Changes in shoot allometry with increasing tree height in a tropical canopy species, *Elateriospermum tapos*

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Summary  Allometry of shoot extension units (hereafter termed “current shoots”) was analyzed in a Malaysian canopy species, *Elateriospermum tapos* Bl. (Euphorbiaceae). Changes in current shoot allometry with increasing tree height were related to growth and maintenance of tree crowns. Total biomass, biomass allocation ratio of non-photosynthetic to photosynthetic organs, and wood density of current shoots were unrelated to tree height. However, shoot structure changed with tree height. Compared with short trees, tall trees produced current shoots of the same mass but with thicker and shorter stems. Current shoots with thin and long stems enhanced height growth in short trees, whereas in tall trees, thick and short current shoots may reduce mechanical and hydraulic stresses. Furthermore, compared with short trees, tall trees produced current shoots with more leaves of lower dry mass, smaller area, and smaller specific leaf area (SLA). Short trees adapted to low light flux density by reducing mutual shading with large leaves having a large SLA. In contrast, tall trees reduced mutual shading within a shoot by producing more small leaves in distal than in proximal parts of the shoot stem. The production of a large number of small leaves promoted light penetration into the dense crowns of tall trees. All of these characteristics suggest that the change in current shoot structure with increasing tree height is adaptive in *E. tapos*, enabling short trees to maximize height growth and tall trees to maximize light capture.

Keywords: biomass allocation, leaf and stem structures, leaf arrangement, Malaysia, tropical rain forest.

Introduction

Tropical rain forests are characterized by a complex canopy structure (Ashton and Hall 1992, Richards 1996) that creates heterogeneous environments for trees (Aoki et al. 1978, Yoda 1978). Most tree species in tropical forests are late successional and shade tolerant (Hubbell and Foster 1986, Kochummen et al. 1990). Because shade-tolerant canopy species experience various environmental conditions during ontogeny, trees of different heights generally have different physiological traits to maximize photosynthetic efficiency in heterogeneous environments (e.g., Oberbauer and Strain 1986, Pearcy 1987, Thomas and Bazzaz 1999). Leaf structure also differs in trees of different heights, and individual leaf area and specific leaf area (SLA) are smaller in the upper canopy than in the understory in most canopy species because of the differences in light environment (e.g., Oberbauer and Strain 1986, Thomas and Ickes 1995).

Most previous studies have focused on differences in leaf traits alone. However, foliage is only one component of tree crown architecture: the modular unit (i.e., a shoot extension unit) is the most essential unit in tree growth and crown development (White 1979, Room et al. 1994). Therefore, to obtain a detailed understanding of tree architecture, we need to examine not only leaf structure, but also the structure of the modular unit. In temperate trees, a modular unit is defined as a current-year shoot (Maillette 1992, Room et al. 1994). Similar shoot units can also be found in tropical species with an intermittent pattern of shoot extension. Here, we define the term “current shoot” as the shoot extension unit produced in one flush and separated from the previous shoot extension unit by the bud scale at its base.

Because biomass allocation patterns determine current shoot structure (i.e., stem length, diameter, leaf number, leaf area, and stem and leaf weights), biomass allocation patterns in leaves and in stems of current shoots should be closely related (Room et al. 1994). Therefore, we hypothesized that not only leaf structure but also current shoot structure will differ between short and tall trees of the same species. For example, the biomass allocation ratio of non-photosynthetic to photosynthetic organs within a current shoot may decrease for taller trees, because rapid growth is less important for tall trees than for short trees. Furthermore, we postulated that, compared with short trees, tall trees produce shorter current shoots with the same amount of biomass. In addition, we hypothesized that a leaf arrangement with longer internodes is necessary for short trees to capture light efficiently. Such differences, if
found, would provide strong evidence that current shoot structure is associated with the adaptation of tree growth to changing environmental conditions during ontogeny.

