



Cool-dry season depression in gas exchange of canopy leaves and water flux of tropical trees at the northern limit of Asian tropics

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Abstract Trees on the northern boundary of Asian tropics experience hot-humid and cool-dry seasons, but little is known about their seasonal dynamics in canopy physiology. We used a canopy crane to reach the canopy of nine tropical tree species and measured canopy leaf gas exchange, water status, and trunk sap flux during the hot-humid and cool-dry seasons in Xishuangbanna, China. We found that most tree species exhibited significant reductions in maximum photosynthetic rate (A_{\max}), stomatal conductance (g_{\max}), predawn and midday leaf water potentials, and maximum sap flux density in the cool-dry season. Compared to the hot-humid season, A_{\max} declined by

19–60%, and maximum water flux declined by –14% (an increase) to 42%. The cool-dry season decline in A_{\max} of four species can be partly explained by an increased stomatal limitation (decreased g_{\max} and intercellular CO_2 concentrations). Therefore, a predicted increase in drought in this region may decrease the carbon sequestration and productivity of these forests. We did not find a tradeoff between performance (A_{\max} in the hot-humid season) and persistence through the cool-dry season; species with higher A_{\max} in the hot-humid season did not show higher percent seasonal declines in the cool-dry season. A_{\max} was significantly and positively associated with the trunk sap flux for both seasons, but the association was weaker in the cool-dry season. Thus, our results suggest that some tradeoffs and trait associations are environment dependent. Our results are important for understanding carbon and water fluxes of seasonal tropical forests and their responses to environmental changes.

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Introduction

The dynamics of tree carbon and water fluxes are driven by environmental factors such as temperature, solar radiations, and relative humidity (Fauset et al.

2019; Dusenge and Way 2017; Way et al. 2015). Seasonal dynamics in these environmental factors can lead to changes in canopy leaf physiological performances, which are species specific (Aragao et al. 2014; Chen and Cao 2015; Siddiq et al. 2017). Tree leaf photosynthesis (A) and water fluxes are sensitive to changes in environmental conditions and reach their maximum values under optimum conditions (Tucci et al. 2010; Yang et al. 2012; Zhang et al. 2014a; Gitelson et al. 2014). In the tropics, the optimum conditions are observed during moderate atmospheric temperature and humidity, which create the suitable driving force (vapor pressure deficit) for water fluxes (Siddiq et al. 2017) and suitable temperature for photosynthesis (Cao et al. 2006; Kumagai et al. 2006; Slot et al. 2017; Slot and Winter 2017). In tropical areas with a seasonality in temperature and/or rainfall, (e.g., marginal tropics), the reduction of temperature and/or rainfall during the cool and/or dry season can result in reduced carbon and water fluxes (Vongcharoen et al. 2018; Frenne et al. 2019; Santanoo et al. 2019). Forests at marginal tropics, e.g., those at the northern edge of Asian tropics, are characterized by a seasonality in temperature and rainfall, which results in a hot-humid season and a cool-dry season. This will probably result in the seasonal changes in canopy leaf physiological performances, which have not been well studied until now. These forests are strong carbon sinks and contribute significantly to the global carbon cycle (Zhang et al. 2006, 2016; Tan et al. 2012; Cristiano et al. 2014), but the physiological mechanisms explaining their high carbon-sink function and seasonal dynamics are not well understood.

The marginal tropical rainforests in Xishuangbanna, China, which are on the northern boundary of Asian tropics, are typical Asian tropical rainforests in terms of species composition and phenology, and an important component of the Indo-Burma diversity hotspot (Myers et al. 2000; Cao et al. 2006; Hua 2013). They are also strong carbon sinks (Zhang et al. 2006) contributing significantly to the global carbon cycle. The tropical forests of this region are under the threat of degradation due to global warming, increasing drought, decreasing fog persistence, and the introduction of exotic species for commercial uses (Singh et al. 2019; Zhang et al. 2014a; Qiu 2010; Li et al. 2006). All these changes may significantly alter the water and carbon cycles of the region. For instance, the carbon fixation of the forests was significantly reduced in this

region due to the drought event in 2010 (Zhang et al. 2012). An understanding of water and carbon fluxes of trees from this region under different environmental conditions will help to predict their response to projected climate change including an increase in climate variability and to develop effective management strategies.

Although there are some studies reporting the seasonal changes in photosynthesis of crops and small trees (Zhang et al. 2014a) and ecosystem-level carbon fluxes of the marginal Asian tropical forests (Zhang et al. 2006), more mechanistic studies are needed to understand their canopy physiology in responding to ambient seasonal environmental changes. For instance, temperate plants are found to follow a general tradeoff between maximum photosynthesis in the favorable season, and persistence through the unfavorable season; species with higher maximum photosynthetic performance (A_{\max}) in the favorable season show higher percent seasonal declines in A_{\max} during the cold or dry season (Zhang et al. 2017). However, it is unknown whether trees from the marginal tropics with less seasonality compared to the temperate regions follow the same tradeoff. Understanding tree physiology and its seasonal dynamics of marginal tropical forests will also help to predict the response of temperate forests that are adjacent to them to future warming, and the response of tropical forests to a predicted increase in climate variability (e.g., seasonal drought or dry spells). Further, a more physiological understanding of these forests can improve the performance of the global land surface models, which are used to understand and predict the global water and carbon fluxes in a changing climate. Marginal tropical and subtropical forests are under-represented in these models (Pan et al. 2020; Gentine et al. 2019; Li et al. 2018).

