Sustained diurnal photosynthetic depression in uppermost-canopy leaves of four dipterocarp species in the rainy and dry seasons: does photorespiration play a role in photoprotection?

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Summary Diurnal and seasonal changes in gas exchange and chlorophyll fluorescence of the uppermost-canopy leaves of four evergreen dipterocarp species were measured on clear days. The trees, that were growing in a plantation stand in southern Yunnan, China, had canopy heights ranging from 17 to 22 m. In the rainy season, Dipterocarpus retusus Bl. had higher photosynthetic capacity ($A_{\text{max}}$) than Hopea hainanensis Merr. et Chun, Parashorea chinensis Wang Hsie and Vatica xishuangbannaensis G.D. Tao et J.H. Zhang (17.7 versus 13.9, 11.8 and 7.7 $\mu$mol m$^{-2}$ s$^{-1}$, respectively). In the dry season, $A_{\text{max}}$ in all species decreased by 52–64%, apparent quantum yield and dark respiration rate decreased in three species, and light saturation point decreased in two species. During the diurnal courses, all species exhibited sustained photosynthetic depression from midmorning onward in both seasons. The trees were able to regulate light energy allocation dynamically between photochemistry and heat dissipation during the day, with reduced actual photochemistry and increased heat dissipation in the dry season. Photorespiration played an important role in photoprotection in all species in both seasons, as indicated by a continuous increase in photorespiration rate in the morning toward midday and a high proportion of electron flow (about 30–65% of total electron flow) allocated to oxygenation for most of the day. None of the species suffered irreversible photoinhibition, even in the dry season. The sustained photosynthetic depression in the uppermost-canopy leaves of these species could be a protective response to prevent excessive water loss and consequent catastrophic leaf hydraulic dysfunction.

Keywords: chlorophyll fluorescence, electron flow, gas exchange, heat dissipation, hydraulic conductivity.

Introduction Canopy leaves are the most important contributors to CO$_2$ fixation of tropical forest ecosystems. On clear days, the upper-canopy leaves of tropical rainforest trees are exposed to high irradiance, high air temperature, but low air humidity, resulting in high leaf-to-air vapor pressure deficit (LAVPD), particularly at midday (e.g., Jones 1992). Upper-canopy leaves may experience hydraulic resistance because of the path length effect of water transport (Koch et al. 2004) and dynamic vessel embolism in the leaves induced by high transpiration rates (Brodribb and Holbrook 2004). Both high LAVPD and hydraulic resistance can induce stomatal limitations to photosynthesis (Meinzer et al. 1997, Ishida et al. 1999b, Bonal et al. 2000, Koch et al. 2004). High irradiance and temperature can induce nonstomatal limitations to photosynthesis through the effects of deactivation of photosynthetic enzymes and the reduction of photochemistry (Shinha et al. 1997, Demmig-Adams and Adams III 2006). Therefore, photosynthetic depression around midday is often found in the upper-canopy leaves.

Recently, Brodribb and Holbrook (2007) identified a close relationship between photosynthetic depression and reduction in leaf hydraulic conductivity ($K_{\text{leaf}}$) in response to decreased leaf water potential ($\Psi_{\text{leaf}}$) in the canopy leaves of tropical rainforest trees. Two major types of diurnal photosynthetic depression in the canopy leaves of tropical rainforest trees have been reported: (1) moderate photosynthetic depression only around midday (e.g., Brodribb and Holbrook 2004, 2007) and (2) sustained depression from late morning onward (e.g., Kenzo et al. 2003, Brodribb and Holbrook 2007). In the first type, $K_{\text{leaf}}$ falls precipitously only after a threshold value of $\Psi_{\text{leaf}}$ is reached, whereas in the second type, $K_{\text{leaf}}$ linearly declines with $\Psi_{\text{leaf}}$.
The first type enables the leaves to assimilate more CO₂, but with greater risk of catastrophic hydraulic dysfunction, probably in shoots as well, whereas the second type provides better protection against catastrophic hydraulic dysfunction at the cost of lower daily CO₂ assimilation.