We analyzed current shoot structure in several trees of the canopy species *Elateriospermum tapos* Bl. (Euphorbiaceae) in a Malaysian rain forest. *Elateriospermum tapos* is found in tropical rain forests in southeastern Asia (Whitmore 1972). This species is dominant in the Jengka Forest Reserve, Peninsular Malaysia (Ho et al. 1987), and in the Belalong Forest, Brunei (Cranbrook and Edwards 1994). Trees of various heights were chosen, to examine differences in current shoot structure in relation to tree height. Our objectives were: (1) to determine whether biomass allocation patterns and current shoot allometry change with tree height in *E. tapos*; and (2) if changes were found, whether they contributed to the growth or maintenance of the crowns.

**Materials and methods**

**Study site and species**

The study was carried out at Pasoh Forest Reserve, Peninsular Malaysia (2°59′ N, 102°18′ E). The Pasoh Forest Reserve is a lowland dipterocarp forest belonging to the Red Meranti-Keruing type, which is dominated by *Shorea* spp. (Red Meranti group) and *Dipterocarpus* spp. (Keruing; Manokaran et al. 1992). The emergent layer averages 46 m in height and the height of the main canopy is 20–30 m (Manokaran and Swaine 1994).

Two hundred and twenty *E. tapos* saplings > 1 cm in diameter at breast height (dbh) were found in the 50-ha permanent plot of the Pasoh Forest Reserve, primarily clustered on a hill (Manokaran et al. 1992). *Elateriospermum tapos* has mono-podial branches with an orthotropic orientation and 3/8 phyllotaxis. Mature trees change leaves annually around February–March (Medway 1972, Whitmore 1972, Cranbrook and Edwards 1994, Osada et al. 2002). In contrast, saplings produce leaves non-synchronously, and leaf emergence is more frequent in saplings in high-light environments than in low-light environments (Osada et al. 2002). In *E. tapos*, branching occurs with sylleptic shoots, i.e., a lateral meristem develops continuously from a terminal meristem at the time of leaf emergence (Hallé et al. 1978). Based on a generalized allometric equation (Thomas 1996a), the asymptotic maximum height of *E. tapos* was estimated to be 42.4 m at the study site (N. Osada, unpublished data).

**Data collection**

Ten *E. tapos* trees growing in similar soil conditions were chosen near trails, and dbh and tree height were measured (7.0–39.6 m in height). Tree height was measured with an extendable rod (for trees < 10 m), or calculated by triangulation from the top of the tree to a 1.5-m rod with a clinometer (for trees > 10 m tall). One leading section of the main trunk (200–250 cm in length, hereafter termed “leader crown”) was harvested from each crown of three trees in May 1998, and from seven trees in December 1999. Each leader crown contained more than 15 shoots and there were no leaves proximal to each leader crown. At both harvests, all current-shoot leaves on these leader crowns were fully expanded and toughened, but had not yet become senescent, so the difference between times of harvest had a negligible effect on the results obtained. None of the harvested leader crowns bore flowers or fruits at the time of harvest.

For each leader crown, we counted the numbers of non-branching and branching (sylleptic) shoots and the number of leaf cohorts attached to all shoots. We then randomly chose and cut from each leader crown 14 to 15 current shoots showing no obvious damage. The clear bud scales made it possible to accurately distinguish current shoots. To investigate biomass allocation patterns, we measured stem length and diameter, petiole length, and leaf length and width of each current shoot shortly after harvesting. All stems and leaves were oven dried at 60 °C and weighed. One-sided leaf area was measured with an area meter (AAM-8, Hayashi Denko, Tokyo, Japan) on photocopies of 50 fresh leaves, randomly sampled from all trees, and an equation to estimate area from leaf length and width was determined:

\[ a_L = 0.753 L_w, \]

where \(a_L\), \(L\), and \(w\) are leaf area, length, and width, respectively \((r^2 = 0.995)\).

