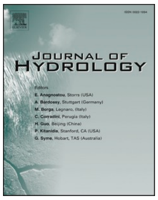
Journal of Hydrology 616 (2023) 128705

Contents lists available at ScienceDirect

Journal of Hydrology

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



Research papers

Water consumption during a leafless period in a dry season in three deciduous tropical timber species

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ARTICLE INFO

This manuscript was handled by Marco Borga, Editor-in-Chief, with the assistance of Yuting Yang, Associate Editor

Keywords:
Bark
Drought
Leafless period
Water loss
Xylem embolism

ABSTRACT

Besides mechanical protection and sugar transport through phloem, barks also transpire some amount of water. Bark transpiration may be a driving force to keep water flux during the leafless period among tropical deciduous trees, but has been hardly investigated. In the current investigation we used the sap flow data to assess the water consumption during leaf loss initiation, total leaf loss period, and leaf flush period in three economically important tropical deciduous timber species i.e, *Anogeissus acuminata*, *Dipterocarpus tuberculatus* and *Tectona grandis*. Eight trees of each species were measured using Granier's heat dissipation sensors, with the circumference ranging from 59 cm to 172 cm (mean 59.84 cm) across the three species. The phenological observation for canopy leaves was also carried out on weekly basis. During the completely leafless period, a significant amount of water flux was detected in all three species, which was correlated with vapor pressure deficit (VPD), and light intensity. The whole tree daily mean water consumption during this leaf-less, flower-less and fruit-less period, mainly due to bark transpiration was around 8–14 kg across the three species. It was about 7 to 18 % of the mean whole-tree daily transpiration in the fully foliated canopies during a typical wet-season period. This water flux was supported by sufficient soil moisture as indicated by the pre-dawn leaf water potential higher than –0.4 MPa in the three species. Further, a significant and positive relationship ($R^2 = 0.32$, $P < 0.005$) was found between tree circumference and whole-tree water consumption during the leaf-less period. The total stand-level water consumption during the leaf-less period ranged from 13 mm to 26.8 mm on a 30 days basis across the three species. Such water flux mainly driven by bark transpiration could have a significant role in maintaining the hydraulic integrity of trees in the dry season, although it could reduce xylem water potential to a risky level of hydraulic dysfunction during a prolonged drought or on dry sites. The study is the first report on bark transpiration in intact trees, scaled to the stand-level, which should be included in the modeling of hydraulic function of plant and ecosystem hydrology.

1. Introduction

Trees regulate water consumption through stomatal opening and closure, but during stomatal closure due to environmental stresses or the leafless durations, some water loss occurs by transpiration through surfaces of branches and trunks (Wittmann and Pfanz, 2008b; Earles et al., 2016). Depending upon the species, the leaf-less period among tropical deciduous trees varies from two weeks to six months or more (Singh and Kushwaha 2005). During the leaf-less period plants have to keep certain water flux to hydrate the xylem and phloem and maintain adequate water in living tissues (Martínez-Vilalta et al., 2019). There have been a few studies (Oren and Pataki 2001; Wittmann and Pfanz 2008a; 2008b; Wolfe 2020) from different trees species reporting water loss through bark transpiration, mainly using the harvesting and gas exchange methods. It has been found that branch bark of Mediterranean *Pinus* protects the xylem from cavitation by supplying water to the xylem conduits hence keeping them hydrated during a dry period when stomata are closed or leaves are shed (Lintunen et al., 2021). However, net efflux of water from stem surfaces may be significant in some ecosystems especially during the different leaf phenological stages (Iida et al.,

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https://doi.org/10.1016/j.jhydrol.2022.128705
Received 5 July 2022; Received in revised form 9 October 2022; Accepted 18 October 2022

2016). In the seasonal tropical climates deciduous trees are important component of total cover. The measurements of the whole-tree water flux during the leaf-less period from deciduous trees in seasonal tropical climates will allow assessment of water consumption that is mainly due to bark transpiration through lenticels, though living tissues may also consume some minor amount of water. Transpiration during a leafless period is not only relevant to plant physiology but may also be an important element of ecosystem hydrology (Van Stan et al., 2021).

Water loss from the stomata and bark surfaces of trees is driven by vapor pressure deficit (VPD) and solar radiation but its magnitude is determined by soil water status around the root zones and the status of leaves on the canopy (Siddiq and Cao 2016; Iidaet al., 2016). Transpirational water consumption of trees reaches its maximum when high transpirational demand (high VPD) is coupled with availability of water in the soil. During water stress conditions, the water loss through stomata is reduced or completely halted to prevent decreasing of xylem water potential to the threshold inducing hydraulic dysfunction (McDowell et al., 2013; Mencuccini et al., 2015). The whole-tree water consumption is also dependent on tree size, as it could be correlated with the leaf and bark surface areas (Siddiq et al., 2017, Siddiq and Cao 2016). Bark of the trunk and branches during the fully leafed canopies has less direct exposure to the solar radiations than during the dry season period of leaf loss. Vapor pressure deficit in the dry season can be high due to high temperature and lower air humidity. Such conditions probably lead to increased loss of water from stem surfaces, provided sufficient water available in the soil (Lintunen et al., 2021). For example Wolfe (2020) found that the species having high bark conductance also had a high stem water deficit especially during the dry season, and some species could have strong stomatal control while losing water during leaf fall (Iida et al., 2016). Therefore, bark transpiration could further decrease plant water potential and even lead to catastrophic hydraulic dysfunction and tree mortality during a prolonged drought (Li et al., 2021). The role of stem surfaces in deciduous trees may be more important than in needle and broadleaf evergreens for maintenance of a low water flux to hydrate the xylem and phloem during leafless periods. Further, the development of the canopy with new leaves require some amount of water and mineral nutrients (Oren and Pataki, 2001) which can only be supplied if the previous xylem remain functioning.

A large proportion of Asian tropical forests are subject to seasonal drought (Corlett, 2016; Zhang et al., 2020) and the frequency and duration of drought in Asian tropics is being exacerbated due to climate change and may continue in the future (Dai, 2011; IPCC, 2021, Wang et al., 2022). Such drought episodes impact the hydrology and phenological behavior of trees and hence their productivity (Duan et al., 2018; Zhao et al., 2013). The duration of leaf flushing was delayed in *Tectona grandis* till the availability of rainwater during a drought (Yoshifuji et al., 2006). It has been reported in the some other species that excessive prolongation of leafless period can also lead to the carbon starvation as well as severe xylem embolism (Adams et al., 2009; Adams et al., 2017). The present study was planned to use the sap flow data from three economically important deciduous timber species in a northern tropical site to answer two questions; 1) how much water are consumed at tree and stand levels during the leafless period for three deciduous tropical tree species? Which could be largely due to bark transpiration?, 2) is dry season sap flux density of leafless period related to environmental factors such as vapor pressure deficit and light intensity?