It has been observed that photosynthetic carbon gain and water flux are coupled (Cowan & Farquhar 1977; Santiago et al. 2004, Brodribb and Feild 2000; Fauset et al. 2019; Siddiq et al. 2019) because both processes are regulated by the stomata. A large water flux enabled by a high transport capacity will result in a high leaf water potential (less negative) during active transpiration at a given evaporative demand, which can potentially facilitate photosynthetic gas exchange (Landsberg et al. 2017). However, environmental conditions of the habitat can shift the coupling between water transport and leaf gas exchange (Sack et al. 2005), and therefore, this

coupling can also be potentially changed due to seasonal changes in environmental conditions. The evaporative cooling strategies will adjust according to seasonal changes in temperature. In the cool season, the needs for cooling through canopy transpiration are less, while in the hot-humid season, the canopy needs a significant amount of evaporative cooling to avoid heat damage. In addition, water flux and stomatal conductance may not be the major limiting factors on photosynthesis in the cool season as tropical trees can be sensitive to chilling-induced photodamage (Levitt 1980; Dungan et al. 2003; Huang et al. 2010; Zhang et al. 2014b; Yang et al. 2017). Therefore, water flux and photosynthesis are not necessarily coupled in the unfavorable season. The other factors such as leaf phenology and leaf age that influence leaf photosynthesis (Kitajima et al. 1997, 2002) can also alter the coupling between water flux and carbon gain in the cool-dry season, as these forests have species with a range of leaf life spans including both evergreen and deciduous species. In general, how this coupling responds to environmental changes, and how it shifts in different seasons are not well understood.

Here, we accessed the canopy of tropical trees in Xishuangbanna with a canopy crane and measured canopy leaf carbon assimilation and water fluxes in the hot-humid and cool-dry seasons. The main objectives of the present study were (1) to quantify the seasonal changes in canopy photosynthesis and water flux of trees at the northern limit of Asian tropics; (2) to test whether the potential cool-dry season declines in A_{\max} of some species of this region is due to increased stomatal limitation, and whether the seasonal changes in environmental conditions shift the coordination between maximum water flux and maximum photosynthetic performances; and 3) to test whether there is a tradeoff between maximum photosynthetic performance (A_{\max} in the hot-humid season) and persistence through the cool-dry season (less percent decline in A_{\max}) across species. We hypothesized that the species with high rates of carbon fixation during the hot-humid season have higher seasonal declines in the cool-dry season according to the performance vs endurance tradeoff (Zhang et al. 2017). It was also hypothesized that most tree species will show significant declines in photosynthesis and water use, mainly caused by an increased stomatal limitation due to decreased water availability. We also hypothesized that the coordination between photosynthesis and water flux will be weaker during the cool-dry season due to the increased

limitation of factors other than water transport (e.g., chilling-induced photoinhibition) on photosynthesis.

Materials and methods

Study site and species

The experimental set-up for this study was established in Xishuangbanna Tropical Botanical Garden (XTBG; 21°54' N, 101°46' E, 580 m a.s.l.), southern Yunnan Province, Southwest China. This region has a typical tropical monsoon climate and, hence, a pronounced hot-humid season with plenty of rains from May to October, and a dry season from November to April. The dry season can further be divided into a cool-dry season from December to February and a hot-dry season from March to April. The mean annual precipitation is 1560 mm, approximately 80% of which falls during the wet season. The mean annual temperature of the study site is 21.7 °C (Cao et al. 2006). In this study, we selected 26 individual trees from 9 species in plantation stands of 40 years old (Table 1). Among the nine studied six species, i.e., *Hopea hainanensis*, *Shorea assamica*, *Vatica magachapoi*, *Mesua ferrea*, *Dalbergia odorifera*, and *Pterocarpus indicus* are naturally distributed in the southern China while the other three species: *Anisoptera laevis*, *Dipterocarpus alatus*, and *Swietenia mahagoni* are exotic trees. The former two species are naturally distributed in northern Thailand and adjoining tropical areas while *Swietenia mahagoni* is naturally found in tropical Caribbean islands of the United States. Among the nine species, six are evergreen while the rest are deciduous (Table 1). The canopy physiological measurements were carried out in September 2012 for the hot-humid season, while the cool-dry season measurements were done during the first week of January 2013. All the deciduous species start shedding their leaves at the end of February or the beginning of March and start flushing new leaves in mid-April.