Photosynthetic depression of forest canopy leaves results in the absorption of excess light energy by chloroplasts. Heat dissipation of excess excitation energy within the light-collecting chlorophyll- and the carotenoid-binding protein complexes of photosystem (PS) II is considered to be one of the major mechanisms of photoprotection (Niyogi 1999, Demmig-Adams and Adams III 2000). Studies on the canopy leaves of tropical rainforest trees have revealed that when midday depression in stomatal conductance (gₛ) limits CO₂ supply to the mesophyll, photorespiration increases (Ishida et al. 1999a, 1999b, Flexas and Medrano 2002). Photorespiration dissipates excess ATP, reducing the energy released from the photosynthetic light reactions and thus minimizing the photodamage (Ishida et al. 1999a, 1999b). Although photorespiration has been studied in many plants, its photoprotective role in rainforest canopy leaves is less known. The protective function of increased heat dissipation and photorespiration could be particularly important in seasonal tropical areas, where low soil water availability during the dry season can lead to a higher probability of xylem embolism and to a decreased gₛ. However, because water deficits have little effect on light absorption by chloroplasts, drought stress increases the risk of photoinhibition (Ishida et al. 2006).

Dipterocarpaceae is the most important tree family both ecologically and economically in tropical Asia, and many dipterocarps are canopy or emergent trees in Asian tropical rainforests (Ashton 1991). Because of their great stature, direct measurements of photosynthetic processes in the canopy leaves of the mature dipterocarp forest trees pose a challenge. Although a few studies have reported photosynthetic measurements of the canopy leaves of dipterocarp species (e.g., Kenzo et al. 2003, 2004, 2006), the majority of our knowledge of photosynthesis in dipterocarps is limited to studies on seedlings or saplings (e.g., Lee et al. 1997, Scholes et al. 1997, Cao 2000a, Leakey et al. 2003, Norisada and Kojima 2005).

In the present study, photosynthetic capacity and diurnal changes in gas exchange and chlorophyll fluorescence in the uppermost-canopy leaves of four dipterocarp species in a plantation stand were compared between the rainy and the dry seasons. We attempted to answer two questions: (1) To what extent does photosynthetic depression occur during a clear day in the uppermost-canopy leaves of these dipterocarp species in the two seasons? and (2) How do photoprotective mechanisms, heat dissipation and photorespiration respond to the photosynthetic depression in the different seasons?

Materials and methods

Study site and species

This study was conducted in a dipterocarp plantation stand of about 7 ha at the Xishuangbanna Tropical Botanical Garden (21°41' N and 101°25' E, 570 m a.s.l.), Chinese Academy of Sciences, southern Yunnan, China. Over 40 dipterocarp species from the tropical areas of Asia have been collected in this stand, of which 13 species are found in southern China. Mean annual temperature is 21.7 °C and mean annual precipitation is 1560 mm with 80% of precipitation occurring from May to October. On clear days, photosynthetic photon flux (PPF), air temperature and vapor pressure deficit (VPD) are higher in the rainy season than in the dry season, with the highest PPF occurring at midday and the highest air temperature and VPD occurring between 1400 and 1600 h (Figure 1).
The monthly temperature, rainfall and sunshine hours for a 1-year period that covers the study periods are shown in Table 1. The soil is sandy alluvium, containing 0.875 g kg$^{-1}$ N, 0.329 g kg$^{-1}$ P and 9.693 g kg$^{-1}$ K at 0–20 cm depth.

The four dipterocarp species selected for the study were introduced to the plantation stand in 1986 – *Dipterocarpus retusus* Bl., *Parashorea chinensis* Wang Hsie and *Vatica xishuangbannaensis* G.D. Tao et J.H. Zhang were from Yunnan Province and *Hopea hainanensis* Merr. et Chun was from the Hainan island, southern China. They are all deep-rooted evergreen climax canopy species of tropical rainforests, with *P. chinensis* being an emergent species above the canopy. The leaf life span (LLS) of *P. chinensis* is about 1 year, with leaf exchange occurring at the start of the rainy season (data not shown). The LLS of the other three species is about 1.5 years with leaf shedding and flush concentrated in the late dry season. *Dipterocarpus retusus* and *H. hainanensis* bloom during May–June, with fruit ripening occurring during November–January. The other species bloom in the early rainy season (May–June), with fruit ripening occurring in the late rainy season (August–September; data not shown).

