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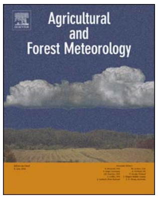

Research Paper

More sensitive response of crown conductance to VPD and larger water consumption in tropical evergreen than in deciduous broadleaf timber trees

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ABSTRACT

The differences in crown conductance sensitivity (*m*) to vapor pressure deficit (VPD) and water consumption between tropical evergreen and deciduous tree are not well-understood despite the importance of such information for the development of plantation and water-resource management strategies in regions that experience seasonal drought and increasing water deficits. To this end, during the wet season we measured sap flow in 60 individual trees representing 21 tropical angiosperm broadleaf timber species (11 evergreen and 10 deciduous) growing in plantations in a marginal tropical area of southwestern China. The results showed that *m* was strongly correlated with reference crown conductance (G_{cref}) at 1 kPa VPD across all species, with a slope value of 0.46, which was significantly different from the proposed theoretical value of 0.6, suggesting the study species as anisohydric. The *m* was positively correlated with tree diameter at the height of 1.3 m (diameter at breast height, DBH) but for a given DBH, *m* was significantly higher in evergreens than in deciduous trees. Further, whole-tree mean daily water consumption was strongly and positively correlated with DBH, but at a given DBH, evergreen species exhibited larger water consumption than deciduous species. Vessel diameter (related to xylem hydraulic conductance) and sapwood area were also positively correlated with DBH, and evergreen species had significantly larger sapwood area than deciduous species at a given DBH. In conclusion, we found that 1) crown conductance of evergreen trees is more sensitive to VPD compared to deciduous species and 2) evergreen trees consume more water than deciduous trees, partly because of having higher peak transpiration rate and, larger sapwood area (i.e., larger xylem area for water transport and storage). Therefore, we suggest that in tropical regions associated with seasonal drought timber plantations with more deciduous species could potentially be considered as a management possibility for achieving a balance between timber production and water conservation, even in the wet season, which needs to be tested at the plantation level.

1. Introduction

Understanding the water use pattern of different tree species and their response to environmental change is essential for developing effective natural and man-made ecosystem management strategies, particularly in areas that currently experience seasonal drought and are predicted to be drier in the future (Ford et al., 2011; Zhang et al., 2014b). Although whole tree water consumption overall scales with tree size (Meinzer et al., 2005; Miyazawa et al., 2014; Otieno et al., 2014; Gao et al., 2015), significant differences in whole-tree water consumption with similar DBH (diameter at 1.3 m height) were found among different species (Dierick et al., 2010; Kallarackal et al., 2013) calling for research on different tree species especially with contrasting leaf habits (Reyes-Garcia et al., 2012). Trees with different leaf habits (*i.e.* evergreen *vs.* deciduous) show remarkable differences in trunk sapwood area, wood density, hydraulic conductance, water storage capacity, and leaf gas exchange characteristics (Choat et al., 2004; Meinzer et al., 2003, 2008; Zhang et al., 2013), all of which would greatly influence the tree's water use amount and pattern. For trees, effective regulation of transpiration under meteorological fluctuations

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is critical for maintaining a balance between photosynthetic carbon gain and transpirational water loss (Buckley, 2005; Hacke et al., 2006; Fiorin et al., 2015). Delay in such responses, when transpirational demand is high could potentially lead to the formation of embolisms (blockage of conduits by air bubbles) in xylem vessels and consequently catastrophic hydraulic failure, potentially resulting in branch or even plant dieback (Tyree and Sperry, 1989; Meinzer et al., 2009; Lens et al., 2011). The objective of the present study was to understand the differences in whole tree water consumption and crown conductance sensitivity to the vapor pressure deficit (VPD) between evergreen and deciduous timber species in tropical China, which is predicted to drier in the future.

Crown conductance (G_c) coupling photosynthesis and transpiration is a variable used to characterize the species-specific response to transpirational demand (Naithani et al., 2012). The relationship between G_c and vapor pressure deficit (VPD) can estimate the crown conductance sensitivity (m) to transpirational demand. A greater sensitivity (faster decrease in stomatal conductance) is associated with a higher stomatal conductance at low VPD (Oren et al., 1999). Partly based upon the stomatal sensitivity, species can be categorized into isohydric and anisohydric, each having advantages and disadvantages in particular growing conditions (Franks et al., 2007; Choat et al., 2012). Isohydric species have strong stomatal control to maintain good leaf water status at the cost of reduced carbon gain. Such behavior is advantageous with a largely fluctuating evaporative demand (Bucci et al., 2004). On the other hand, anisohydric species possessing a weak stomatal control generally have longer carbon assimilation than isohydric species (Konings and Gentine, 2016). Such behavior is favored in conditions with constantly sufficient soil water supply (Bush et al., 2008; Kumagai and Porporato, 2012).

