

# Architectural and allometric differences among *Scaphium* species are related to microhabitat preferences

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## Summary

1. Interspecific comparisons were made among *Scaphium* species (Sterculiaceae): *S. borneense* (Merr.) Kosterm., *S. longipetiolatum* (Kosterm.) Kostermans, and *S. macropodum* (Miq.) Beumee ex Heyne to test the hypothesis that variations in their architecture and allometry are related to the microhabitat conditions of stands where the species regenerate preferentially.

2. The species studied are shade-tolerant canopy trees. They occur in a tropical rainforest in Lambir Hills National Park, Sarawak, East Malaysia (sympatric at the community level), where the study was conducted, but show an allopatric pattern of distribution among microhabitats due to localized edaphic conditions. *Scaphium longipetiolatum* occurs primarily in stands on clay-rich soils, whereas *S. borneense* occurs primarily in stands on sandy soils. Stands on clay-rich soils are more shaded, and gaps form less frequently than in stands on sandy soils.

3. *Scaphium longipetiolatum* initiated branching at a smaller tree size than *S. borneense* and *S. macropodum*, which did not produce branches until stems reached several centimeters in diameter.

4. The monoaxial saplings of *S. borneense* and *S. macropodum* expanded their crown area by producing bigger leaves. The branched saplings of *S. longipetiolatum* expanded their crown area by developing lateral branch systems.

5. An analysis of interspecific differences in above-ground allometries revealed that the growth pattern of monoaxial saplings, which emphasizes leader growth, leads to rapid height growth. In contrast, that of the branching saplings of *S. longipetiolatum* prioritizes shade tolerance.

6. The architecture and allometry of each *Scaphium* species gave some potential advantage over the other *Scaphium* species in stands where the former regenerates preferentially, that is, the advantages of each phenotype were context-dependent.

*Key-words:* Adaptation, allocation, regeneration niche, saplings, tropical rainforest, tree architecture

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## Introduction

Trees show great variation in architecture (Hallé, Oldemann & Tomlinson 1978), and tree architecture has a major influence on performance through its effect on leaf display (Ashton 1978). Recent investigations have demonstrated that the above-ground architecture and allometry of trees are closely related to each species' growth and survival (Aiba & Kohyama 1997; Chazdon 1986; King 1990; Kohyama 1987; 1991; Kohyama & Hotta 1990).

King (1990), Kohyama (1987) and Kohyama & Hotta (1990) hypothesized that understorey trees and saplings display an adaptive allocation pattern among leaves, branches and stems that maximizes the future probability that trees can grow to reproduce. Kohyama (1987) showed that variation in the architecture and allometry of understorey saplings in a Japanese warm-temperate forest was related to the trade-off between height growth (to exploit potential opportunities to reach better-lit conditions) and horizontal growth (to increase actual production). King (1990) found that understorey saplings of canopy trees were better adapted for height growth than permanent understorey trees in neotropical forests. Kohyama & Hotta (1990) hypothesized that the advantage of maintaining and expanding photosynthetic area at a given height is

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relatively smaller than that conferred by rapid height growth in habitats where fast growth rates are possible and steep vertical light gradients occur, as in tropical rain forests. Kohyama (1991) demonstrated mathematically that the optimal allocation for maximizing a sapling's rate of height growth depended on light conditions. He proposed that temporal and spatial fluctuations in the understorey light environment induce allometric variations among coexisting saplings. It is now accepted that allometric and architectural variations influence the growth and survival of tree species, and can lead to their equilibrium coexistence by promoting niche differentiation during regeneration (Grubb 1977).

However, most previous studies compare the architecture and allometry of trees belonging to different taxonomic groups, and few examine interspecific differences within a genus (Ackerly & Donoghue 1998; Chazdon 1986; Thomas 1996). It is necessary to compare the architecture and allometry of trees within closely related species for two reasons. First, a hierarchically structured phylogeny undermines the comparison of two phenotypes across two higher taxa (Felsenstein 1985), and this often leads to serious statistical problems (Kelly & Purvis 1993). The simplest way to factor out a phylogenetic explanation is to compare species within closely related taxa or the same taxon (Kelly & Purvis 1993). Within a taxonomic group, comparisons are more likely to be free of phylogenetic constraints.

