Sapling Structure and Regeneration Strategy in 18 Shorea Species Co-occurring in a Tropical Rainforest

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INTRODUCTION

Juvenile trees have suites of structural traits that differ markedly among species. This variety in traits such as crown architecture, biomass allocation and leaf characters is assumed to reflect their diversified regeneration strategies, i.e. regeneration niche (sensu Grubb, 1977), and hence to promote their coexistence (e.g., Horn, 1971). From this perspective, many ecologists have attempted to elucidate the ecological functions of the structure of tree seedlings and saplings. As a result, two inevitable trade-offs in structure are now known to be tightly correlated with potential growth speed and shade tolerance, i.e. the ability to survive in the shaded understorey.

One is the architectural trade-off between a less-branched narrow crown supported by a slender trunk (small crown) and a well-branched wide crown on a thick trunk (large crown; King, 1990; Kohyama, 1987, 1991). A small crown could be advantageous for rapid height growth under relatively bright conditions, such as in gaps, whereas a large crown may increase light capture in shaded environments. The second is a trade-off relationship between a robust structure and a structure advantageous for carbon gain, which is mainly related to allocation patterns to organs and leaf structure. Despite early predictions that shade-tolerant plants should maximize light interception (Givnish, 1988), they seem to have thicker lamina, smaller leaf area ratio and greater allocation to roots than light-demanding species, which minimize biomass loss rather than maximize carbon gain (Walters et al., 1993a; Kitajima, 1994; Cao and Ohkubo, 1998; Walters and Reich, 1999, 2000).

Although these two trade-off axes have been well investigated, some critical questions remain unanswered. First, do these trade-offs in structural traits contribute to the differentiation of plant strategies even among species within a single taxonomic or functional group? Many previous studies compared contrasting functional groups and distantly related taxa, although species within a single taxon or functional group can also show considerable differences in both their structure and their shade tolerance (Ashton, 1995; Ackerly and Donoghue, 1998; Davies, 1998; Montgomery and Chazdon, 2002). Especially in tropical rain forests, dozens of species within a single large genus coexist sympatrically and show various structural characters. As competition is thought to be more severe among these phylogenetically and ecologically related species, whether niche differentiation exists and how it occurs is a more critical question for these species. Secondly, how are the two axes, i.e. the architectural trade-off and the biomass partitioning and leaf structure trade-off, related to each other? In some studies that compared species from different

Key words: Allocation, architecture, Borneo, dipterocarps, regeneration strategy, sapling, shade tolerance, seedling, Shorea.

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taxa and functional groups, species with a small crown showed more investment to the trunk and less to leaves than species with a large crown (Kohyama, 1987; Kohyama and Hotta, 1990; Takahashi et al., 2001), suggesting further synthesis of structural traits on a single trade-off axis. However, all of these studies of sapling architecture were conducted on the basis of height or above-ground mass, without evaluating the allocation to roots. Hence, the relationship between the two axes, both of which are related to shade tolerance, remains unclear.

Diversification of congeneric tree species is a particular feature of Asian tropical forests, and structural variation seems to be one significant mechanism that allows the stable coexistence of these species (Thomas, 1996, 2004). One such diversified genus, Shorea (Dipterocarpaceae), dominates the canopy and the emergent layers of Bornean dipterocarp forests and many species coexist sympatrically there. All species in the genus Shorea are considered non-pioneer species with a restricted distribution in primary or relatively undisturbed forests, although they may show different levels of shade tolerance (Turner, 1990; Ashton, 1995; Still, 1996; Barker et al., 1997). These conditions provide an excellent opportunity to compare the sapling structure of many species within a single genus and with similar life histories. Despite the merits of using this genus, little is known about the shade tolerance of these species. Therefore, co-variation was tested between structure and three indices of shade tolerance: the maximum net photosynthetic rate, the wood density of mature trees and seed size. The maximum net photosynthetic rate can be considered to be an index of the potential for carbon assimilation in high-light environments (Walters et al., 1993a), and wood density is negatively correlated with the innate growth speed (e.g. Muller-Landau, 2004). Therefore, these two traits should be negatively and positively correlated with shade tolerance, respectively, and inversely correlated with the potential growth rate. While these two indices represent shade tolerance throughout the life history of the tree, seed size correlates with the temporal shade tolerance just after germination, and the correlation diminishes within a few years (Poorter and Rose, 2005). Such trends are often observed even among ecologically similar species (Reich et al., 1995; Still, 1996; Davies, 1998; Suzuki, 1999) and, by using these indices, subjective, qualitative measures of shade tolerance were avoided.

