Changes in photosynthesis and leaf characteristics with tree height in five dipterocarp species in a tropical rain forest

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Summary Variations in leaf photosynthetic, morphological and biochemical properties with increasing plant height from seedlings to emergent trees were investigated in five dipterocarp species in a Malaysian tropical rain forest. Canopy openness increased significantly with tree height. Photosynthetic properties, such as photosynthetic capacity at light saturation, light compensation point, maximum rate of carboxylation and maximum rate of photosynthetic electron transport, all increased significantly with tree height. Leaf morphological and biochemical traits, such as leaf mass per area, palisade layer thickness, nitrogen concentration per unit area, chlorophyll concentration per unit dry mass and chlorophyll to nitrogen ratio, also changed significantly with tree height. Leaf properties had simple and significant relationships with tree height, with few intra- and interspecies differences. Our results therefore suggest that the photosynthetic capacity of dipterocarp trees depends on tree height, and that the trees adapt to the light environment by adjusting their leaf morphological and biochemical properties. These results should aid in developing models that can accurately estimate carbon dioxide flux and biomass production in tropical rain forests.

Keywords: Dipterocarpaceae, leaf morphology, nitrogen content, palisade layer, photosynthetic capacity, Sarawak.

Introduction

The vertical structure of a forest is complex and multilayered, resulting in great variation in light availability with height (Yoda 1978, Kimmins 1997). Most canopy trees experience diverse light conditions during their lifetime, starting as seedlings on the poorly lit forest floor but gaining access to the well-lit canopy layer at maturity. Many tree species have different photosynthetic capacities at light saturation ($A_{\text{max}}$) according to growth stage or light conditions, or both, as a result of differences in leaf morphological and biochemical properties (Körner 1994, Larcher 2003). It is well known that sun leaves have higher leaf nitrogen and leaf mass per area (LMA), corresponding to higher $A_{\text{max}}$, than shade leaves. Shade leaves have a higher leaf chlorophyll content and are thinner and thus have a lower dark respiration rate and light compensation point ($I_c$) than sun leaves (Lambers et al. 1998). However, there is little information on the variations in leaf photosynthetic, morphological and biochemical traits in tropical rain forests, which account for a substantial fraction of global primary production (Chapin et al. 2002, Kumagai et al. 2004). To guide development of models of carbon dioxide ($\text{CO}_2$) fixation in tropical rain forests (see review by Ehleringer and Field 1993), there is a need for a detailed understanding of the changes in leaf physiological and morphological characteristics with depth in the forest profile.

Tropical rain forests have a particularly complex and multilayered vertical structure (Whitmore 1998). The crown surface of emergent trees in tropical rain forests are exposed to high solar irradiances (Chazdon et al. 1996), but less than 1% of the solar radiation incident above the canopy typically reaches the forest floor. Carswell et al. (2000) and Rijkers et al. (2000) conducted studies to determine how tree leaves respond to the drastic differences in light conditions at differing heights under the closed canopy of a tropical rain forest and reported that $A_{\text{max}}$, LMA and leaf nitrogen content increased significantly with tree height in some neotropical forest trees, though neither report gave much information about large canopy trees or emergent trees.

Studies designed to determine if photosynthetic capacity of canopy and emergent trees increases with height in the tropical rain forest have shown that an age- or size-dependent decrease in leaf nitrogen content and an increase in LMA parallel the ontogenetic decrease in $A_{\text{max}}$ in some canopy species (Yoder et al. 1994, Fredericksen et al. 1996, Bond 2000, Thomas and
Winner 2002, Koch et al. 2004). In general, a decline in leaf nitrogen content causes a reduction in $A_{\text{max}}$ in tall trees (Bond 2000, Niinemets 2002). Because $A_{\text{max}}$ may also depend on LMA (Thomas and Winner 2002), an increase in LMA with tree size leads to an increase in resistance to CO2 diffusion within the leaf and eventually, a decrease in $A_{\text{max}}$ (Terashima et al. 2001, Niinemets 2002). It is possible, however, that tropical canopies and emergent trees achieve a high $A_{\text{max}}$ by developing a leaf mesophyll structure that is adjusted to the tropical forest canopy environment. Kenzo et al. (2004) reported that, in some canopy species with high $A_{\text{max}}$ ($\sim 20$ µmol m$^{-2}$ s$^{-1}$) in the tropical rain forest of Southeast Asia, $A_{\text{max}}$ had a higher positive correlation with leaf mesophyll structure, such as leaf palisade layer thickness and surface area of mesophyll cells per unit leaf area ($A_{\text{leaf}}/A_{l}$), than with area-based leaf nitrogen concentration and LMA. We therefore hypothesized that tree height of tropical canopy species does not limit $A_{\text{max}}$.