Trees were planted in a grid, with $3 \times 2$ m between individuals. In 2004, the canopy height of *D. retusus* was about 19 m and the canopy height of the other species was about 17 m, with the corresponding trunk diameters at a breast height of about 20 and 18 cm. Mean height and diameter growth rate of the four species are 0.88–1.05 m year$^{-1}$ and 0.82–1.23 cm year$^{-1}$, respectively.

### Leaf water potential

We accessed the upper canopies of the trees with a crane mounted on a truck that was driven along the paths around the stand. Predawn ($\Psi_{pd}$) and midday ($\Psi_{md}$) leaf water potentials were measured on a canopy leaf of each of three to five trees per species with a pressure chamber (SKPM 1400, Skye Instruments, Powys, UK). We measured $\Psi_{md}$ in the rainy season between August 30 and September 2, 2004, and measured $\Psi_{pd}$ and $\Psi_{md}$ on the same days in the late dry season between March 5 and 9, 2007 and again in the rainy season between August 25 and 26, 2008.

### Photosynthetic light response curves and chlorophyll concentration

During the measurement periods in the rainy season 2004 and in the late dry season 2007, photosynthetic light response curve data were obtained by measuring a fully expanded leaf from each of three to four trees per species between 0800 and 1100 h (to avoid midday depression in photosynthesis), with a portable infrared gas analyzer (LI-6400, Li-Cor, Lincoln, NE). Before measurements, leaves were fully adapted to sunlight on clear days or to artificial light of 1000 $\mu$mol m$^{-2}$ s$^{-1}$ provided by the integrated LED light source for about 15 min on cloudy days. The PPF varied from 2000, 1500, 1000, 500, 200, 100, 50 and 20 to 0 $\mu$mol m$^{-2}$ s$^{-1}$. Net assimilation rate ($A_n$) at each PPF was recorded when it was stable (usually 3–5 min), with CO$_2$ concentration inside the leaf chamber maintained at 380 $\mu$mol mol$^{-1}$. During the measurements, the ambient air humidity was 55–65% and 35–50%, and leaf temperature was about 28 and 23 °C in the rainy and dry seasons, respectively. Mean maximum air temperatures in the wet and the dry periods were similar (Table 1); lower leaf temperature in the dry period is consistent with lower mean daily temperature in the dry period.

Maximum assimilation rate ($A_{max}$) and dark respiration rate ($R_d$) were derived from the photosynthetic light response curves that were fitted with a non-rectangular hyperbola equation (Leverenz 1987):

$$A_n = \left\{ \frac{(PPF)\Phi + A_{max} - \left[((PPF)\Phi + A_{max})^2 - 4\Phi A_{max}C\right]^{0.5}}{2C - R_d} \right\}$$

where $C$ is the convexity of the curve and $\Phi$ is the apparent quantum yield that was calculated as the slope of the $A_n$ versus PPF relationship between 0 and 100 $\mu$mol m$^{-2}$ s$^{-1}$. The PPF at 0.9 $A_{max}$ was taken as the light saturation point (LSP). The coefficients of determination for all regressions of the photosynthetic light response curves were >0.98.