In this study, the biomass allocation and plant architecture of juveniles (0.1–1.5 m tall) were analysed on a whole-plant basis, while considering ontogeny, in 18 co-occurring climax species of the genus Shorea in a Bornean tropical rainforest. The specific questions addressed were (a) which suite of morphological traits co-variates with the indices of shade tolerance and (b) how do the two aspects of plant structure, i.e. architecture and allocation, correlate with each other?

**MATERIALS AND METHODS**

**Study site and species**

This study was conducted at Lambir Hills National Park, Sarawak, Malaysia (4°2′N, 113°50′E, 150 m a.s.l.). Consistently high temperatures, with no distinct dry season, characterize the climate of this region. The mean annual temperature and annual precipitation are approx. 26 °C and 2700 mm (Nakagawa et al., 2000). The park is 6949 ha in area and is entirely covered with a primary lowland mixed dipterocarp forest on nutrient-poor sandy clay or clay-rich soils (Yamakura et al., 1995).

Trees of the genus Shorea (Dipterocarpaceae) are dominant in the canopy and the emergent layer of the lowland mixed dipterocarp forest of West Malesia (Ashton, 1991). This genus is highly diversified in Borneo, and 129 species have been recorded on the island (Newman et al., 1996). Of the approx. 70 species of the genus Shorea that occur in Lambir, 18 species, for which enough saplings of a comparable size (0.1–1.5 m tall) could be collected, were analysed. Table 3 provides details of the species analysed. The species were sampled from six taxonomic sections, which are thought to differ in terms of shade tolerance (cf. Still, 1996), i.e. species of section Shorea are considered highly shade tolerant, while some species of sections Brachyptera, Mutica, Ovalis and Pachyparpae seem to be relatively light demanding. Most of the selected species were emergent trees (maximum height >50 m), although two lower species, S. biawak and S. macroptera, which reached up to 30 m were included.

**Biomass partitioning and other structural traits**

In August 2003, approx. 20 sound saplings of various sizes (0.1–1.5 m in height) of each species were sampled to determine their allometric relationships. All sampled individuals grew under closed canopies. For S. ochracea, only 18 individuals were sampled because of its rarity. Also sampled were 10–15 saplings of each species excluding S. ochracea, in November 2003. After the trunk height (the vertical distance from the ground to the highest apex), crown width in two directions at right angles (including the widest width) and crown depth (the vertical distance from the lowest to the highest leaves) had been measured, the entire plant body was harvested. After harvest, hemispherical photographs were taken at 1-m height to measure canopy openness for three randomly selected individuals per species. Canopy openness was consistently low (5.9 ± 0.7%, mean ± s.d.), indicating that the light environment under the closed canopy was homogenous. After recording the stem diameter at ground height in two directions at right angles, the sampled saplings were divided into three parts: root, stem and leaf lamina. In the latter sampling period, the stem was further divided into the main trunk and branches. Though S. ochracea was sampled only in the first sampling period, any individual of the species sampled lacked branches. Petioles were treated as stems in the first sampling and as the trunk or branches in the latter. For each sapling, the total leaf area and maximum individual leaf area were measured using the software LIA32 for Windows 95 (ver. 0.371B1, K. Yamamoto) after scanning the images. All parts of the saplings were weighed after being oven-dried at 60 °C for at least 5 d. The crown projection area and crown volume of each individual were approximated as an ellipse and an ellipsoid of revolution.
Indices of shade tolerance