The second reason is that the coexistence of closely related species is central to understanding the maintenance of biodiversity in tropical rainforests (Ashton 1988). One remarkable feature of this biodiversity is the presence of a series of sympatric congeneric species in some genera (Ashton 1982; Fedorov 1966; Kochummen, LaFrankie & Manokaran 1990; Rogstad 1990; Whitmore 1984). Such species differ at fewer gene loci, and therefore in fewer life-history characteristics, because they share the same ecological and physiological heritage via their common ancestry (Rogstad 1989). Consequently, the equilibrium coexistence of the sympatric species should be more difficult than that among species of different taxonomic groups. The mechanisms for the maintenance of biodiversity may therefore be critical for the coexistence of such species.

This paper analyses interspecific variations in the architecture and allometry of three species from a genus of shade-tolerant canopy trees, *Scaphium* Schott & Endl., in a tropical rainforest. The species are sympatric at the community level, but allopatric among microhabitats due to localized edaphic conditions. *Scaphium borneense* (Merr.) Kosterm. and *S. longipetiolatum* (Kosterm.) Kostermans occur primarily on sites covered by sandy and clay-rich soils, respectively, whereas *S. macropodum* (Miq.) Beumee ex Heyne occurs on sites covered by both soil types (Yamada *et al.* 1997; 1999). Our aims are (1) to describe differences in the growth and survival of saplings in terms of inter-

specific differences in above-ground architecture and allometry; and (2) to answer the question: are differences in growth and survival related to the microhabitat conditions of stands where each species regenerates preferentially?

## Materials and methods

### STUDY SPECIES AND SITES

*Scaphium* is a small genus of large, briefly deciduous trees that includes six species (Yamada *et al.* 1999). Three of the six species, *S. borneense*, *S. longipetiolatum* and *S. macropodum*, were investigated here. The genus is endemic to the Indo-Malaysian sub-kingdom defined by Good (1974), and is distributed throughout Indochina, Malaysia, Borneo and Sumatra (Yamada *et al.* 1999). Each species is shade-tolerant, and saplings are abundant beneath closed canopies (Yamada *et al.* 1999). *Scaphium macropodum*, the most widespread species, reaches heights of >45 m in Borneo (Yamada & Suzuki 1996). The trees flower on bare twigs after leaf fall (Kostermans 1953), and produce fruits with a boat-shaped wing derived from a dehiscent follicle. The dispersal distance of the fruit seldom exceeds 50 m from the base of the parent tree (Yamada & Suzuki 1997).

This study was performed in an equatorial foothill forest in Lambir Hills National Park, East Malaysia (latitude 4°12' N, long 114°00' E). The park is covered by ≈7000 ha of primary mixed dipterocarp forest. Annual rainfall averages around 320 cm. A 52 ha research plot was established in the forest (Yamakura *et al.* 1996). *Scaphium borneense*, *S. longipetiolatum* and *S. macropodum* occur in the park (Yamada *et al.* 1999), and each contributes trees to the forest's main continuous canopy. The observed maximum d.b.h. measurements (diameter at breast height, 130 cm above ground) in the research plot were 40.7, 53.0 and 57.3 cm for *S. borneense*, *S. longipetiolatum* and *S. macropodum*, respectively (Yamada *et al.* 1999). Details of the climate, soils, vegetation and physiography in both forest and research plot are provided by Watson (1985) and Yamakura *et al.* (1996).

These *Scaphium* species coexist in the plot because they reduce direct competition by niche differentiation (Yamada *et al.* 1999). The plot is covered by two different soil types, clay-rich and sandy soils. The distributions of *S. longipetiolatum* and *S. borneense* are restricted to clay-rich and sandy soils, respectively; *S. macropodum* occurs on both soil types.

### DATA SAMPLING

All *Scaphium* trees larger than 1 cm d.b.h. that were found in the southern part of the research plot (25 ha in total area) were identified and their d.b.h. were measured from February to March 1996. At the same time we recorded the maximum number of lobes

of each palmate leaf on each tree, and whether it had branches.

