Forest Ecology and Management 418 (2018) 47–54

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Nocturnal transpiration in 18 broadleaf timber species under a tropical seasonal climate☆

Zafar Siddiq[b,c,d], Kun-Fang Cao[a,*]

[a] Plant Ecophysiology and Evolution Group, State Key Laboratory for Conservation and Utilization of Subtropical Agro-bioresources, Guangxi Key Laboratory of Forest Ecology and Conservation, College of Forestry, Guangxi University, Nanning, Guangxi 530005, China
[b] Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Mengla, Yunnan 666303, China
[c] Department of Botany, Government College University, Lahore 54000, Pakistan
[d] University of Chinese Academy of Sciences, Beijing 100039, China

ARTICLE INFO

Keywords:
Nocturnal sap flux density
Seasonal variation
Vapor pressure deficit
Water recharge
Wood density

ABSTRACT

Global increase in night time as compared to day time temperatures results in an increased nocturnal VPD, which possibly increases nocturnal transpiration of plants. However, there are few studies on nocturnal transpiration of plantations in the tropics. Here, we investigated the ratio of nocturnal to daily transpiration and its seasonal differences in timber plantations of tropical angiosperm tree species in low land seasonal tropical botanical garden in southwest China. We measured sap flow in 18 tree, comprising of nine evergreen and nine deciduous species, during three months in the wet season and three months in the dry season between 2012 and 2013. We partitioned the nocturnal sap flux density (SFD) into nocturnal transpiration and trunk water recharge. We also measured wood density to investigate its relationship with nocturnal sap flux density. Our results showed that the mean nocturnal (whole night-time) VPD was linearly correlated with mean nocturnal SFD ($R^2 > 0.41$–0.73 across species) in both the wet and dry seasons. During the wet season, the ratio of nocturnal SFD to daily SFD was 0.12–0.19 and 0.15–0.2 among evergreen and deciduous species, respectively. During the dry season, this ratio increased to 0.18–0.28 for evergreen species. For evergreen species, the nocturnal trunk water recharge and nocturnal transpiration in the wet season were between 11.37–59.80% and 40.20–88.62% of nocturnal SFD, respectively. For deciduous species, these values were 18.10–66.26% and 81.90–33.73%, respectively. We found an inverse relationship between nocturnal SFD and wood density ($R^2 = 0.24$, $P = \leq 0.05$) across the 18 studied species. In conclusion, this study demonstrates a substantia amount of nocturnal transpiration in a number of tropical tree species, even in the wet season and increased nocturnal transpiration in evergreen species in dry season. However, there was not any significant difference of the nocturnal SFD between evergreen and deciduous species during the wet season. Nocturnal transpiration is constrained by wood density across species. High nocturnal air temperature will result in increased transpirational demand and hence water loss at night. Our findings revealed important implications for nocturnal transpiration on soil-plant equilibrium and hydrology of forest ecosystems in the seasonal tropics.

1. Introduction

The first decade of the 21st century was recorded as the warmest since 1850s and the predicted global average surface air temperature rise is projected to be between 2 and 4 °C by 2040, with larger increases observed at night, especially in the tropics (IPCC, 2007; Anderegg et al., 2015; Davy et al., 2017; IPCC, 2014). Such a rise in nocturnal temperature will result in the increase in nocturnal vapor pressure deficit (VPD), which will inevitably affect the movement of water fluxes in plants (Fu et al., 2016; Zeppel et al., 2014; Way and Oren, 2010). Although complete stomatal closure is often assumed at night, in many plants the stomata remain partially open, due to high nocturnal vapor pressure deficit (VPD), ample water at the roots and high wind speed (Oren and Pataki, 2001; Fisher et al., 2007). Incomplete stomata closure results in nocturnal water loss in plants, and is considered maladaptive in terms of carbon fixation (Alvarado-Barrientos et al., 2014). However, nocturnal transpiration incurs other benefits for plants, such as improving nutrient acquisition (Masle et al., 1992; McDonald et al., 2002), nocturnal refilling of embolized conduits resulting from daytime transpiration (Snyder et al., 2003), oxygen delivery to xylem parenchyma in

☆ This article is part of a special issue entitled "Current advances in plant water-relations research, implications for forest management and restoration stemming from the Ecosummit 2016 conference", published in the Journal of Forest Ecology and Management 418, 2018.

* Corresponding author.
E-mail address: kunfangcao@gxu.edu.cn (K.-F. Cao).

https://doi.org/10.1016/j.foreco.2017.12.043
Received 31 October 2017; Received in revised form 16 December 2017; Accepted 22 December 2017
Available online 27 December 2017
0378-1127/

the trunks of larger trees, prevention of excess leaf turgor at night and enhanced carbon uptake in the early morning hours (Donovan et al., 2001; Gansert, 2003; Daley and Phillips, 2006; Resco de Dios et al., 2016). Despite the importance of nocturnal sap flow for plant functioning, there is limited research on the nocturnal sap flow behavior of trees from the seasonal tropics, where nocturnal VPD is greater than 1 kPa in most hours before mid-night during the dry season, thus increasing transpirational demand.

Forest plantations with monoculture of fast-growing species consume more water than the native forests, mainly due to the more responsive to VPD, having larger sapwood conducting area and greater leaf area index (Kupper et al., 2016; Kunert and Cardenas, 2015). Such plantations also consume more water at night as well (Kagawa-Viviani et al., 2009). Natural forests with a diverse species assembly demonstrated a more dynamic response to climatic drivers in terms of transpiration, and vice versa for monoculture plantations with trees of uniform age and size. Hence, natural forests and monoculture plantations can differ in their impact on the hydrology of watersheds (Kunert and Cardenas, 2015).

The reported contribution of nocturnal transpiration (E_n) to total daily transpiration (24-h period) is highly variable, yet a growing body of evidence have shown that E_n may constitute a significant, yet largely unaccounted component of the water balance in different ecosystems (Dawson et al., 2007; Fisher et al., 2007; Oishi et al., 2008). Global syntheses have found that the percentage of nocturnal transpiration to daily transpiration in woody plants to be 12%, although values up to 30–60% have also been observed (Field and Holbrook, 2000; Snyder et al., 2003; Wallace and McJannet, 2010; Forster, 2014). High nocturnal transpiration was reported for wet areas such as rainforests (Wallace and McJannet, 2010) or in species that were less prone to atmospheric or soil water deficit. For example the ratio of night to daytime transpiration was up to 25% in tropical ecosystems, while 15% in Mediterranean ecosystems and 14% in neotropical savanna ecosystems (Dawson et al., 2007). Irrespective of the species, significant amount of nocturnal transpiration was observed in the plants immediately after a rainfall event following a period of soil water deficit, which can affect the daily water budget. Thus, nocturnal transpiration is an important component in estimating the water budget of forest plantations.

Nocturnal transpiration can also be affected by the intra- and interspecific variation in physiological traits such as wood density, which determines the water storage and transport (Meinzer et al., 2009; Chave et al., 2009; Resco de Dios et al., 2013). Species with high wood density have thick and small vessels and usually have low sap flux density (SFD) (Zimmermann, 1983; Tyree and Ewers, 1991; Siddiq et al., 2017). However, the relationship between wood density and nocturnal SFD has not been well investigated in tropical tree species. Nocturnal transpiration can also be affected by the species responses to seasonal changes in climatic drivers such as VPD (Daley and Phillips, 2006; Phillips et al., 2010; Rosado et al., 2012; Zeppel et al., 2010).