Seasonal differences of climatic variables

There were distinct differences in the atmospheric temperature between the hot-humid and cool-dry seasons of the studied year. The mean daily temperature during the cool-dry season was 18 °C, while it

Table 1 List of species studied, their scientific names, abbreviations, family, DBH range, and replicates

| Scientific name | Abbreviation | Family | Leaf phenology | DBH range (cm) | Number of trees |
|----------------------------------------------|--------------|------------------|----------------|----------------|-----------------|
| * <i>Anisoptera laevis</i> Ridl | Al | Dipterocarpaceae | Evergreen | 31, 33, 37 | 3 |
| * <i>Dipterocarpus alatus</i> Roxb. Ex G.Don | Da | Dipterocarpaceae | Evergreen | 30, 37, 58 | 3 |
| <i>Hopea hainanensis</i> Merr. & Chun | Hh | Dipterocarpaceae | Evergreen | 19, 29, 32 | 3 |
| <i>Shorea assamica</i> Dyer | Sa | Dipterocarpaceae | Evergreen | 17, 20 | 2 |
| <i>Vatica magachapoi</i> Blanco | Vm | Dipterocarpaceae | Evergreen | 20, 22 | 3 |
| <i>Mesua ferrea</i> L. | Mf | Calophyllaceae | Evergreen | 16, 22 | 4 |
| <i>Dalbergia odorifera</i> T.C.Chen | Do | Leguminosae | Deciduous | 18, 19, 23 | 3 |
| <i>Pterocarpus indicus</i> Willd | Pi | Leguminosae | Deciduous | 20, 31 | 2 |
| * <i>Swietenia mahagoni</i> (L.) Jacq | Sm | Meliaceae | Deciduous | 31, 43, 55 | 3 |

Asterisk indicates the exotic species, while the rest are indigenous to southern China

was 25 °C in the hot-humid season. The mean atmospheric vapor pressure deficit (VPD) during the cool-dry season was 0.3 kPa, while in the hot-humid season, it was 0.73 kPa. The average solar radiation in the cool-dry season was 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$, while in the hot-humid season, it was 640 $\mu\text{mol m}^{-2} \text{s}^{-1}$. During normal sunny days, the duration of hourly mean day light with photosynthetic photon flux density (PPFD) > 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the hot-humid season was from 9:00 to 19:00, while during the cool-dry season, the duration was 10:00–18:00 on the top of tree canopies. Thus, there was a two hours difference in light availability to canopy leaves between the hot-humid and cool-dry seasons. The rainfall during the hot-humid months was > 200 mm per month, while in the cool-dry season, it was < 100 mm per month (Fig. 1a–d).

Canopy gas exchange and leaf water potentials

To access the canopies with the height range of 25–35 m, we used a canopy crane mounted on a truck. Trees close to the edges of the stands were not used to minimize potential edge effects. The maximum (light-saturated) leaf photosynthesis (A_{max} ; $\mu\text{mol m}^{-2} \text{s}^{-1}$) and stomatal conductance (g_{smax} ; $\text{mol m}^{-2} \text{s}^{-1}$) were measured using a portable photosynthesis measurement system (LI-6400; LI-COR, Nebraska, USA) under ambient conditions on sunny days for both hot-humid and cool-dry seasons. The maximum gas exchange was measured between 09:00 and 11:00. The chamber temperature during the measurement

time of the hot-humid season was approximately 23 °C, and the leaf to air vapor pressure deficit (VPD_{leaf}) was approximately 1.0 kPa. During the cool-dry season, the chamber temperature was 17 °C and the VPD_{leaf} was 0.7 kPa. The PPFD within the chamber was set at 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ as the maximum gas exchange rates were achieved at this level and to avoid photoinhibition. For each tree, six to eight new fully developed mature leaves from different sun-exposed canopy-top terminal branches of two to four individuals per species were selected to measure canopy gas exchange at the top of the canopy. For each tree, six to eight stable values of photosynthetic rate and stomatal conductance were logged and stored in the LI-6400 instrument, and the average value of each species was calculated. Intrinsic water use efficiency was calculated by dividing the photosynthetic rate with stomatal conductance (Farquhar et al. 1982). The intercellular values of carbon (C_i ; $\mu\text{mol mol}^{-1}$) were also obtained from the LI-6400 while measuring the gas exchange. The leaf water potentials were measured on-site from five to six leaves per tree using a pressure chamber (PMS, Albany, OR, USA). Predawn leaf samples were collected and measured in the field between 06:00 and 07:00, whereas midday samples were collected between 12:30 and 14:30 on sunny days.

Sap flow and meteorological data

We used the daily maximum sap flow data (water flux; peak sap flux density during the day; $\text{g m}^{-2} \text{s}^{-1}$) of