The maximum net photosynthetic rate ($A_{\text{max}}$) of saplings under the closed canopy was quantified in the field using a portable infrared gas analyser (LI6400; LI-COR Incorporated, Lincoln, NB, USA) in November 2003. Although it is better to measure $A_{\text{max}}$ under high light conditions to use as an index of shade tolerance, $A_{\text{max}}$ was measured under shaded conditions to reduce the variation in site conditions where the plants grow, given that the light conditions of the shaded understorey are far more homogenous than that of a naturally generated high-light site, i.e. gaps of various size and age. All measurements were conducted in the morning (0700–1000 h). During all measurements, the airflow rate through the chamber was 500 ml min$^{-1}$, and the air temperature was maintained at 27°C. The CO$_2$ concentration of the air was kept at 450 mg kg$^{-1}$, which is a typical value in the forest understorey, where CO$_2$ from the canopy accumulates, and the humidity was sufficiently high (approx. 80%). Light was provided artificially with a light bulb. Three to four approx. 1-m-tall saplings of each species that grew under a closed canopy were selected and the youngest fully expanded leaf on each sapling used for the measurements. After acclimation at a photon flux density of 80%, light was provided artificially with a light bulb. All parameters measured in this study are summarized in Table 1 with abbreviations and units.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Definition</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>TM</td>
<td>Total dry mass</td>
<td>g</td>
</tr>
<tr>
<td>RM</td>
<td>Root dry mass</td>
<td>g</td>
</tr>
<tr>
<td>SM</td>
<td>Stem dry mass</td>
<td>g</td>
</tr>
<tr>
<td>BM</td>
<td>Branch dry mass</td>
<td>g</td>
</tr>
<tr>
<td>LM</td>
<td>Leaf lamina dry mass</td>
<td>g</td>
</tr>
<tr>
<td>LA</td>
<td>Total leaf area</td>
<td>$10^2$ cm$^2$</td>
</tr>
<tr>
<td>$L_{\text{max}}$</td>
<td>Maximum individual leaf area</td>
<td>$10^2$ cm$^2$</td>
</tr>
<tr>
<td>CA</td>
<td>Crown projection area</td>
<td>$10^2$ cm$^2$</td>
</tr>
<tr>
<td>CV</td>
<td>Crown volume</td>
<td>$10^3$ cm$^3$</td>
</tr>
<tr>
<td>H</td>
<td>Plant height</td>
<td>cm</td>
</tr>
<tr>
<td>D</td>
<td>Diameter of stem at ground height</td>
<td>mm</td>
</tr>
<tr>
<td>SV</td>
<td>Seed volume</td>
<td>cm$^3$</td>
</tr>
<tr>
<td>$A_{\text{max}}$</td>
<td>Net photosynthetic rate per leaf area</td>
<td>$\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$</td>
</tr>
<tr>
<td>WD</td>
<td>Wood density of matured tree</td>
<td>g cm$^{-3}$</td>
</tr>
</tbody>
</table>

respectively. All parameters measured in this study are summarized in Table 1 with abbreviations and units.

Data analysis

The allometric relationships between the parts of an individual plant were used to analyse the structural properties and growth patterns of saplings. All parameters except branch mass (BM) were log-transformed before regression. For the interspecific comparison of regression lines, standardized major axis estimations and ANCOVA-like comparisons were applied using (S)MATR (Version 1; Falster et al., 2003). Standard regression methods were used to predict the dependent variables. Total dry mass (TM) was adopted as the independent variable in all regressions, and root dry mass (RM), stem dry mass (SM), leaf dry mass (LM), total leaf area (LA), projected crown area (CA), crown volume (CV), height (H) and stem diameter at ground height (D) were selected as the dependent variables to obtain eight regression lines. Quadratics were applied to the relationship of $L_{\text{max}}$ (maximum individual leaf area) to TM in the non-linear regression, because in some species the increase in leaf size diminished with growth. To estimate BM, a non-linear regression was applied following the general model of Klinkhamer et al. (1992), $Y = a(X - c)^b$, because small saplings lacked branches. The relation of $L_{\text{max}}$ on TM and BM on TM was excluded from the ANCOVA-like test by (S)MATR, as there was no way to statistically compare such a complicated regression.

Significant differences were found not only in the intercepts but also in the slopes; therefore, for further analyses, estimated values were obtained instead of the direct comparison of the regression parameters. Each sapling characteristic that was treated as a dependent variable was estimated against a TM of 5 and 30 g, which approximated the lower and upper limits of the common range of TM for the 18 species. Although regression will sometimes fail to properly predict values at the extreme of the range, these two values are actually not at the extreme of regression for most species. Even for the species for which prediction was done at the extreme, the high correlation coefficients indicated that the predicted values were reliable. Pairwise simple correlations and principal component analysis (PCA) were performed on the log-transformed estimated values to clarify the correlations between any pair of structural traits and the constellations among traits by unifying parameters into some principal components (PC). To incorporate BM, which included zero values, into the analysis, 0-1 was added to all values before log-transformation. Although other values such as 0-01 were tested, the resultant pattern was robust. In the PCA, factors with an absolute loading larger than 0-468 were considered, which corresponds to a percentage of risk <0-05 in the present case, which was significant. Finally, the correlations between the PCA score and three indices of shade tolerance were calculated to examine which structural variation correlated with shade tolerance.