Nocturnal sap flux density does not necessarily indicate nocturnal transpiration. The recharge of depleted water storage in the tree trunk is a significant component of daily sap flux (Phillips et al., 2003). However, the positive correlation between nocturnal SFD and VPD suggests that nocturnal SFD can be mostly attributed to nocturnal transpiration (Green et al., 1989; Hogg and Hurdle, 1997). The nature of the relationship between nocturnal SFD and nocturnal VPD (either linear or non-linear) can indicate the control over nocturnal transpiration i.e, the threshold of the nocturnal VPD contorting the nocturnal transpiration, depending upon the soil water status of the particular site (Rosado et al., 2012). Benyon (1999) observed that the nocturnal sap flux density in *Eucalyptus* was not solely the result of recharge of trunk water storages, since the sap flux rates increased during the night after several hours of zero flow rates. Furthermore, high rates trunk water recharge followed days with high cumulative sap flux, but night flux also occurred in nights preceded by low daytime sap flux (Daley and Phillips, 2006).

The selective analysis of days with day-time mean VPD in the range from 1.0 to 2.0 kPa (although this threshold can vary across ecosystems), combined with evenings with rainfall (VPD less than 0.05 kPa), can be used to partition the nocturnal water recharge and nocturnal transpiration (Fisher et al., 2007; Wang et al., 2011; Alvarado-Barrientos et al., 2014). Wang et al. (2011) reported that species with high day-time SFD had high nocturnal SFD as well. This could be due to the increase in day-time SFD in the dry season when VPD was higher and there was lack of water stress for plants as well (Siddiq and Cao, 2016). Similarly they may also increase nocturnal SFD, provided there is enough transpirational demand (VPD).

The seasonal tropics, with distinct wet and dry seasons, have wide seasonal differences in temperature and VPD, and consequently could result in different seasonal nocturnal sap flow behavior, which can impact the water budget and soil-plant equilibrium of a particular site (Bucci et al., 2004). At present, only a few studies (Fisher et al., 2007; Wang et al., 2011; Rosado et al., 2012) have reported the seasonal behavior of nocturnal sap flow of tropical trees. Here, we studied the nocturnal transpiration and trunk water recharge of 18 timber species plantations in tropical seasonal climate in Southwest China. Our previous study showed that the evergreen trees at the present study site can access stable soil water resources near their root zones, even in the dry season (Siddiq and Cao, 2016). Hence we hypothesized that the evergreen tree species can meet the nocturnal transpirational demand due to the availability of soil water even in the dry season. We addressed the following questions.

1. What is the ratio of nocturnal transpiration in nocturnal sap flux density of studied species?
2. Does the nocturnal transpiration increase in the dry season compared to the wet season in the evergreen species?
3. Is nocturnal sap flux density constrained by wood density across deciduous and evergreen species?

2. Materials and methods

2.1. Study site and species

This 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.), in southern Yunnan Province, Southwestern China. This region has a tropical seasonal climate and thus features a pronounced dry season; that can be divided into a cool dry season (November to February) and a warm dry season (March to April). The wet season is from May to October. Mean annual precipitation is 1560 mm, of which ~80% occurs during the wet season. The mean annual temperature is 21.7 °C (Cao et al., 2006). We selected 18 timber tree species comprising nine evergreen and nine deciduous trees (Table 1) in plantation stands located next to each other in the arboretum of XTBG, with an average of three replicates per species, fewer than three individuals were available in some species. The species name, wood density, diameter at breast height (DBH), and the number of replicates are as presented in Table 1. The plantation was established in 1980s, each species was planted as monocultural stands with a distance of about 3–4 m between the individuals and with the stand density of approximately 1100 trees ha^{-1}. The present tree height ranged from 20 to 35 m (as measured with a laser range finder) and the DBH ranged from 10 to 65 cm. The canopy crown of the sampled trees was distinct and thus they were not competing for solar radiation.

2.2. Sap flow and climatic data

The sap flow measurements were made at DBH, during three months of the wet season (June - August) and three months of dry season (mid-February to mid-May) in 2012–2013. Since the rain started in the end of May, mid-May 2013 was still warm and dry. Each tree was equipped with two sets of 2 cm long lab-made thermal dissipation sap flow measuring sensors (Granier, 1987), which were installed at 90°

Table 1
Species, abbreviation (code), mean wood density, range of diameters at 1.3 m height (DBH) and replicate number.

Scientific name	Code	Mean wood density (± SE)	DBH range (cm)	No. of trees
Evergreen trees				
Anisoptera laevis Ridl.	Al	0.60 (± 0.2)	31–37	3
Dipterocarpus alatus Roxb. ex G.Don	Da	0.54 (± 0.01)	30–55	3
Hopea hainaniensis Merr. & Chun	Hh	0.75 (± 0.01)	19–30	3
Hopea hongayensis Tardieu	Hng	0.81 (± 0.01)	20	1
Shorea assamica Dyer	Sa	0.76 (± 0.01)	17–20	2
Shorea chinensis Merr.	Sc	0.66 (± 0.02)	16–25	3
Vatica guangxiensis S.L. Mo	Vg	0.73 (± 0.09)	16–24	4
Mesua ferrea L.	Mf	0.81 (± 0.02)	16–22	3
Phoebe puwenensis W.C. Cheng	Pb	0.52 (± 0.02)	20–29	3
Deciduous trees				
Albizia falactoria	Af	0.6 (± 0.01)	43–48	2
Anogeisus acuminata	Aa	0.83 (± 0.04)	21–37	5
Dalbergia odorifera	Do	0.92 (± 0.02)	18–23	3
Dalbergia fusca	Df	0.78 (± 0.01)	31–41	3
Dipterocarpus tuberculatus	Dt	0.51 (± 0.02)	19–40	4
Leucaena leucocephyla	Ll	0.53 (± 0.01)	21–23	2
Peltophorum tonkinense	Pt	0.54 (± 0.01)	23–33	2
Pterocarpus indicus	Pi	0.57 (± 0.02)	20–31	2
Swietenia mahogany	Sm	0.55 (± 0.01)	31–55	3

angles to the stem and positioned directionally opposite to one another along the same compass position. The sap flow sensors consisted of a thermocouple surrounded by a heating coil and a reference sensor, and all sensors were connected to four data loggers (CR-1000, Campbell Scientific, Inc. Utah USA) with 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. Sensors were monitored bi-weekly, with malfunctioning sensors being immediately replaced.

Sap flux density (SFD, g m^{-2} s^{-1}) was calculated using the calibrated Granier's equation (Granier, 1987) following Bush et al. (2010) method of calibration and developed our own equation for the study species (Siddiq et al., 2017; Table S 3). For *Dipterocarpus alatus*, *Mesua ferrea*, *Shorea chinensis* and *Vatica guangxiensis* species-specific equations were used while for the rest of species we used the generalized equation was employed. The calibration detail is mentioned in Siddiq et al. (2017). We selected the maximum temperature difference between heated and non-heated sensors for each night in our analysis to avoid any possible error in estimating sap flux density. Zero sap flow was observed after midnight, when the maximum temperature difference was recorded between heated and non-heated sensors (Lu et al., 2004).