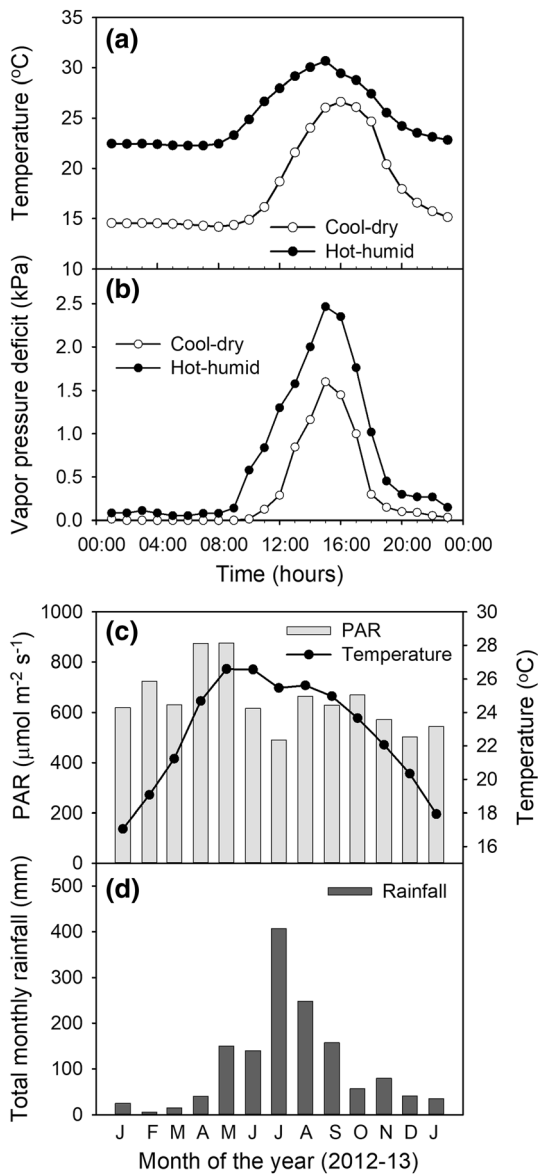


Fig. 1 Diurnal changes in average temperature (a) and vapor pressure deficit (VPD; b) of the cool-dry season (January) and hot-humid season (September); Seasonal dynamics in mean monthly temperature, mean photosynthetic active radiations (PAR) (c), and total monthly rainfall (d) during the years of measurements (2012–2013)

hot-humid and cool-dry seasons from the sap flow measurements for the same trees that were used to measure canopy photosynthetic gas exchange. Sap flow was measured using Granier-type heat dissipation sap flow sensors (Granier 1987) from 2012 to

2013, and the daily maximum sap flow data of the same days with canopy gas exchange measurements were used for this study. The technique involves the heating of one sensor using an electrical source, while the other sensor was not heated and used as the reference sensor. The temperature difference between these two sensors was used to calculate the sap flux density. The details are mentioned in Siddiq et al. (2019). The original Granier equation was calibrated to calculate the sap flux density, as that Granier equation can substantially underestimate the sap flux density of tropical trees (Siddiq et al. 2017). The hourly mean meteorological data, i.e., temperature, solar radiations, relative humidity, and rainfall were collected from the Xishuangbanna Tropical Rain Forest station, situated about 900 m away from the study site.

Data analysis

The effect of species and season on canopy gas exchange (A_{max} and g_{smax}) were analyzed by a two-way ANOVA using SPSS (IBM version 19). The differences in maximum canopy photosynthesis (A_{max}), stomatal conductance (g_{smax}), water use efficiency, intercellular CO_2 concentration, predawn and midday leaf water potentials between the two seasons, for the individual species, were analyzed using a *t* test. Duncan's method was used for the comparison of mean A_{max} and g_{smax} between the hot-humid and cool-dry seasons across the studied deciduous and evergreen species. A linear regression was fitted to the relationships between percentage decline in A_{max} and g_{smax} from the hot-humid to the cool-dry season to test whether the potential decline in A_{max} was associated with decrease g_{smax} . The relationship between A_{max} of hot-humid season and the absolute or percent decline in A_{max} during the cool-dry season was also fitted with a linear regression to test the potential tradeoff between maximum performance and persistence through the cool-dry season. The association of maximum photosynthetic rate or stomatal conductance with the maximum sap flux density was analyzed with a linear regression to test the coupling between water flux and photosynthesis for both seasons. The generation of graphics and regression analyses were carried out using the Sigmaplot software (version-12.5; Systat Software Inc. USA).

Results

Variations across species

The studied species showed high variations in canopy photosynthetic gas exchange (A_{\max} and $g_{s\max}$), water use efficiency, and midday leaf water potentials in both the hot-humid and cool-dry seasons. The significant effect of species and season, and species–season interaction was observed among the studied species (Table 2). Further, evergreen species had significantly higher A_{\max} during both the hot-humid and cool-dry seasons (Table 3). The $g_{s\max}$ of the hot-humid season was significantly higher in evergreen than in deciduous trees, while no significant difference was detected between the two groups of trees in the cool-dry season (Table 3). The highest A_{\max} across species were found in *D. alatus*, i.e., $18.71 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $11.59 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the hot-humid and cool-dry seasons, respectively. The lowest A_{\max} in the hot-humid season was observed in *S. assamica*, ($6.85 \mu\text{mol m}^{-2} \text{s}^{-1}$). In the cool-dry season, the lowest A_{\max} was found in *M. ferrea*, which was $3.24 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 2). The highest stomatal conductance was found in *D. alatus*, which were 0.37 and $0.20 \text{ mol m}^{-2} \text{s}^{-1}$ during the hot-humid and cool-dry seasons, respectively. The lowest $g_{s\max}$ during the hot-humid season was found in *S. assamica* ($0.039 \text{ mol m}^{-2} \text{s}^{-1}$). In the cool-dry season, the lowest $g_{s\max}$ was found in *M. ferrea*, which was $0.031 \text{ mol m}^{-2} \text{s}^{-1}$. The species also showed high variations in their water use efficiency in both seasons, ranging from 49.42 to $204.65 \mu\text{mol mol}^{-1}$ during the hot-humid season, and 55.45 – $190.04 \mu\text{mol mol}^{-1}$ in