For each of the three species, 10 trees that showed no evidence of past breakage were collected in May 1996 from a closed stand near, but outside, the research plot; these trees were 30–300 cm tall. All samples of *S. borneense* and *S. macropodum* were monoaxial and had not yet begun to develop branches. The sample trees were cut at ground level and the following dimensions were measured: tree height; two stem diameters (at right angles to each other) at 10% of the tree's height above ground; two crown diameters including the maximum width (also at right angles to each other); petiole lengths; and leaf-blade lengths of all leaves. The mean trunk diameter was defined as the geometric mean of the two stem diameters measured. The area of the crown was calculated as the projection of an ellipse defined by the two crown diameters.

The sample trees were cut into four fractions: leaves, petioles, branches and stems. The fractions were dried at 80 °C for 1 week in an oven, and their oven-dry mass (DM) were measured. The total DM of the petioles and branches was defined as the DM of the leaf support tissue ( $W_{LS}$ ). Leaf area was determined with a scanner (Epson EP Scan GT-8000, Seiko-Epson Co., Japan) combined with area-determination software based on ADOBE PHOTOSHOP 2.5 J (Adobe Systems, Inc., USA). Tree height and the length of the biggest leaf on the tree were measured for a further 10 trees for each species, with heights ranging from 300 to 1100 cm. The lengths of six leaves from canopy trees of each species were also measured.

#### DATA ANALYSIS

The allometric relationship between the sizes of two parts of an organism,  $X$  and  $Y$ , can often be described by a simple power function:

$$\log Y = K + h \log X \quad \text{eqn 1}$$

where  $K$  and  $h$  are parameters obtained by linear regression of the log-transformed values of  $X$  and  $Y$ . However, many scientists have pointed out that the standard regression method is unsuitable for calculating allometric relationships in which the two variables are covariant or are subject to error. As a result, alternative regression methods have been recommended for bivariate data (LaBarbera 1989; Niklas 1994; Suzuki & Ashton 1996). Here we used the standard regression method (equation 1) because it remains valid when the goal is only to detect interspecific variations, not to calculate regression parameters (Kohyama 1987; Kohyama & Hotta 1990). Differences between the regression relationships for the three species were examined using analysis of covariance. All were log-transformed using base 10. The dimensions and abbreviations used in the analysis of allometric relationships are listed in Table 1.

**Table 1.** Units and symbols for the parameters analysed in the study

Parameter	Units	Symbol
Tree height	cm	$H$
Stem diameter at breast height	cm	$D_{0.1}$
Crown projection area	cm <sup>2</sup>	$A_C$
Total leaf area	cm <sup>2</sup>	$A_L$
Above-ground mass	g DM	$W$
Mass of stem	g DM	$W_S$
Mass of branches	g DM	$W_B$
Mass of leaf blade	g DM	$W_{BL}$
Mass of petiole	g DM	$W_P$
Mass of leaf-support tissue	g DM	$W_{LS}$

## Results

### DIFFERENCES IN ABOVE-GROUND ARCHITECTURE

Figure 1 shows d.b.h. frequency distributions for the *Scaphium* trees in the southern part of the plot. Most *S. longipetiolatum* trees in the d.b.h. class 1–2 cm, and all trees >2 cm d.b.h., had branches. For *S. borneense* most trees <3 cm d.b.h. had no branches, whereas most trees >3 cm d.b.h. had branches. Most *S. macropodum* <10 cm d.b.h. had no branches, but most trees >10 cm d.b.h. did. For all species, all trees >21 cm d.b.h. had branches. These data suggest that the tree size at which branching initiation begins differs between species: *S. longipetiolatum* initiates branching at the smallest tree size, and *S. macropodum* at the largest.

Leaf forms and their patterns of ontogenetic change differed among the species. *Scaphium longipetiolatum* deployed only ovate leaves, and the leaf form did not change ontogenetically. In contrast, *S. borneense* and *S. macropodum* had ovate leaves as seedlings, developed palmate leaves on a monoaxial stem before the initiation of branching, and retained ovate leaves again after the initiation of branching. The number of lobes of palmate leaves increased with increasing tree size. The maximum number of lobes was five for *S. borneense* and nine for *S. macropodum*.