Climatic-data such as air temperature (°C), relative humidity (%), photosynthetic active radiation (PAR; μ mol m^{-2} s^{-1}), wind speed (m s^{-1}), and rainfall (mm) were obtained from the Tropical Rainforest Ecosystem Station at XTBG, located at a distance of ~900 m from the plantation stands. Vapor pressure deficit (VPD) was calculated from the air temperature and humidity data for the duration of the study (Campbell and Norman, 1998).

2.3. Determination of wood density

The trunk sapwood wood density (g cm^{-3}) of the study species was measured using a wood 5 mm increment borer. Two cores were extracted at DBH from each tree of a species, sealed in plastic vials, and transported to the laboratory immediately. After removing the pith with a razor blade, the cores were placed in a small graduated cylinder with water to determine the volume. The samples were then oven-dried at 80 °C to a constant weight to obtain the dry mass. Density was then determined by dividing the dry mass by the volume of the sample.

2.4. Data analysis

From the data of the daily sap flux density, night time was defined as the PAR < 20 μ mol m^{-2} s^{-1} (Daley and Phillips, 2006; Wang et al., 2011). To partition the nocturnal sap flow into nocturnal trunk water recharge and nocturnal transpiration, we first selected 2–3 days in both wet and dry seasons, when the daytime VPD and PAR were similar to a sunny day with mid-day VPD > 2.5 kPa but rained in the evening for 2–3 h and consequently VPD was ≤0.05 kPa. We assumed no nocturnal transpiration of canopy leaves after an evening rain of 2–3 h due to the lack of VPD as a driving force for sap flux density. Therefore, the sap flux density of that night was considered as trunk water recharge. This amount of trunk water recharge was subtracted from the nocturnal sap flux density of the evening without rain and the remaining amount of sap flux density of that night was taken as the nocturnal transpiration driven by the VPD > 0.5 kPa (Fisher et al., 2007; Rosado et al., 2012; Alvarado-Barrientos et al., 2014). The seasonal and species-specific percentage of nocturnal transpiration and trunk water recharge to daily sap flux density were estimated for the three months in both the wet and dry season. For deciduous species, only the nocturnal sap flux density data of the wet season only was used, while for evergreen species, the data of both wet and dry seasons were used. A T-test was performed (1) for the ratio of nocturnal SFD to daily SFD, during the wet season between evergreen and deciduous species, (2) for the ratio of nocturnal SFD to daily SFD between wet and dry season in evergreen species, (3) for the nocturnal VPD between wet and dry season. The T-tests and the linear relationships of each night mean nocturnal SFD with mean nocturnal VPD and with the day-time mean SFD for the wet and dry season were analyzed using Sigma-plot v.12 (Systat Software Inc. USA). The slopes of linear relationship between mean nocturnal SFD and mean nocturnal VPD for evergreen species in the wet and dry season were compared using SMART package of R programme version 3.23 (Warton et al., 2006).

3. Results

The mean night time VPD in the dry season (0.30 kPa ± 0.01) was larger than the mean in the wet season (0.21 kPa ± 0.01) at the significance level of $P < .05$. Across studied species, a significant amount of nocturnal sap flow was observed (Figs. 1 and 2). The integrated daytime sap flux density was not significantly different between the days with rainy evening and the days preceding an evening without rain (Fig. S 2). Significant correlation between mean nocturnal VPD and nocturnal SFD was found for both wet and dry season across species with R^2 values of between 0.41 and 0.73 respectively (Fig. 3, Table S 1). For most evergreen species, the relationship slope between mean nocturnal VPD and nocturnal SFD was significantly larger in the dry than the wet season (Table S 2), indicating larger response to nocturnal VPD in the dry season in most of these species. In both seasons, mean daytime SFD was not significantly correlated with mean nocturnal SFD for all but one species *Shorea assamica* (Fig. 4).

Nocturnal SFD was not correlated with nocturnal wind speed (Fig. S 1). During the wet season, the ratio of nocturnal SFD to daily SFD ranged from 0.12 to 0.19 among evergreen species and from 0.15 to 0.2 among deciduous species, hence there was no significant difference in the ratio of nocturnal SFD to daily SFD across evergreen and deciduous species in the wet season. However, in the dry season, this ratio increased significantly among six evergreen species, to between 0.18 and 0.28 (Fig. 5a and b). The partitioning of nocturnal sap flux density into