To test this hypothesis, we determined the effects of tree height on leaf photosynthesis and on leaf morphological and biochemical properties, in five dipterocarp species. We studied specimens ranging from seedlings on the poorly lit forest floor to mature canopy trees in the brightly lit canopy layer, which we accessed with a canopy crane (Ozanne et al. 2003). We paid particular attention to differences in photosynthetic capacity and leaf traits with depth within the closed canopy, rather than with crown position of each individual.

**Materials and methods**

**Study site**

The study was carried out in an experimental plot (200 × 200 m) in an intact lowland mixed dipterocarp forest in Lambir Hills National Park, Sarawak, Malaysia (4°20′ S, 113°50′ E, 150–250 m a.s.l.), in September 2002. Mean height of the canopy was 30–40 m and some emergent trees reached 50 m. An 80-m tall canopy crane with a 75-m-long rotating jib was constructed in the center of the plot to provide three-dimensional access, from close to the forest floor to the top of the canopy (Sakai et al. 2002, Ozanne et al. 2003, Kumagai et al. 2004).

The study area has a humid tropical climate, with weak seasonal changes in rainfall and temperature (Kato et al. 1995). Annual precipitation at the study site averaged 2429 mm from 2000 to 2003. Mean annual temperature from 2000 to 2003 was 26.3 °C, with monthly means that varied from 25.6 °C in February to 27.0 °C in May.

**Plant material and canopy openness**

We selected 65 individuals of five dipterocarp species, from seedlings to mature trees (Table 1). The species were *Dipterocarpus globosus* Veiq. (DG), *Dryobalanops aromatica* Gaertn. f. (DA), *Shorea acuta* Ashton (SA), *S. beccariana* Burck (SB) and *S. macroptera* Dyer (SM). All are evergreen trees that grow to the forest canopy layer. In particular, DG, DA and SB are common emergent species at the study site (Itoh et al. 1995, Lee et al. 2002).

Tree heights ranged from 0.6 to 53 m. The seedlings and saplings (0.6–5m tall) were chosen from, or close to, gaps ($n = 3$ for each species) and from beneath a closed canopy ($n = 3$ for each species). Canopy openness at the top of the trees studied was estimated from hemispherical photographs (Coolpix 5000, Nikon; Fisheye Converter FC-E8, Nikon, Tokyo, Japan; Yamamoto 2000).

**Gas exchange measurements**

Leaf gas exchange rate was measured with a portable photosynthesis apparatus (LI-6400, Li-Cor, Lincoln, NE). All measurements were made between 0800 and 1100 h to avoid the midday depression in photosynthesis (Ishida et al. 1996, Hiromi et al. 1999, Kenzo et al. 2003). We measured fully expanded and apparently non-senescing leaves taken from the top of the crown (the same positions as the canopy openness measurements). To ensure that leaf age was not a variable within and across species, the age of the leaves of the study species was estimated from position on the branch, leaf texture and, particularly, leaf color (Sobrado and Medina 1980, Ishida et al. 1996) measured with a chlorophyll meter (SPAD-502, Konica Minolta Holdings, Tokyo, Japan). Gas exchange measurements were made on the third to fifth leaf from the shoot apex, for which the SPAD values were fairly stable (Ishida et al. 1996, Kenzo et al. 2004).

**$A$–$PPF$ curve measurements**

The relationship between photosynthetic photon flux (PPF) and carbon assimilation rate ($A$) was determined for three leaves from each tree. Photosynthetic photon flux, CO2 concentration and temperature in the chamber were controlled at 0 to 1800 µmol m$^{-2}$ s$^{-1}$, 360 ppm and 30 °C, respectively. Illumination was supplied by an internal LED light source (Li-Cor, LI-640B). From the gas exchange measurements, $A_{\text{max}}$ and $I_{\text{c}}$ were estimated. Light compensation point, defined here as the instantaneous compensation point, is the PPF at which photosynthesis just balances respiration (Ashton and Turner 1979).