Leaves measured for photosynthetic light response curves were collected in the morning and analyzed for chlorophyll concentration by the method described by Johnston et al. (1984).
Diurnal changes in gas exchange and chlorophyll fluorescence

Diurnal changes in gas exchange and chlorophyll fluorescence were measured in at least eight intact, fully expanded sunlit leaves at the uppermost-canopy of three to four trees per species, at 1–2 h intervals from the early morning to the late afternoon. Measurements were made on clear days in the rainy season 2004 on August 30 for \textit{D. retusus} and \textit{P. chinensis}, August 31 for \textit{H. hainanensis}, and September 2 for \textit{V. xishuangbannaensis}, and in the late dry season 2007 on March 5 for \textit{V. xishuangbannaensis}, March 6 for \textit{H. hainanensis}, March 5–6 for \textit{P. chinensis} and March 9 for \textit{D. retusus}. Dew on the leaf surfaces in the early morning was dried with tissue paper before the measurements. We measured $A_n$, $g_s$, and LAVPD with the Li-Cor LI-6400 gas analyzer.

Immediately after each gas exchange measurement, chlorophyll fluorescence was measured on other parts of the same leaves, avoiding the shading effect of the previous gas exchange measurement, with a portable fluorometer (FMS2, Hansatech Instruments Ltd., Norfolk, UK). Steady-state chlorophyll fluorescence ($F_s$) and maximal fluorescence ($F_{m}'$) in the light-adapted state were determined. Incident PPF was measured with a quantum sensor attached to the leaf clip holder.

The leaf temperature was determined with a thermocouple. Incident PPF was measured with a quantum sensor attached to the leaf clip holder.

The photons absorbed by the PSII antennae were divided into fractions in photochemistry dissipation ($\Phi_{\text{PSII}}$), regulated non-photochemical dissipation ($\Phi_{\text{NPQ}}$), and constitutive ($\Phi_{\text{C}}$) and fluorescence ($\Phi_{\text{F}} = \Phi_{\text{TD}} + \Phi_{\text{C}}$) energy dissipation, according to the following formulae (Hendrickson et al. 2004)

\begin{align}
\Phi_{\text{PSII}} &= 1 - F_s/F_m', \\
\Phi_{\text{TD}} &= F_s/F_m, \\
\Phi_{\text{NPQ}} &= F_s/F_m' - F_s/F_m.
\end{align}

where $F_m$ is the predawn maximum fluorescence. To determine $F_m$, at the end of the diurnal photosynthetic measurements, twigs were collected and the based ends were cut with a sharp razor when the remaining had submerged in water. They were kept in darkness overnight with the cut ends remaining submerged in water. Next morning, minimum fluorescence ($F_o$) was measured under dim measuring light, and then $F_m$ was measured following a pulse of actinic light of 5000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Maximum quantum yield of PSII was calculated as $F_v/F_m = (F_m - F_o)/F_m$.

Total electron transport rate ($J_T$) through PSII was estimated according to Krall and Edwards (1992)

\begin{equation}
J_T = \Phi_{\text{PSII}}L_{\text{abs}}(\text{PPF})0.5.
\end{equation}

where $L_{\text{abs}}$ is the leaf absorptance that is 0.92 for \textit{D. retusus} and \textit{H. hainanensis}, 0.91 and 0.89 for \textit{P. chinensis} and \textit{V. xishuangbannaensis}, respectively, measured with a portable spectrometer attached to an integrated sphere (USB4000, Ocean Optics, Dunedin, FL). These leaf absorptance values are close to those of dipterocarp leaves from a Bornean heath forest (Cao 2000b).

We divided $J_T$ into two components, $J_C$ and $J_O$, representing the electron flows devoted to carboxylation and oxygenation of RuBP, respectively. On the assumption that electron flow to the Mehler-ascorbate peroxidase reaction is negligible, $J_O$, $J_C$, and photorespiration rate ($R_d$) were calculated as (Valentini et al. 1995)

\begin{align}
J_O &= 2/3(J_T - 4(A_n + R_d)), \\
J_C &= 1/3(J_T + 8(A_n + R_d)), \\
R_d &= 1/12(J_T - 4(A_n + R_d)),
\end{align}

where $R_d$ is the dark respiration rate of the leaves. In the dry season, $R_d$ was determined after the leaves were dark adapted under a black cloth for 3 min after each diurnal measurement of chlorophyll fluorescence. In the rainy season, $R_d$ was derived from the photosynthetic light response curve with calibration according to actual leaf temperature. A $Q_{10}$ of 2.2 that was averaged from a range of tropical rainforest species was used (Meir et al. 2001).