RESULTS

Interspecific differences in allometry and structural traits

For all chosen allometric relations, significant interspecific differences among the regression lines were found...
Table 2. Interspecific differences in allometric relationships calculated as standardized major axis after log-transformation of each variable

<table>
<thead>
<tr>
<th>log x–log y</th>
<th>Sample size</th>
<th>n</th>
<th>Slope</th>
<th>Intercept</th>
</tr>
</thead>
<tbody>
<tr>
<td>log TM–log RM</td>
<td>567</td>
<td></td>
<td>35.27</td>
<td></td>
</tr>
<tr>
<td>log TM–log SM</td>
<td>254</td>
<td></td>
<td>53.49</td>
<td></td>
</tr>
<tr>
<td>log TM–log LM</td>
<td>567</td>
<td></td>
<td>24.06</td>
<td>8.63</td>
</tr>
<tr>
<td>log TM–log CA</td>
<td>567</td>
<td></td>
<td>71.88</td>
<td></td>
</tr>
<tr>
<td>log TM–log CV</td>
<td>567</td>
<td></td>
<td>76.11</td>
<td></td>
</tr>
<tr>
<td>log TM–log H</td>
<td>567</td>
<td></td>
<td>12.25</td>
<td>17.53</td>
</tr>
</tbody>
</table>

*Significant at P < 0.01. The test statistics is \( -2\log A \) by \((S)MATR\) for slope and \( F \) ratio for intercept. The set of degree of freedom is \((17, n - 18)\). Test for intercept is applicable only when difference in slope is not significant.

(ANCOVA, \( P < 0.01; \) Table 2). Of the eight relationships, six showed significant differences in their slopes; differences were seen in the intercepts only in the relationship of TM vs. LM and TM vs. D.

The structural characters predicted from the least square regression for a TM of 5 and 30 g are shown in Table 3. At 5 g, H ranged from 22 cm (\( S. \) ochracea) to 57 cm (\( S. \) exelliptica). Only four species, \( S. \) cf. andulensis, \( S. \) curtisi, \( S. \) ovata and \( S. \) scrobiculata, had branched by this stage, and these species had a small \( L_{\text{max}} \) (15–28 cm\(^2\)) in common. At 30 g, the shortest species was \( S. \) ochracea (57 cm) and the tallest was \( S. \) crassa (118 cm). Although most species had developed branches by this stage, some species with a large \( L_{\text{max}} \) (188–231 cm\(^2\)), i.e. \( S. \) amplexicaulis, \( S. \) beccariana, \( S. \) falciferoidea and \( S. \) ochracea, still lacked branches.

Simple and multiple correlation patterns in structure among the 18 species

The pairwise simple correlation coefficients for ten morphological traits at two ontogenetic stages are summarized in Table 4, and some representative correlations are shown in Fig. 1 as scatter plots. At 5 g, the positive correlations between LM vs. LA, LA vs. CA, and \( L_{\text{max}} \) vs. D and the negative correlations between SM vs. LM and BM vs. \( L_{\text{max}} \) were significant (Table 4, \( P < 0.05 \) after sequential Bonferroni correction; also see Fig. 1 for SM vs. LM). The positive correlation between SM vs. H was also relatively strong, although the correlation was only marginally significant after sequential Bonferroni correction (\( P < 0.1 \)). At 30 g, the positive correlations between LA vs. CA, \( L_{\text{max}} \) vs. D and CA vs. CV and the negative correlation between BM vs. \( L_{\text{max}} \) were significant (see Fig. 1 for LA vs. CA, \( L_{\text{max}} \) vs. D and BM vs. \( L_{\text{max}} \)). The correlations between RM vs. H, LA vs. CV and \( L_{\text{max}} \) vs. CA were also relatively strong, although the significances were marginal.

In both ontogenetic stages, >80% of the total variance was explained by three principal components. The factor loadings of the first and second principal component are summarized as scatter plots in Fig. 2. At 5 g, the first axis, whose contribution was 34%, had significant positive correlations with SM and H and negative correlations with LM, LA and CA. This axis summarizes a trade-off relationship between investment in leaves and investment in the trunk (and consequently, attained height). The second axis, which explained 30% of the variance, was positively correlated with CV, BM, H and CA and negatively correlated with D, \( L_{\text{max}} \) and RM. This axis contrasts species with well-branched, large crowns consisting of small leaves supported by a thin trunk with species with small crowns consisting of large leaves supported by a thick trunk. The third axis, which contributed 17%, showed a strong negative correlation with RM and a weak positive correlation with SM and \( L_{\text{max}} \) (data not shown). This axis mainly represents variation in allocation to the roots.