2. Materials and methods

2.1. Study site and species

The study was carried out in the monsoon plantation stands of three tropical deciduous timber species i.,e *Anogeissus acuminata*, *Dipterocarpus tuberculatus*, and *Tectona grandis*, in Xishuangbanna Tropical Botanical Garden (XTBG; 21° 54′59.99″ N, 101°. 14′60.00″ E, 580 m a.s.l.), southern Yunnan Province, Southwest China. This region has a typical tropical monsoon climate with a pronounced dry season from November to April. The mean annual precipitation is 1560 mm, of which ~80 % occur during the wet season (May to October). The mean annual temperature of the study site is 21.7 °C (Fig. 1; Cao et al., 2006). The region has the mountain-valley topography, and the soil formation from the siliceous rocks, rock substrate of sandstone and limestone (Zhu, 2006). These plantation stands have not been subject to pruning and contain a herbaceous ground cover. Eight replicate trees of each species were selected for the sap flow measurement and phenological observation.

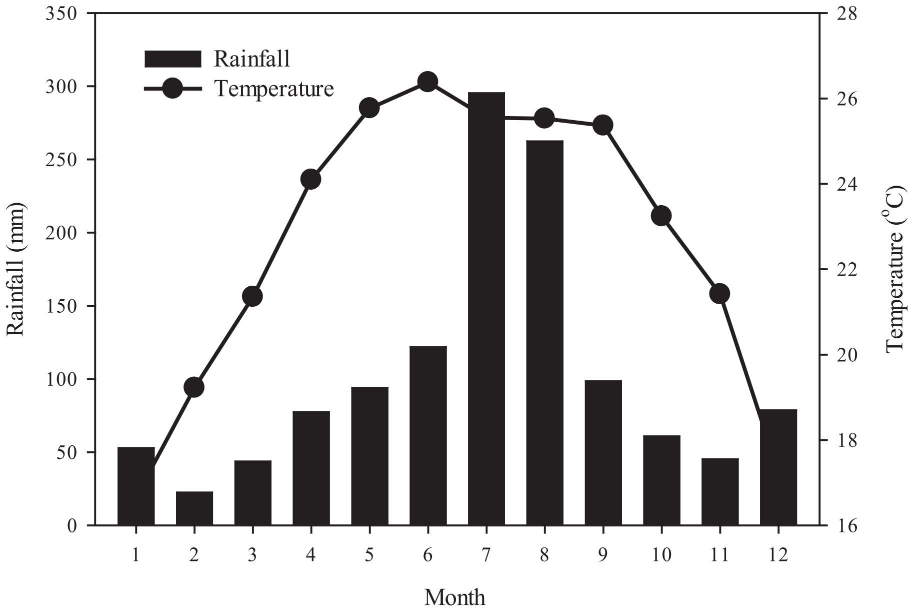

Fig. 1. Annual pattern of mean monthly rainfall and temperature of the study site during 2011–2016.

Table 1
Species scientific names, family, circumference range of sample trees, number of replicates, stand basal area and stand density.

Sr no.	Scientific Name	Family	Circumference range (cm)	Replicates	Stand basal area per hectare	Stand density per hectare
1.	*Anogeissus acuminata* (Roxb. Ex Dc.) Guillaum & Perr.	Combretaceae	69–116	8	23 m^2	475
2.	*Dipterocarpus tuberculatus* Roxb.	Dipterocarpaceae	62–123	8	19 m^2	225
3.	*Tectona grandis* L.f.	Verbenaceae	59–174	8	39 m^2	450

2.2. Phenological observations

The phenological observation of each of the eight trees was made on weekly basis from February to May 2016. Three canopy branches from each tree were tagged and the number of leaves on each target branch were counted to estimate the percentage of leaves remaining.

2.3. Water flux through bark transpiration

The water flux through bark transpiration was inferred from the sap flow measurements (2015–2016) on eight trees of each of the three timber species. For assessing the water flux during the leafless period the sap flow data from February to May 2016, representing the duration of leafless and new leaf appearance and a week spa flow data of September 2015 representing the fully developed canopy leaves in the wet season were used. The circumference range of the sample trees are indicated in Table 1. The laboratory made Granier's heat dissipation (Granier, 1987) sap flow sensors were fixed at trunks of 1.3 m height from the ground, in the outer 2 cm and 4 cm of sapwood of trees. Each sensor consisted of a thermocouple surrounded by a heating coil and a reference sensor. All sensors were connected to data loggers (CR-1000, Campbell) connected with a multiplexer (AM 16/32, Campbell) and supplied with a constant power of 0.2 W to heat the sensors. Each tree was equipped with two sets of sensors installed at 90° to the stem and directionally opposite to each other. The sensors were protected from mechanical damage and solar radiation using aluminum foil. Data were logged every 30 s and averaged over 60 min intervals, for storage in the data loggers. The sensors were monitored bi-weekly and malfunctioning sensors were immediately replaced. The sap flux density ($g\ m^{-2}\ s^{-1}$) was calculated using the baseliner program version 3.0.7. (C-H_2O Ecology Group, Nicholas School of the Environment, Duke University, Durham, North Carolina, USA). The average values from two paired sensors were used to calculate the sap flux density for each individual tree. Because the original Granier's equation is not universal for all the species and should be calibrated as it could underestimate the sap flow (Taneda and Sperry 2008; Bush et al.,2010; Hultine et al., 2010). We used the calibrated Granier's equation developed by Siddiq et al., (2017) for these species to calculate their sap flux density. The zero flow was established as the maximum difference between the heated and non-heated sensors, which was attained late mid-nights; as there was no biophysical driving force due to low VPD (Eliades et al.2018; Fig. S1).