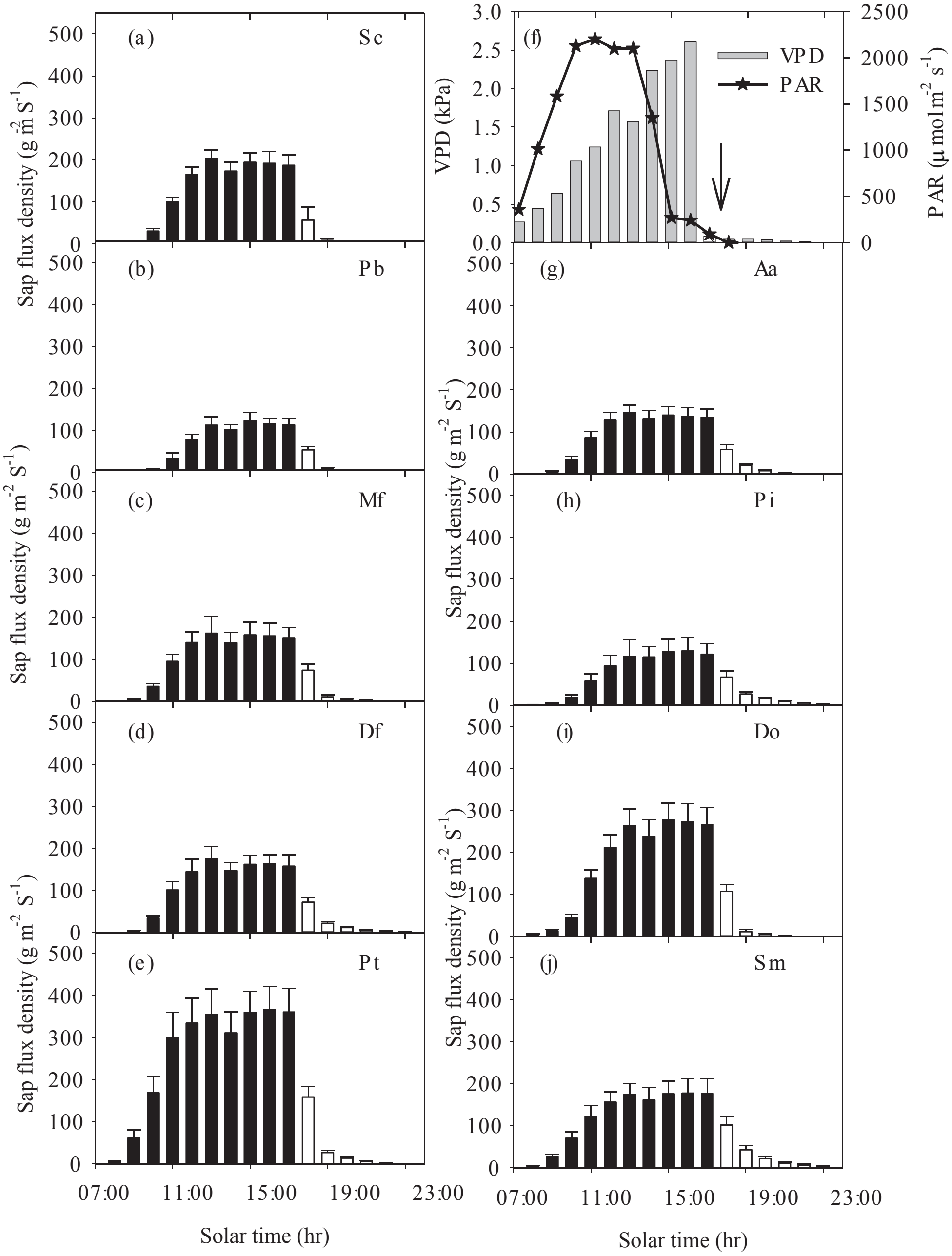

Fig. 1. Sap flux density on a sunny day with VPD > 2.5 kPa at midday and rainy evening with VPD < 0.05 kPa at 19:00. The bars indicate species mean and standard error; black bars indicate day-time sap flux density, white bars indicate nocturnal trunk water recharge. The arrow indicates the occurrence of rain in the evening. Species codes are afore mentioned in Table 1.

nocturnal trunk water recharge and nocturnal transpiration showed that for evergreen species, the nocturnal trunk water recharge and nocturnal transpiration in the wet season were 11.37–59.80% and 40.20–88.62% of nocturnal SFD, respectively. For the deciduous species, nocturnal trunk water recharge and nocturnal transpiration were 18.10–66.26% and 33.73–81.90% of nocturnal SFD, respectively (Fig. 5c and d). A significant and inverse correlation between nocturnal SFD and wood density across 18 study species was found in the wet season ($R^2 = 0.24$, Fig. 6).

4. Discussion

Across all studied species, the nocturnal SFD was largely a separate phenomenon between nocturnal water recharge and nocturnal transpiration. Average nocturnal transpiration accounted for 3.0–6.8% of daily SFD in the wet season and 4.5–14.7% of the daily SFD in the dry season. Such nocturnal water usage in monoculture plantation can have the consequences on the water economy, and thus is a useful estimate for the selection of plantation species based upon their seasonal nocturnal transpiration behavior. Monoculture plantations with more responsive species to VPD and hence higher nocturnal transpiration can lead to substantial nocturnal water loss in tropics, as shown by evergreen species of this study in dry season. High levels of nocturnal transpiration can affect the soil hydraulic redistribution of water; a process critical for the maintenance of root viability (Domec et al., 2012; Baurele et al., 2008). In addition it can create a disequilibrium between predawn leaf water potential and the soil water status (Bucci et al., 2004). The values of nocturnal transpiration reported in this study are comparable to those reported in other species from other ecosystems: the nocturnal transpiration was 5% of total daily water use in *Eucalyptus grandis* (Benyon, 1999), 12.8% in *Populus trichocarpa* Torr. & Gray × *P. deltoids* Bartr ex. Marsh (Kim, 2000), 6% in *Malus sylvestris* L. and 19% in *Actinidia deliciosa* Chev. (Green et al., 1989).

In this study, VPD had the largest influence among other climatic variables on the magnitude of nocturnal transpiration. This was congruent with the findings for *Populus tremuloides* Michx. by Hogg and

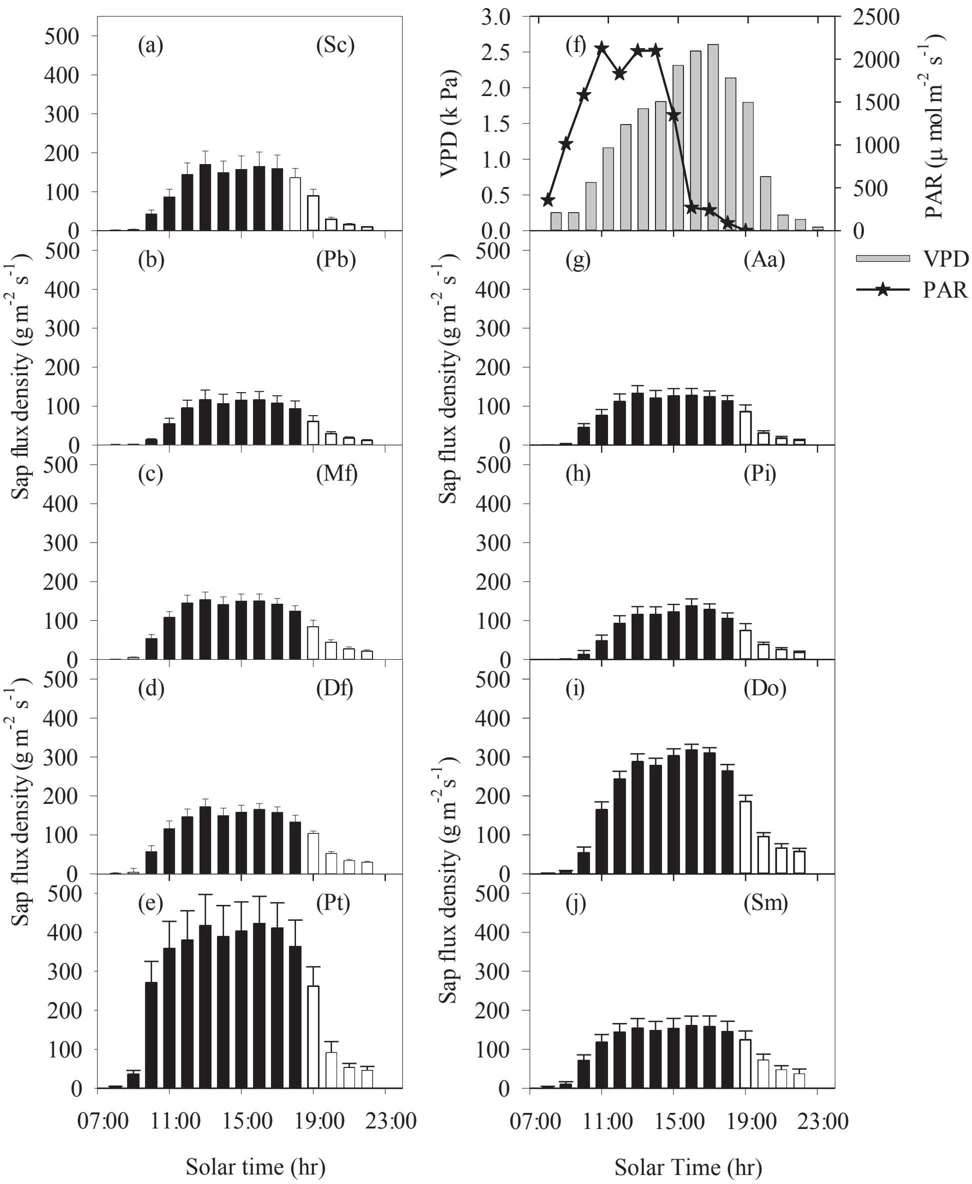

Fig. 2. Sap flux density on a clear day with VPD ≤ 2.5 kPa at midday and evening without rain (VPD > 1 kPa). Bars indicate species means with stand error, black bars indicate day-time sap flux density; white bars indicate nocturnal sap flux density. Species codes are afore mentioned in Table 1.

