DIFFERENCES IN GROWTH TRAJECTORY AND STRATEGY OF TWO SYMPATRIC CONGENERIC SPECIES IN AN INDONESIAN FLOODPLAIN FOREST

TOSHIHIRO YAMADA,2,5 OKA PUTU NGAKAN,3 AND EIZI SUZUKI4

1Faculty of Environmental and Symbiotic Sciences, Prefectural University of Kumamoto, Kumamoto 862-8502, Japan;
2Faculty of Agriculture, Hasanudin University, Makassar 90245, Indonesia; and
3Faculty of Science, Kagoshima University, Kagoshima 890-0065, Japan

Whole-plant development trajectories and sapling leaf displays were compared for two sympatric congeneric species, Pterospermum diversifolium and P. javanicum, in a tropical floodplain forest in East Kalimantan, Indonesia. We assessed their growth strategies and developed hypotheses for their coexistence within the community. Pterospermum diversifolium retains a monaxial growth habit that promotes quick stem elongation; thus, it is taller when branches are initiated than is P. javanicum. The species differed significantly in height growth and total crown expansion per unit increment of biomass: monaxial P. diversifolium saplings devote more effort to stem elongation, whereas branched P. javanicum saplings devote more effort to branch expansion. Monaxial P. diversifolium sustained more severe self-shading than P. javanicum. The sapling growth strategy of P. diversifolium appears to be static, optimizing leaf display for current light conditions. The advantages of these strategies depend on context, and the two species may coexist within a community by adopting different regeneration niches based on differing understory light conditions: P. diversifolium is favored over P. javanicum at high light levels, but the opposite is true at low light levels.

Key words: allometry; architecture; coexistence; Indonesia; interspecific comparison; Pterospermum diversifolium; Pterospermum javanicum; regeneration niche; Sterculiaceae.

A tree’s architecture is made up of many component traits at different levels of organization, such as the leaf, shoot, branch, and stem. These traits influence a plant’s growth and survival through their combined effects on leaf display (Ashton, 1978). Tree architecture has long been of interest, and its adaptive significance for growth and survival has been discussed by many researchers. Horn (1971) demonstrated mathematically that a monolayer arrangement of foliage within a crown is effective for assimilation under closed canopies, whereas multilayer arrangements are more effective in canopy gaps. Kohyama (1987) and King (1990) emphasized the importance of tree architecture from the viewpoints of static functioning (which optimizes leaf display under current light conditions) and dynamic functioning (which enhances the opportunistic use of light following disturbance).

Understanding these functions led researchers to two important findings concerning tree architecture. First, sapling architectures are related to the mature height of a species (King, 1990; Aiba and Kohyama, 1997). Because static functioning is more important for permanent understory shrubs, they should have an architecture that leads to increased leaf area while minimizing self-shading within their crowns. In contrast, dynamic functioning is more important for young saplings of canopy species, and they should have an architecture that reduces the biomass requirement per unit of height growth. Second, temporal and spatial fluctuation in the understory light environment induces allometric variations among coexisting understory saplings and promotes the coexistence of different species at equilibrium by accelerating the diversification of regeneration niches (Grubb, 1977). Kohyama (1991) demonstrated this phenomenon mathematically, and Aiba and Kohyama (1997) did it empirically. These research efforts led to broad acceptance that architectural and allometric variations influence the growth and survival of tree species and can lead to their coexistence at equilibrium. Hence, information about tree architecture can be a strong tool in assessing species’ growth strategies.

However, most previous research has compared the architecture of trees belonging to different taxonomic groups. Interspecific comparisons should be done using closely related species for two reasons. The first reason is that the coexistence of closely related species with similar ecological and physiological characteristics is central to our understanding of the maintenance of biodiversity (Ashton, 1988). The second reason is phylogenetic constraint. A hierarchically structured phylogeny undermines the comparison of two phenotypes across two higher taxa, and can lead to serious statistical problems (Felsenstein, 1985). Interspecific comparisons within a genus are most likely to weaken this phylogenetic constraint. Furthermore, previous researches compared species architectures only for juveniles, not for the entire development trajectory through to maturity. Only a few researchers have studied a species’ growth trajectory from the juvenile stage to reproductive maturity (Alvarez-Buylla and Martinez-Ramos, 1992; Thomas, 1996; Yamada and Suzuki, 1996; Aiba and Kohyama, 1997). As Poorter and Werger (1999) pointed out, the outcome of interspecific comparisons is very sensitive to the choice of ontogenetic trajectory reflected in the comparison, and thus the entire development trajectory from seedling to reproductive maturity should be studied.