the cool-dry season. The intercellular CO_2 concentration also varied highly across species. In the hot-humid season, it ranged from 100 to $350 \mu\text{mol mol}^{-1}$, while in cool-dry season, it ranged from 174 to $28 \mu\text{mol mol}^{-1}$ (Fig. 2c, d). The predawn leaf water potential ranged from -0.26 MPa (*D. alatus*) to -0.53 MPa (*A. laevis*) in the hot-humid season, and it ranged from -0.46 MPa (*M. ferrea*) to -0.81 MPa (*V. magachopoi*) in the cool-dry season. The midday leaf water potential ranged from -0.62 MPa (*D. alatus*) to -2.0 MPa (*M. ferrea*) in the hot-humid season, and it ranged from -1.0 MPa (*D. alatus*) to -2.56 MPa (*S. assamica*) in the cool-dry season.

Seasonal declines in canopy photosynthetic gas exchange and water flux

The seasonal dynamics in maximum photosynthetic rate (A_{\max}) and stomatal conductance ($g_{s\max}$) differed among individual species (Table 2). Significant seasonal declines in the values of A_{\max} were found in six out of the nine species, while the other three species did not significantly change (Fig. 2a). Significant seasonal declines in $g_{s\max}$ were found in only four species. Two species showed significant increases in $g_{s\max}$ in the cool-dry season, and four species showed significant declines of $g_{s\max}$ in the cool-dry season, while the remaining three species showed no change (Fig. 2b). The percentage of photosynthesis reduction in the cool-dry season compared to the hot-humid season ranged from 19% in *S. mahagoni* to 60% in *M. ferrea*. Three species showed a significant decline in water use efficiency in the cool-dry season compared to the hot-humid season, while two species showed significant increases and the other three species showed no change (Fig. 2c). Four species showed significant declines in the intracellular CO_2 concentration in the cool-dry season compared to the hot-humid season, while three species showed significant increases and two species showed no change (Fig. 2d). For daily maximum sap flux density, five out of the nine species showed significant declines in the cool-dry season compared to the hot-humid season, while the other four species (*D. odorifera*, *H. hainanensis*, *S. assamica* and *S. mahagoni*) did not show significant differences between the two seasons (Fig. 3). A significant decline in predawn leaf water potential in the cool-dry season (compared to the hot-

Table 2 Two-way ANOVA results for the effect of species and season on photosynthetic rate and stomatal conductance

| Predictor | SS | df | F | P |
|-----------------|-----------|----|---------|----------|
| Species | | | | |
| A_{\max} | 14,700.47 | 8 | 1429.12 | < 0.0001 |
| $g_{s\max}$ | 9.46 | 8 | 2651.2 | < 0.0001 |
| Season | | | | |
| A_{\max} | 3393.76 | 1 | 2639.4 | < 0.0001 |
| $g_{s\max}$ | 0.250 | 1 | 559.055 | < 0.0001 |
| Species: season | | | | |
| A_{\max} | 7833.78 | 8 | 76.19 | < 0.0001 |
| $g_{s\max}$ | 1.879 | 8 | 526.31 | < 0.0001 |

Table 3 Duncan's test result for the comparison of mean A_{\max} and g_{smax} between the hot-humid and cool-dry seasons across the studied deciduous and evergreen species

| | | <i>F</i> value | <i>P</i> value |
|-----------|------------------------------------------|----------------|----------------|
| Season | A_{\max} (Deciduous, Evergreen) | | |
| Hot-humid | 9.54 (\pm 1.16), 12.46 (\pm 4.81) | 61.17 | < 0.001 |
| Cool-dry | 6.33 (\pm 1.71), 7.384 (\pm 3.905) | 18.26 | < 0.01 |
| Season | g_{smax} (Deciduous, Evergreen) | | |
| Hot-humid | 0.06 (\pm 0.002), 0.20 (\pm 0.01) | 221.95 | < 0.001 |
| Cool-dry | 0.10 (\pm 0.003), 0.11 (\pm 0.002) | 3.75 | 0.053 |

humid) was found in six out of the nine species (not in *A. laevis*, *D. odorifera*, and *M. ferrea*). A significant cool-season decline in midday leaf water potential was found in seven species but not in *M. ferrea* and *P. indicus* (Fig. 4a, b).

Relationship between water flux and photosynthetic gas exchange

A significant and positive relationship ($R^2 = 0.50$; $P < 0.01$) was found between the percent decline of A_{\max} and the percent decline in g_s from the hot-humid to the cool season (Fig. 5). A significant and positive relationship was also found between maximum sap flux density and photosynthetic rate in both the hot-humid and cool-dry seasons, although the relationship was weaker during the cool-dry season as compared to that of the hot-humid season (Fig. 6a). There was also a significant and positive relationship between maximum sap flux density and stomatal conductance in the hot-humid season (Fig. 6b). The relationship between sap flux density and stomatal conductance during the cool-dry season was not significant ($P > 0.1$, Fig. 6b). No relationship between the A_{\max} of the hot-humid season and the percent decline in A_{\max} from the hot-humid to the cool-dry season has been found across species (relationship not shown).