2.4. Whole-tree and stand-level water consumption

The daily whole-tree water consumption during the leaf loss initiation, leaf-less period and the leafed canopy month for each species was calculated by multiplying the active sapwood area by the integral of 24-h sap flux density. Whole-tree sap flux density was calculated by multiplying the flow per area sensed at 2 cm by the area of a ring between the outer most xylem and 2 cm, similarly, for the flow of the ring from 2 cm to 4 cm. Among all the trees the active sapwood was not >4 cm. 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 1.3 m height. After 12–16 h, a 5 mm and 5–8 cm long core was taken just above the injection point to measure the active sapwood area by assessing the dye color travelled on the xylem core (Clearwater et al., 1999). The cores were taken after the sap flow measurements, to avoid any damage to the trees. The active sapwood areas for these species was not >4 cm. The contributions of sap flow sensed at 2 cm and 4 cm were added to determine the whole tree total sap flow ($g\ h^{-1}$), which was multiplied by the sapwood area and then integrated over 24 h to estimate whole-tree daily followed by weekly water consumption for comparison. During this period, trees were devoid of leaves or other structures external to the stems such as flowers, and fruits. Thus, the flux in this period was considered mainly due to transpiration from the stem surfaces (bark), as the physiological activities of living tissues could consume a minor amount of water.

The stand-level bark transpiration was estimated based on the survey of 20 m × 20 m plots in the plantation stands of three species. All the trees with circumference >30 cm were measured for circumference. The circumference ranges of trees were 69–116 cm, 62–123 cm, and 59–174 cm for *A. acuminata*, *D. tuberculatus* and *T.grandis* respectively. The stand density and basal areas for the three species are provided in Table 1. The stand-level transpiration ($mm\ d^{-1}$) was estimated using the following formula (Wullschlegeret al., 2001; Kumagai et al., 2008):

$$E = \frac{1}{A_{plot}} * \sum_{j=1}^{n} WU_j$$

where WU_j is the daily water use of tree j ($kg\ d^{-1}$) during the leaf-less period, and A_{plot} is the plot area (m^2). The daily stand-level bark transpiration was integrated to weekly or monthly basis.

2.5. Pre-dawn leaf water potential

In order to assess the soil water status around the root zones of the trees, the pre-dawn leaf water potential (Ψ_L) was measured on site with a pressure chamber (PMS, Albany, OR, USA) during the days when only few leaves were left on the canopy. For *Tectona* the leaf water potential was measured during the last week of February, while for *Anogeissus* and *Dipterocarpus* it was measured in mid-March 2016. For each tree 5–6 complete and healthy leaves were collected at 6:00 to 7:00 am for water potential measurement.

2.6. Meteorological data

The meteorological data (temperature, relative humidity, and photosynthetic active radiation (PAR) were obtained from the climatic station of XTBG, which is situated approximately 900 m away from the sap flow measurement site. The hourly mean values of the meteorological variables were used in the analysis. The vapor pressure deficit (VPD) was calculated from air temperature and relative humidity (Campbell and Norman, 1998).

2.7. Data analysis

The statistical analyses and graphics were made using sigma Plot (version-12.5; Systat Software Inc. USA. The relationships between the hourly mean VPD, PAR and sap flux density during the leafless and leaf flushing periods were analyzed using linear regression. As day-time mean VPD and PAR during these periods were strongly correlated ($R^2 = 0.45$, $P < 0.0001$), we only presented the results of the correlation between mean sap flux density and VPD.

3. Results

3.1. Phenological observations for canopy foliage status

The three species varied in the timing and duration of leaf fall but all were leafless for several weeks. *Tectona grandis* started to shed the leaves in the second week of January and completed leaf shedding at the end of February. In *A. acuminata* and *D. tuberculatus* leaf shedding initiated in the first week of March and completed in the last week of March. The duration of complete leaflessness for *T. grandis* was 6 weeks but 4 weeks for both *A. acuminata* and *D.tuberculatus*. All the species had their new crown of leaves by the beginning of May (Fig. 2 a). The weekly sap flux density varied across the three species, and was >1096 g cm^{-2} $week^{-1}$ even during the leafless weeks (Fig. 2 b).