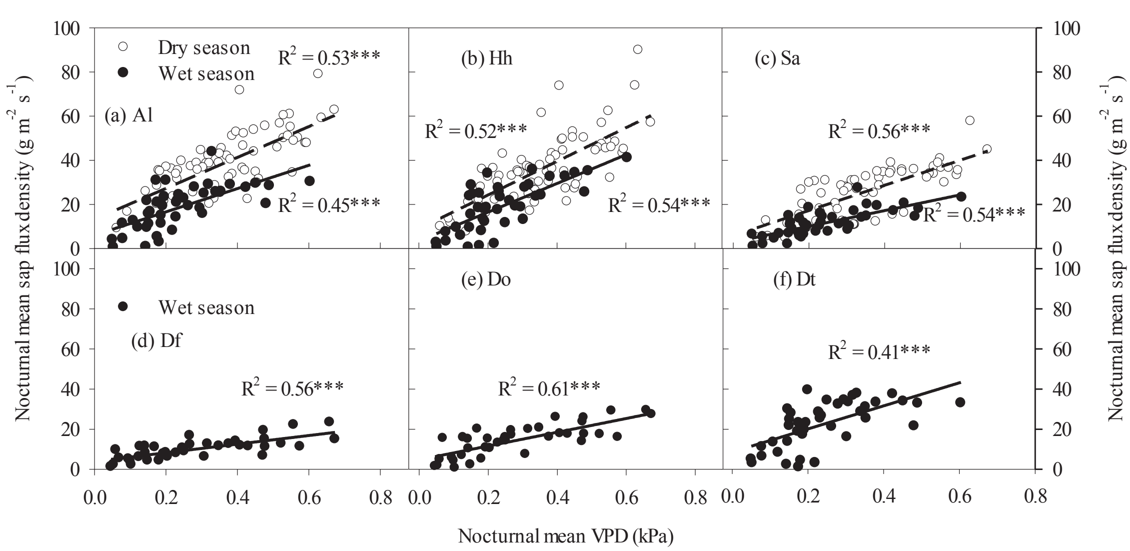

Fig. 3. The representative relationship from few days of seasonal nocturnal mean sap flux density with nocturnal mean VPD (a–f) among evergreen species in wet and dry season (a–c) and deciduous species in the wet season only (d–f). *** indicates $P < .0001$.

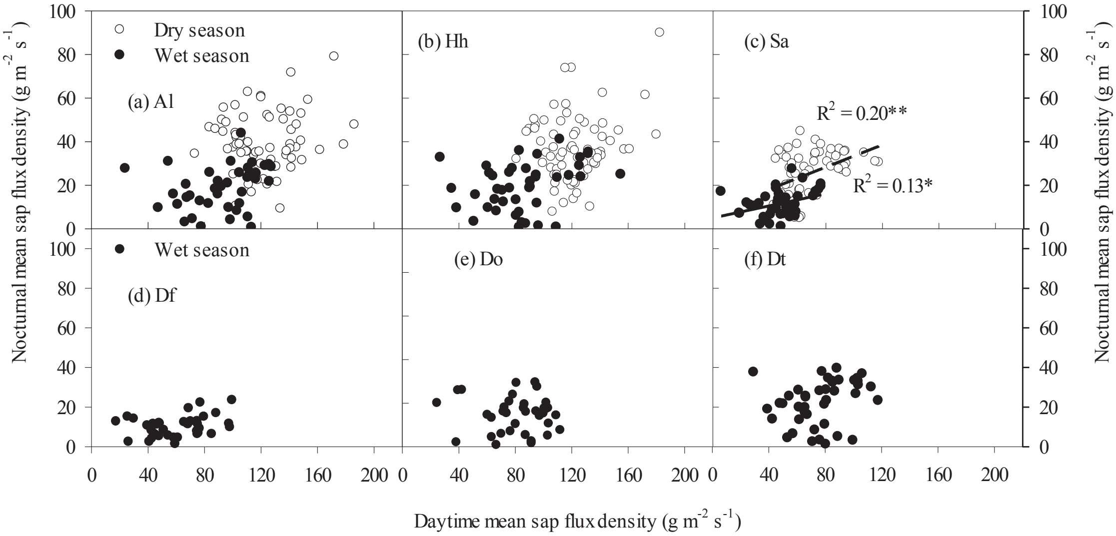

Fig. 4. The representative relationship from few days of seasonal nocturnal mean sap flux density with daytime mean sap flux density among evergreen species (a–c) in wet and dry season and deciduous species (d–f) in the wet season only. ** indicates $P < .001$, * $P < .01$. The relationship was non-significant in the panels a, b and d–f, as indicated by the absence of trend line.

Hurdle (1997). On the other hand, other studies conducted in some other ecosystems found that the variation in nocturnal SFD is best explained by nocturnal VPD and wind speed e.g, in a mix deciduous forest trees (Daley and Phillips, 2006), *Eucalyptus* (Benyon, 1999), *Malus*, and *Actinidia* plantations (Green et al., 1989). Contrary to these findings, our results showed no relationship between nocturnal sap flux density and wind speed. This may be due to the present study site being typically sheltered from wind. The absence of a correlation between nocturnal VPD and nocturnal SFD would indicate that the nocturnal sap flow only contributed to the recharge water loss during day-time transpiration. However, our results showed the substantial amount of nocturnal SFD depending on the magnitude of nocturnal VPD,