Crown conductance sensitivity to transpirational demand (vapor pressure deficit, VPD) is associated with many aspects of tree structure and function such as water storage, tree size, and leaf habit (Naithani et al., 2012; Klein and Niu, 2014). Moreover, m is strongly linked with xylem hydraulic safety; species with high xylem vulnerability to cavitation generally exhibit a more sensitive response to VPD (Bush et al., 2008). m can also be influenced by leaf habit (Hasselquist et al., 2010), particularly because of differences in leaf biomass, sapwood area, wood density and vessel size between evergreen and deciduous species (Reyes-Garcia et al., 2012; Tomlinson et al., 2013). In general, deciduous species have lower wood densities and wider vessels than evergreen, and thus higher xylem hydraulic conductance and greater water storage capacity (Zhang et al., 2013), all of which render deciduous trees more vulnerable to dehydration induced-embolism than evergreens (Choat et al., 2004). Such disparities could result in differences in their diurnal responses to VPD and water use strategies.

Whole-tree water consumption is also related to crown conductance and its response to VPD (Oren et al., 2001; Klein et al., 2013; Zhu et al., 2015). Trees with high crown conductance under favorable conditions consume more water to offset higher levels of evaporative demand (Oren et al., 1999) due to higher whole-tree hydraulic conductance (Litvak et al., 2012; McCulloh and Woodruff, 2012). On the other hand, trees can reduce whole-plant water use by down-regulating G_c under drought conditions, an adaption to avoid hydraulic failure (Kumagai et al., 2008; Igarashi et al., 2015).

In areas using both evergreen and deciduous trees for timber plantations, understanding their differences in water consumption and response to change in environmental conditions (*e.g.* VPD) could be helpful for species selection. Information about water consumption of timber tree species can also be used to assess their hydrological impacts on regional water cycles and forecast their responses to climate change, which can be helpful for plantation and regional water-resource management (Attia et al., 2015; Roman et al., 2015). Since many tropical regions are becoming drier (Van Loon and Laaha, 2015; Wang et al., 2015; Corlett, 2016), understanding the water consumption of different tropical timber species is crucial for developing sustainable water-use strategies. We studied the whole-tree water use and crown conductance response to VPD in 10 deciduous and 11 evergreen broadleaf timber tree species in a site of Southwest China with a tropical seasonal climate to address the following questions: 1) Under non-limiting growth conditions, do evergreen and deciduous broadleaf trees differ in their crown conductance response to changes in VPD? and 2) Are there significant differences in whole-tree daily water consumption between the evergreen and deciduous species in this region? Further, we studied the potential mechanisms explaining the possible differences between evergreen and deciduous species in terms of xylem water transport (indicated by vessel diameter), sapwood area, and sapwood hydraulic capacitance.

2. Materials and methods

2.1. Study site and species

The study was carried out in plantation stands in the Xishuangbanna Tropical Botanical Garden (XTBG; 21° 54/N, 101° 46/E, 580 m a.s.l.) of southern Yunnan Province, in southwestern China. This region has a typical tropical monsoon climate and thus features, a pronounced dry season (November–April). Mean annual precipitation in the study area is 1560 mm, of which ~80% occurs during the wet season (May–October) and mean annual temperature is 21.7 °C (Cao et al., 2006). We selected 21 evergreen and deciduous timber tree species (Table S1) in nearby plantation stands in the arboretum of XTBG, with an average of three replicates per species, for some species, however, fewer than three individuals were available. Five of the 21 species were non-native to the region, with four (*Anisoptera laevis*, *Dipterocarpus alatus*, *Dipterocarpus tuberculatus* and *Tectona grandis*) native to northern Thailand and adjoining areas, and one (*Swietenia mahagoni*) native to United States tropical islands. The remaining 16 species were native to southern China. Of these, two species (*Shorea chinensis* and *Phoebe puwenensis*) are generally considered to be representative of the forest vegetation types in Xishuangbanna (Cao and Zhang, 1997). The species names, leaf habit, DBH, and replicates that were used are presented in Table S1. All species have diffuse-porous wood, with the exception of *Tectona grandis*, which has ring-porous wood.

2.2. Sap flow and climatic data

Sap flow measurements were made at 1.3 m DBH, in the outer 2 cm depending on tree diameter, using home-made thermal dissipation sap flow sensors (Granier, 1987) during 3 months of the wet season (June–August) in 2012. Each tree was equipped with two sets of 2 cm long sensors, which were installed at 90° angles to the stem and positioned directionally opposite to one another along the same compass position. Sap flow sensors consisted of a thermocouple surrounded by a heating coil and a reference sensor, and all sensors were connected to data loggers (CR-1000, Campbell) with a multiplexer (AM 16/32, Campbell) 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, for storage in the data loggers. Sensors were monitored bi-weekly, with malfunctioning sensors were immediately replaced. Sap flux density (SFD, $g\,m^{-2}\,s^{-1}$) was calculated using BaseLiner v. 4.0. (Oishi et al., 2016; C-H_2O Ecology Group, Nicholas School of the Environment, Duke University, Durham, North Carolina, USA) using our calibrated Granier's equations (Granier, 1987), as recent studies have pointed out that the original Granier's equation is not universal and should be calibrated as it could underestimate the sap flow of some trees especially ring-porous species (Taneda and Sperry, 2008; Bush et al., 2010; Hultine et al., 2010). We calibrated the equation for 5 diffuse-porous and one ring-porous species using excised stems from 6 to 9 trees per species with diameter range of 3.82–9.55 cm (Table S3) following Bush et al. (2010) and Hua-Xiu et al. (2016). We generated species-specific equations for both five diffuse- and one ring-porous species and one generalized equation by pooling the data of five diffuse-porous species. For calculating sap flux density we used species-specific equations for the trees that we made calibration, while for the rest of diffuse porous species the generalized equation was used. The average values from two paired sensors were used to calculate the sap flux density for each individual tree.