Leaf size also differed between species (Fig. 2). The ovate leaves of *S. longipetiolatum* became larger as the trees grew taller until they reached ≈100 cm in height, and their size remained constant thereafter. The maximum length of these ovate leaves was 65 cm. The size of palmate leaves on monoaxial saplings increased with tree size for both *S. borneense* and *S. macropodum*, which had maximum leaf lengths of 97 and 149 cm, respectively. The ovate leaves on branched trees in the canopy layer were smaller than in the younger trees; the mean leaf lengths were 20.3 (SD = 3.57), 30.1 (SD = 5.70) and 29.4 (SD = 3.20) for *S. borneense*, *S. longipetiolatum* and *S. macropodum*, respectively. Significant differences were found in pairs of *S. borneense* and *S. longipetiolatum*, and of *S. borneense* and *S. macropodum* (Tukey's HSD test

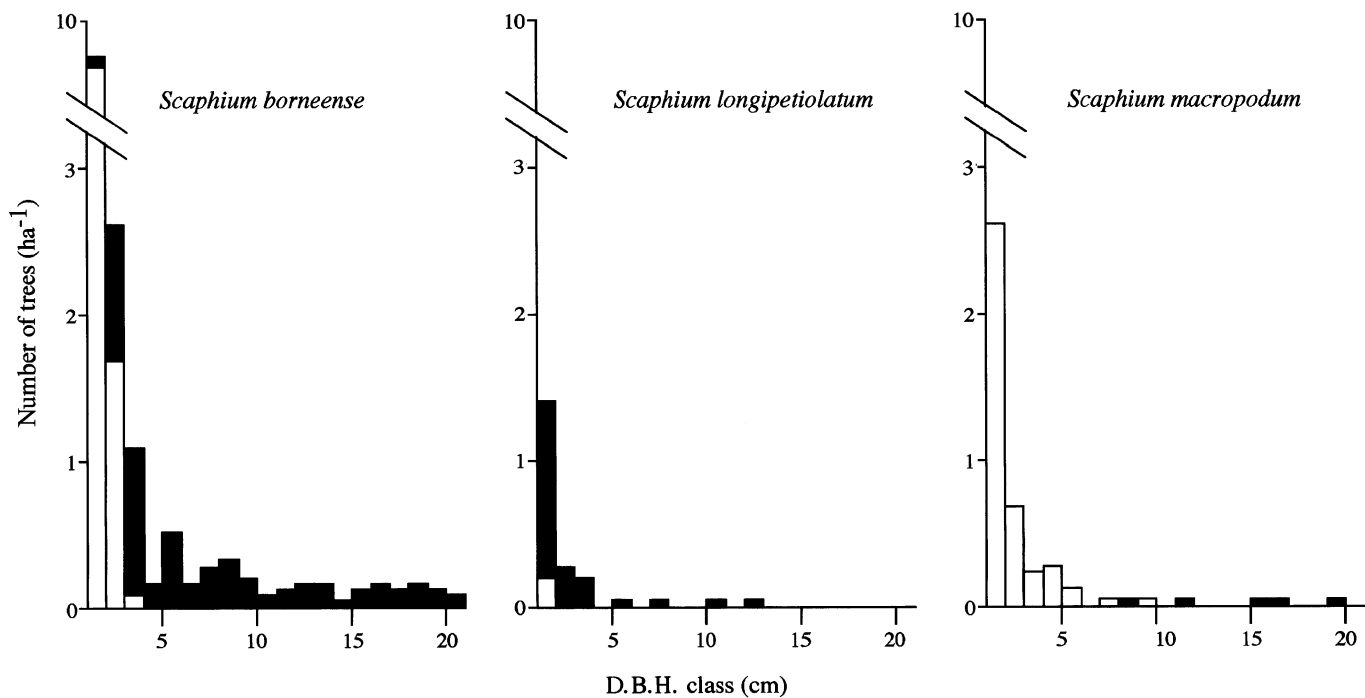


Fig. 1. Frequency distribution of diameter at breast height for *S. borneense*, *S. longipetiolatum* and *S. macropodum* in the southern half of a 52 ha study plot in Lambir Hills National Park (Sarawak, East Malaysia). Open and solid columns show monoaxial and branched trees, respectively.