**$A$–$C_i$ curve measurements**

The $A$–$C_{i}$ curves were made with the LI-6400 equipped with a CO2 injector (Li-Cor, LI-6400–01). The PPF and temperature in the chamber were maintained at 1000–1500 µmol m$^{-2}$ s$^{-1}$ and 30 °C, respectively. The leaf selection criteria were the same as for $A$–$PPF$ curve measurements. The $A$–$C_{i}$ curves were analyzed by the mechanistic model of CO2 assimilation proposed by Farquhar et al. (1980) and modified by Sharkey (1985) and Harley and

<table>
<thead>
<tr>
<th>Species</th>
<th>Code</th>
<th>Individual</th>
<th>$H_{\text{max}}$ (m)</th>
<th>$H_{\text{min}}$ (m)</th>
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<tr>
<td><em>Dipterocarpus globosus</em></td>
<td>DG</td>
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<tr>
<td><em>Dryobalanops aromatica</em></td>
<td>DA</td>
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<td>15</td>
<td>39.5</td>
<td>1.0</td>
</tr>
<tr>
<td><em>Shorea beccariana</em></td>
<td>SB</td>
<td>11</td>
<td>52.5</td>
<td>1.0</td>
</tr>
<tr>
<td><em>Shorea macroptera</em></td>
<td>SM</td>
<td>12</td>
<td>27.5</td>
<td>0.7</td>
</tr>
</tbody>
</table>
Sharkey (1991). From the A–C\textsubscript{i} curve, maximum rate of carboxylation (V\textsubscript{cmax}, µmol m\textsuperscript{-2} s\textsuperscript{-1}) and maximum rate of photosynthetic electron transport (J\textsubscript{max}, µmol m\textsuperscript{-2} s\textsuperscript{-1}) were estimated by nonlinear regression techniques (KaleidaGraph ver 3.52; Harley et al. 1992, Wullschleger 1993).

Following the gas exchange measurements, the leaves were collected and their area, blade thickness and fresh mass measured. The leaves were then divided into three groups: one for measuring dry mass and nitrogen content; one for chlorophyll analysis; and one for observation of mesophyll structure.

**Leaf nitrogen and chlorophyll determination**

Leaf nitrogen and carbon contents were determined with an NC analyzer (Sumigraph NC-900, Shimadzu, Kyoto, Japan) after leaves had been dried at 60 °C for 3 days and their dry mass measured. Chlorophyll was extracted with dimethyl sulfoxide (DMSO) (Barnes et al. 1992, Shinano et al. 1996) and absorbances at 664.9 and 648.2 nm were determined spectrophotometrically (UV-1400, Shimadzu, Kyoto, Japan).

**Leaf mesophyll structure**

Leaves selected for observation of mesophyll structure were fixed in FAA (40% formaldehyde:acetic acid:70% ethanol; 2:1:17, v/v) and transverse slices prepared. The transverse slices were frozen in a drop of distilled water and sectioned with a sliding microtome. Transverse sections (about 150 to 530 µm thick) were observed and photographed with the aid of a light microscope (BH-2, Olympus, Tokyo, Japan). Transmitted light images of transverse sections were also obtained with a confocal laser scanning microscope (LSM-310, Carl Zeiss, Oberkochen, Germany; Kitin et al. 1999). The thicknesses of the leaf blade and palisade layer were determined from a micrograph at 200× magnification. The surface area of mesophyll cells per unit leaf area (A\textsubscript{mes}/A\textsubscript{L}) was estimated by the method of Nobel (1999).

**Statistical analysis**

Scatter plots of leaf morphological and physiological properties with tree height were analyzed by linear regression. Differences between leaf properties of species were tested by analysis of covariance (ANCOVA; SPSS v.11.5), with species as the main factor and tree height as a covariable (Sokal and Rohlf 1995, Rijkers et al. 2000).