Climatic data were obtained from the Tropical Rainforest Ecosystem Station at XTBG, located at a distance of ~900 m from the plantation stands. Vapor pressure deficit was calculated from air temperature and humidity.

2.3. Whole-tree water use and crown transpiration

Whole tree sap flows in up to three ring-shaped stem cross-sections were calculated from the radial profile(s) and, the active sapwood area of the particular depth, multiplied by the mean sap flux density of the particular depth. The active sapwood area of each sample tree was determined using the dye injection method. A dye solution of 0.1% safranin was injected into the sapwood at DBH. After 12 h or even longer duration, a 5 mm core was taken just above the injection point to measure the active sapwood area by assessing the dye color travelled on the xylem core. For the species with sapwood depth larger than 2 cm, the radial profile of sap flux density was measured using the sensors fixed at 4 cm, and 6 cm depth of sapwood, avoiding the contact with hardwood (Clearwater et al., 1999). Twenty two trees (including at least 1–2 trees of each species) were fixed with the sensors at a depth of 4 cm and 12 trees with the sensors at a depth of 6 cm. For trees in which sapwood depths extended beyond 2 cm but were not fixed with sensors at the 4 cm or 6 cm, the sap flux density was estimated as the proportional declines of sap flux density with the increase in sapwood depth obtained from those trees measured at different sapwood depths of the same species. The radial profile of sap flux density for each species was estimated by normalizing measurements from the 4 cm and 6 cm depths by 2 cm. In order to measure. The contributions of different cross-sections were added to determine the whole tree total sap flow (g h^{-1}) and then integrated over a day to estimate whole-tree daily water use (DWU, kg d^{-1}). We estimated crown transpiration (E_c) by dividing the whole tree water use by the crown projected area (Chen et al., 2011), which was estimated using the formula for the area of an ellipse (A_e):

$$A_e = \pi\,(0.5X) \times (0.5Y) \tag{1}$$

where X is the crown length and Y is the width measured perpendicularly to X (Gotsch et al., 2010).

2.4. Crown conductance and species behavior

The hourly mean crown conductance (G_c) to water vapor (mmol m^{-2} s^{-1}) was calculated from hourly mean E_c and VPD using the equation developed by Monteith and Unsworth (1990).

$$G_c = \frac{KG(T)EC}{VPD} \tag{2}$$

where K_G is the conductance coefficient (115.8 + 0.4236T; kPa m^3 kg^{-1}) which accounts for the temperature effect on the psychrometric constant, latent heat of vaporization, specific heat of air at constant temperature, and density of air; E_c is the crown transpiration; T is the air temperature; and *VPD* is the vapor pressure deficit (Phillips and Oren, 1998). Values for G_c were converted from m s^{-1} to mmol m^{-2} s^{-1} following Pearcy et al. (1989). Eq. (2) assumes the following conditions: (1) VPD is close to the leaf-to-air VPD, and thus boundary layer conductance is high; (2) there is no vertical gradient in VPD through the canopy; and (3) there is negligible water stored above the sap flux density measurement position. The first two conditions were assumed to be met due to distances between trees in the plantation stands being large enough to ensure that individual tree canopies did not overplay and therefore canopies receive adequate sun-light and air circulations. Additionally, our analysis showed that there was lack of correlation of G_c with wind speed at our study site (Data not shown). The conditional sampling approach and hourly average of G_c was applied to meet the third condition that is., we selected data when VPD exceeded 0.6 kPa and photosynthetic active radiation was also not a limiting factor (> 1000 μ mol m^{-2} s^{-1}) (Ewers and Oren, 2000; Meinzer et al., 2013; Gao et al., 2015). The hourly G_c average could also average out the time lag between crown transpiration and our sap flow measurements at DBH, as the time lag between canopy and basal sap flow were mostly less than 30 min in tropical trees, with decreasing time lag in smaller trees (Kume et al., 2008; Chen et al., 2016).

Table 1
Results of the Type III SS ANOVA analysis. The effect of diameter at breast height (DBH) and leaf habit on the sensitivity of crown conductance to VPD (*m*).

Predictor	SS	Df	F	*P*
DBH (cm)	1.98	1	10.95	< 0.001
Leaf habit	2.07	1	11.43	< 0.001
DBH: leaf habit	0.62	1	3.46	0.073

The sensitivity of G_c in response to changes in VPD (*m*) was determined from the slope of the relationship between G_c and ln VPD ($-dG_c$/dln VPD) following equation proposed by Oren et al. (1999).

$$G_c = G_{cref} - m(lnVPD) \tag{3}$$

where *m* is defined as the crown conductance sensitivity and G_{cref} is the reference conductance at 1 kPa VPD. For categorizing the evergreen and deciduous trees behavior as isohydric or anisohydric the slope value obtained from the pooled *m* data of all the individual trees from all the species against G_{cref} was compared with the proposed theoretical value 0.6 (Oren et al., 1999). A species can be indicated as isohydric if the slope value is not significantly different from the proposed theoretical value of 0.6, otherwise the species is isohydric.