**Data analysis**

Total biomass of current shoots \(b_T\), stem biomass \(b_S\), total leaf biomass \(b_{LT}\) and leaf weight ratio (LWR, ratio of leaf weight to total biomass of current shoot; Chiaratto et al. 1989) within a current shoot were determined as follows:

\[ b_T = b_S + b_{LT}, \]

\[ \text{LWR} = b_{LT}/b_T. \]

Stem biomass \(b_S\) is a function of wood density \(\delta_w\) and stem volume, and stem volume is a function of stem length \(l_s\) and diameter \(d_s\). Stem biomass was thus determined as:

\[ b_S = \delta_w \left( \frac{\pi d_s^2 l_s}{4} \right). \]

Total leaf biomass \(b_{LT}\) was determined from individual leaf blade weight \(w_B\), petiole weight \(w_p\) and leaf number \(n_L\), whereas individual leaf blade weight and SLA were used to determine individual leaf area \(a_L\):

\[ b_{LT} = n_L (w_B + w_p), \]

\[ a_L = w_B \text{SLA}. \]

We analyzed biomass allocation patterns within current shoots based on these variables. For stem and leaf allocation patterns, we applied an analysis of covariance (ANCOVA) to investigate whether trees of different heights produce different...
shoot structures with the same amount of biomass (Kohyama 1987, Kohyama and Hotta 1990):

\[ \ln y = b_0 + b_1 \ln x, \]  

(5)

where \( x \) and \( y \) are any two components of shoot structure, and \( b_0 \) and \( b_1 \) represent parameters obtained by linear regression. Least squares regression was used to determine the allometric relationships because it is appropriate when the objective is to detect variations and not to calculate regression parameters (Kohyama 1987, Kohyama and Hotta 1990). First, homogeneity of slopes was tested, and if no difference was found among slopes, ANCOVA was conducted to test for differences among adjusted means. If \( b_1 \) differs among individuals, then individuals with larger \( b_1 \) will show a greater increase in \( y \) per increment of \( x \). On the other hand, if \( b_0 \) differs, but \( b_1 \) does not, then individuals with a larger \( b_0 \) will have a consistently larger amount of \( y \) at any \( x \). Thus, these two parameters characterize differences in shoot structure between trees of different heights. We determined whether the differences occurred only in the intercept \( b_0 \) or also in the slope \( b_1 \).

In addition to the allometric analyses, differences in leaf shape among individuals were considered, because shape affects the degree of mutual shading of leaves on a shoot. The mean distance of leaf area from the stem was used as an index of mutual shading of leaves (Takenaka 1994). According to computer simulations, shoots with leaves having a large mean distance are less susceptible to mutual shading than shoots with leaves having a small mean distance (Takenaka 1994). Because leaves of E. tapos are oblong and almost symmetric, petiole length plus half of leaf length was taken as the distance, and this value was normalized by dividing it by the square root of leaf area (Takenaka 1997).

The analysis of Takenaka (1994) assumes that all the leaves within a shoot are of similar size. However, any difference in leaf size within a shoot will strongly affect the degree of mutual shading. Therefore, to examine whether changes in leaf size are sequential along a shoot, the Kendall rank correlation was applied between leaf order and petiole length or leaf length for each current shoot.

### Results

**Shoot traits and biomass allocation within current shoots**

The proportions of shoots with 1, 2 and ≥ 3 cohorts of leaves within each leader crown are shown in Figure 1a. The proportion of shoots with ≥ 2 cohorts of leaves decreased and the proportion of shoots with only 1 cohort of leaves increased with increasing tree height. The proportion of sylleptic shoots was 9.5 ± 10.4% (mean ± SD) and was unrelated to tree height (Figure 1b). We therefore examined the structure of non-branching current shoots only in relation to tree height.

Total biomass and LWR of current shoots were unrelated to tree height (Figure 2), indicating that similar biomass was allocated to current shoots, irrespective of tree height. Wood density varied significantly among trees, but was unrelated to tree height (Figure 2).