**Results**

**Relationship between canopy openness and tree height**

Canopy openness varied from 5–10% in the understory to more than 90% at 40 m aboveground. Canopy openness increased roughly linearly with tree height up to 30 m, then increased more rapidly to 90% at 40 m (Figure 1). In gaps, canopy openness was about 20%, and direct sunlight usually reached the leaves. On sunny days, irradiances were around 5 to 20 µmol m\textsuperscript{-2} s\textsuperscript{-1} in the forest understory and at least 1800 µmol m\textsuperscript{-2} s\textsuperscript{-1} in the canopy layer.

**Leaf photosynthetic properties and tree height**

Photosynthetic rate at light saturation and I\textsubscript{c} increased significantly with tree height both within and across species (Figures 2A and 2B). There were no interspecific differences in V\textsubscript{cmax} and J\textsubscript{max} with tree height (ANCOVA; P > 0.05), except for A\textsubscript{max} of canopy individuals of SB. The I\textsubscript{c} value of understory seedlings was relatively low, usually less than 10 µmol m\textsuperscript{-2} s\textsuperscript{-1}.

Maximum rate of carboxylation by Rubisco (V\textsubscript{cmax}) and maximum rate of photosynthetic electron transport (J\textsubscript{max}) increased significantly with tree height (Figures 2C and 2D). No interspecific differences in V\textsubscript{cmax} or J\textsubscript{max} with tree height were observed (ANCOVA; P > 0.05), except for DG where these parameters hardly changed with height. However, when gap seedlings of DG were excluded from the regression, both V\textsubscript{cmax} and J\textsubscript{max} of DG increased significantly with tree height (P < 0.05). A positive correlation between V\textsubscript{cmax} and J\textsubscript{max} was observed both within and across species (data not shown). The slope of the regression line of J\textsubscript{max} versus V\textsubscript{cmax} varied from 1.37 (SB) to 1.77 (DA), with r\textsuperscript{2} varying from 0.50 to 0.81.

**Leaf morphological and biochemical properties and tree height**

Leaf blade thickness and LMA increased significantly with tree height (Figures 3A and 3B). Interspecific differences were found between SA and the other species. Of the species studied, SA had the thickest leaf blade and highest LMA (ANCOVA; P < 0.05). The thickness of the palisade layer and A\textsubscript{mes}/A\textsubscript{L}—both indicators of the degree of development of leaf mesophyll structure—increased with tree height, and no inter-
specific differences were identified (Figures 3C and 3D). Leaf density (LMA/leaf blade thickness) increased significantly with tree height in all species (Figure 3E), with interspecific differences only between DA and DG (ANCOVA; $P < 0.05$).

The relationship between area-based nitrogen concentration ($N_{area}$) and tree height was similar to the other traits and no significant interspecific difference was found (Figure 4A). Although area-based chlorophyll concentration did not vary with tree height (data not shown), mass-based chlorophyll concentration ($Chl_{mass}$; Figure 4B) and the chlorophyll to nitrogen ratio (Chl/N ratio; Figure 4C) decreased with tree height in all species, with no interspecific differences identified. However, $Chl_{mass}$ and the Chl/N ratio differed between gap seedlings and seedlings beneath the closed canopy.

**Relationship between $A_{max}$ and leaf characteristics**

Significant correlations were found between $A_{max}$ and LMA (Figure 5A; $r^2 = 0.63$, $P < 0.001$) and between $A_{max}$ and $N_{area}$ (Figure 5B; $r^2 = 0.57$, $P < 0.001$). Interspecific differences were found between SB and the other species (ANCOVA; $P < 0.05$). For all species, the highest correlation coefficients were between $A_{max}$ and properties of leaf mesophyll structures, such as the thickness of the palisade cell layer (Figure 5C; $r^2 = 0.76$, $P < 0.001$) and $A_{max}/A_i$ (Figure 5D; $r^2 = 0.72$, $P < 0.001$) and no interspecific differences were found.

**Relationship between light compensation point and leaf characteristics**

Negative correlations were found between $I_c$ and $Chl_{mass}$ (Figure 6A), and between $I_c$ and Chl/N (Figure 6B). There were interspecific differences between $I_c$ and $Chl_{mass}$. Two groups could be distinguished: between DA, DG and SA, SB and SM (ANCOVA; $P < 0.05$). The only interspecific difference in the relationship between $I_c$ and Chl/N was between DG and SM (ANCOVA; $P < 0.05$).