2.5. Sapwood capacitance

In order to estimate sapwood capacitance, two cores were collected from each tree at a height of 1.3 m with a 5 mm increment corer, then sealed in plastic vials, and immediately transported to the laboratory to quantify fresh weight and volume, with wood volume determined using the water displacement method. Trees of similar size to the trees to which sensors were attached were selected for core extraction. Cores were allowed to hydrate overnight in distilled water and then blotted to remove excess water prior to saturated weight measurement. Dry weights for each individual tree were measured by placing the samples in a drying oven at 70 °C for 48 h. Relative water content of each core was determined by comparing the cores fresh weight, saturated weight, and dry weight.

The second sample core was cut into 10 mm segments and placed in a small plastic sample cup for use in measurement of sapwood water potential for which a WP-4 Dew point Potential meter (Decagon Devices, Inc. USA) was used. WP-4 was allowed to stabilize for 30 min before samples were placed in the meter chamber, and meter was set to continuous mode; following three consecutive readings, sample was weighed on a digital balance. The sample cup was removed from the WP-4 and set aside for 20–30 min, after which its water potential and weight were once again measured. This procedure was repeated until sapwood water potential reached approximately −5 MPa to −10 MPa, depending upon the species. Sapwood capacitance (C, expressed as 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 comparisons among species in the absolute amounts of water released per unit decline in water potential (Scholz et al., 2007).

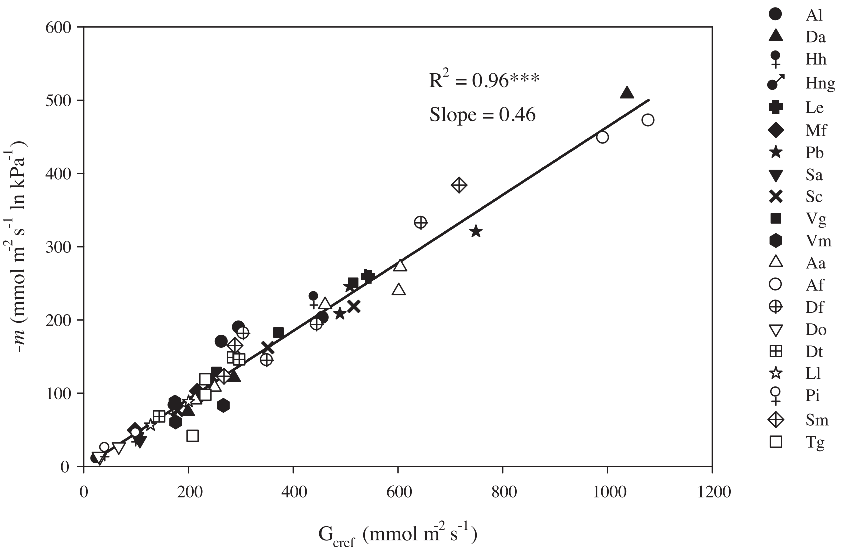

Fig. 1. The relationship between the crown-level stomatal sensitivity (m) and reference crown conductance (G_{cref}) at 1 kPa vapor pressure deficit (VPD), across evergreen (closed symbols) and deciduous species (open symbols). Significance: ***: $P < 0.0001$. The species codes are listed in Table S1.

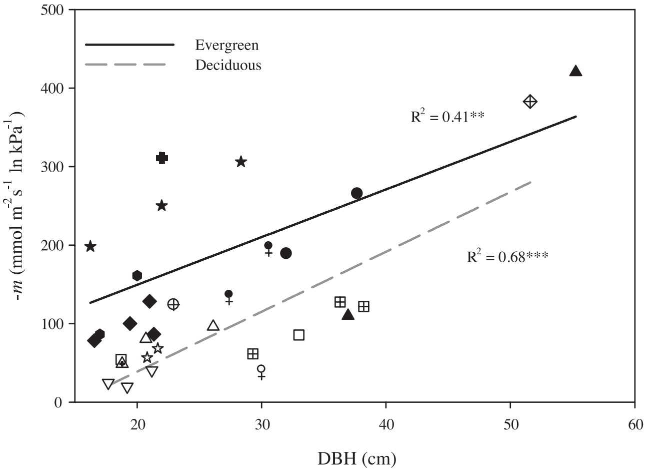

Fig. 2. Relationship between the crown conductance sensitivity to VPD (m) and diameter at breast height (DBH) in evergreen (closed symbols) and deciduous trees (open symbols) with similar DBH ranges. **, $P < 0.001$.

2.6. Hysteresis

The diurnal hysteresis between sap flux density and VPD, for an individual tree, was calculated as the area of difference between the curves of the hourly mean of SFD and VPD (Matheny et al., 2014). Both SFD and VPD were rescaled so that they ranged between 0 and 1, and thus, SFDmax and VPDmax were both equal to 1. The two curves were subtracted from one another to create a difference function, and then the area under the difference function was estimated using a Riemann-type integral of areas in the intervals between sampling times. Each interval area was approximated using the sum of a rectangle and a triangle between the difference function line and the zero line, and all areas were taken as absolute values so that the total area of the difference between the difference curve and the zero line was estimated.