**Current shoot allometry**

Stem shape parameters (Equation 5), such as diameter and length, changed with tree height. Significant differences were found among trees of different heights, not in the slope but in the intercept of the allometric relationship between \( \log_e \) stem diameter and \( \log_e \) stem dry weight (Table 1). Thus, tall trees had current shoots with shorter and thicker stems than short trees (Figure 3).

Leaf characteristics within current shoots also changed with tree height. Significant differences among trees of different heights were found only in the intercepts for the two allometric relationships (Table 1). Leaf number was greater in tall trees than in short trees (Figure 4), suggesting that mean leaf weight was less in tall trees. Both total leaf area (Figure 4) and SLA were smaller for tall trees than for short trees \((r = -0.928, P < 0.001)\). Thus, leaders of tall trees produced more leaves, of lower dry mass and smaller specific area, than leaders of short trees of the same biomass.

To investigate the structural constraints in current shoots, we analyzed indices of leaf structure in relation to stem diameter and length. Slopes did not differ in any of the allometric relationships, whereas intercepts differed among trees of different heights (Table 1). Total leaf area, mean leaf area, total leaf weight, and mean leaf weight were smaller for shoot stems of a given diameter in tall trees than in short trees (Table 2). Thus, current shoot stems of similar diameter supported...
less leaf biomass in tall trees than in short trees. Because tall
trees had current shoots with shorter stems for a given stem di-
ameter than short trees, and the relationship between diameter
and leaf number did not change with tree height, tall trees ar-
ranged the same number of leaves along shorter internodes.
This indicates that mutual shading among leaves on current
shoots was greater in tall trees than in short trees.

Leaf shape and arrangement
Leaf shape also affected the degree of mutual shading. The
mean distance of leaf area from the shoot stem did not differ
among trees of different heights, because the decrease in leaf
length with increasing tree height was greater than the de-
crease in petiole length, and because leaf length per width was
unrelated to tree height (Figure 5). Therefore, mean distance
did not explain the difference in mutual shading among trees
of different heights.

Overall, mutual shading was considered more severe in cur-
rent shoots of tall trees than of short trees. However, we ob-
tained evidence that trees reduced mutual shading within
current shoots by producing leaves of different sizes, related to
leaf order. Within current shoots, petiole and leaf lengths were
shorter in distal leaves than in proximal leaves, especially for
shoots that had many leaves (Figure 6), and this trend was par-
ticularly obvious for petiole length. This suggests that, for cur-
rent shoots having many leaves, the production of smaller
leaves acropetally along the stem results in a reduction in mu-
tual shading.

Discussion
Total biomass and leaf weight ratio (LWR) of current shoots
were unrelated to tree height (Figure 2). Thus, the relative im-
portance of stem and leaf biomass of current shoots did not
change with tree height. This finding contrasts with the LWR of a whole tree, which is larger in taller trees than in shorter trees (e.g., Shukla and Ramakrishnan 1984, Ardhana et al. 1988). Biomass allocation to support mass is considerably larger for tall trees than for short trees, and this may decrease the LWR of tall trees at the level of individual trees. In our study, effects of tree height and light environment were correlated because we selected short trees from the understory. We note that our results may also be influenced by light environment (cf. Sterck and Bongers 2001).

Shoot stem structure changed with increasing tree height: current shoots of tall trees had thicker and shorter stems than current shoots of short trees (Figure 3). Because saplings of canopy trees cannot achieve sexual maturity until they emerge above the canopy (Kohyama 1987), height growth is important for their successful regeneration. As a tree grows toward its maximum height, however, its growth rate declines gradually because of hydraulic limitations (Ryan and Yoder 1997), mechanical constraints (King 1986, Aiba and Kohyama 1996), or increased allocation to reproduction (Kohyama 1993, Thomas 1996b). In E. tapos, leaf biomass allocation also changed: compared with short trees, tall trees produced current shoots with more leaves of lower dry mass and smaller area per leaf mass. Thomas and Ickes (1995) showed that leaf size and tree size exhibit a non-monotonic relationship, and that leaf size is maximized at stem diameters close to the species-specific size at reproductive onset for two *Garcinia* species. Yamada et al. (2000) found that leaf size increased with increasing height.