Discussion

Our study quantified the seasonal dynamics in canopy leaf photosynthetic gas exchange, and trunk water flux of nine tree species at the northern limit of the Asian tropics. The studied tree species showed high variations in canopy photosynthetic performances and

trunk water flux, as well as their seasonal changes (two-way ANOVA; Table 2). This pattern suggests diversified responses of trees in the marginal tropics to the seasonal unfavorable conditions and diverged strategies in achieving high annual carbon assimilation. Our results did not support the hypothesis that species with high photosynthetic rates in the hot-humid season will have more percent declines in cool-dry season, i.e., a photosynthetic performance vs. persistence tradeoff, as found in temperate plants (Zhang et al. 2017). The absence of a tradeoff between photosynthetic performances under favorable conditions and persistence through the unfavorable season (low seasonal declines) in marginal tropical trees could be because the “stress” level in the cool-dry season of this region is not strong enough to make this tradeoff detectable. Also, the leaf age effects (Field 1983, 1987; Kitajima et al. 1997, 2002) and potential different strategies in responding to seasonal stress between evergreen and deciduous species may confound the potential tradeoff.

Six out of nine species studied showed significant declines in the maximum photosynthesis rate in the cool-dry season. However, despite significant declines, the cool-dry season canopy photosynthetic rate of the studied species ranged from 3.24 to 11.59 $\mu\text{mol m}^{-2} \text{s}^{-1}$, indicating a significant amount of net carbon gain during the cool-dry season. This finding provides a physiological explanation of the ecosystem-level carbon sequestration during the cool-dry season in this region and their great contribution to the global carbon cycles (Zhang et al. 2006). Furthermore, soil and tree nocturnal respiration is lower due to lower temperatures during the cool-dry season (Barbour et al. 2005; Anderegg et al. 2015; Siddiq and Cao 2018), which can also contribute towards more

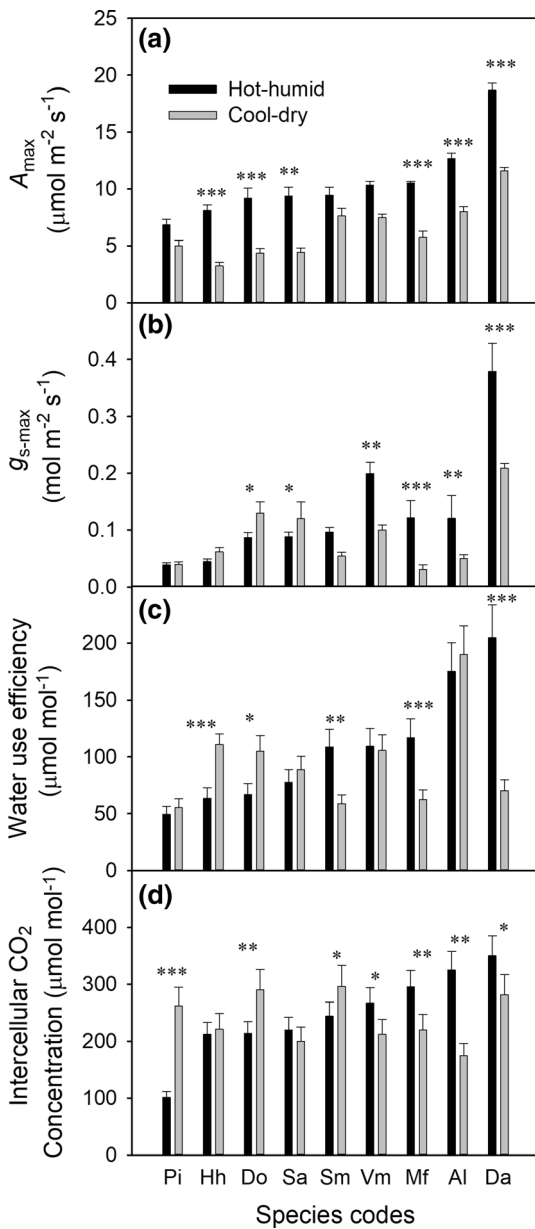


Fig. 2 Maximum photosynthetic rate (A_{\max} , **a**), stomatal conductance ($g_{s-\max}$, **b**), water use efficiency (**c**), and intercellular CO_2 concentration (**d**) of nine tropical tree species in the hot-humid and cool-dry seasons, where $***P < 0.0001$, $**P < 0.001$, $*P < 0.01$, ns indicates non-significance. Bars indicate species means + SEs and the asterisks indicate the significant seasonal differences in the individual species. Species codes are listed in Table 1

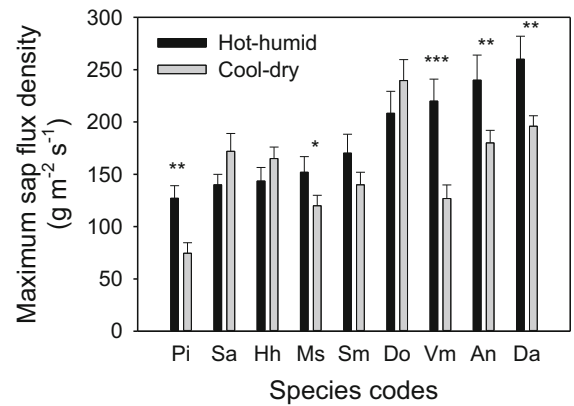


Fig. 3 Maximum sap flux density in the hot-humid and cool-dry seasons of nine tropical tree species. Species codes are listed in Table 1, where $***P < 0.0001$, $**P < 0.001$, $*P < 0.01$, ns indicates non-significance. Bars are species means + SEs, the asterisks indicate the significant seasonal differences in the individual species