At 30 g, PC1 was relatively dominant, explaining 39% of the total variance. The axis was correlated positively with CV, CA, BM and LA and negatively with \( L_{\text{max}} \), D and RM. This axis is very similar to the second axis at 5 g and summarizes the trade-off relationship between a large crown consisting of small leaves and a small crown consisting of large leaves. PC2, which accounted for 26% of the total variance, had positive correlations with LM, LA and D. The interspecific variation in the investment in leaves is summarized in this axis. In addition, PC3, whose contribution was 22%, had positive correlations with SM and H and a negative correlation with RM, which represented a trade-off relationship between the attained height and the allocation to roots at this ontogenetic stage.

Correlation between structural characters and indices of shade tolerance

The \( A_{\text{max}} \) of saplings (approx. 1 m high) growing in non-gap sites ranged from 2.6 (\( S. \) exelliptica) to 4.6 \( \mu \text{mol} \text{m}^{-2} \text{s}^{-1} \) (\( S. \) amplexicaulis) (Table 3b). Wood densities of these species obtained from the literatures ranged from 0.50 (\( S. \) acuta and \( S. \) cf. andulensis) to 0.97 (\( S. \) scrobiculata). These two indices of shade tolerance showed a significant negative correlation (\( r = -0.71 \), \( P < 0.001 \); data not shown), suggesting their validity as an index of shade tolerance through the tree life history. Furthermore, these values generally support the empirical knowledge that some species of section Brachyptera, Mutica, Ovalis and Pachycarpae are relatively light-demanding and species of section Shorea are shade tolerant. Seed size, which represents a different aspect of the regeneration strategy, was not strongly correlated with the other two indices.

The results of the correlation test between the PCA score of each species at both stages and three indices of regeneration strategy are shown in Table 5. At 5 g, only the correlation between PC1 and TD was marginally positive (\( r = 0.62 \), \( P = 0.06 \) after the sequential Bonferroni correction). At 30 g, PC1 had a significant negative correlation with seed size (\( r = -0.63 \), \( P < 0.05 \)). The negative correlation between PC2 and TD was also significant at this stage (\( r = -0.67 \), \( P < 0.05 \)), and the positive correlation between PC2 and \( A_{\text{max}} \) was relatively strong, although it was not significant (\( r = 0.54 \), \( P = 0.11 \)). The positive correlation
between PC3 and seed size was also strong, although it was only marginally significant ($r = 0.61, P = 0.05$).

**DISCUSSION**

**Allometry and structure of 18 Shorea species**

In six of the eight allometric relationships tested, significant differences in slopes were found among the species (Table 2). This indicates that the order of species for certain traits such as RM, SM, CA, CV and H per TM can shift with growth. Spearman’s rank correlation coefficients for these characters at two ontogenetic stages were 0.83, 0.37, 0.69, 0.76 and 0.83, respectively, indicating that a certain level of ontogenetic shift exists among these species. Such ontogenetic drift in plant structure is a general phenomenon in juvenile trees as well as in herbs (Poorter and Pothmann, 1992; Walters et al., 1993b; Poorter, 1999; Walters and Reich, 1999). Predicted values of the morphological traits (Table 3) were comparable to values previously reported for saplings in tropical rain forests (Kohyama and Hotta, 1990; Lusk, 2002), temperate evergreen forests (Kohyama, 1987; Lusk, 2002), and temperate deciduous forests (Cao and Ohkubo, 1998; DeLucia et al., 1998; Takahashi et al., 2001). However, the variations among Shorea species in this study were unexpectedly high, given that all of the previous studies had compared taxonomically or ecologically diverse species. For example, Lusk (2002) compared eight species belonging to various functional groups (e.g. shrubs and tall trees, pioneer and climax species) and reported leaf mass ratios ranging from 0.11 to 0.37 and leaf area ratios ranging from 30.8 to 56.7 cm$^2$ g$^{-1}$.