**Discussion**

**Changes in photosynthetic capacity and light compensation point with tree height**

Photosynthetic capacity was not limited by tree height in the studied tropical canopy tree species, supporting our hypothesis. For the five dipterocarp species studied, $A_{max}$ had a simple relationship with tree height (Figure 2A). Rijkers et al. (2000) also found a significant relationship between $A_{max}$ and tree height in four neotropical species. The slope and intercept of their linear regression line (0.16 and 4.69, respectively) corresponded closely with the values of 0.16 and 4.69 that we obtained. These findings may be important when developing
models for CO₂ fixation in tropical forests, although further studies are needed in diverse tropical forests.

The photosynthetic parameters \( V_{\text{cmax}} \) and \( J_{\text{max}} \) increased significantly with tree height, as well as with \( A_{\text{max}} \) (Figures 2C and 2D), indicating that leaves exposed to high irradiances have high rates of carboxylation and electron transport capacity per unit area. Wullschleger (1993), who reviewed the ranges of values of \( V_{\text{cmax}} \) and \( J_{\text{max}} \) in tropical forest species (\( n = 22 \)), based mostly on wild plants and experimental plants growing in natural conditions or greenhouses, quoted values of 9–126 (for \( V_{\text{cmax}} \)) and 30–222 (for \( J_{\text{max}} \)). Variations in \( V_{\text{cmax}} \) and \( J_{\text{max}} \) in our study are consistent with these ranges. The highest values of \( V_{\text{cmax}} \) and \( J_{\text{max}} \) in our study were about twice the values found in the canopy of neotropical trees (Carswell et al. 2000), indicating that dipterocarp species have a high photosynthetic capacity over a wide range of irradiances.

At the dimly lit forest floor, \( I_c \), although low, seemed sufficient to maintain positive net gas exchange (Figure 2B). The \( I_c \) was below 10 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) for most of the non-gap seedlings we studied. Eschenbach et al. (1998) reported simi-

Figure 3. Relationships between tree height and: leaf thickness (A); leaf mass per area (LMA; B); palisade layer thickness (C); mesophyll cell surface area per unit leaf area (\( A_{\text{mes}}/A_{\text{a}} \); D); and leaf density (E). Values are means for each individual across all replicate leaves. The regression lines are: A, \( y = 206 + 4.76x; r^2 = 0.69, P < 0.001 \); B, \( y = 69.7 + 2.76x; r^2 = 0.84, P < 0.001 \); C, \( y = 38.3 + 1.97x; r^2 = 0.83, P < 0.001 \); D, \( y = 20.1 + 1.05x; r^2 = 0.86, P < 0.001 \); and E, \( y = 0.34 + 0.003x; r^2 = 0.53, P < 0.001 \). Symbols: □ = Dipterocarpus globosus; ◇ = Dryobalanops aromatica; ○ = Shorea acuta; □ = Shorea beccariana; and △ = Shorea macroptera.
larly low $I_c$ values for 11 woody species in the Malaysian rain forest, but some pioneer species displayed higher values. Many authors have reported that PPF beneath the canopy of tropical rain forests ranges between 5 and 20 µmol m$^{-2}$ s$^{-1}$ (Pearcy 1983, Chazdon 1988, Barker et al. 1997, Eschenbach et al. 1998). Thus, the low $I_c$ of the non-gap seedlings indicates that our study species are well suited to the low light conditions beneath the closed canopy of tropical rain forests.

Leaf photosynthetic traits in relation to leaf morphological and biochemical properties

Differences in photosynthetic characteristics such as $A_{\text{max}}$ and $I_c$ with tree height were closely related to leaf morphological and biochemical traits. It is well known that $A_{\text{max}}$ is strongly affected by various leaf characteristics, such as leaf thickness (MacClendon 1962, Koike 1988), leaf mesophyll structure ($A_{\text{mes}}/A_a$; Nobel 1975, Koike 1988, Hanba et al. 1999, Kenzo et al. 2004) and nitrogen content (Field and Mooney 1986, Evans 1989, Reich et al. 1999). Generally, age- and size-dependent declines in leaf nitrogen concentration seem to be reflected in a reduction in $A_{\text{max}}$ in tall trees (Bond 2000, Niinemets 2002); however, we found that leaf nitrogen concentration increased with tree height in these tropical canopy species. Although high LMA may also limit $A_{\text{max}}$ (Terashima et al. 2001, Niinemets 2002), dipterocarp canopy trees have a well-developed leaf mesophyll structure, including a thick palisade layer and high $A_{\text{mes}}/A_a$, which is responsible for reduced leaf internal resistance to CO$_2$ diffusion, as well as a high LMA (Hanba et al. 1999, Kenzo et al. 2004). Our results suggest that high leaf nitrogen concentration and a well-developed mesophyll structure helps maintain high $A_{\text{max}}$ in the upper-canopy leaves.