2.7. Vessel diameter

The cores collected for estimation of sapwood area were also used to measure vessel diameter. Cores were softened by soaking in a solution of glycerol and ethanol (1:1 by volume) for 3–4 months, after which a sliding microtome was used for making core transverse sections of 20–40 μ m thickness. For each core, three to four sections were prepared by staining the sections in safranin. Eight to 10 images of stained cores were taken using a digital camera (DFC 295, Leica Germany) mounted on a microscope (DM 2500, Leica, Germany), which were analyzed using IMAGE J software. The vessel lumen diameter (major and minor axis) was measured in each cross-section, with at least 80–100 vessels measured for each tree.

2.8. Data analysis

We analyzed the effect of leaf habit and DBH on m. As m was strongly correlated with DBH, for this analysis we excluded some trees with larger DBH values from the deciduous group to ensure that we were comparing trees with similar DBH ranges of both evergreen (n = 17, DBH = 16.24–55.25 cm) and deciduous (n = 17, DBH = 18.70–51.59 cm) species. Slope or intercept values for evergreen and deciduous trees were compared, with comparisons of the variations explained by each component (DBH and leaf habit) conducted via Type III SS ANOVA using R software (R Core Team, 2013). The hysteresis area for each species was calculated as described above. Hysteresis area for each trees represented the sampling unit and t-tests were used to compare the hysteresis of deciduous versus evergreen species for the selected DBH ranges of trees.

We plotted whole-tree DWU use against DBH for evergreen and deciduous species using separate power models for each. In order to compare the whole-tree DWU, capacitance, sapwood area, and vessel diameter between the two types of trees, the data were natural log-transformed and the slopes of DBH against the variables were compared using the 'SMART' R-package (Warton et al., 2006). Two separate models were fitted when the slopes differed significantly (DWU and sapwood area) whereas only one regression model was fitted for the variables (capacitance, vessel diameter) for which no significant difference in either linear slope or intercepts between evergreen and deciduous trees were detected. The relationships between the traits were analyzed using the regression analysis in Sigma-plot v.10 (Systat Software Inc. USA). Finally, the significance of differences in sapwood area and vessel diameter between the evergreen and deciduous trees were tested using a one-way ANOVA.

3. Results

3.1. Factors influencing the sensitivity of crown conductance

Leaf habit and DBH were found to have significant effects on m ($P < 0.001$, Table 1), together accounting for 72% of total variation. The slope value 0.46 of the relationship between m and G_{cref} for all the