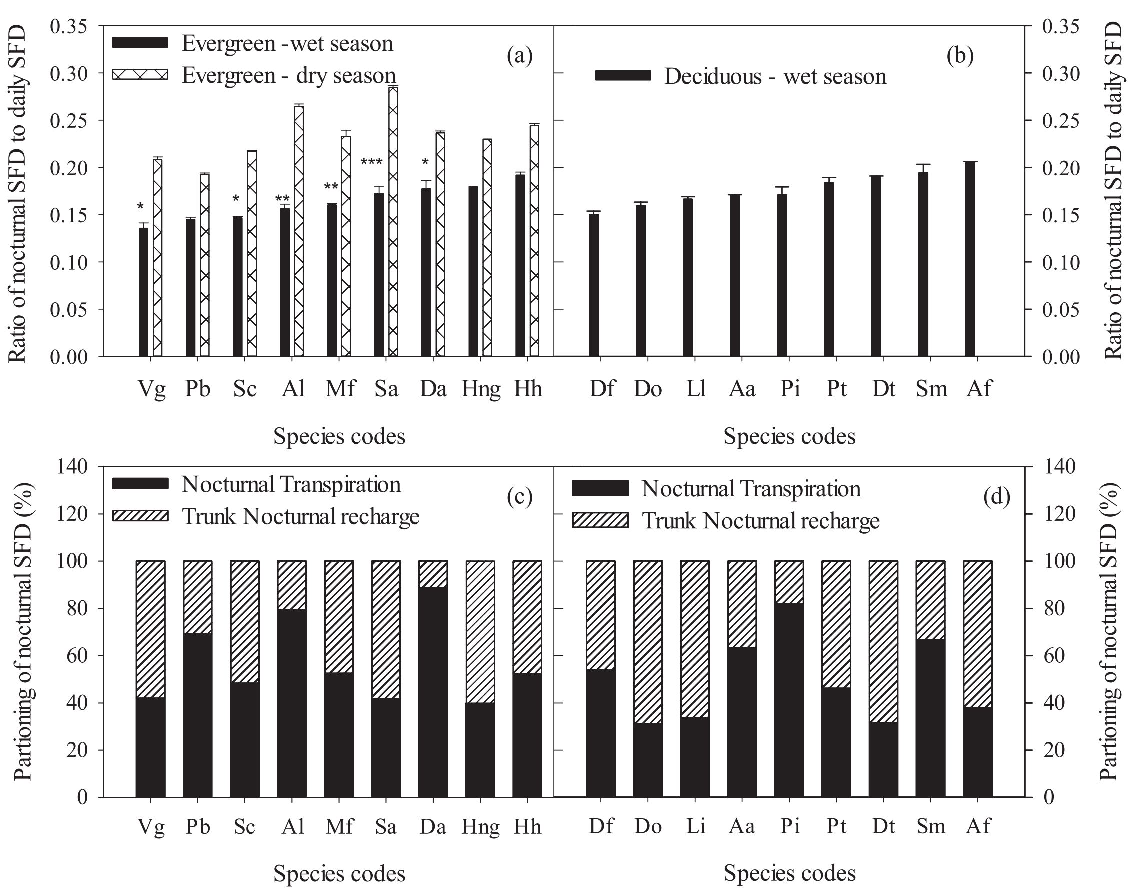

Fig. 5. The ratio of nocturnal SFD to daily SFD in the wet and dry seasons among evergreen species (a) and in the wet season for deciduous species (b). The error bars indicate standard error. Species codes are mentioned in Table 1. *** indicates $P < .0001$, ** indicates $P < .001$, * indicates $P < .01$. Partioning of nocturnal sap flux density into nocturnal trunk water recharge and transpiration in the wet season for evergreen species (c) and deciduous species (d).

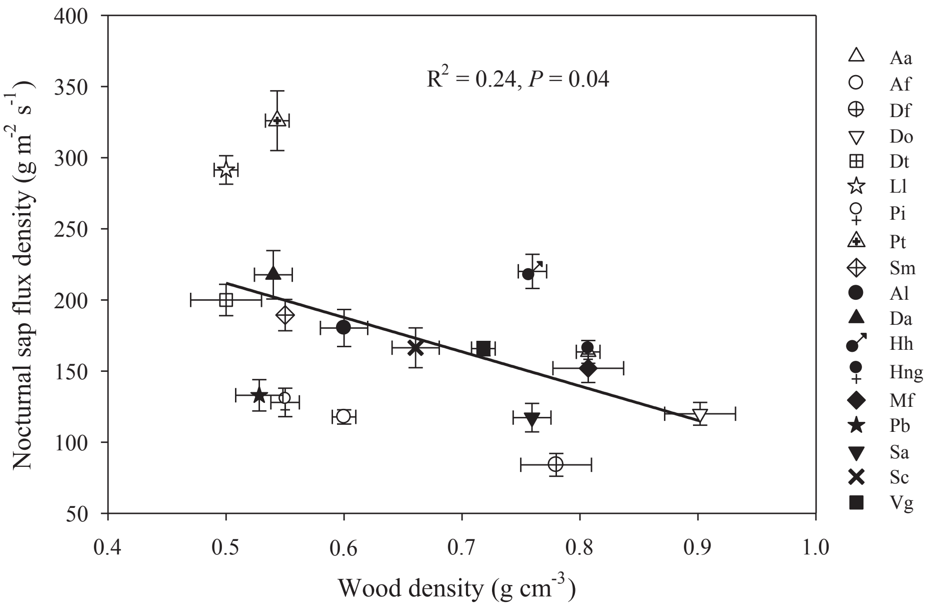

Fig. 6. Correlation between mean total nocturnal sap flux density and mean wood density in the wet season. Each symbol represents the mean wood density of each species. Open symbols indicate deciduous, and filled symbols represent evergreen species.

indicating both nocturnal recharge and transpiration. This was also supported by a higher nocturnal sap flux density in the dry season as compared to wet season among evergreen species, which was attributed to the increased VPD. The significant linear relationship between mean nocturnal VPD and mean nocturnal SFD across studied species indicated that the VPD values were below threshold levels, otherwise the non-linear relationship would have been found due to the lack of enough soil moisture near the root zones.

As shown in Fig. 3, VPD > 0.2 kPa may be sufficient to drive nocturnal transpiration and a significant increase in mean nocturnal VPD in the dry season (mean 0.30 kPa) compared to the similar time window the wet season (mean 0.21 kPa) was found. In addition, our results also demonstrated that VPD was the main factor driving nocturnal SFD in both seasons. In general, VPD remains high (> 1.0 kPa) for several hours after sunset, and sap flux density during this time is often assumed as the recharging of trunk water. However, our analysis indicated substantial nocturnal transpiration occurring during these hours. To some extent this appeared to counter the notion that plants maximize carbon gain and minimize water loss (Cowan, 1977). In a previous study, we found that the loss of water at night was mainly due to the ability of a tree to access a stable water source both in the wet and dry seasons (Siddiq and Cao, 2016). Therefore, in the presence of accessible soil moisture and the VPD > 0.2, the plants can transpire water in the night.

The lack of a significant difference in the ratio of nocturnal sap flux density to daily sap flux density between the evergreen and deciduous species could be due to the similar responses of nocturnal SFD per unit sapwood area to transpiration demand. Wet season lacks water stress and hence the tropical trees can increase both daytime and night transpiration (Siddiq et al., 2017). The other possibility for the absence of a significant difference between evergreen and deciduous species can be their similarity in leaf mass and wood density. Our results also highlighted the variation in nocturnal SFD caused by ecophysiological differences across species, as shown by the significant correlation between nocturnal SFD and wood density. Across the study species, the inverse relationship between wood density and nocturnal sap flux density indicated that species with low wood density hence, more sapwood water storage (Zhang et al., 2013) may have higher nocturnal sap flux density. This is consistent with previous findings of wood density being the constraining factor for sap flux density (Litvak et al., 2012; Resco de Dios et al., 2013; Gao et al., 2015). This inverse relationship also highlighted species strategies for the resistance against cavitation, with high wood density species relying on their wood structure (small and thick vessels) while low wood density species relying on their water storage capacity with large vessels (Bucci et al., 2004; Woodruff et al., 2007; McCulloh et al., 2012; Johnson et al., 2009, 2011). A larger decline in nocturnal sap flux density among deciduous species was due to a wider range of wood density (0.5–0.9 g cm^{-3}; Fig. 6), indicating the limits of hydraulic conductance (nocturnal sap flow). The seasonal difference in nocturnal sap flux density across species was also due to differences in their response to nocturnal VPD (Table S 2). Most evergreen species increased nocturnal sap flux density in the dry season due to their larger response to higher nocturnal VPD (< 1.0 kPa). Such sap flux density response to VPD may provide an advantage by more tightly coupling transpiration and carbon capture. Firstly, with sufficient water near the root zones in dry season, the species could continue responding to lower VPD levels even during the night. This enables the trees to continue photosynthesizing until sunset and resume photosynthesis rates earlier in the morning. Consequently, it maximizes the ratio of photosynthesis to transpiration and avoids lags between assimilation and stomatal opening (Oren and Pataki, 2001; Resco de Dios et al., 2016).