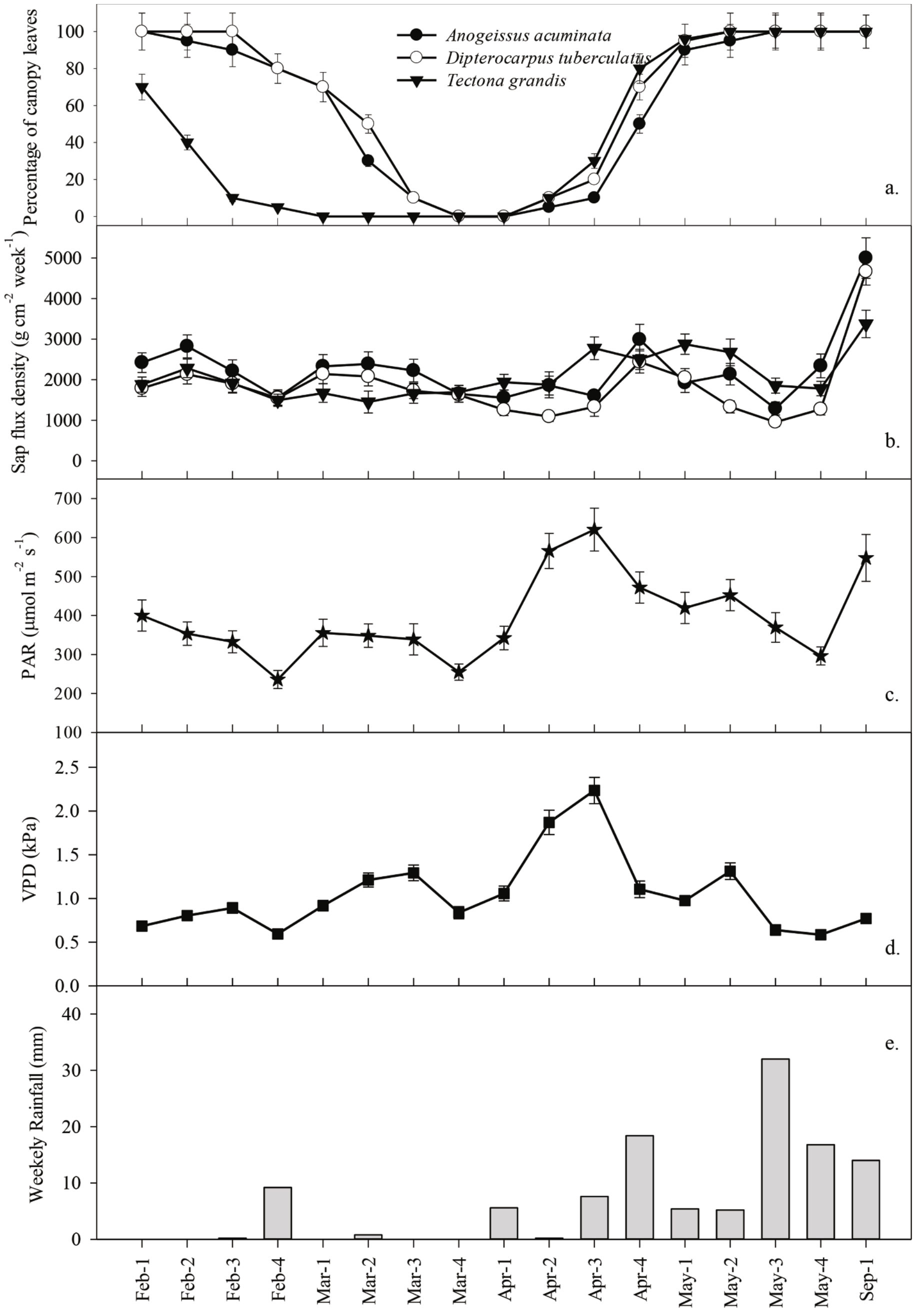

Fig. 2. Weekly time series of leaf phenology, meteorological variables, and sap flux density. Percentage of leaves on canopy (a), daily integrated weekly scaled average sap flux density of all measured trees of each species (b), daytime mean photosynthetic active radiations (PAR, c), and vapor pressure deficit (VPD, d), and weekly total rainfall (e) across the three studied species. Where, Feb, Mar, Apr, 1–4, indicate the first, second, third and fourth week of February, March 2016, while Sep-1 indicates the 1st week of September 2015.

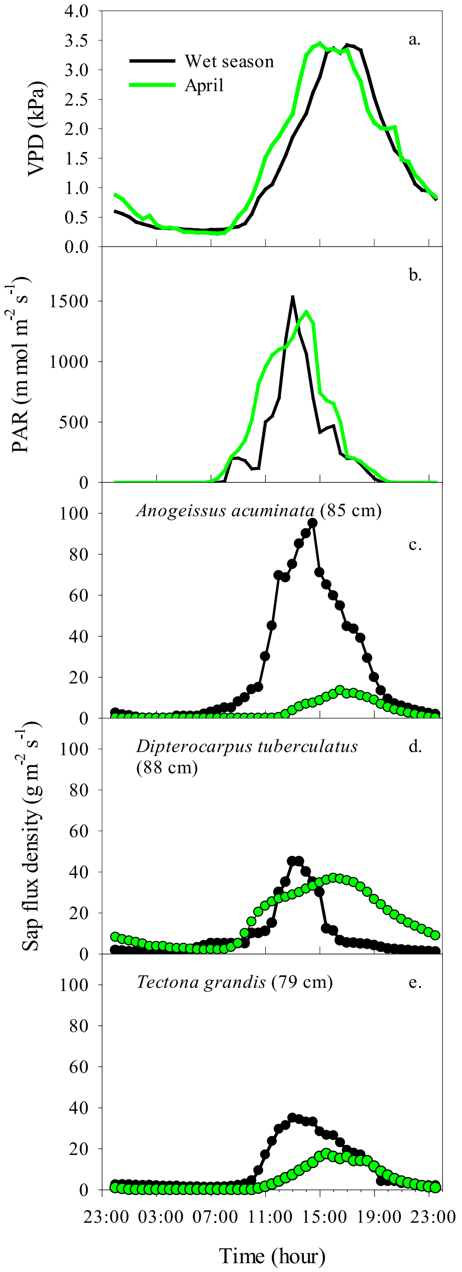

Fig. 3. Diurnal pattern of hourly mean vapor pressure deficit (VPD, a), photosynthetic active radiations (PAR, b), sap flux density in *Anogeissus acuminata* (c), *Dipterocarpus tuberculatus* (d) and *Tectona grandis* (d) during a day of 1st week of September 2016 wet season (fully developed leaves) and April 2015 (leafless day) with circumference for each tree.

3.2. Diurnal pattern of VPD, PAR, and sap flux density

The hourly mean diurnal pattern of VPD and PAR showed the similar diurnal peaks but the peaks of diurnal sap flux density for each species was significantly different during the month of March and April 2016 (Fig. 3). In *A. acuminata* the daily mean sap flux density in the leafless month of April and during the wet season week of September were 16 g m^{-2} s^{-1} (±2.02), and 30 g m^{-2} s^{-1} (±4.91), respectively, while in *D. tuberculatus* it was 3.2 g m^{-2} s^{-1} (±0.62) and 7.9 g m^{-2} s^{-1} (±1.45) and in *T. grandis* it was 11 g m^{-2} s^{-1} (±1.81) and 5 g m^{-2} s^{-1} (±0.95) (Fig. 2 b). The sap flux density during the leafless month was significantly lower, *P* = < 0.001, 0.003 and 0.001 for *A. acuminata* and *D. tuberculatus* and *T. grandis* respectively, during leafless day of April as compared to the wet season day of September.

3.3. Meteorological variables and plant water potential

In March the weekly mean VPD and PAR ranged from 0.83 kPa (±0.071) to 1.29 kPa (±0.093) and 254.72 µ m^2 *sec*$^{-1}$ (±45.8) to 355.71 µ m^2 *sec*$^{-1}$ (±33.81) respectively, while in April the VPD and PAR ranged from 1.0 (±0.087) to 2.23 (±0.02) and 342.45 µ m^2 *sec*$^{-1}$ (±44.88) to 620.57 µ m^2 *sec*$^{-1}$ (±77.99) respectively. And in May the weekly mean VPD and PAR ranged from 0.58 (±0.03) to 1.31 (±0.089) and 296.45 µ m^2 *sec*$^{-1}$ (±35.71) to 454.42 µ m^2 *sec*$^{-1}$ (±62.34) respectively (Fig. 2 c-d). While, the mean wet season VPD was 0.7 (±0.081) and PAR 595 µ m^2 *sec*$^{-1}$ (±59.91). The VPD was significantly higher in the dry season weeks of March and April as compared to the wet season week of September (P < 0.001) while, PAR was not significantly different between the dry season weeks and wet season week (P > 0.05). The weekly rainfall ranged from 0 mm to 32 mm from February to April 2016 (Fig. 2, panel e).

For all the species, the hourly mean sap flux density in March and April were strongly correlated with hourly mean VPD ($R^2 > 0.65$, $P < 0.0001$, Fig. 4 a-i). Similarly, a significant ($P < 0.001$) and positive relationship ($R^2 = 0.41–0.76$) was found between the daily sap flux density and the daytime mean PAR, across the three species during the months of March and April (Fig. 5). The mean pre-dawn leaf water potential prior to leaf-shedding for *A. acuminata*, *D. tuberculatus* and *T. grandis* was –0.24 MP (±0.025), –0.18 MPa (±0.01) and –0.31 MPa (±0.02), indicating good water status of the studied plants.