This paper analyzes interspecific differences in whole-plant development trajectories and leaf displays for two sympatric congeneric species, Pterospermum diversifolium and P. javanicum, in a tropical floodplain forest in East Kalimantan, Indonesia. We assessed their growth strategies and developed hypotheses for their coexistence within the community. Pterospermum diversifolium retains a monaxial growth habit that promotes quick stem elongation; thus, it is taller when branches are initiated than is P. javanicum. The species differed significantly in height growth and total crown expansion per unit increment of biomass: monaxial P. diversifolium saplings devote more effort to stem elongation, whereas branched P. javanicum saplings devote more effort to branch expansion. Monaxial P. diversifolium sustained more severe self-shading than P. javanicum. The sapling growth strategy of P. diversifolium appears to be static, optimizing leaf display for current light conditions. The advantages of these strategies depend on context, and the two species may coexist within a community by adopting different regeneration niches based on differing understory light conditions: P. diversifolium is favored over P. javanicum at high light levels, but the opposite is true at low light levels.

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developmental trajectories from seedlings to reproductive maturity for two sympatric congeneric species, Pterospermum diversifolium Bl. and P. javanicum Jungh. (Sterculiaceae) in a floodplain rain forest in Indonesia. We characterize the growth strategies of the two species from the viewpoint of their individual growth trajectories and propose mechanisms for the coexistence of the two congeneric species within a forest community in terms of their different growth strategies.

**MATERIALS AND METHODS**

**Study species**—The genus *Pterospermum* Scherb. is characterized by medium to large trees and consists of about 20 species distributed from India to southern China and the Moluccas (Kochummen, 1972). According to Kochummen, these species are fast-growing, light-demanding trees that regenerate only in canopy gaps and on the fringes of forests. However, in our study site in the Indonesian tropical floodplain forest, we found many *Pterospermum* trees under closed canopies. In particular, we found two species (*P. javanicum* and *P. diversifolium*) growing under these conditions. These species form part of a continuous canopy at about 30 m aboveground and can become part of the emergent layer.

**Study site**—We performed our study in an equatorial floodplain forest in Labanan (Berau, East Kalimantan, Indonesia; latitude 1°52'30" N, longitude 117°12'00" E). The forest was designated as a 100 ha forest reserve in the Labanan concession of PT. Inhutni I, Indonesia. Records of precipitation at the Tanjun Redeb airport (ca. 20 km from the study site) from 1971 to 2000 gave an average annual precipitation of 2012 mm.

A 100 × 100 m permanent sample plot was established within the forest in 2002 at an altitude of 30 m, and all trees greater than 4.8 cm DBH (diameter at breast height, 130 cm above the ground) were tagged with an aluminum number plate; the trees were then identified, their DBH was measured, and their location was mapped (E. Suzuki, Faculty of Science, Kagoshima University, unpublished data). *Endertia spectabilis* Steenis & de Wit of the Fabaceae (Caesalpinioideae) was abundant within the plot. Dipterocarp trees from the genera *Shorea*, *Dryobalanops*, *Parashorea*, and *Anisoptera* were also present. Numerous species belonging to the Euphorbiaceae, Ebenaceae, Annonaceae, Sapindaceae, and many other families formed the main continuous canopy at a height of about 30 m. *P. javanicum* was the fifth most abundant tree species in the plot; *P. diversifolium* was the 34th most abundant species. We found 97 and 265 individuals of *P. diversifolium* and *P. javanicum*, respectively, in the 1-ha plot. The values of the index of skewness for the frequency distribution of tree heights in the plot were positive for each species, which suggests that some big trees were present with many small trees, generating the inverse J-shaped frequency distribution typically observed for shade-tolerant species with plentiful regeneration.

**Nondestructive sampling**—All *Pterospermum* trees in the plot were identified to the species level, then were tagged using numbered plastic tapes. Each tree’s location was mapped, and tree height was measured in August 2002. Tree height was defined as the height of the top of the crown for trees greater than 4.8 cm in DBH. For smaller trees, the same value was defined as stem height. In addition, the diameters at ground level and the crown widths of all *Pterospermum* trees that appeared to be sound and that showed no evidence of past breakage were measured by averaging two measurements, and the height at the lowest leaf (or branch, if present) was recorded. We also recorded the presence or absence of branches. To increase our sample of large trees, we added 11 trees that lay outside the plot and measured tree height, height at the lowest leaf (or branch), the stem diameter at ground level and crown diameter (again, using two measurements). The stem diameter (*D*, in centimeters) and crown width (*C*, in meters) were defined as the geometric mean of two measurements of the respective diameters. The crown depth (*C*<sub>c</sub>, in meters) was defined as the difference between tree height (*H*, in meters) and the height of the lowest leaf (or branch).