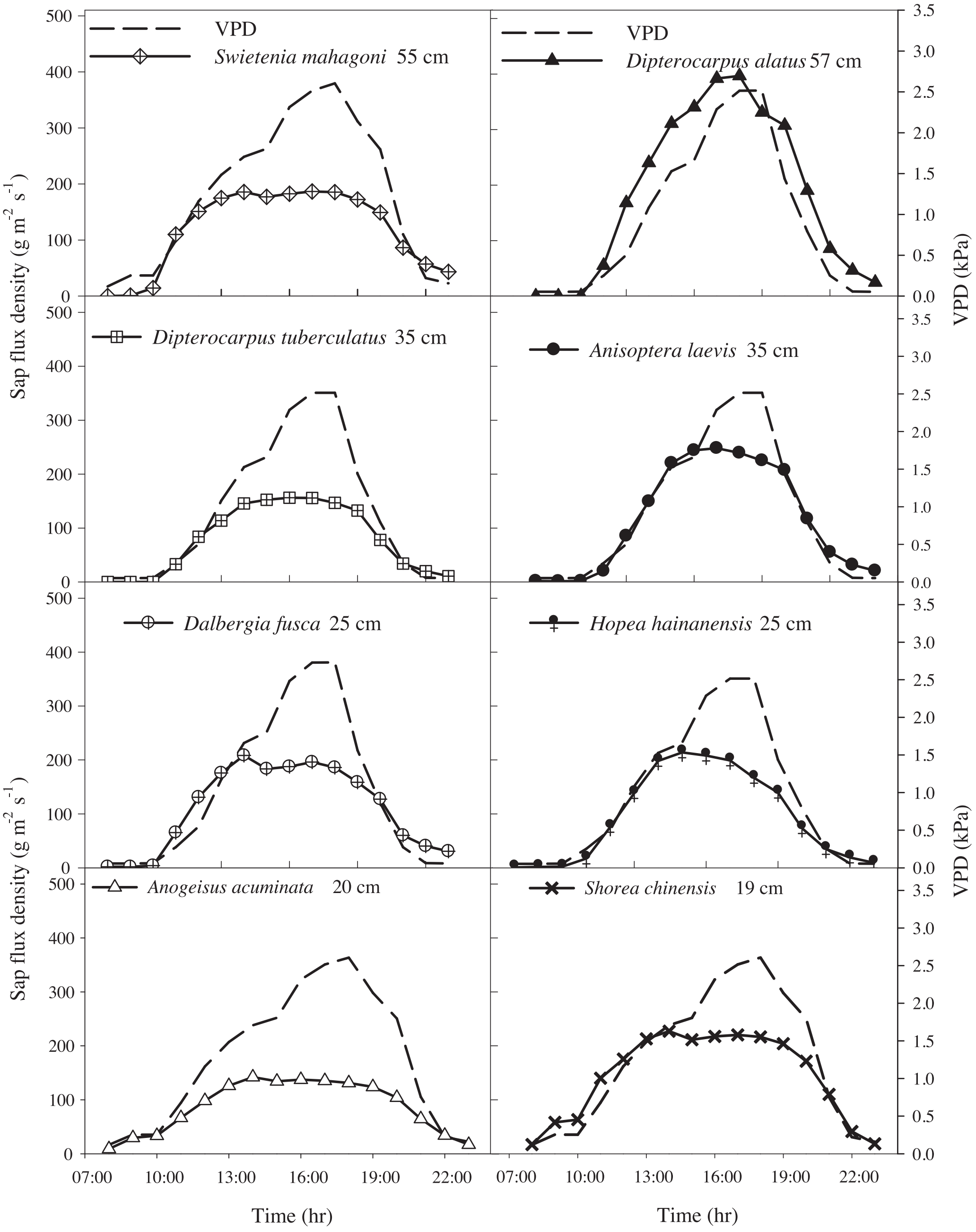

Fig. 3. Representative diurnal patterns of hourly mean sap flux density (SFD, solid lines) and vapor pressure deficit (VPD, dashed lines) of deciduous (open symbols) and evergreen (closed symbols) trees of comparable DBH. The values followed the species name are DBH of the trees.

60 individual trees of the two groups (Fig. 1) was significantly smaller than the proposed theoretical value of 0.6, indicating anisohydric behavior of both deciduous and evergreen species of the present study according to Oren et al. (1999).

A significantly positive relationship between DBH and m was found for both groups, albeit with a significantly higher intercept ($P < 0.0001$) in evergreen species than in deciduous species (Fig. 2), indicating that evergreen have a more sensitive crown conductance response to VPD than deciduous at this range of DBH.

3.2. Diurnal pattern of sap flux density

Sap flow calculated using the calibrated equations was 2–5 times higher compared to that using the Granier's equation for diffuse porous and about 7 times for ring porous species (Figs. S1 and S2). The SFD of both evergreen and deciduous species exhibited similar diurnal patterns for VPD, but with different hysteresis, which was overall significantly greater in deciduous trees than in evergreens, especially at midday, when the SFD of deciduous trees showed higher hysteresis to VPD than did in evergreen species (Fig. 3). The difference in hysteresis between evergreen and deciduous trees was not that obvious in lower DBH range (< 20 cm), while evergreen trees show distinctly lower hysteresis than that of deciduous trees at the higher DBH range (≥ 19 cm; Fig. 4a). Further, paired t-tests of evergreen and deciduous trees of comparable DBH ranges revealed that evergreen had a significantly lower hysteresis ($P < 0.05$) than the deciduous trees (Fig. 4b).

3.3. Whole tree water use in relation to sapwood properties

Whole-tree daily water use (DWU) was closely associated with DBH for both evergreen and deciduous species, but at a given DBH, evergreen species had significantly higher whole-tree DWU than deciduous species (Fig. 5a). Although sapwood area was also related with DBH in both groups (Fig. 5b), sapwood area at a given DBH was significantly