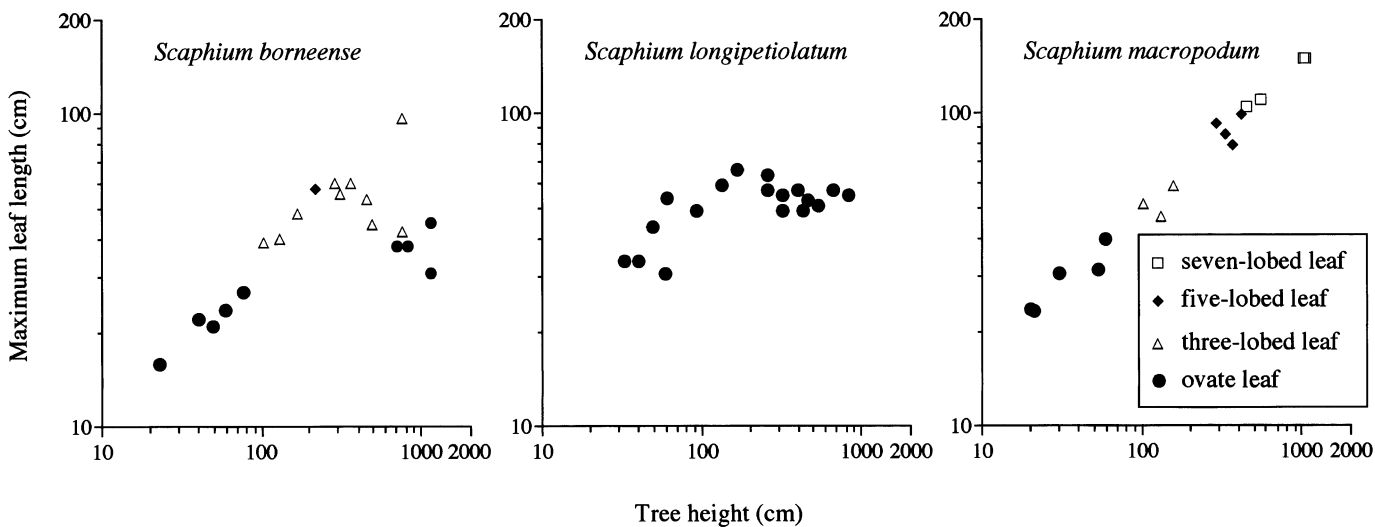


Fig. 2. Relationship between tree height and length of largest leaf. Each symbol represents one tree. Leaf length is defined as the sum of blade and petiole lengths.

for pairwise comparisons,  $P < 0.01$ ), but the difference between *S. longipetiolatum* and *S. macropodum* was not significant ( $P > 0.5$ ).

#### DIFFERENCE IN ABOVE-GROUND ALLOMETRY

Allometric relations differed significantly among species. Table 2 summarizes the analysis of differences in allometric relations. The value of the regression parameter  $K$  differed significantly in nine of the 11 regressions, but the only other significant difference was in  $h$  in the  $W_p$  versus  $W_{BL}$  regression. This suggests

that the allometric differences among the species show the same tendency at all sapling sizes.

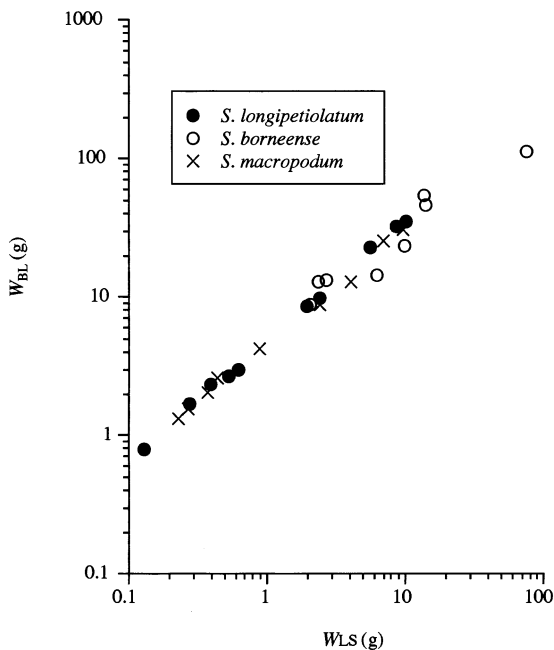
*Scaphium borneense* grew tallest for any given value of  $D_{0.1}$ , whereas *S. longipetiolatum* was shortest. For a given  $H$ , *S. borneense* and *S. longipetiolatum* had the narrowest and widest crowns ( $A_c$ ), respectively. Furthermore, for a given  $H$ , *S. longipetiolatum* possessed the largest  $W_s$ ,  $W_{LS}$  and  $W_{BL}$  values, and so the largest  $W$ . In contrast, *S. borneense* had the smallest  $W_s$ ,  $W_{LS}$  and  $W_{BL}$  values, and thus the smallest  $W$ . *Scaphium macropodum* was intermediate in its characteristics. For a given  $W$ , *S. longipetiolatum* allocated more dry matter to  $W_{BL}$  and  $W_{LS}$  and less to  $W_s$  than the other species.