Hydraulic conductivity and wood traits

Four to six uppermost-canopy shoots from three to four trees per species which were exposed to full sunlight were collected in the morning in the rainy season, cut in water, and transported to the laboratory to determine the maximum hydraulic conductivity ($k_h$), as described by Santiago et al. (2004). Deionized water under a pressure of 0.2 MPa was pumped through a 25-cm-long shoot segment for 15–20 min to remove the embolism, then $k_h$ was calculated as the water flow rate through the shoot segment under a low gravitational pressure (5 kPa) generated by a hydraulic head of 50 cm (Sperry et al. 1988). Leaf-specific hydraulic conductivity ($k_l$) was calculated as the ratio of $k_h$ to the total leaf area distal to the stem segment.

Wood density of a shoot was determined as the ratio of sapwood dry mass (dried at 80 °C for 48 h) to its wet volume, which was determined by the displacement of water. Some wood segments of the shoots were stored in 1:1 (v/v) ethanol:glycerol for 2 months and then transverse sections of about 5 $\mu\text{m}$ thickness were cut with a microtome. Vessel diameter and density were measured with the aid of a microscope.

Data analysis

The effects of season and species on leaf water potentials, photosynthetic traits, predawn $F_v/F_m$ and chlorophyll
concentrations were evaluated by the two-way analysis of variance (ANOVA). Differences in vessel diameter and density, wood density and \( k_1 \) among species were tested by one-way ANOVA. Differences in the regression lines of \( A_n \) against \( g_s \) and \( g_s \) against LAVPD between seasons were compared by the analysis of covariance (ANCOVA). Slopes of the regression lines were compared first. If slopes between two regression lines were not significantly different, then the intercepts were compared using a common slope. Relationships between fractions of light energy partitioning and PPF and between \( g_s \) and \( J_0/J_C \) ratio were analyzed by linear regressions.

Results

Water status, photosynthetic and hydraulic characteristics

In most cases, season and species had significant effects on leaf water potentials, photosynthetic characteristics, predawn \( F_o/F_m \), chlorophyll concentrations and Chl a/b ratios (Table 2). Dipterocarpus retusus had the highest \( A_{max} \) and \( V. \) xishuangbannaensis had the lowest \( A_{max} \), with a 52–64% reduction in \( A_{max} \) among species in the dry season compared with the rainy season (cf. Figure 2). In the dry season, the values of \( \Phi \) and \( R_d \) were significantly reduced in three species, whereas LSP, chlorophyll concentrations and Chl a/b ratios decreased in two species compared with the corresponding values in the rainy season. In all species in both seasons, predawn \( F_o/F_m \) remained above 0.7.

Dipterocarpus retusus had the largest vessels, lowest vessel and wood densities, and highest \( k_1 \) among species (Table 3), which was consistent with its high \( A_{max} \) (Table 2). In the rainy season, \( A_{max} \) was negatively correlated with wood density \( (r^2 = 0.84, P = 0.08 \text{ and } n = 4) \) and positively correlated with vessel diameter \( (r^2 = 0.86 \text{ and } P = 0.07) \) and \( k_1 \) \( (r^2 = 0.70, P = 0.16 \text{ and } n = 4) \).