**Destructive sampling**—Thirty-five and 28 trees of *P. javanicum* and *P. diversifolium*, respectively, with stem heights ranging from 20 to 150 cm,
Table 1. Coefficients for the generalized allometry, $1/Y = 1/A X^a + 1/Y^*$, where $X$ and $Y$ are the sizes of two parts of an organism. $A$ and $b$ are regression parameters that approach those of the simple allometry (Table 2) for small values of $X$ and $Y^*$ represents the asymptotic maximum value of $Y$. These parameters were obtained by applying an iterative nonlinear regression that minimizes the sum of squares of the residuals (RSS) using natural log-transformed values of $Y$.

| $X$ | $Y$ | $A$ (m cm$^{-3}$) | $b$ | $Y^*$ (m) | $A$ (m cm$^{-3}$) | $b$ | $Y^*$ (m) | $P$ for between-species difference
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<td>$D$</td>
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<td>1.66</td>
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<td>0.914</td>
<td>1.35</td>
<td>49.2</td>
<td>6.66**</td>
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<td>$C_D$</td>
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<td>1.95</td>
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<td>$C_C$</td>
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<td>0.643</td>
<td>0.97</td>
<td>20.8</td>
<td>3.99*</td>
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† Significance levels: no asterisk $P > 0.05$, * $P < 0.05$, and ** $P < 0.01$. 

were destructively sampled to permit a detailed analysis of allometric relationships for the juvenile trees. These samples were collected from around the plot under closed canopies. Only trees that appeared sound were selected for sampling. All sampled $P. diversifolium$ lacked branches (hereafter, these are referred to as "monoaxial"), but 89% of the sampled $P. javanicum$ had branches. A crown projection photograph (top view) of all samples was taken before sampling. The juvenile trees were then cut at ground level, and the following parameters were measured: stem height, stem diameter at ground level and crown diameter (two measurements each, as described in the previous section), height at the lowest leaf and branch (whichever one occurred first), number of branches originating at the main stem, number of leaves on the tree, and length (from petiole base to leaf tip) of the longest leaf on the tree. The leaf area and the dry masses of petioles, leaf blades, stems, and branches were also measured. Stem height and the length of the longest leaf on the tree were measured for an additional 14 trees for $P. diversifolium$ with heights ranging from 200 to 600 cm. To determine the leaf size of the mature trees, we measured the lengths of 10 leaves from a mature tree taller than 30 m for each species. From these data, we determined stem height, stem diameter, crown width, crown depth, oven-dry stem mass ($M_s$, in grams), leaf mass ($M_l$, in grams), support mass ($M_{support} =$ petiole dry mass + branch dry mass, in grams), and total mass ($M = M_s + M_l + M_{support}$) for each sample tree.

Data analysis—We compared the allometric relationships for the two species for development of the entire plant using data derived from nondestructive sampling. To examine interspecific differences in juvenile allometric relationships in more detail, we used data derived from destructive sampling. For our analysis of the juvenile allometries, we examined three combinations of allometric pairs: (1) length dimensions (the top three pairs in Table 2), (2) length and mass dimensions (the fourth and fifth pairs in Table 2), and (3) mass dimensions (the sixth through eighth pairs in Table 2). For the analysis of whole-plant development, we lacked mass data and thus examined only allometries relating to length dimensions.

We first tested the linearity of the allometric relationship. The linearity model for an allometric relationship between the sizes of two parts ($X$ and $Y$) of an organism used a simple model of the form:

$$Y = AX^a,$$

where $A$ and $b$ are parameters obtained by a Model II linear regression (reduced major-axis regression, RMA) of the natural log-transformed values of $X$ and $Y$ (LaBarbera, 1989; Niklas, 1994). The nonlinearity model for an allometric relationship used a generalized allometry (Aiba and Kohyama, 1996, 1997; Thomas, 1996):

$$1/Y = (1/AX^a) + (1/Y^*),$$

where $A$ and $b$ are parameters that approach those of the simple allometry for small values of $Y$, and $Y^*$ is a parameter that represents the asymptotic maximum value of $Y$. The parameters are obtained by applying an iterative, nonlinear regression program that minimizes the sum of squares of the residuals (RSS) using values of $Y$ transformed using natural logarithms. In this case, the use of a nonlinear function necessitates the use of a Model I technique because there is no generally accepted form of Model II for nonlinear regressions (Thomas, 1996). The expanded allometry has fewer degrees of freedom because of more constants, and the RSS in Eq. 2 is smaller than that in the simple allometry (Eq. 1).