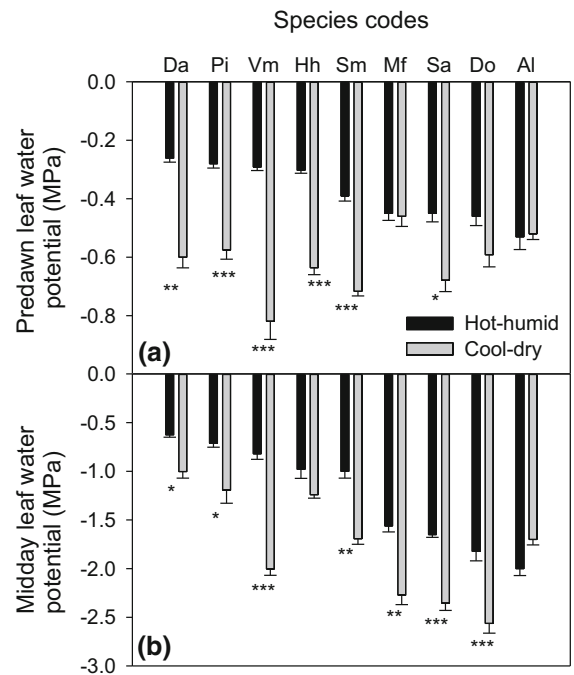


Fig. 4 Predawn leaf water potential (**a**) and midday leaf water potential (**b**) in the hot-humid and cool-dry seasons. Species codes are listed in Table 1, where: $***P < 0.0001$, $**P < 0.001$, $*P < 0.01$. Bars indicate species means + SEs and the asterisks indicate the significant seasonal differences in the individual species

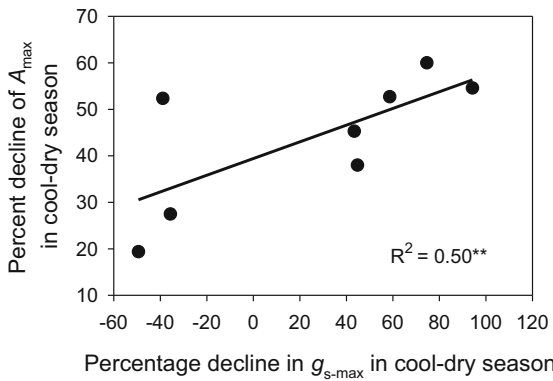


Fig. 5 The relationship between percent seasonal decline in A_{max} and g_{s-max} from the hot-humid to the cool-dry season across nine tropical tree species studied. The line is a linear regression fitted to the data, where $**P < 0.001$

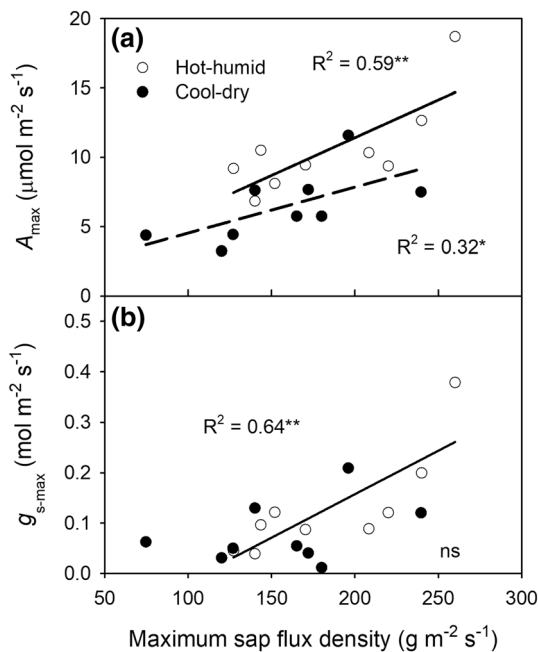


Fig. 6 Maximum photosynthetic rate (**a**; A_{max}) and stomatal conductance (**b**; g_{s-max}) in relation to maximum sap flux density in hot-humid season (open dots) and cool-dry season (closed dots) across the studied species. Solid lines are linear regressions fitted to the hot-humid season data and the dashed line is a linear regression fitted to the cool-dry season data, where $**P < 0.001$, $*P < 0.01$, ns indicates that the relationship during the cool-dry season between g_s and sap flux density was not significant

positive ecosystem carbon accumulation in the cool-dry season. The water loss of the trees, indicated by leaf stomatal conductance and tree sap flux density,

also declined during the cool-dry season in five species. This could be beneficial to these trees for water conservation in the cool-dry season. Water conservation in the cool-dry season is important for trees as most tree species experienced some degree of drought stress indicated by predawn water potentials being lower than -0.5 MPa, and as low as -0.8 MPa. The leaf water potentials were generally reflecting the rainfall pattern; a significantly lower rainfall in the cool-dry season will result in dryer soils and, therefore, lower leaf water potentials. Interestingly, the VPD in the cool-dry season was lower compared to the hot-humid season despite lower rainfall (Fig. 1). Lower VPD and, thus, lower transpirational demand can be the reason for lower water flux in the cool-dry season (Fig. 3; Siddiq and Cao, 2016). Since the VPD was lower in the cool-dry than in the hot-humid season (due to lower temperatures), the lower midday leaf water potentials in the cool-dry season compared to the hot-humid season cannot be explained by an increased transpirational demand. Rather, it should be related to decreased soil water content.