Diurnal courses in gas exchange between seasons

Diurnal values of \( A_n \) and \( g_s \) in \( H. \) hainanensis, \( P. \) chinensis and \( V. \) xishuangbannaensis were strongly reduced in the dry season compared with the rainy season (Figure 3). In both seasons, all species displayed depression in \( A_n \) from midmorning onward with a slight recovery in the afternoon in some cases (Figure 3) in response to decreases in leaf temperature and LAVPD (data not shown). In both seasons, diurnal depression in \( g_s \) started even earlier than that in \( A_n \) for all species except for \( H. \) hainanensis in the rainy season and \( V. \) xishuangbannaensis in the dry season, which had low \( g_s \) throughout the day. In some cases, the maximum values of \( A_n \) obtained from the diurnal measurements were lower than those derived from the photosynthetic light response curves (Table 2), presumably reflecting the effects of microclimate fluctuations on gas exchange during the diurnal measurements.
There were significantly positive correlations between $A_n$ and $g_s$ in both seasons for all species ($r^2 > 0.15, P < 0.05$), indicating increased photosynthetic water-use efficiency. Nevertheless, the comparison of the regressions of $g_s$ versus LAVPD between seasons revealed that $g_s$, at a given LAVPD was significantly reduced in the dry season in all species (ANCOVA, $P < 0.05$).

**Allocation of photons absorbed by PSH antennae and electron flow**

The allocation patterns of PPF used in photochemistry and heat dissipation were similar across species (Figure 5). With an increase in PPF, the fraction of photons allocated to $\Phi_{PSII}$ decreased and the fraction to $\Phi_{NPQ}$ increased. In the dry season, at a given PPF, the fraction of the photons allocated to $\Phi_{PSII}$ decreased and the fraction to $\Phi_{NPQ}$ increased in all species. There is no change in values of $\Phi_{OD}$ with PPF or between seasons (data not shown).

Nonwithstanding the sustained depression in photosynthetic rate, $J_T$ remained at a high level in all species throughout the day (Figure 6). In both seasons, $R_l$ in the morning (with the exception of *V. xishuangbannaensis* in the dry season) gradually increased toward midday. Overall, about 30–65% of electron flow was allocated to photorespiration (data not shown but see $J_O/J_C$ ratios in Figure 6). In most cases, $J_O/J_C$ was $> 1$ around midday, indicating that the $R_l$ exceeded the carboxylation rate. The $J_O/J_C$ ratio increased with decreasing $g_s$ when $g_s$ was below 0.1 mol m$^{-2}$ s$^{-1}$, and $J_O/J_C$ stabilized when $g_s$ was above 0.1 mol m$^{-2}$ s$^{-1}$ (Figure 7). Diurnal $J_T$ was lower in the dry season than in the rainy season, consistent with the downregulation of photosynthetic rate and $\Phi_{PSII}$. The synchronous downregulation of carbon assimilation (Figure 3), photorespiration (Figure 6), and dark respiration rate (in three of the four study species, Table 2) in the dry season indicated decreased activity of ribulose-1, 5-bisphosphate carboxylase/oxygenase.

**Discussion**

**Photosynthesis in the rainy and dry seasons**

In the rainy season, $A_{\text{max}}$ values of the uppermost-canopy leaves of all species varied greatly (Table 2) but are within the range reported for a dozen other dipterocarp species in southeast Asia (e.g., Eschenbach et al. 1998, Kenzo et al. 2003, 2004, Ishida et al. 2006). All the species showed sustained photosynthetic depression from midmorning onward (Figure 3). Midday depression in carbon gain on sunny days is common in the canopy leaves of tropical forest trees (e.g., Zotz and Winter 1996, Meinzer et al. 1997, Ishida et al. 1999a, 1999b, Bonal et al. 2000, Brodribb and Holbrook 2004), and is believed to be caused by high temperature, irradiance, or VPD, or a combination thereof (e.g., Ishida et al. 1999b, 2006, Muraoka et al. 2000). However, the strong sustained photosynthetic depression as found in our study has rarely
been reported (Kenzo et al. 2003, Brodribb and Holbrook 2007). Brodribb and Holbrook (2007) reported that the sustained photosynthetic depression in the canopy leaves of two tropical tree species in a neotropical seasonal rain forest is due to the sensitive response of their $K_{\text{leaf}}$ to water loss by leaf transpiration as indicated by a linear

Table 3. Wood structure and leaf-specific hydraulic conductivity ($k_l$) of D. retusus, H. hainanensis, P. chinensis and V. xishuangbannaensis. Different letters indicate significant differences in the mean values among species at $P < 0.05$. Data are mean values ± SE of three to four plants.