3.4. Whole tree daily water consumption in leafless and leafy states

During the leaf-less weeks of the months of March and April, the mean daily water consumption in *A. acuminata*, *D. tuberculatus* and *T. grandis* was 14 kg (2.01 ± SE), 13 kg (1.98 ± SE), and 8.1 kg (2.11 ± SE) respectively (Fig. 6 a) with mean circumference 87 cm, 86 cm and 99 cm for *A. acuminata*, *D. tuberculatus* and *T.grandis*, respectively. The mean wet season week whole-tree water use for *A. acuminata*, *D. tuberculatus* and *T.grandis* was 80 kg, 100 kg and 126 kg, respectively. During these two months in dry season, the percentage daily water consumption to the whole tree daily water use the in a representative wet season weak as 7 %, 13 % and 18 % for *T.grandis*, *D.tuberculatus* and *A. acuminata* respectively (Fig. 6 b). The total stand-level water consumption on a 30-day basis during the leafless period was 26.85 mm, 18 mm and 13.6 mm for *A. acuminata*, *D. tuberculatus* and *T.grandis* respectively (Fig. 6 c). Further, across species, a significant ($R^2 = 35$, $P < 0.006$) and positive relationship was found between the tree circumference and mean daily water consumption during the leaf-less period (Fig. 7). At comparable circumference among the three species, *Tectona grandis* consumed less water than the other two species.

4. Discussion

On the average the whole tree water consumption of the studied species ranged from 8 kg to 14 kg during the four-six leaf-less weeks which was 7 % – 18 % of water consumed by these species during the wet season week of September. Such water flux could assist these species in the xylem functioning during these weeks. The strong correlation between sap flux density and VPD in the leafless period indicates that water consumption during the leafless period mainly resulted from bark transpiration, though other physiological activities such as living tissues and bud development might consume some minor amount of water. This

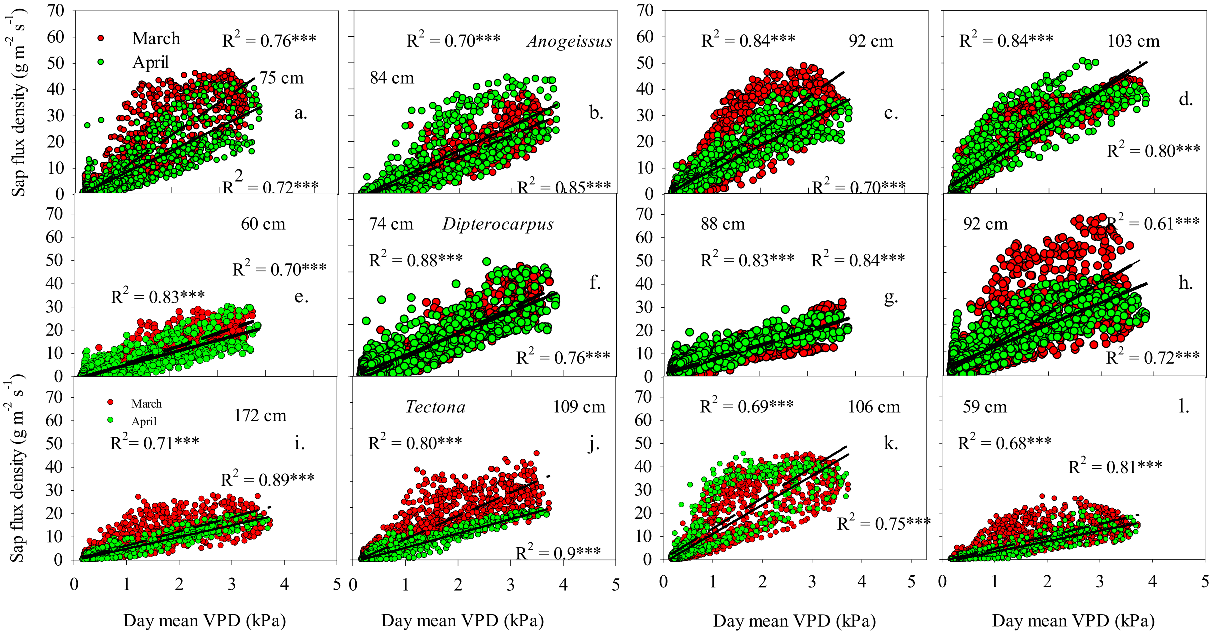

Fig. 4. Relationship of hourly mean sap flux density with hourly mean VPD in four representative trees of the three species (*Anogeissus acuminata* a-d, *Dipterocarpus tuberculatus* e-h, and *Tectona grandis* i-l) from 1st March to 20th April 2016. Each panel has the tree circumference along with the R^2 and *P* values of linear regression.

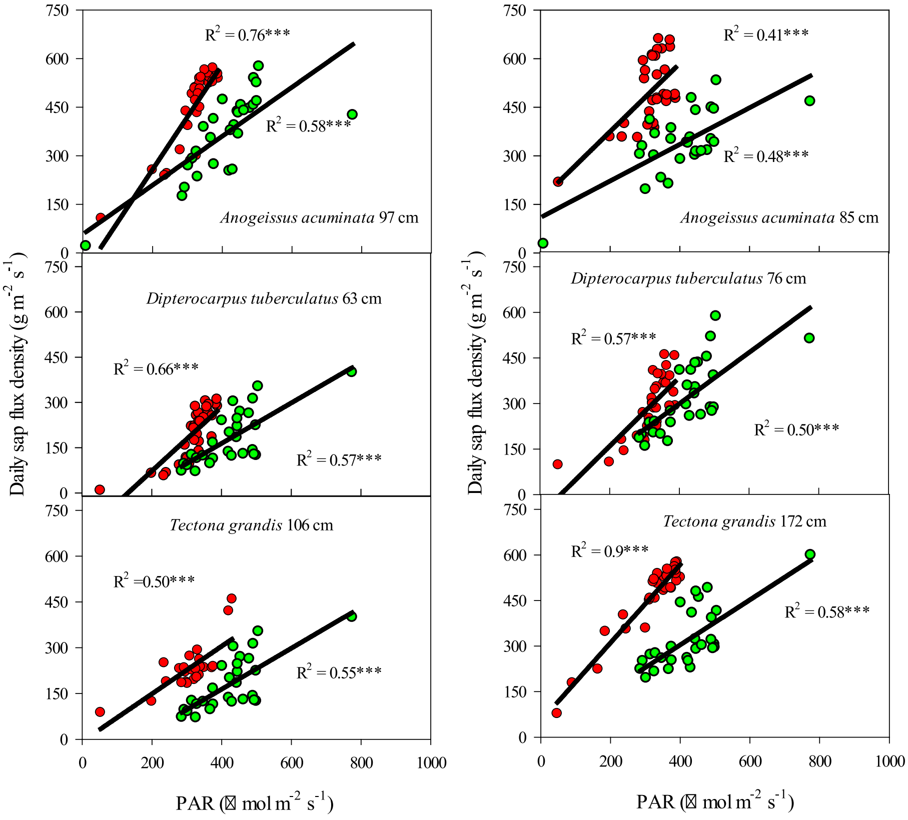

Fig. 5. Relationship of day-time mean photosynthetic active radiations (PAR) with daily mean sap flux density in the month of March (red symbols) and April (green symbols) in the three studied species, for the representative trees with the circumference.