**Table 2.** Differences in the allometric relationships between 11 pairs ( $X, Y$ ) of dimensions (see Table 1) based on equation 1,  $\log Y = K + h \log X$  (see text for details) among three sympatric *Scaphium* species

No.	$X$	$Y$	$F$ for difference†		Common $h$	$K$ for‡		
			$h$	$K$		<i>S. macropodum</i>	<i>S. longipetiolatum</i>	<i>S. borneense</i>
1	$D_{0.1}$	$H$	1.651	54.984**	1.687	84.5351	<b>64.869</b>	<b>179.489</b>
2	$H$	$A_C$	1.948	23.044**	1.176	17.4377	<b>21.7014</b>	<b>8.42341</b>
3	$H$	$W$	1.397	28.284**	1.862	0.00857	<b>0.01207</b>	<b>0.00471</b>
4	$H$	$W_S$	2.086	34.974**	2.087	0.00207	<b>0.00246</b>	<b>0.00103</b>
5	$H$	$W_{LS}$	1.642	29.277**	1.669	0.00124	<b>0.00277</b>	<b>0.00091</b>
6	$H$	$W_{BL}$	1.653	14.399**	1.422	0.01426	<b>0.02736</b>	<b>0.01033</b>
7	$W$	$W_{BL}$	3.049	4.518*	0.777	<b>0.51473</b>	<b>0.75263</b>	0.59099
8	$W$	$W_S$	0.435	5.029*	1.110	<b>0.43893</b>	<b>0.35925</b>	0.42796
9	$W$	$W_{LS}$	1.692	11.586**	0.900	<b>0.0778</b>	<b>0.14191</b>	0.08610
10	$W_P$	$W_{BL}$	4.753*	–	–	–	–	–
11	$W_{LS}$	$W_{BL}$	0.186	1.156	–	–	–	–

†Significance levels are denoted by no asterisks, one asterisk, and two asterisks for  $> 0.05$ ,  $P < 0.05$  and  $P < 0.01$ , respectively.

‡Bold and underline show the largest and smallest values, respectively, among the three species.



**Fig. 3.** Allometric relationship between leaf blade dry mass ( $W_{BL}$ ) and DW of the leaf's support tissues ( $W_{LS}$ , the sum of DW of petioles and branches) for *Scaphium* trees. Each symbol represents one tree.

The slope of the allometric relationship between  $W_{BL}$  and  $W_P$  differed among the species. However, no interspecific differences in allometry were observed between  $W_{BL}$  and  $W_{LS}$  (Fig. 3).

## Discussion

The three *Scaphium* species showed different patterns of ontogenetic change in leaf and tree form (Fig. 2). These differences are related to the different growth strategies the species adopted during the transition from the sapling stage to adulthood.

A branching architecture such as that of *S. longipetiolatum* diverts resources to lateral branches at the expense of elongation growth of the main stem at low tree heights; these branches soon become useless in photosynthesis as a result of shading. However, this branching architecture allows *S. longipetiolatum* to expand its crown width more than those of the other two species, and to deploy more leaves at a given height, providing superior shade tolerance. In contrast, the monoaxial architecture of *S. borneense* and *S. macropodum* concentrates resources on leader growth at the cost of a smaller total crown area. This growth habit may have advantages if the species can survive to reach the heights of the surrounding canopy, but is disadvantageous in terms of decreased shade tolerance.