<table>
<thead>
<tr>
<th></th>
<th>D. retusus</th>
<th>H. hainanensis</th>
<th>P. chinensis</th>
<th>V. xishuangbannaensis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vessel diameter (μm)</td>
<td></td>
<td>92.8 ± 4.4 a</td>
<td>59.3 ± 4.0 b</td>
<td>60.7 ± 4.3 b</td>
</tr>
<tr>
<td>Vessel density (no. mm$^{-2}$)</td>
<td>36 ± 1 c</td>
<td>82 ± 7 b</td>
<td>78 ± 5 b</td>
<td>114 ± 21 a</td>
</tr>
<tr>
<td>Wood density (g cm$^{-3}$)</td>
<td>0.48 ± 0.02 c</td>
<td>0.53 ± 0.01 b</td>
<td>0.51 ± 0.02 bc</td>
<td>0.59 ± 0.02 a</td>
</tr>
<tr>
<td>$k_l$ (mmol m$^{-1}$ s$^{-1}$ MPa$^{-1}$)</td>
<td>66.8 ± 10.2 a</td>
<td>33.7 ± 7.0 b</td>
<td>33.3 ± 6.0 b</td>
<td>29.9 ± 7.9 b</td>
</tr>
</tbody>
</table>

Figure 3. Diurnal courses of net photosynthetic rate ($A_n$) and $g_s$ in the uppermost-canopy leaves of D. retusus, H. hainanensis, P. chinensis and V. xishuangbannaensis in the rainy (closed circles) and dry (open circles) seasons. Measurements were made on a single clear day between late August and the beginning of September in the rainy season 2004 and in March in the hot dry season 2007 for all species except for P. chinensis in the dry season, when measurements were made on two consecutive clear days and were combined. Data are mean values ± SE of 8–13 leaves from three to four plants of each species.
reduction in $K_{\text{leaf}}$ with $\Psi_{\text{leaf}}$. Although the variation in wood structure among our species was large (Table 3), they had similar daily patterns of photosynthesis (Figure 3), perhaps reflecting a convergent adaptation to canopy environmental conditions to prevent catastrophic hydraulic dysfunction and to maintain the water balance of the canopy leaves (Brodribb and Holbrook 2007).

In the dry season, $A_{\text{max}}$ was significantly reduced in all species, which might be associated with decreases in water potential and concentrations of chlorophyll and nitrogen or increases in VPD or photoinhibition. However, chlorophyll concentrations of the species were not significantly reduced in the dry season (Table 2). Moreover, predawn $F_{\text{v}}/F_{\text{m}}$ in the dry season remained high ($>0.79$) in all species, indicating that there is no irreversible photoinhibition (Demmig-Adams and Adams III 2006). Bota et al. (2004) had reported that photosynthetic enzymes are affected only when drought stress is intense. Therefore, in the dry season, increased stomatal limitation caused by low leaf water potentials (Table 2), high VPD (Figure 4), and probable decreases in nitrogen concentration (Ishida et al. 2006) contributed to the sharp reduction in photosynthetic capacity in the study species. Moreover, the cool dry season that had lasted for 4 months before our measurements in March (Table 1) could have had long-lasting negative effects on the physiology of our dipterocarp trees, as found in five mango cultivars grown at the same site (Elsheery et al. 2007).