High foliar chlorophyll concentration (Chl mass) and Chl/N ratio leaves were related to low $I_c$, permitting better acclimation under poor light at the sapling stage (Figures 4B and 4C). There was a negative correlation between Chl mass and $I_c$ (Figure 6A), indicating that high Chl mass contributes to light-harvesting efficiency at low irradiances (Lambers at al. 1998). In the model of Hikosaka and Terashima (1995), increased allocation of leaf nitrogen to chlorophyll-protein complexes under shade increases the efficiency of incident light capture (Björkman 1981). The Chl/N ratio therefore acts as an indicator of the allocation of leaf nitrogen to chlorophyll-protein complexes of the light-harvesting component (Kimura et al. 1998, Kull and Niinemets 1998, Koike et al. 2001). In our study, the Chl/N ratio of all species increased with decreasing tree height (Figure 4C), and the ratio was negatively correlated with $I_c$ (Figure 6B). These findings support the model of Hikosaka and Terashima (1995) and suggest that the study
species are able to change their light-harvesting component, allowing ready adaptation of photosynthetic capacity to the variable light conditions encountered by seedlings in gaps and beneath the closed canopy.

In conclusion, our results suggest that $A_{\text{max}}$ is not limited by tree height in tropical canopy tree species. We found simple and significant linear relationships between tree height and both leaf photosynthetic characteristics (e.g., $A_{\text{max}}$, $I_c$, $J_{\text{max}}$ and $V_{\text{cmax}}$) and leaf morphological and biochemical traits (e.g., LMA, $N_{\text{area}}$, Chl$_{\text{mass}}$, Chl/N ratio), which in turn affect photosynthetic traits, with some differences among the dipterocarp species studied. These relationships, involving leaf properties of forest understory seedlings up to mature canopy trees, may allow more accurate modeling of CO$_2$ flux and biomass production in tropical rain forests than hitherto. We also obtained evidence that dipterocarp species can optimize leaf anatomy and physiology to make the best use of the variable light encountered from the seedling stage to adulthood.

Figure 5. Light-saturated photosynthetic rate ($A_{\text{max}}$) versus: leaf mass per area (LMA; A); nitrogen content per area ($N_{\text{area}}$; B); palisade layer thickness (C); and mesophyll cell surface area per unit leaf area ($A_{\text{mes}}/A_{\text{a}}$; D). Values are means for each individual across all replicate leaves. The regression lines are: A, $y = 1.11 + 0.05x$; $r^2 = 0.63$, $P < 0.001$; B, $y = 0.67 + 0.102x$; $r^2 = 0.57$, $P < 0.001$; C, $y = 1.67 + 0.08x$; $r^2 = 0.76$, $P < 0.001$; and D, $y = 1.85 + 0.15x$; $r^2 = 0.72$, $P < 0.001$. Symbols: $\bullet$ = Dipterocarpus globosus; $\Diamond$ = Dryobalanops aromatica; $\bigcirc$ = Shorea acuta; $\square$ = Shorea beccariana; and $\triangle$ = Shorea macroptera.

Figure 6. Light compensation point ($I_c$) versus: chlorophyll content per unit dry mass (Chl$_{\text{mass}}$; A); and chlorophyll to nitrogen ratio (Chl/N ratio; B). The regression lines are: A, $y = 35.5 - 6.98x$; $r^2 = 0.51$, $P < 0.001$; and B, $y = 39.3 - 5.06x$; $r^2 = 0.43$, $P < 0.001$. Symbols: $\bullet$ = Dipterocarpus globosus; $\Diamond$ = Dryobalanops aromatica; $\bigcirc$ = Shorea acuta; $\square$ = Shorea beccariana; and $\triangle$ = Shorea macroptera.
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