We examined the linearity and nonlinearity of the allometric relationships by means of an ordinal extension of the analysis of variance (Snedecor and Cochran, 1980):

$$F = (n - 3)[(RSS \text{ for simple allometry}) - (RSS \text{ for expanded allometry})] / (RSS \text{ for expanded allometry}), \tag{3}$$

with degrees of freedom equal to $(1, n - 3)$. When nonlinearity was statistically supported by the $F$ test ($P < 0.05$), we adopted the expanded allometry for our analysis. Although it is debatable whether the $F$ test can be applied to nonlinear regressions, the approach seems justified in our study because this approach generated nearly identical results to those generated by means of an $F$ test using sequential polynomial regressions (Aiba and Kohyama, 1996; Thomas, 1996).

Because the $F$ test showed that all the juvenile allometries were linear or provided a better fit by means of simple allometry than by using expanded allometry, we used the simple allometry for our interspecific comparison. For this comparison, we applied an ordinal ANCOVA test, which is commonly used to compare allometric relationships (Kohyama, 1987; Kohyama and Hotta, 1990; Kohyama and Grubb, 1994). Although this test is based on the Model I regression method, we chose to use it for two reasons: (1) we were not interested in specifying the values of the regression parameters, but rather in detecting differences in parameters between the species, and (2) the related species would presumably show similar errors or deviations.
For both species, the taller monoaxial trees had the larger leaf size, but after the initiation of branching, leaf sizes decreased with tree height (Fig. 2). The ANCOVA in which species was treated as a factor, leaf size was the variate, and \( H \) was the covariate yielded a nonsignificant interaction term and a significant species term \( (F = 22.65, df = (1, 53), P < 0.001) \); the leaf size of \( P. \) diversifolium was larger than that of \( P. \) javanicum of the same height. Besides this, the size at which branching began was larger in \( P. \) diversifolium than in \( P. \) javanicum. Consequently, the maximum leaf size of the former was also larger than that of the latter: it reached about 80 cm. The lengths of 10 leaves from a mature tree averaged 19.71 cm, with a SD of 2.69 cm for \( P. \) diversifolium vs. 11.77 cm (SD = 2.17 cm) for \( P. \) javanicum. Monoaxial \( P. \) diversifolium increased its total number of leaves slowly as tree height increased, whereas \( P. \) javanicum rapidly increased the

**RESULTS**

**Interspecific differences in whole-plant development trajectories**—The tree size at which the first branches appeared differed between the species, with \( P. \) javanicum initiating branching at lower heights than \( P. \) diversifolium (Fig. 1). Some trees of \( P. \) diversifolium had not yet developed branches at heights of 6–7 m, but all trees of \( P. \) javanicum taller than 2 m had branches.

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Because the \( F \) test showed that all allometric relationships for whole-plant development, with the exception of the \( D-C \) relationship for \( P. \) diversifolium, were nonlinear or provided a better fit by means of the expanded allometry, we compared allometric relations for the two species using the expanded allometries. For this comparison we used an ordinal extension of the analysis of variance:

\[
F = \left(\frac{n}{n - 6}\right)\left(\frac{\sum RSS_{\text{species}}}{\sum RSS_{\text{r}}}ight)
\]

with degrees of freedom equal to \((3, \Sigma n - 3)\).

**Evaluation of self-shading**—We adopted a simplified approach to empirical measurement of the degree of self-shading (DSS) caused by upper leaves within a crown (Chazdon, 1985; Yamada et al., 2000a). The DSS value (expressed as a percentage) is defined as the ratio of the sum of overhead projections of the leaf area of all leaves within a crown to the sum of projected areas of leaves overlapped (shaded) by upper leaves; a crown with no leaves shaded by upper leaves would have a DSS value of 0%. This ratio is based on the simple assumption that a given leaf undergoes no self-shading if no upper leaves overlap it horizontally (i.e., if their vertical projection does not overlap that of the lower leaf).

