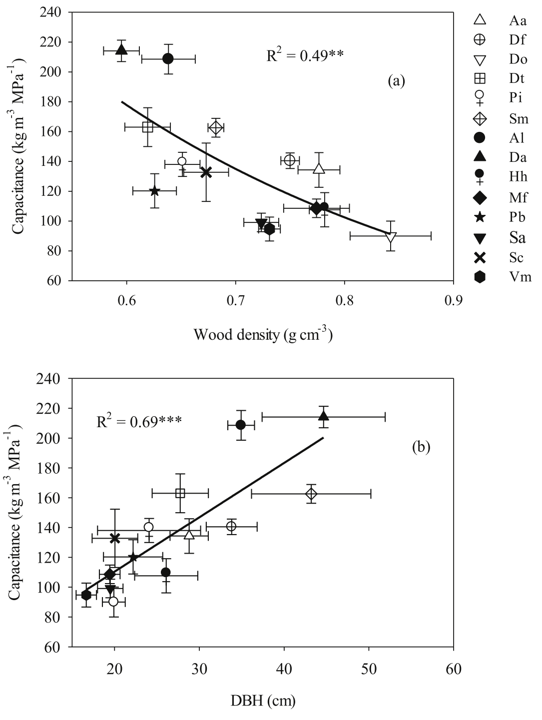

Fig. 3. Relationship of trunk sapwood capacitance with trunk wood density (a) and diameter at breast height (DBH, b) across six deciduous (open symbols) and eight evergreen species (filled symbols). Species codes are listed in Table 1. Symbols and whiskers are species means ± SEs, *** indicate $P < 0.0001$ and **$P < 0.001$.

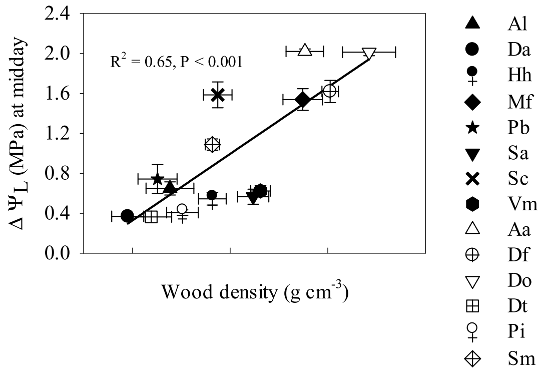

Fig. 4. Relationship between decline in leaf Ψ at midday from pre-dawn and trunk wood density across six deciduous (open symbols) and eight evergreen species (filled symbols). Species codes are listed in Table 1. Symbols and whiskers denote species means + SEs.