### Table 3. Structural characteristics of the saplings of 18 Shorea species growing in the shaded forest understorey

<table>
<thead>
<tr>
<th>Species</th>
<th>Section</th>
<th>RM</th>
<th>SM</th>
<th>BM</th>
<th>LM</th>
<th>LA</th>
<th>$L_{\text{max}}$</th>
<th>CA</th>
<th>CV</th>
<th>H</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>S. acuta</td>
<td>Mutica</td>
<td>1.3</td>
<td>1.8</td>
<td>0.0</td>
<td>1.7</td>
<td>2.1</td>
<td>0.49</td>
<td>4.6</td>
<td>1.5</td>
<td>37</td>
<td>4.5</td>
</tr>
<tr>
<td>S. agami</td>
<td>Anthoshorea</td>
<td>1.7</td>
<td>1.7</td>
<td>0.0</td>
<td>1.5</td>
<td>1.7</td>
<td>0.65</td>
<td>3.6</td>
<td>1.1</td>
<td>30</td>
<td>4.8</td>
</tr>
<tr>
<td>S. amplexicaulis</td>
<td>Pachycarpae</td>
<td>1.4</td>
<td>1.7</td>
<td>0.0</td>
<td>1.4</td>
<td>1.9</td>
<td>0.53</td>
<td>3.9</td>
<td>1.4</td>
<td>37</td>
<td>4.6</td>
</tr>
<tr>
<td>S. cf. andulensis</td>
<td>Brachyptera</td>
<td>1.2</td>
<td>1.6</td>
<td>0.3</td>
<td>1.7</td>
<td>2.4</td>
<td>0.28</td>
<td>5.2</td>
<td>3.7</td>
<td>37</td>
<td>4.4</td>
</tr>
<tr>
<td>S. beccariana</td>
<td>Pachycarpae</td>
<td>1.3</td>
<td>1.3</td>
<td>0.0</td>
<td>2.0</td>
<td>2.7</td>
<td>0.71</td>
<td>5.0</td>
<td>5.7</td>
<td>40</td>
<td>4.5</td>
</tr>
<tr>
<td>S. biawak</td>
<td>Shorea</td>
<td>1.5</td>
<td>2.4</td>
<td>0.0</td>
<td>1.1</td>
<td>1.9</td>
<td>0.40</td>
<td>3.5</td>
<td>2.3</td>
<td>47</td>
<td>4.1</td>
</tr>
<tr>
<td>S. crassa</td>
<td>Shorea</td>
<td>1.1</td>
<td>2.5</td>
<td>0.0</td>
<td>1.1</td>
<td>1.6</td>
<td>0.34</td>
<td>3.7</td>
<td>2.5</td>
<td>56</td>
<td>4.1</td>
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<tr>
<td>S. curtissi</td>
<td>Mutica</td>
<td>1.0</td>
<td>1.9</td>
<td>0.2</td>
<td>1.7</td>
<td>2.6</td>
<td>0.27</td>
<td>6.5</td>
<td>7.9</td>
<td>56</td>
<td>4.1</td>
</tr>
<tr>
<td>S. exelliptica</td>
<td>Shorea</td>
<td>1.2</td>
<td>2.2</td>
<td>0.0</td>
<td>1.3</td>
<td>1.8</td>
<td>0.33</td>
<td>3.7</td>
<td>2.9</td>
<td>57</td>
<td>4.1</td>
</tr>
<tr>
<td>S. falciferoides ssp.</td>
<td>Pachycarpae</td>
<td>1.4</td>
<td>2.0</td>
<td>0.0</td>
<td>1.4</td>
<td>2.0</td>
<td>0.54</td>
<td>4.3</td>
<td>4.2</td>
<td>40</td>
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<td>S. laxa</td>
<td>Richetioiides</td>
<td>1.4</td>
<td>1.5</td>
<td>0.0</td>
<td>1.8</td>
<td>1.9</td>
<td>0.69</td>
<td>3.1</td>
<td>2.2</td>
<td>35</td>
<td>4.4</td>
</tr>
<tr>
<td>S. macroptera ssp.</td>
<td>Anthoshorea</td>
<td>1.6</td>
<td>1.5</td>
<td>0.0</td>
<td>1.7</td>
<td>2.1</td>
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<td>5.0</td>
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<td>29</td>
<td>4.7</td>
</tr>
<tr>
<td>S. ovalis ssp. sarawakensis</td>
<td>Ovalis</td>
<td>1.1</td>
<td>2.0</td>
<td>0.0</td>
<td>1.5</td>
<td>2.3</td>
<td>0.39</td>
<td>6.3</td>
<td>1.9</td>
<td>35</td>
<td>4.8</td>
</tr>
<tr>
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<td>Mutica</td>
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<td>1.8</td>
<td>0.3</td>
<td>1.4</td>
<td>2.0</td>
<td>0.15</td>
<td>4.7</td>
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<td>Pachycarpae</td>
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<td>2.2</td>
<td>0.0</td>
<td>1.4</td>
<td>2.0</td>
<td>0.52</td>
<td>4.1</td>
<td>3.9</td>
<td>40</td>
<td>4.8</td>
</tr>
<tr>
<td>S. scrobiculata</td>
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<td>0.3</td>
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<td>35</td>
<td>3.8</td>
</tr>
<tr>
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<td>Brachyptera</td>
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<td>3.4</td>
<td>0.71</td>
<td>6.6</td>
<td>7.0</td>
<td>43</td>
<td>4.9</td>
</tr>
</tbody>
</table>