Our study showed a substantial amount of nocturnal transpirational water loss, with variation among species, and being constrained by wood density. If climate change leads to an increased nocturnal VPD (due to increased temperature) in the seasonal tropics, forests will consume more water through nocturnal transpiration. Such water loss can impact the soil-plant equilibrium and hydrology of forest ecosystems and watersheds. Our findings can also be used to improve the models for the hydrology of tropical plantations and native forests and prediction of the impacts of global warming on hydrology. The mixture of evergreen and deciduous trees in native and plantation forests could help to balance the productivity and conservation of water in a tropical seasonal climate.

Acknowledgements

The authors are grateful to the horticulture department of XTBG for permitting the experiment and the Tropical Rain Forest Ecosystem Station of XTBG for providing the climatic data. We are also thankful to Mr. MA Hong for the field assistance, to Drs. Uromi M. Goodale and Alison K.S. Wee for improving the language. The research was supported by the National Natural Science Foundation of China (grants 31470469, 31170399) and the CAS 135 programme (XTBG-T01).

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.12.043.

References

Alvarado-Barrientos, M.S., Holwerda, F., Geissert, D.R., Muñoz-Villers, L.E., Gotsch, S.G., Asbjornsen, H., Dawson, T.E., 2014. Nighttime transpiration in a seasonally dry tropical montane cloud forest environment. Trees 29, 259–274.

Anderegg, W.R., Ballantyne, A.P., Smith, W.K., Majkut, J., Rabin, S., Beaulieu, C., Birdsey, R., Dunne, J.P., Houghton, R.A., Myneni, R.B., Pan, Y., Sarmiento, J.L., Serota, N., Shevliakova, E., Tans, P., Pacala, S.W., 2015. Tropical nighttime warming as a dominant driver of variability in the terrestrial carbon sink. Proc. Natl. Acad. Sci. USA 112, 15591–15596.

Baurele, T.L., Richards, J.H., Smart, D.R., Eissenstat, D.M., 2008. Importance of internal hydraulic rdistribution for prolonging the lifespan of root in dry soil. Plant Cell Environ. 31, 177–186.

Benyon, R.G., 1999. Nighttime water use in an irrigated *Eucalyptus grandis* plantation. Tree Physiol. 19, 853–859.

Bucci, S.J., Goldstein, G., Meinzer, F.C., Franco, A.C., Campanello, P., Scholz, F.G., 2004. Mechanisms contributing to seasonal homeostasis of minimum leaf water potential and predawn disequilibrium between soil and plant water potential in Neotropical savanna trees. Trees 19, 296–304.

Bush, S.E., Hultine, K.R., Sperry, J.S., Ehleringer, J.R., Philips, N., 2010. Calibration of thermal dissipation sap flow probes for ring and diffuse porous trees. Tree Physiol. 30, 1545–1554.

Campbell, G.S., Norman, J.M., 1998. Water vapor and other gases. In: Campbell, G.S., Norman, J.M. (Eds.), An Introduction to Environmental Biophysics, second ed. Springer, New York, pp. 37–51.

Cao, M., Zou, X.M., Warren, M., Zhu, H., 2006. Tropical forests of Xishuangbanna, China. Biotropica 38, 306–309.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., Zanne, A.E., 2009. Towards a worldwide wood economics spectrum. Ecol. Lett. 12, 351–366.

Cowan, I.R., 1977. Stomatal behavior and environment. In: Preston, R.D., Woodhouse, H.W. (Eds.), Advances in Botanical Research. Academic Press, San Francisco, pp. 117–228.

Daley, M.J., Phillips, N.G., 2006. Interspecific variation in nighttime transpiration and stomatal conductance in a mixed New England deciduous forest. Tree Physiol. 26, 411–419.

Davy, R., Esau, I., Chernokulsky, A., Outten, S., Zilitinkevich, S., 2017. Diurnal asymmetry to the observed global warming. Int. J. Climatol. 37, 79–93.

Dawson, T., Burgess, S., Tu, K., Oliveira, R., Stantiago, L., Fisher, J., Simonin, K., Ambrose, A., 2007. Nighttime transpiration in woody plants from contrasting ecosytems. Tree Physiol. 27, 561–576.

Domec, J.C., Ogee, J., Noormets, A., Jouangy, J., Gavazzi, M., Treasure, E., Sun, G., McNulty, S.G., King, J.S., 2012. Interactive effects of nocturnal transpiration and climate change on the root hydraulic redistribution and carbon and water budgets of southern United States pine plantations. Tree Physiol. 32, 707–723.

Donovan, L., Linton, M., Richards, J., 2001. Predawn plant water potential does not necessarily equilibrate with soil water potential under well-watered conditions. Oecologia 129, 328–335.

Field, T.S., Holbrook, N.M., 2000. Xylem sap flow and stem hydraulics of the vessel less angiosperm Drimys granadensis (Winteraceae) in a Costa Rican elfin forest. Plant Cell Environ. 23, 1067–1077.

Fisher, J.B., Baldocchi, D.D., Misson, L., Dawson, T.E., Goldstein, A.H., 2007. What the towers don't see at night: nocturnal sap flow in trees and shrubs at two AmeriFlux sites in California. Tree Physiol. 27, 597–610.

Forster, M.A., 2014. How significant is nocturnal sap flow? Tree Physiol. 34, 757–765.

Fu, Y.H., Liu, Y., De Boeck, H.J., Menzel, A., Nijs, I., Peaucelle, M., Penuelas, J., Piao, S., Janssens, I.A., 2016. Three times greater weight of daytime than of night-time temperature on leaf unfolding phenology in temperate trees. New Phytol. 212, 590–597.

Gansert, D., 2003. Xylem sap flow as a major pathway for oxygen supply to the sapwood of birch (*Betula pubescens* Ehr.). Plant Cell Environ. 26, 1803–1814.

Gao, J., Zhao, P., Shen, W., Niu, J., Zhu, L., Ni, G., 2015. Biophysical limits to responses of water flux to vapor pressure deficit in seven tree species with contrasting land use regimes. Agric. For. Meteorol. 200, 258–269.

Granier, A., 1987. Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. Tree Physiol. 3, 309–319.

Green, S.R., McNaughton, K.G., Clothier, B.E., 1989. Observations of nighttime water use in kiwifruit vines and apple trees. Agric. For. Meteorol. 48, 251–261.

Hogg, E.H., Hurdle, P.A., 1997. Sap flow in trembling aspen: implications for stomatal responses to vapor pressure deficit. Tree Physiol. 17, 501–509.

IPCC, 2007. Climate change 2007: the physical science basis. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK, pp. 10–104.

IPCC, 2014. Summary for policymakers. In: Field, C.B., Barros, V.R., Dokken, D.J., Mach, K.J., Mastrandrea, M.D., Bilir, T.E., Chatterjee, M., Ebi, K.L., Estrada, Y.O., Genova, R. C., Girma, B., Kissel, E.S., Levy, A.N., MacCracken, S., Mastrandrea, P.R., White, L.L. (Eds.), Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK, and New York, NY, USA, pp. 1–32.