Figure 4. Dependences of $A_n$ on $g_s$ and $g_m$ on LAVPD in the uppermost-canopy leaves of D. retusus, H. hainanensis, P. chinensis and V. xishuangbannaensis in the rainy (closed circles) and dry (open circles) seasons.
Photoprotection mechanisms

During a diurnal course, with an increase in PPF, the fraction of light energy allocated to $\Phi_{\text{PSII}}$ decreased, whereas that to $\Phi_{\text{NPQ}}$ increased in all species in both seasons (Figure 5), demonstrating flexible regulation between photochemical and non-photochemical quenching in the dipterocarp canopy leaves, as observed in many of the previous studies (e.g., Flexas and Medrano 2002, Franco and Lättge 2002, Hendrickson et al. 2004). All species allocated a lower proportion of light energy to $\Phi_{\text{PSII}}$ and a higher proportion of light energy to $\Phi_{\text{NPQ}}$ at a given PPF in the dry season than in the rainy season (Figure 5), which should be associated with the inactivation of photosynthetic reaction centers and the enhancement of heat dissipation (cf. Flexas and Medrano 2002). Light energy allocated to $\Phi_{\text{NPQ}}$ is dissipated as heat mainly through de-epoxidation of the xanthophyll cycle, thereby protecting the photosynthetic apparatus (Niyogi 1999).

We found that photorespiration played an important role in photoprotection in the uppermost-canopy leaves of the study species. Throughout the day in both seasons, a large proportion of electron flow was allocated to photorespiration (30–65% of the total electron transport, Figure 6), and in both seasons $R_l$ increased from midmorning reaching its highest value around midday in all species, except for $V. \text{xishuangbannaensis}$ in the dry season (Figure 6). A similar diurnal course of $R_l$ has been reported for the sunlit leaves of $Quercus \text{cerris}$ L. in a dry summer in central Italy (Valentini et al. 1995). High photorespiration has also been reported in a Japanese herb ($Arisaema \text{heterophyllum}$ Bl.) in natural high light, where $J_0/J_T$ reached 60% (Muraoka et al.
and in four neotropical savanna species where \( J_O/J_C \) was over 40% (Franco and Lütge 2002). In our study species, \( J_O/J_C \) increased linearly with decreasing \( g_s \) when \( g_s \) was below 0.1 mol m\(^{-2}\) s\(^{-1}\) (Figure 7), indicating the acceleration of oxygenation under strong stomatal limitation to photosynthesis, as also reported by other studies (Ishida et al. 1999a, 1999b, Flexas and Medrano 2002, Guan et al. 2004). Flexas et al. (2006) had found that photochemistry and biochemistry generally fail when \( g_s \) is below 0.1–0.05 mol m\(^{-2}\) s\(^{-1}\); however, our data showed that photorespiration played an important role in photoprotection under this condition. Other electron sinks, such as cyclic electron transport around PSI, Mehler reaction and nitrate reduction, dissipate < 5% of the total light energy absorbed by leaves under moderate drought stress (cf. Flexas and Medrano 2002). We sampled leaves at the top of the trees that were fully sunlit, when a large proportion of leaves within the canopy were partially or largely shaded. Therefore, it is likely that the strong sustained photosynthetic depression and the high rates of photorespiration occurred only in the uppermost-canopy leaves with the maintenance of high CO\(_2\) assimilation rates at the whole-tree level.

No sustained photoinhibition was detected in the uppermost-canopy leaves of any species in either season.
(Table 2), indicating that dynamic regulation among carboxylation, oxygenation and heat dissipation during a day effectively balances light energy for the canopy leaves of these species. Ishida et al. (2006) had also found no irreversible photoinhibition in the canopy leaves of four tropical tree species, including two dipterocarp species in seasonal rain forests in Thailand whose predawn $F_v/F_m$ values remained high ($>0.7$) even in the dry season. At a savanna site where annual rainfall is about half of that at our study site in the same region, photoinhibition occurs in the exposed leaves of some woody species only when drought stress becomes extremely severe (Zhang et al. 2007).

In conclusion, the study species displayed pronounced and sustained photosynthetic depression from midmorning onward in both seasons, with strongly reduced photosynthesis and photochemistry and enhanced thermal dissipation in all species in the dry season. During a diurnal course, all species were able to regulate light energy allocation between photochemistry and heat dissipation dynamically. Photorespiration played an important role in photoprotection in these dipterocarp species. The sustained diurnal photosynthetic depression could be a protective response to prevent severe hydraulic dysfunction in the dipterocarp canopy leaves.

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**References**