The maximum net photosynthetic rate of the saplings, seed volumes and wood density are also shown.
For the definitions and units, see Table 1.
These ranges were only slightly wider for leaf mass ratio (0-17–0-34, re-calculated from Table 3), and even narrower for leaf area ratio (24-0–55-0 cm² g⁻¹) than the ranges of values shown in the present study, although only non-pioneer species within a single genus were selected. In contrast, the variation in the leaf area index (total leaf area per crown projection area), which represents the extent of self-shading of crown architecture, was relatively small compared with the value for neotropical species reported by Sterck et al. (1999). The leaf area index in the 18 species in the present study ranged from 0-39 to 0-74, while Sterck et al. (1999) found a range from 0-28 to 0-95 in comparing only four species. This may be partly because they selected species with compound leaves, which were excluded from the present study.

### Multiple correlation of structural traits

An allocation trade-off between SM and LM was clear at 5 g (Table 4 and Fig. 1), which suggests that the 18 species are diverse along the axis representing the functional trade-off between height growth per mass and assimilation potential at this ontogenetic stage. However, this trend no longer existed at 30 g, and the weak correlation among allocation...
traits indicates that interspecific differences in allocation cannot be explained by any single trade-off axis at this stage. The strong correlation between LM and LA at 5 g means that LA is mainly determined by leaf mass ratio at this stage. Conversely, at the later stage, the difference in specific leaf area also seems important because the correlation is not as strong at 30 g. A positive correlation between LA and CA was found at both stages. As the incremental rate is larger for CA for interspecific comparisons (in case of 30 g, logCA = 1.1logLA + 0.13), leaf area index decreases in large-crowned leafy species. A positive correlation between Lmax and D was also observed at both stages. This relationship seems analogous to Corner’s Rules, which predict a correlation between individual leaf size and twig diameter (e.g. Corner, 1949; Cornelissen, 1999; Westoby and Wright, 2003), although the functional or physiological meaning of this is not clear. At 30 g, the correlation between BM and Lmax was also strong. It is reasonable that species with smaller leaves need to allocate more to branches to increase leaf area, while avoiding self-shading. The correlation between CA and CV was very strong at 30 g, but not as strong at 5 g. This is because at a younger stage, several large leaves arranged in a plane or small leaves arranged three-dimensionally can realize a large CA at that stage, while at a later stage, a large CA cannot be achieved without branches. The correlation between allocation (RM, SM, BM and LM) and architecture (CA, CV, H and D) was generally not as strong, suggesting that architecture is not as strictly determined by biomass allocation. For example, H was not dependent on BM, while it was partly dependent on SM, at both ontogenetic stages, although it has been hypothesized that the allocation to the lateral expansion of branches reduces the attained height for a given mass. That is, since the trade-offs between SM and other organs (LM at 5 g and RM at 30 g) were very strong, the trade-off between SM and BM was negligible.

The PCA satisfactorily summarized the structural variation of these 18 species into three principal components at both stages (cumulative contribution > 80%). At 5 g, the trade-off between height growth and investment in leaves, which results from an allocation trade-off between SM and LM, and a gradient from species with a well-branched, three-dimensional crown supported by a thin trunk to species with a crown consisting of several large leaves without branches supported by a thick trunk, explained similar portions of the total morphological variation. The relatively unimportant third axis mainly represents the independence of the allocation to roots from these two major axes. At 30 g, the first axis summarizes the trade-off relationship between well-branched, large crowns consisting of small leaves and less-branched, small crowns consisting of large leaves. This axis is relatively independent of allocation traits other than BM, indicating that crown architecture (CA and CV) and allocation do not converge on a single axis, as has been reported in some studies that have compared species from contrasting groups. The other two axes account for the interspecific difference in allocation. The second axis represents the difference in the investment
to leaves and the third axis shows the difference in SM and resultant height growth efficiency.