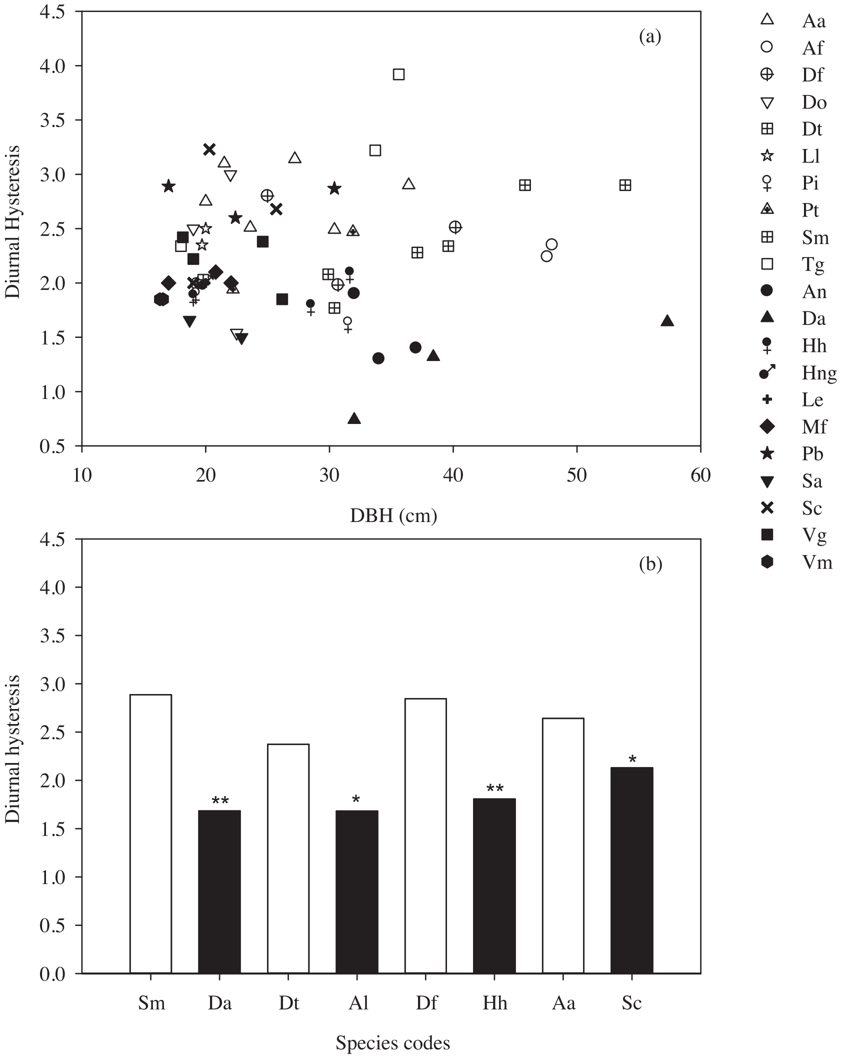

Fig. 4. Diurnal hysteresis between sap flux density and vapor pressure deficit (VPD) of evergreen (closed) and deciduous (open) trees across different DBH ranges (a). Comparative diurnal hysteresis of diurnal hourly mean sap flux density in representative deciduous and evergreen trees of comparable DBH shown in Fig. 3(b), $**P < 0.01$, $*P < 0.05$. Species codes are listed in Table S1.

larger in evergreen than deciduous species. Sapwood depth ranged from 2 to 6 cm in evergreen and 2–4 cm in deciduous trees. Sapwood capacitance was positively associated with DBH for the pooled data of 60 trees from the two groups (Fig. 5c) and there was a significant and positive relationship between vessel diameter and DBH (Fig. 5d) across all species.

4. Discussion

The objectives of the present study were to compare (1) crown conductance sensitivity to the vapor pressure deficit (VPD) and (2) water consumption between evergreen and deciduous timber species during the wet season. A more sensitive response to VPD (higher m) and larger whole-tree mean daily water consumption in evergreen compared to deciduous trees were found. Further, larger daily water consumption by evergreen trees appears to be related to their higher peak crown conductance and sap flux density (SFD), which is facilitated by their larger sapwood area (*i.e.*, larger xylem area for water transport and storage). Our results provide new insights on the differences in water use between tropical evergreen and deciduous timber trees and the findings have important implications for species selection in tree plantations and water-resource management.

Evergreen and deciduous broadleaf timber trees show differences in their range of SFD (Fig. 3) and sensitivity (m) in G_c response to VPD (Table S2). However, the slope of the relationship between m and G_{cref} (0.46) for all the trees was smaller than the proposed theoretical value of 0.6 (Oren et al., 1999), suggesting anisohydric behavior of both deciduous and evergreen species. Notably, this needs further confirmation by the measurements of dynamics of leaf water potential and leaf stomatal conductance. In seasonal tropical forests, such anisohydric behavior favors the maximization of water use under high evaporative demand with the lack of water stress in the wet season (Zhu et al., 2015; Kumagai et al., 2015). Our finding of anisohydric behavior in tropical trees during wet season agrees with the findings of Kumagai and Porporato (2012), Igarashi et al. (2015) and Koning and Gentine (2016). Further, higher m in evergreen species than deciduous at a given DBH was found, and is at least partly related to their higher peak SFD and G_{cref}, as indicated by the positive relationship between m and G_{cref} (Fig. 1 and Oren et al., 1999).

Our results revealed that evergreen trees had larger daily water consumption than deciduous trees (Fig. 5a) mainly because of their higher peak SFD and crown conductance (*i.e.* maximum or reference crown conductance; G_{cref}). Higher G_{cref} is associated with higher m (Fig. 1 and Oren et al., 1999). It is possible that species with high m (more sensitive stomatal response for closing to high VPD) also have more sensitive response to increasing VPD and light (stomatal opening) in the morning, which allows sap flow and crown conductance to increase faster and reach higher peak values before VPD getting too high during the day. The hysteresis of sap flow behind VPD (light and temperature, both coincide with VPD pattern, Fig. S3) was smaller in evergreen trees compared to deciduous trees particularly with larger DBH (Fig. 3), which allowed them to reach high transpiration earlier