Johnson, D.M., Woodruff, D.R., McCulloh, K.A., Meinzer, F.C., 2009. Leaf hydraulic conductance, measured in situ, declines and recovers daily: leaf hydraulics, water potential and stomatal conductance in four temperate and three tropical tree species. Tree Physiol. 29, 879–887.

Johnson, D.M., McCulloh, K.A., Meinzer, F.C., Woodruff, D.R., Eissenstat, D.M., 2011. Hydraulic patterns and safety margins, from stem to stomata, in three eastern U.S. tree species. Tree Physiol. 31, 659–668.

Kagawa-Viviani, K.A., Sack, L., Duarte, K., James, A.S., 2009. Hawaiian native forest conserves water relative to timber plantations: species and stand traits influence water use. Ecol. Appl. 19 (6), 1429–1443.

Kim, H., 2000. Transpiration of Hybrid Poplar in Eastern Washington. University of Washington, Seattle, WA, pp. 107 M.Sc. Thesis.

Kunert, N., Cardenas, A., 2015. Are mixed tropical tree plantations more resistant to drought than mnocultures? Forests 6 (6), 2029–2046.

Kupper, P., Ivanova, H., Sober, A., Rohula-Okunev, G., Sellin, A., 2016. Night and daytime water relations in five fast-growing tree species: effect of environmental and endogenous variables. Ecohydrology.

Litvak, E., McCarthy, H.R., Pataki, D.E., 2012. Transpiration sensitivity of urban treesin a semi-arid climate is constrained by xylem vulnerability to cavitation. Tree Physiol. 32, 373–388.

Lu, P., Urban, L., Zhao, P., 2004. Thermal dissipation probes (TDP) method for measuring sap flow in trees: theory and practice. Acta Bot. Sin. 46 (6), 631–646.

Masle, J., Farquhar, G.D., Wong, S.C., 1992. Transpiration ratio and plant mineral-content are related among genotypes of a range of species. Aust. J. Plant Physiol. 19, 709–721.

McCulloh, K.A., Johnson, D.M., Meinzer, F.C., Voelker, S.L., Lachenbruch, B., Domec, J.C., 2012. Hydraulic architecture of two species differing in wood density: opposing strategies in co-occurring tropical pioneer trees. Plant Cell Environ. 35, 116–125.

McDonald, E.P., Erickson, J.E., Kruger, E.L., 2002. Can decreased transpiration limit plant nitrogen acquisition in elevated CO_2? Funct. Plant Biol. 29, 1115–1120.

Meinzer, F.C., Johnson, D.M., Lachenbruch, B., McCulloh, K.A., Woodruff, D.R., 2009. Xylem hydraulic safety margins in woody plants: coordination of stomatal control of xylem tension with hydraulic capacitance. Funct. Ecol. 23, 922–930.

Oishi, A.C., Oren, R., Stoy, P.C., 2008. Estimating components of forest evapotranspiration: a footprint approach for scaling sap flux measurements. Agric. For. Meteorol. 148, 1719–1732.

Oren, R., Pataki, D., 2001. Transpiration in response to variation in microclimate and soil moisture in southeastern deciduous forests. Oecologia 127, 549–559.

Phillips, N.G., Lewis, J.D., Logan, B.A., Tissue, D.T., 2010. Inter- and intra-specific variation in nocturnal water transport in *Eucalyptus*. Tree Physiol. 30, 586–596.

Phillips, N.G., Ryan, M.G., Bond, B.J., McDowell, N.G., Hinckley, T.M., Čermák, J., 2003. Reliance on stored water increases with tree size in three species in the Pacific Northwest. Tree Physiol. 23, 237–245.

Resco de Dios, V., Trunbull, H.M., Barbour, M.M., Josephine, O., Ghannoum, O., Tissue, D.T., 2013. Soil phosphorous and endogenous rhythms exert a larger impact than CO_2 or temperature on nocturnal stomatal conductance in *Eucalyptus tereticornis*. Tree Physiol. 33, 1206–1215.

Resco de Dios, V., Loik, M.E., Smith, R., Aspinwall, M.J., Tissue, D.T., 2016. Genetic variation in circadian regulation of nocturnal stomatal conductance enhances carbon assimilation and growth. Plant Cell Environ. 39, 3–11.

Rosado, B.H.P., Oliveira, R.S., Joly, C.A., Aidar, M.P.M., Burgess, S.S.O., 2012. Diversity in nighttime transpiration behavior of woody species of the Atlantic Rain Forest, Brazil. Agric. For. Meteorol. 158–159, 13–20.

Siddiq, Z., Cao, K.F., 2016. Increased water use in dry season in eight deiperocarp species in a common plantation in the northern boundary of Asian tropics. Ecohydrology 9, 871–881.

Siddiq, Z., Chen, Y.J., Zhang, Y.J., Zhang, J.L., Cao, K.F., 2017. More sensitive response of crown conductance to VPD and larger water consumption in tropical evergreen than in deciduous broadleaf timber trees. Agric. For. Meteorol. 247, 399–407.

Snyder, K.A., Richards, J.H., Donovan, L.A., 2003. Night-time conductance in C3 and C4 species: do plants lose water at night? J. Exp. Bot. 54, 861–865.

Tyree, M.T., Ewers, F.W., 1991. The hydraulic architecture of trees and other woody plants. New Phytol. 119, 345–360.

Wallace, J., McJannet, D., 2010. Processes controlling transpiration in the rainforests of north Queensland, Australia. J. Hydrol. 384, 107–117.

Wang, H., Zhao, P., Holscher, D., Wang, Q., Lu, P., Cai, X.A., Zeng, X.P., 2011. Nighttime sap flow of Acacia mangium and its implications for nighttime transpiration and stem water storage. J. Plant Ecol. 5, 294–304.

Warton, D.I., Wright, I.J., Falster, D.S., Westoby, M., 2006. Bivariate line-fitting methods for allometry. Biol. Rev. Camb. Philos. Soc. 81, 259–291.

Way, D.A., Oren, R., 2010. Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data. Tree Physiol. 30, 669–688.

Woodruff, D.R., McCulloh, K.A., Warren, J.R., Meinzer, F.C., Lachenbruch, B., 2007. Impacts of tree height on leaf hydraulic architecture and stomatal control in Douglas-fir. Plant Cell Environ. 30, 559–569.

Zeppel, M., Tissue, D., Taylor, D., Macinnis-Ng, C., Eamus, D., 2010. Rates of nocturnal transpiration in two evergreen temperate woodland species with differing water-use strategies. Tree Physiol. 30, 988–1000.

Zeppel, M.J., Lewis, J.D., Phillips, N.G., Tissue, D.T., 2014. Consequences of nocturnal water loss: a synthesis of regulating factors and implications for capacitance, embolism and use in models. Tree Physiol. 34, 1047–1055.

Zhang, Y.J., Meinzer, F.C., Qi, J.H., Goldstein, G., Cao, K.F., 2013. Midday stomatal conductance is more related to stem rather than leaf water status in subtropical deciduous and evergreen broadleaf trees. Plant Cell Environ. 36, 149–158.

Zimmermann, M.H., 1983. Xylem Structure and the Ascent of Sap. Springer, Berlin Heidelberg, New York.