**Sapling structure and regeneration strategy**

At 5 g, the correlation between the PCA score of any axis and the three indices of shade tolerance among 18 species was not very strong. Only the positive correlation between PC1 score and TD was marginally significant. This correlation means that the trade-off between height growth efficiency and carbon gain co-varies with growth speed or shade tolerance. Since light-demanding species have a larger leaf area than shade-tolerant species, the result that fast growers have a larger LM and LA, which enable them to grow fast and be competitive in high-light conditions, agrees with previous studies. Conversely, we found that slow growers had a larger investment in the trunk and greater stature per unit mass. With these traits, slow growers might escape from the shaded understory in relatively short period. In addition to this ecological reason, their dense wood may physically enable them to be slim compared with fast growing, light-wood species. Moreover, at 30 g, the correlation between PC2 score and WD was significant, suggesting that fast growers are characterized by a larger LM and LA, even within a functional group. The correlation between PC2 score and $A_{\text{max}}$ was also relatively strong, although not significant at this stage, further supporting this view. At this stage, LM and LA were in weak trade-off with RM (Fig. 1 and Table 4); hence, slow growers were characterized by a large RM and small LM and LA. This tendency is also reasonable, as the large allocation to roots, especially to non-structural carbon, which enables juveniles to temporarily tolerate a negative carbon balance arising from herbivory, physical damage or shading by competitors (Canham *et al.*, 1999), is a strategy that is advantageous under low-light conditions (Kobe, 1997).

The score of first axis at 30 g, which mainly summarizes the trade-off in crown architecture and leaf size, showed a significant negative correlation with seed size. As previous studies have indicated that shade-tolerant or ‘pessimistic’ species (species which can tolerate waiting longer for a gap to form) are characterized by well-branched, larger crowns, while light-demanding or ‘optimistic’ species (species supposing a shorter time before gap formation) have less-branched, small crowns (Kohyama 1987, 1991), it was expected that species with a higher wood density, lower maximum photosynthetic rate and larger seeds would have larger crowns and vice versa. However, the present results show that in the 18 species studied, crown architecture (and leaf size) is virtually independent of wood density and photosynthetic rate, and the trend for seed size was contrary to the prediction. Small-seeded species formed large crowns and large-seeded species formed small crowns. The present simple correlation analysis showed that $H$ per unit mass is not affected by crown size or the investment in branches (Table 4), while leaf area index, an index of self shading, was dependent on crown size, as described above. This independence of $H$ per unit mass from crown architecture suggests that the functional trade-off between height growth and light capturing may not exist in these 18 species. Rather, also this trend seems similar to Corner’s Rules, i.e. small-leaved species tend to have small fruit and branch more frequently than large-leaved species. In a comparison of 17 *Acer* species, Ackerly and Donoghue (1998) found that the crown architecture of saplings was independent of Corner’s Rules through evolution. However, the strong correlation among sapling architecture, leaf size, and seed size found in the present study is thought to be rather general, because a tight relationship between leaf size and crown architecture has been reported (Kohyama, 1987; Cao and Ohkubo, 1998; King, 1998, 1999), as well as a correlation between leaf size and seed size (Cornelissen, 1999; Westoby and Wright, 2003). The strength and validity of the relationship may be size dependent; hence, the difference may be due to the inclusion of larger saplings in the study by Ackerly and Donoghue (1998). In either case, the ecological merit of such a correlation among crown size, leaf size and seed size remains enigmatic, primarily because Corner’s Rules are empirical rules. In addition, at 30 g, the positive correlation between PC3 score and seed size was marginally significant. This relationship can be understood as poorly dispersed large-seeded species require efficient height growth to escape shaded conditions.

Overall, the present results suggest that the allocation trade-off between leaves and other organs, which co-varies with wood density and to a certain extent with photosynthetic capacity, accounts for the difference in regeneration strategy, even in congenic non-pioneer species. On the other hand, the correlation between the crown architecture, which is relatively independent of biomass allocation, and shade tolerance seems to be weak in closely related species, though it is obvious that species of different functional groups are characterized by specific crown architecture (King, 1990). Further comparative studies of the structure of closely related species, as well as a discussion of the results with respect to growth dynamics, are required to clarify the generality of these trends and to understand how tree species with a variety of structural traits compete and coexist.

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**LITERATURE CITED**