We calculated DSS values for each of the destructively sampled trees. These samples had grown under closed canopies, and under these conditions light coming from angles nearer to the horizon is likely to be intercepted by the stems and crowns of neighboring trees. Most of the light captured by a tree’s leaves, therefore, would come from angles nearer to the vertical, and reducing the extent of self-shading could significantly increase the tree’s whole-crown carbon gain.

Leaf margins of all leaves in photographs of the crowns taken from directly overhead were traced onto tracing paper, and the leaves drawn on the tracing paper were painted. Leaf margins of shaded parts were likewise traced and painted. Leaves completely shaded by upper leaves and not visible in these views were accounted for by photographing the crowns with the shading leaves removed. All these papers were scanned, and the total area and total views were accounted for by photographing the crowns with the shading leaves painted. Leaves completely shaded by upper leaves and not visible in these views were accounted for by photographing the crowns with the shading leaves removed. All these papers were scanned, and the total area and total shaded leaf area for all leaves within a crown were determined by counting painted pixels using an area meter programmed in Photoshop 5.0 (Adobe Inc., San Jose, California, USA).

**RESULTS**

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![Fig. 4. Whole-plant developmental trajectories of height vs. diameter (A), crown depth vs. diameter (B), and crown width vs. diameter (C) for Pterospermum diversifolium (○) and P. javanicum (○). Fitted lines were generated using a generalized allometric function (Eq. 2); continuous lines represent P. diversifolium and dashed lines represent P. javanicum.](image-url)
number of leaves as a function of tree height after the initiation of branching (Fig. 3). Therefore, monoxial trees deployed relatively few large leaves on the main stem, whereas branched trees produced relatively many small leaves on branches. Hence, the monoxial trees expanded their crown by producing larger leaves, whereas branched trees expanded their crowns by the elaboration of branches.

The curves for diameter vs. height (D–H) differed significantly between the species (F = 6.66, df = (3, 276), P < 0.001). The curve for *P. javanicum* had a smaller slope and a greater asymptotic (maximum) value for D than in the curve for *P. diversifolium* (Table 1, Fig. 4A). There was no significant difference in the diameter vs. crown depth (C–D) curves between the species (Table 1, Fig. 4B). The diameter vs. crown width (D–C) curves for *P. diversifolium* and *P. javanicum* differed significantly (F = 3.09, df = (3, 276), P < 0.05); the curve for *P. javanicum* had a greater slope and a smaller asymptotic (maximum) value of C than did the curve for *P. diversifolium* (Table 1, Fig. 4C).

### Interspecific differences in juvenile allometries

The simple allometric relationship best described the juvenile allometries. The slopes of the regression curves for the D–H relationships differed between the species; the curve for *P. diversifolium* had a significantly greater slope than the curve for *P. javanicum* (Table 2, Fig. 5A). The D–C and D–C relationships for *P. diversifolium* and *P. javanicum* did not differ significantly (Table 2, Fig. 5B, 5C). However, the D–C curve for *P. javanicum* had a greater (less negative) Y intercept than the curve for *P. diversifolium*, and this difference was nearly significant (P = 0.057).

The slopes of the total mass vs. height (M–H) relationships differed significantly between the species; the curve for *P. diversifolium* had a significantly greater slope than that for *P. javanicum* (Table 2, Fig. 6A). The intercepts of the M–C relationships differed significantly between the species; *P. javanicum* had a greater (less negative) Y intercept than *P. diversifolium* (Table 2, Fig. 7A). In the curves for the total mass vs. leaf mass and vs. support mass relations (M–M, M–M, and M–M, respectively), the slopes differed significantly; the M–M, curve for *P. diversifolium* had a steeper slope than in the curve for *P. javanicum*, whereas the opposite was true for the M–M, curves (Table 2, Fig. 7B and 7C).

### Leaf display

Monoaxial *P. diversifolium* had relatively high DSS values, especially for saplings with H taller than 0.8 m, the DSS values were mostly greater than 10% (Fig. 8). A few monoxial *P. javanicum* had comparably high values of DSS, but the DSS values for branched *P. javanicum* were lower than 10% in most cases. The median DSS values for *P. diversifolium* and *P. javanicum* were 12.6 and 7.19%, respectively, and these values differed significantly (Mann-Whitney U test, P < 0.05).