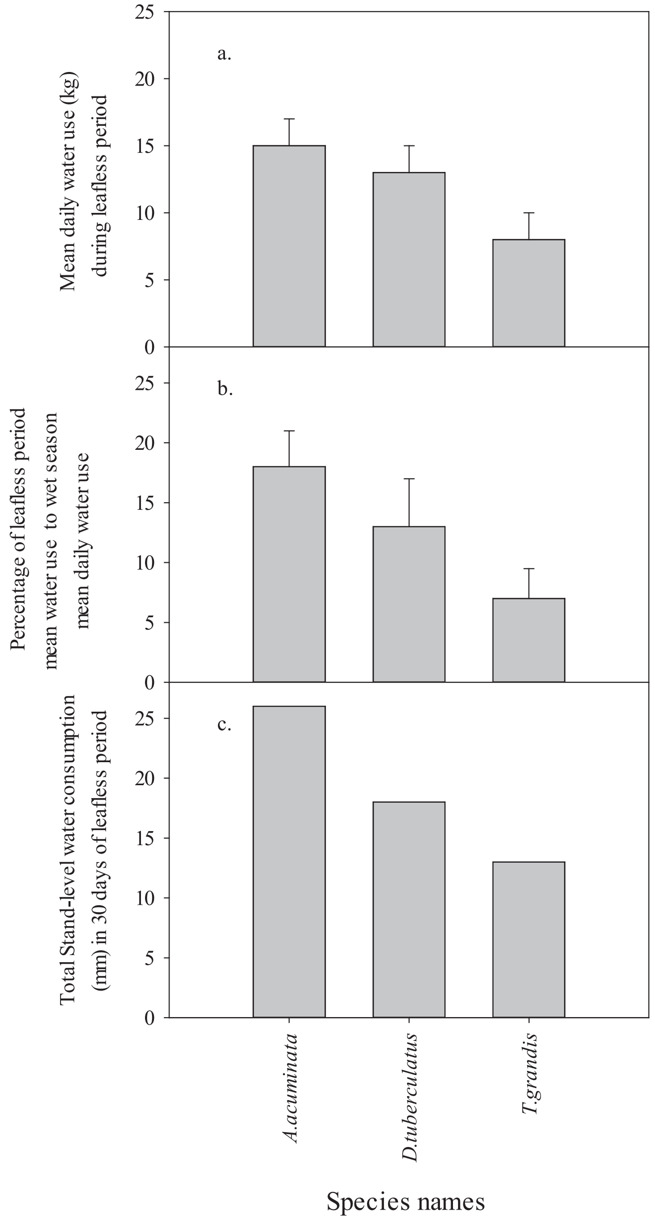

Fig. 6. The mean daily water use during leaf-less period (a), its percentage to the wet season week whole-tree daily water use (b), and total stand-level water consumption on 30-day basis during leaf-less period (c) across the three studied species.

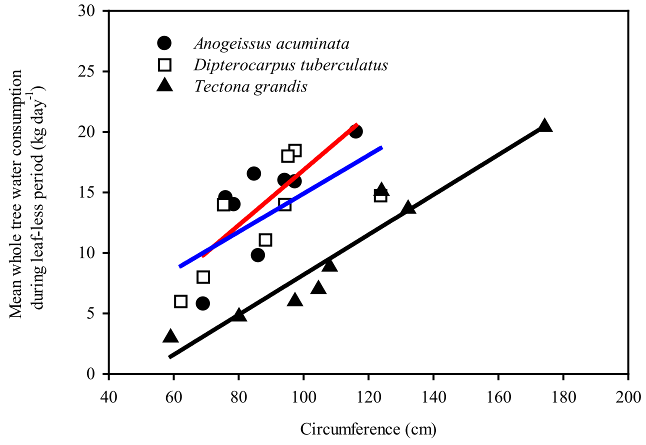

Fig. 7. The relationship between mean whole-tree daily water use during leafless period and circumference of the three tree species. Each symbol represents the replicate trees of the particular species. Red line indicates *Anogeissus acuminata* ($R^2 = 0.51$, $P = 0.02$), blue line indicates *Dipterocarpus tuberculatus* (R^2 0.48, $P = 0.04$) while black line indicates *Tectona grandis* ($R^2 = 0.91$, $P = 0.001$).

water flux could be supported by the presence of water around their root zones, which enabled them to meet the evaporative demand in the hot-dry period of March-April. Even during the initial hours of night there could be a significant amount of flux due to evaporative demand, but it could include both the stem refilling as well as night-time transpiration during a leaf-less period (Siddiq and Cao 2018). The nocturnal water use of leaf-less duration among these species is 5–16 % of the day-time water use, which is among the range reported by Fisher et al., 2007 and Eliades et al., 2018.This amount of water-use can also have adaptive significance of cooling the bark surface so that reducing night respiration.

The total stand-level transpiration during the leaf-less period varied from 13.6 mm to 26.8 mm monthly among the three species, while the outcrossing the total rainfall of 14 mm during this leaf-less duration. To our knowledge, this paper is the first report about stand-level water consumption during leaf-less period in the intact trees. This amount of water lost mainly through bark transpiration should be considered in modeling of ecosystem hydrology. It should be noted that use of thermal dissipation method for sap flow can have some error due to natural temperature gradient, which could be a limitation of the present study (Reyes-Acosta and Lubczynski 2014; Fuchs et al., 2017; Flo et al., 2019), but the use of calibrated equation for these species and the estimation of active sapwood area could minimize the expected errors.