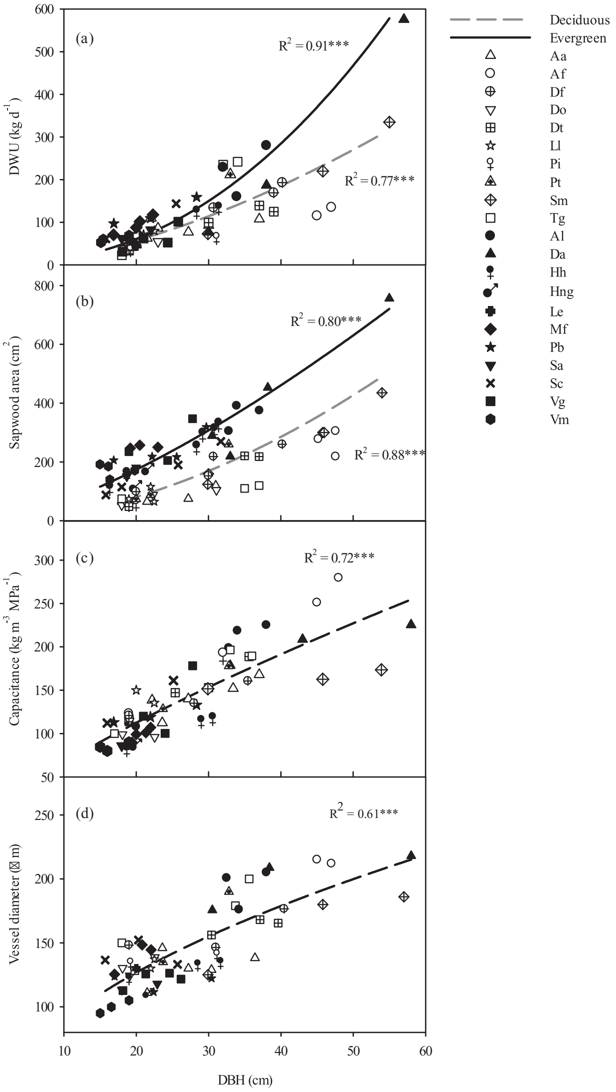

Fig. 5. Relationship between DBH (diameter at a height of 1.3 m) and whole-tree daily mean water use (DWU; a), sapwood area (b), sapwood capacitance (c), and sapwood vessel diameter (d) in deciduous (open symbols) and evergreen (filled symbols) species. For all the panels power function $y = a(x)^b$ was fitted. The values of coefficients and scaling exponents of panel (a) for deciduous and evergreen trees were; “$y = 0.3751(x)^{1.682}$”; “$y = 0.0769(x)^{2.231}$” respectively. ***$P < 0.0001$.

than deciduous trees and reach higher peak transpiration. In contrast, large deciduous trees showed higher hysteresis of SFD to increased VPD in the morning (and slower increase in transpiration in terms of time), therefore their canopy transpiration (as indicated by SFD) increased relative slowly in the morning (Zhang et al., 2014a). Notably, although the duration of peak SFD was longer in deciduous trees, the comparatively lower peak SFD values resulted in lower rates of DWU (Fig. 5a). On the other hand, the sharp decline in transpiration in the afternoon when the VPD was reaching the highest, which agrees with their higher m (stomatal closure), resulted in a shorter time for peak values in evergreen trees. Additionally, higher peak SFD in evergreen could also be because of their longer leaf life spans and therefore potentially higher total leaf area.

Higher peak SFD, faster increase in sap flow and transpiration in the morning and higher m in evergreen species could all be linked with their hydraulic properties: larger sap wood area. The larger sapwood area for a given DBH in evergreen species indicated a larger xylem area for water transport and a larger volume for water storage in the trunk (Klein et al., 2013), which could allow them to have faster (in terms of time) increase in crown transpiration as light intensity, temperature and VPD increase in the morning and consequently higher peak transpiration values. However, depletion in water storage and potentially lower canopy leaf water potentials due to higher peak transpiration could result in sharp declines in transpiration in the afternoon, which agrees with higher m in evergreen trees and the positive relationship between m and G_{cref} (Fig. 1 and Oren et al., 1999). Moreover, as the trees of both evergreen and deciduous species included in our analysis have similar vessel diameters at a given DBH (Fig. 5d) and possibly similar hydraulic conductivity per xylem area, the larger sapwood area and therefore larger area for water transport and storage could be the main hydraulic reason for the faster increase in transpiration in the morning, higher peak SFD, and larger water use in evergreen species.

The present study has established models for estimating whole-tree daily water use in tropical timber species, which can be used to estimate the stand-level water consumption of plantations during the wet season in the study region (Fig. 5a). The species included in the present study are mainly represented by the two families, Dipterocarpaceae and Fabaceae (Table S1), and all have high economic value (Raes et al., 2013; Jalonen et al., 2014). Our findings regarding the difference in water consumption in these evergreen and deciduous tropical angiosperm tree species can be used for species selection to optimize water use in commercial timber plantations (Reyes-Garcia et al., 2012; Gao et al., 2014). Notably, annual water use of evergreen timber trees could be even higher than deciduous trees as they consume water in the dry season as well when the latter are leafless. Some evergreen species may even consume more water during the dry season than in the wet season if their roots are capable of assessing stable ground water sources, enabling them to meet the high evaporative demand of the dry season (Siddiq and Cao, 2015). Southern China represents the major reservoir for meeting the country's fresh water needs (Barriopedro et al., 2012), although the study region was suffered from frequent droughts over the past several years (Sun and Yang, 2011; Qi et al., 2012; Zhang et al., 2014a). Large-scale monoculture plantations of introduced fast-growth timber species, such as rubber and eucalypts, consume enormous amounts of water (Morris et al., 2004; Tan et al., 2011), exacerbating the water deficit in this region. Based on the predictions of climate change and water scarcity in the future, we suggest that the plantations composed of more deciduous trees can potentially be a solution to conserve water resources for this region, which needs to be tested at the plantation level.

5. Conclusion

Our results show that tropical evergreen angiosperm timber species have higher sensitivity of crown conductance to VPD, and consume more water through transpiration than deciduous angiosperm species even in a wet season. Larger water consumption is largely due to their higher peak transpiration rate, and sap flux density, which is facilitated by their higher sapwood area (*i.e.* larger active xylem area for water transport and storage). Our results also indicate the anisohydric behavior of tropical angiosperm trees (both evergreen and deciduous). Based on our results, we recommend a potential management possibility that plantations with less evergreen species and more deciduous species could be used to enhance water conservation for plantation systems in the tropical regions with a monsoonal climate and increasing water deficit, which needs to be tested at the plantation level.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agrformet.2017.08.028.

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