Our results suggest that the cool-dry season decline in A_{max} in some tree species can be explained by an increased stomatal limitation. The percent decline in A_{max} in the cool-dry season is significantly associated with the percent decline in g_s , suggesting that the decline in A_{max} can be at least partly explained by increased stomatal limitation. This is at least true for four species (*A. laevis*, *D. alatus*, *M. ferrea*, and *V. magachopai*). For these four species showing significant seasonal declines in A_{max} , their g_{smax} and C_i also declined significantly in the cool-dry season compared to the hot-humid season (Fig. 2). For them, decreased g_s is limiting CO_2 uptake, resulting in lower C_i and A_{max} in the cool-dry season. For the other two showing significant declines in A_{max} (*P. indicus*, *H. hainanensis*), their g_{smax} and C_i showed increases or no change in the cool season. Therefore, their decreases in A_{max} cannot be explained by increased stomatal limitation but can probably result from low-temperature-induced photoinhibition, as found in crops and tree seedlings in the region (Huang et al. 2010; Zhang et al. 2014b), or reduced photosynthetic carboxylation capacity under lower temperatures (Kumarathunge et al. 2019). In addition, leaf age may also be a possible factor explaining seasonal declines in A_{max} (Field 1983, 1987; Kitajima et al. 1997, 2002). A recent study (Bielczynski et al. 2017)

emphasizes that both increased leaf and plant ages can cause declines in photosynthetic performance. For evergreen trees, because they continuously flush leaves throughout the year in this region and we selected newly-fully-developed leaves for measurements, the leaf age effect on A_{\max} should be minor. For one deciduous species showed seasonal declines in A_{\max} (*P. indicus*) but not in $g_{s\max}$, the age effect could at least partly explain the decline in A_{\max} because the leaves were six weeks away from shedding during the cool-dry season measurements. However, no declines in A_{\max} were found in the other two deciduous species. Notably, two species with more southern and warmer native distribution limits (*A. laevis* and *D. alatus*; see materials and methods) showed the highest A_{\max} among all the studied species in both the hot-humid and cool-dry seasons. This suggests their high physiological plasticity in responding to changes in temperatures and contradicts our general understanding that species with warmer native habitats have lower resistance to low temperatures (Armando et al. 2016; Korner 2016).

Our study found a seasonal shift in the coupling between water flux and photosynthesis, and the coupling is weakened during the cool-dry season. The coupling of canopy photosynthesis and trunk water flux during both the hot-humid and cool-dry seasons indicate the canopy level synchronization of these two processes, supporting Drake et al. (2018). However, although the photosynthetic rate and the trunk water flux remained significantly associated during the cool-dry season, the coefficient of the relationship was lower compared to the hot-humid season. The same pattern was found for the relationship between stomatal conductance and trunk water flux. It was significant in the hot-humid season but became not significant during the cool-dry season. The weaker coupling between canopy photosynthesis and trunk water flux during the cool-dry season compared to the hot-humid season could be because there are more other limiting factors on canopy photosynthesis rather than water supply in the cool-dry season. For instance, chilling can induce declines in leaf photosynthetic electron transport (Huang et al. 2010; Zhang et al. 2014c) and carboxylation activity (Kumarathunge et al. 2019). Also the leaf age effect (Field 1983, 1987; Kitajima et al. 1997, 2002) may also change the coupling.

Conclusion

In conclusion, the studied trees showed a high variation in seasonal dynamics of canopy leaf gas exchange at the northern limit of Asian tropics. Three species showed no seasonal declines in A_{\max} , while the rest also maintained positive carbon assimilation during the cool-dry season, suggesting that the forests are productive throughout the year. These results also provide a physiological explanation for the carbon-sink function of the forests in the cool-dry season (Zhang et al. 2006). The seasonal declines in gas exchange are associated with increased stomatal limitation in some but not all the tree species, suggesting that further warming and increased VPD may have different impacts on limiting photosynthesis of different species. Variations in the response to seasonal changes in temperatures and soil water content also suggest a potential shift in species composition of the forests under climate change. Further, some of the tree species showed water stress with predawn water potentials being as negative as -0.8 MPa in the cool-dry season, indicating that an increase in drought in this region (Jia and Pan 2016; Zhang et al. 2019) could further exacerbate the water stress and decrease the carbon sequestration potential of tropical forests in this region. In addition, we did not find the hypothesized tradeoff between maximum photosynthetic performance under favorable conditions and persistence through the unfavorable season as found in temperate plants. We also found a seasonal shift in the coupling between water flux and photosynthesis. Therefore, our study confirms that a lot of trait correlations and tradeoffs are environment or climate-dependent (Sack et al. 2005).

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Data availability Data Availability can be provided on request.

Declarations

Conflict of interest The authors declare that they have no competing interest.

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