During the leafless period of April the day-time VPD averaged 1.3 kPa but had a maximum above 2.2 kPa and the maximum water flow 54 %, 35 %, and 27 % of mean wet season whole-tree daily water flow in *A. acuminata*, *D. tuberculatus* and *T.grandis*, respectively. The mean ratio of whole-tree water consumption during the leafless period to that in wet season was 0.07 – 0.18 among these species. It remains to be determined whether water consumption during leafless period is involved in fixation of carbon in barks of twigs and small branches in these species (De Roo et al., 2020). This water flux may also hydrate the xylem vessels and facilitate the flushing of new leaves, even some water for the refilling or recharge of xylem vessels, but that amount of water must be lost from the bark (Klein et al., 2016; Wolfe, 2020). Lintunen et al., (2021) using gas exchange methods, reported that bark transpiration can range from 6 to 11 % to 64 – 78 % depending upon the species and environmental conditions.

Among the three studied species, at a similar circumference, teak had less bark transpiration than *A. acuminata* and *D. tuberculatus*, which could probably be due to the bark morphology of *Tectona garndis* such as having lower density of lenticels. It could also be due to the less soil water accessibility of its roots, as indicated by its more negative pre-dawn leaf water potential as compared to the other two species. Although, *Tectona grandis* had the greater basal area and tree density as compared to the other two species. It should be noted that the presence of a herbaceous a cover in forest understory can have an indirect effect on bark transpiration rates of trees, as the absence of leaves allow more solar radiations reaching the ground cover, which could enhance understory growth and thus relatively more soil water will be up-taken by the herbaceous vegetation (Eliades et al., 2022). However, the increased soil water uptake can be counter-balanced by the increase of net rainfall reaching the ground due to less rainfall interception by the leaf-less canopies (Del Campoa et al., 2022). The present study plantation stands also have a herbaceous ground cover and could have the similar counter balance of water availability.

During a dry period when stomata are closed and leaves are shed, trees must keep a low amount of water. Such water flux is important to avoid massive embolism formation and the refilling of embolized vessels (Delzon and Cochard 2014). Hence, the water flux during leafless period is important determinant for the survival trees in a drought (McDowell et al., 2013; Mencuccini et al., 2015). During the leafless or drought period the foliar carbon assimilation is much limited (Li et al., 2021), the water flux driven by bark transpiration also plays an important role in tree carbon balance through bark photosynthesis, providing nutrients to the living tissues in sapwood and barks (De Roo et al., 2020). It has been reported that sapwood and bark can store a significant amount of water, which can be utilized during the water stress condition (Siddiq et al., 2017; Lintunen et al., 2021). However, in dry sites or in a severe drought, bark transpiration may result in a decrease of plant water potential to the level of catastrophic hydraulic dysfunction and death of living cells in xylem and phloem, and consequently tree mortality (Cuneo et al., 2016). As the stand-level water consumption mainly through bark transpiration during the leafless period was more than the rainfall during the leaf-less duration, it can substantially impact the ecosystem water cycle, especially with the increasing drought linked with climate change.

5. Conclusion

The three deciduous species consumed considerable amount of water mainly through bark transpiration during the leafless period, which was correlated with the evaporative demand, light intensity, and also tree size. The water flux during the leafless period could be important in hydrating the sapwood and thus maintain hydraulic function, but could result in xylem water potential decrease to the risky level of hydraulic dysfunction during a prolonged drought. This amount of water consumption should be included in the whole tree water budget, while modeling hydraulic functioning of trees during a drought, ecosystem hydrology, and also need to be considered for the consequence of arboriculture.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

Acknowledgements

The authors thank National Forest Ecosystem Research Station at Xishuangbanna of XTBG, for providing the climatic data, and to the horticulture department of XTBG for permitting the experiment. The authors are also grateful to Dr. Uromi Manage Goodale for the language editing of manuscript. Two anonymous reviewers are also acknowledged for the constructive comments to improve the manuscript. The work was supported by National Natural Science Foundation of China (31170399, 41861144016, and 32071735).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jhydrol.2022.128705.

References

Adams, H.D., Guardiola-Claramonte, M., Barron-Gafford, G.A., et al., 2009. Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. Proc. Natl. Acad. Sci. U.S.A. 106, 7063±7066.

Adams, H.D., Zeppel, M.J.B., Anderegg, W.R.L., et al., 2017. A multi-species synthesis of physiological mechanisms in drought-induced tree mortality. Nat. Ecol. Evol. 1, 1285–1291.

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, 2nd 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.

Clearwater, M.J., Meinzer, F.C., Andrade, J.L., Goldstein, G., Holbrook, N.M., 1999. Potential errors in measurement of nonuniform sap flow using heat dissipation probes. Tree Physiol. 19, 681–687.

Corlett, R.T., 2016. The impacts of droughts in tropical forests. Trends in Plant Sciences 21 (7), 584–593.

Cuneo, I.F., Knipfer, T., Brodersen, C.R., McElrone, A.J., 2016. Mechanical failure of fine root cortical cells initiates plant hydraulic decline during drought. Plant Physiol. 172, 1669–1678.

Dai, A., 2011. Drought under global warming: a review. WIREs Clim. Change 2, 45–65.

Del Campoa,A.D., Otsukib, K., Serengilc, Y., Blancod, J. A., Yousefpoure, R., Weif, X. 2022. A global synthesis on the effects of thinning on hydrological processes: Implications for forest management. Forest Ecol. Manage., 519, 120324. 10.1016/j.foreco.2022.120324.

Delzon, S., Cochard, H., 2020. Recent advances in tree hydraulics highlight the ecological significance of the hydraulic safety margin. New Phytol. 203, 355–358.

De Roo, L., Salomón, R. L., Steppe, K. 2020. Woody tissue photosynthesis reduces stem CO2 efflux by half and remains unaffected by drought stress in young *Populus tremula* trees. Plant Cell Environ. 43 (2014) 981–991.

Duan, S., He, H.S., Spetich, M., 2018. Effects of growing-season drought on phenology and productivity in the west region of central hardwood forests, USA. Forests 9, 377.

Earles, J.M., Sperling, O., Silva, L.C.R., McElrone, A.J., Brodersen, C.R., North, M.P., Zwieniecki, M.A., 2016. Bark water uptake promotes localized hydraulic recovery in coastal redwood crown. Plant, Cell Environ. 39, 320–328.

Eliades, M., Bruggeman, A., Djuma, H., Lubczynski, M.W., 2018. TreeWater dynamics in a semi-arid, *Pinus brutia* Forest. Water 10, 1039. https://doi.org/10.3390/w10081039.