![Figure 3. Intercepts of the allometric relationships between stem biomass and stem diameter (a), and stem biomass and stem length (b) of current shoots for 10 trees of different heights. Correlation coefficients are shown with significance level (** = P < 0.01, * = P < 0.05).](image)

![Figure 4. Intercepts of the allometric relationships between total leaf biomass and leaf number (a) and total leaf area (b) of current shoots for 10 trees of different heights. Correlation coefficients are shown with significance level (** = P < 0.01, * = P < 0.01).](image)

Table 2. Values of intercepts ($b_0$) of the allometric regression for the two component variables of shoot structure. Significance levels: * = P < 0.10, ** = P < 0.01, *** = P < 0.001, others P > 0.10.

<table>
<thead>
<tr>
<th>Tree height (m)</th>
<th>Stem diameter versus</th>
<th>Leaf diameter versus</th>
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<tr>
<td></td>
<td>Stem length</td>
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<tr>
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$r^1$ Correlation coefficients between tree heights and intercepts.
before branching, but decreased after branches were produced in three *Scaphium* species. In contrast, in *E. tapos*, leaf size decreased monotonically with increasing tree height, even though trees mature at a height of about 20–30 m (Osada et al. 2002). This suggests that, in *E. tapos*, changes in leaf size are more closely related to tree height than to the onset of reproduction or branching status, and that changes in light environment or hydraulic stress with tree height play important roles in determining leaf size.

As predicted, changes in stem and leaf structures of current shoots with increasing tree height interacted to determine the overall current shoot structure. Because tall trees supported less leaf biomass on shoot stems of a given diameter than short trees, both mechanical and hydraulic stresses may be reduced in tall trees.

Changes in stem and leaf structures of current shoots directly affected patterns of mutual shading among leaves. Based on a computer simulation, Takenaka (1994) showed that mutual shading within a shoot was reduced by (1) smaller total leaf area per shoot length, (2) less leaves per shoot and (3) larger mean distance of leaf area from the stem. In *E. tapos*, total leaf area per shoot length and mean distance of leaf area from the stem did not change with tree height. However, the number of leaves per shoot changed with tree height. Tall trees had more leaves with shorter internodes than short trees, suggesting that mutual shading is more severe in tall trees than in short trees. Short trees adapt to low irradiance by reducing mutual shading and producing leaves with a large SLA. In contrast, because tall trees receive high light energy, which often exceeds the light saturation point of the leaves of typical canopy species (Zotz and Winter 1996), the effect of mutual shading may be less important than in short trees. Even so, mutual shading in tall trees was reduced by the production of smaller leaves in distal than in proximal parts of current shoots. It is noteworthy that tall trees produced a large number of small leaves rather than a small number of large leaves of the same mass. Because the proportion of sylleptic shoots did not change and because stem lengths of current shoots decreased with increasing height, shoot density (number per volume) in tall trees may be greater than in short trees. This suggests that tall trees may reduce mutual shading of adjacent shoots by producing smaller leaves. Horn (1971) concluded that more light can penetrate the dense crowns of tall trees that have a
large number of small leaves than a small number of large leaves.

In addition to morphological traits, the phenology of leaf emergence and stem elongation also affected the growth patterns of *E. tapos*. Mature *E. tapos* trees produce leaves annually (Medway 1972, Whitmore 1972, Cranbrook and Edwards 1994, Osada et al. 2002). In contrast, saplings under high-light conditions produce leaves two to three times a year, whereas saplings under low-light conditions produce leaves only once a year (Osada et al. 2002). Therefore, short saplings can produce current shoots more than once a year, in which case total shoot elongation per year will exceed that of one current shoot. This phenological plasticity further accelerates height growth of saplings. All of these characteristics suggest that changes in current shoot structure with increasing tree height are adaptive in *E. tapos*, i.e., shoot structure appears to maximize growth in short trees and maximize light capture in tall trees.

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