The leaf size of the monoaxial saplings of *S. borneense* and *S. macropodum* increased with tree size (Fig. 2). Since the total leaf area required for growth and survival of a tree increases with tree size in juveniles, monoaxial saplings must overcome constraints on crown expansion due to their growth habit; producing large, lobed leaves is one way to expand the leaf area when the tree cannot expand the crown area by lateral branches. In effect, the large, palmate leaves of monoaxial saplings are functionally equivalent to a lateral branch system. The fact that leaves became smaller in all three species once branch initiation begins supports this hypothesis: leaves need not be as large if the lateral branch systems can expand the crown area instead.

Seven-lobed leaves were larger than leaves with fewer lobes (Fig. 2). Yamada & Suzuki (1996) discussed the adaptive significance of this growth form from the viewpoints of improving leaf-gas exchange and the efficiency of crown-level light capture. In general, larger leaves photosynthesize less efficiently than a collection of smaller leaves with the same total leaf area, because a larger leaf has a thicker boundary layer which increases resistance to gas exchange (Yabuki

1985). Each lobe of a palmate leaf can behave as if it were a single leaf (Raschke 1960), and the leaf's shape mimics the effect of growing small leaves. This increases photosynthetic rates compared with non-lobed leaves of the same leaf area. Furthermore, compound leaves permit the penetration of more light into a diffuse canopy (Horn 1971), and the development of lobes on leaves contributes to increasing the overall light interception of the tree (Niklas 1989). For these reasons, the development of lobes by the larger leaves of *S. borneense* and *S. macropodum* should contribute to increasing the overall light interception of the crown.

Givnish (1978) proposed that a large part of a petiole's strength is derived from turgor pressure and the development of fibrous materials. If this is true, petioles should not be as costly to grow as a woody branch that bears the same mass of leaves. However, our results contradict this: the allometric relationship between  $W_{BL}$  and  $W_{LS}$  did not differ among species (Fig. 3). This suggests that the cost of leaf support is the same for petioles and branches. The potential of a monoaxial stem for quick height growth with large leaves probably does not derive from energy savings made by using petioles to replace woody branches; instead it derives from energy saving due to reduced investment in lateral growth by concentrating shoot growth in the apical meristem.

The allometric analyses are consistent with the growth strategies of the three *Scaphium* species. Kohyama (1987) compared the allometric relationships for the above-ground parts of saplings in a warm temperate forest, and suggested that allometric variations relate to the manner in which each species copes with the unpredictability of gap formation. He proposed a dichotomy in the strategies of understorey saplings: 'optimists', with superior growth rates under improved light conditions, and 'pessimists', with superior shade tolerance. The monoaxial saplings of *S. borneense* and *S. macropodum* had narrower crowns and more slender stems than *S. longipetiolatum*, and could grow tall for any given  $W$  (Table 2). These characteristics favour vertical growth at the expense of shade tolerance, and *S. borneense* and *S. macropodum* therefore meet the criteria for optimists. In contrast, the saplings of *S. longipetiolatum* meet the criteria for pessimists. They require more dry matter than the saplings of the two other species to attain a given height (Table 2), but if the three species have comparable photosynthetic capacities per unit DM of leaf blade, *S. longipetiolatum* is likely to be the most shade-tolerant because it has invested the most resources in  $W_{BL}$  for any given  $W$  (Table 2).

Itoh (1995) analysed the structures and understorey light conditions of stands growing on sandy and clay-rich soils. He found that stands on sandy soils were typically very dense, with abundant small trees, whereas stands on clay-rich soils consisted mostly of large trees, with relatively sparse small trees. Forest-floor light regimes also differed between the two types of

stand; the understories of stands on clay-rich soils were more shaded than those on sandy soils (Itoh 1995). Itoh also proposed that gap formation would be more frequent and predictable on sandy than on clay-rich soils. The monoaxial architecture and the allometric pattern of *S. borneense* might have some advantage over those of *S. longipetiolatum* on sandy soils, where there is less shade and more frequent gap formation. In contrast, *S. longipetiolatum* might be better adapted to stands on clay-rich soils, which have heavier shade and less frequent gap formation. Therefore the architecture and allometry of the three *Scaphium* species in the present study appears to be adapted to the respective understorey light regimes of the forest where each species mainly regenerates.

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