Eliades, M., Bruggeman, A., Djuma, H., Christofi, C., Kuells, K., 2022. Quantifying evapotranspiration and drainage losses in a semi-arid nectarine (*Prunus persica* var. *nucipersica*) field with a dynamic crop coefficient (Kc) derived from leaf area index measurements. Water, 14, 734. 10.3390/w14050734.

Fisher, J.B., Baldocchi, D.D., Misson, L., Dawson, E.T., 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.

Flo, V., Vilaltaa, M.J., Steppe, K., Schuldt, B., Poyatos, R., 2019. A synthesis of bias and uncertainty in sap flow methods. Agric. For. Meteorol. 271, 362–374. https://doi.org/10.1016/j.agrformet.2019.03.012.

Fuchs, S., Leuschner, C., Link, R., Coners, H., Schuldt, B., 2017. Calibration and comparison of thermal dissipation, heat ratio and heat field deformation sap flow probes for diffuse-porous trees. Agric. For. Meteorol. 244–245, 151–161. https://doi.org/10.1016/j.agrformet.2017.04.003.

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

Hultine, K.R., Nagler, P.L., Morino, K., Bush, S.E., Burtch, K.G., Dennison, P.E., Glenn, E. P., Ehleringer, J.R., 2010. Sap flux-scaled transpiration by tamarisk (Tamarix spp.) before, during and after episodic defoliation by the salt cedar leaf beetle (Diorhabda carinulata). Agric. For. Meteorol. 150, 1467–1475.

Iida, S.I., Shimizu, T., Tamai, K., Kabeya, N., Shimizu, A., Ito, E., Ohnuki, Y., Chann, S., Keth, N., 2016. Interrelationships among dry season leaf fall, leaf flush and transpiration: insights from sap flux measurements in a tropical dry deciduous forest. Ecohydrol 9, 472–486.

IPCC, 2021. Climate Change 2021, The Physical Science Basis, Summary for Policymakers. Intergovernmental Panel on Climate Chang, Switzerland.

Klein, T., Cohen, S., Preisler, Y., Rotenberg, E., and Yakir, D. 2016. Diurnal dynamics of water transport, storage and hydraulic conductivity in pine trees under seasonal drought. iForest 9, 710–719.

Kumagai TO, Tateishi M, Shimizu T, Otsuki K. 2008. Transpiration and canopy conductance at two slope positions in a Japanese cedar forest watershed. Agric. Forest Meteorol. 148 (10):1444–1455.

Li, Y., Xu, Y., Zhang, W., Zhuang, Q., Zhang, Y., Cai, P. 2021. Carbon and water fluxes are more sensitive to drought than heat in terrestrial ecosystems in China, J. Hydrol., 603, Part D, 127177.

Lintunen, A., Preisler, Y., Oz, I., Yakir, D., Vesala, T., Hölttä, T., 2021. Bark transpiration rates can reach needle transpiration rates under dry conditions in a semi-arid forest. Front. Plant Sci. 12.

Martínez-Vilalta, J., Anderegg, W.R.L., Sapes, G., Sala, A., 2019. Greater focus on water pools may improve our ability to understand and anticipate drought induced mortality in plants. New Phytol. 223, 22–32.

McDowell, N.G., Fisher, R.A., Xu, C., Domec, J.C., Hölttä, T., Mackay, D.S., et al., 2013. Evaluating theories of drought-induced vegetation mortality using a multimodel experiment framework. New Phytol. 200, 304–321.

Mencuccini, M., Minunno, F., Salmon, Y., Martínez-Vilalta, J., Hölttä, T., 2015. Coordination of physiological traits involved in drought-induced mortality of woody plants. New Phytol. 208, 396–409.

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

Reyes-Acosta, J.L., Lubczynski, M.W., 2014. Optimization of dry-season sap flow measurements in an oak semi-arid open woodland in Spain. Ecohydrology 7, 258–277.

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. Ecohydrol. 9 (5), 871–881.

Siddiq, Z., Cao, K.F., 2018. Nocturnal transpiration in 18 broadleaf timber species under a tropical seasonal climate. For. Ecol. Manage. 418, 47–54.

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.

Singh, K. P., C. P. Kushwaha. 2005. Emerging paradigms of tree phenology in dry tropics. Curr. Sci., 89, 6, Temporary Publisher, pp. 964–75.

Taneda, H., Sperry, J.S., 2008. A case-study of water transport in co-occurring ring-versus diffuse-porous trees: contrasts in water status, conducting capacity, cavitation and vessel refilling. Tree Physiol. 28:1641–1651.

Van Stan, J.T., Dymond, S.F., Klamerus-Iwan, A., 2021. Bark-Water interactions across ecosystem states and fluxes. Front. For. Glob. Change 4.

Wang, S., Ancell, B., Yang, Z.L., Duan, Q., Anagnostou, E.N., 2022. Hydroclimatic extremes and impacts in a changing environment: observations, mechanisms, and projections. J. Hydrol. 608, 127615.

Wittmann, C., Pfanz, H., 2008a. Anti-transpirant functions of stem periderms and their influence on corticular photosynthesis under drought stress. Trees 22, 187–196.

Wittmann, C., Pfanz, H., 2008b. General trait relationships in stems: a study on the performance and interrelationships of several functional and structural parameters involved in corticular photosynthesis. Physiol. Plantarum 134, 636–648.

Wolfe, B.T., 2020. Bark water vapour conductance is associated with drought performance in tropical trees. Biol. Lett. 16, 20200263.

Wullschleger, S.D., Hanson, P.J., Todd, D.E., 2001. Transpiration from a multi-species deciduous forest as estimated by xylem sap flow techniques. For. Ecol. Manage. 143 (1–3), 205–213.

Yoshifuji, N., Kumagai, T.O., Tanaka, K., Tanaka, N., Komatsu, H., Suzuki, M., Tantasirin, C., 2006. Inter-annual variation in growing season length of a tropical seasonal forest in northern Thailand. Forest Ecol. Manag. 229 (1-3):333–339.

Zhang, J., Lu, H., Jia, J., Shen, C., Wang, S., Chu, G., Wang, L., Cui, A., Liu, J., Wu, N., Li, F., 2020. Seasonal drought events in tropical East Asia over the last 60,000 y. Proc. Natl. Acad. Sci. 117, 30988–30992.

Zhao, J., Zhang, Y., Song, F., Xu, Z., Xiao, L., 2013. Phenological response of tropical plants to regional climate change in Xishuangbanna, south-western China. J. Tropical Ecol. 29 (2), 161–172.

Zhu, H., 2006. Forest vegetation of Xishuangbanna, south China. For. Stud. China 8, 1–58.