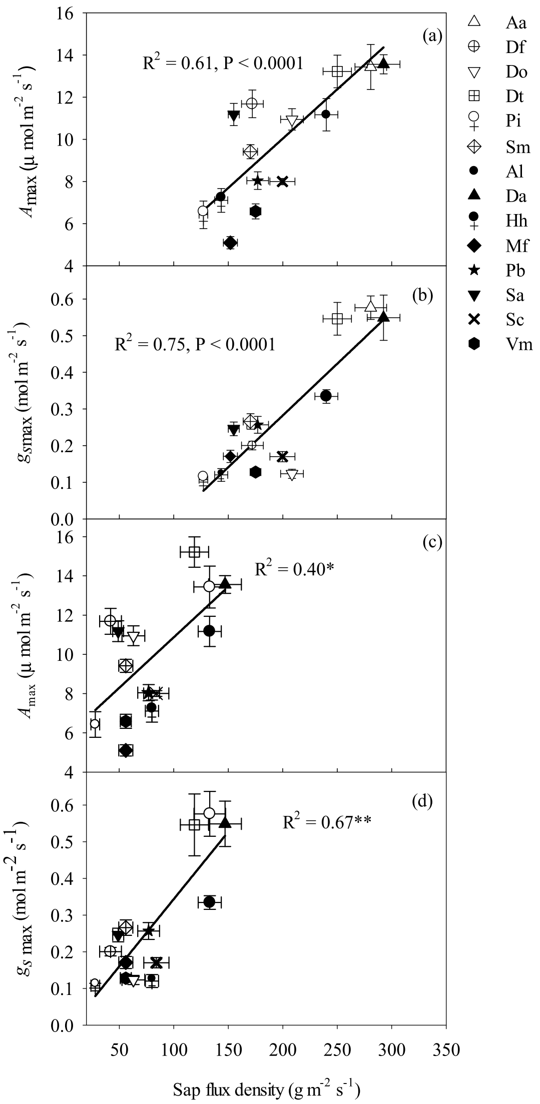

Fig. 5. The maximum photosynthetic rate A and maximum stomatal conductance g_s in relation to sap flux density (maximum; Panel a,b) and sap flux density at 11:00 (Panel c,d). The species codes are listed in 1. Symbols and whiskers denote species means + SEs. Open symbols indicate deciduous while filled symbols indicate evergreen species.

Although the role of C in canopy physiology has been described in some previous studies (Meinzer et al., 2008; Gleason et al., 2014; Oliva et al., 2015), we further found that trunk C not only plays an important role in determining maximum A and g_s in the morning, but is also related to higher A and g_s at midday. The importance of water storage in determining and maintaining canopy photosynthesis is further supported by the significant relationship between DBH and C Large trees (larger DBH) not only have a higher C but also a larger volume of trunk sapwood (Siddiq et al., 2017) compared with small trees, indicating a larger water storage pool to provide water for transpiration in the formers (Fig. 1 b). A large amount stored trunk water, being a closely available water source for the canopy leaves, enables trees to maintain high A and g_s with sufficient water supply from the water stored in trunks at midday, which has also been reported in other studies (Holtta et al., 2009; Richards et al., 2014). This also is further supported by the positive relationship between maximum A and g_s and tree water transport efficiency (suggested by maximum sap flux density at midday) in the morning and at midday (Fig. 5). More efficient vertical water transport may not only facilitate the transport of water from the soil and roots to the trunk, but could also facilitate the delivery of water from the trunk storage pool to the canopy leaves. Further, there is a time lag between maximum canopy gas exchange (reached at 11:00) and maximum sap flux density (reached at midday). Therefore, maximum canopy A and g_s have stronger relationships with maximum sap flux density (midday) than with sap flux density in the morning (11:00; Fig. 5). This time lag is probably because of the contribution of trunk water storage, which supports the importance of hydraulic capacitance in achieving maximum canopy gas exchange in the morning.

In addition, we found that species with a high A and g_s (Al, Da, and Dt, with maximum A and $g_s \geq 10\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$and $0.35\ \text{mol m}^{-2}\ \text{s}^{-1}$, respectively) showed greater midday declines in A and g_s. However, the larger A and g_s declines in these trees species did not result in lower midday A and g_s than those species (Hh, Mf, Pi, and Sc) with lower values of the both A and g_s ($\leq 8\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ and $< 0.2\ \text{mol m}^{-2}\ \text{s}^{-1}$, respectively). These latter four species (Hh, Mf, Pi, Sc) also had a lower range of capacitance and sap flux density than Al, Da, and Dt, indicating the advantage of species with high morning gas exchange during the rainy season in terms of daily carbon gain. No distinct differences in hydraulic and gas exchange performances were found between evergreen and deciduous species, probably because both groups show large interspecific variation within the groups (e.g. Fig. 1).

5. Conclusion

In conclusion, we found a high variation in canopy leaf photosynthetic performance among selected tropical trees in SW China. Further, our study revealed that the trunk hydraulic characteristics of tropical forest trees are associated with canopy leaf water status and the diurnal maintenance of canopy transpiration and carbon assimilation. Both water storage (capacitance and water storage pool size) and vertical water transport (indicated by maximum sap flux density) play important roles in determining canopy photosynthetic performance. Collectively, the findings of our study indicate a strong coordination between tree trunk hydraulic traits and canopy physiological performance in tropical trees.

Authors contributions

Zafar Siddiq, and Kun-Fang Cao designed the study. Zafar Siddiq, Shi-Dan Zhu conducted the field experiments. Zafar Siddiq, Yong-Jinag Zhang and Kun-Fang Cao analyzed the data and all authors contributed the manuscript writing.

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