### DISCUSSION

**Growth strategy of juveniles**—The most rapid height growth of stems can be attained by producing a slender stem, with a high degree of taper from the base of the stem to its apex, as well as by reducing the amount of energy allocated to horizontal growth (i.e., branches), maintaining a low specific stem mass, or a combination of these approaches (Poorter and Werger, 1999). The monoxial growth habit is considered to be an adaptation that favors rapid height growth because it reduces the amount of energy allocated to horizontal growth (Givnish, 1978). Because a large part of the strength of the petiole and rachis derives from turgor pressure and fibrous materials, development of these structures consumes less energy than the production of woody branches bearing the same load. Therefore, a monoxial growth habit with large, expendable leaves (Givnish, 1984) maximizes the amount of energy available for vertical growth at a given stem height and thus promotes rapid height growth. Consequently, juvenile *P. diversifolium*, which retained a monoxial growth habit for longer (until a larger tree size) than *P. javanicum* and deployed large leaves directly on the stem during monoxial growth, follow a dynamic function of tree architecture to enhance the opportunistic use of light after a disturbance rather than a static function that optimizes leaf display under current lighting conditions.

The observed D–H and M–H relationships for juveniles support the hypothesis that *P. diversifolium*’s growth strategy emphasizes height growth. Curves for this species have a significantly higher slope for the D–H and M–H relationships than *P. javanicum*. This means that *P. diversifolium* attains more height growth than *P. javanicum* for a given increment in D and M. The slopes of the D–H curves for *P. diversifolium* and *P. javanicum* were 1.90 and 1.33, respectively. These values are much greater than the values for models based on constant stress or elastic similarity, which are 0.50 and 0.67, respec-

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Table 2. Results of the regression analysis using the simple allometry (lnY = AlnX + b) between selected pairs (X, Y) of dimensions using the reduced major axis method for *Pterospermum diversifolium* and *P. javanicum*. Differences in the allometric relationships between the two species were analyzed using an ANCOVA test, whose results are also shown.

<table>
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<tr>
<th>Y–X</th>
<th>Coefficients for <em>P. diversifolium</em></th>
<th>Coefficients for <em>P. javanicum</em></th>
<th>F2 for Common b (same value used for both species)</th>
<th>Adjusted A based on common b for <em>P. diversifolium</em></th>
<th>Adjusted A based on common b for <em>P. javanicum</em></th>
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‡ Significance levels: no asterisk = P > 0.05 and * = P < 0.01.
Fig. 5. Juvenile allometries relating to length dimensions: height vs. stem diameter (A), crown depth vs. stem diameter (B), and crown width vs. stem diameter (C) for *Pterospermum diversifolium* (●) and *P. javanicum* (○). Fitted lines used a simple allometric function (eq. 1). Continuous lines represent *P. diversifolium*; dashed lines represent *P. javanicum*.

Fig. 6. Juvenile allometries relating to length and mass dimensions: height vs. total mass (A) and crown width vs. total mass (B) for *Pterospermum diversifolium* (●) and *P. javanicum* (○). Fitted lines used eq. 1; continuous lines represent *P. diversifolium*; dashed broken lines represent *P. javanicum*.

tively (McMahon, 1973; Sposito and Santos, 2001). This means that the safety margin for stem rigidity (i.e., the ratio of actual stem diameter to the theoretical calculated minimal diameter to prevent elastic buckling) decreased with increasing tree size. Similar trends have been reported for other tropical Sterculiaceae (Yamada et al., 2000b, 2001) and for many other tree taxa (King, 1990; Sposito and Santos, 2001). Rapid height growth would be favored over stem stability by juvenile trees in tropical forests, in which vertical gradients in relative light availability are steeper than in forests outside the tropics (Yoda, 1974).

Juvenile *P. diversifolium* had smaller crown widths and higher values of DSS than *P. javanicum*. Because monoaxial growth must initially expand crown width by displaying larger leaves, horizontal growth is limited compared with trees that adopt a branching growth habit. Furthermore, the monoaxial growth habit develops large leaves toward the stem’s leader, leading to significant self-shading of lower leaves. Consequently, the static function of tree architecture of *P. diversifolium* is inferior to that of *P. javanicum*. Unlike *P. diversifolium*, *P. javanicum* branched well starting at a younger age. The branching growth habit expands crown area by making and expanding branches with small leaves, thereby distributing the leaves more widely to achieve a low DSS and create a monolayer crown shape. Therefore, *P. javanicum*’s architecture is more effective in terms of increasing survival at a given height or under darker conditions than is the case for *P. diversifolium*.

**Growth trajectories**—Many researchers have suggested that a nonlinear function for the generalized allometry would better...
Fig. 7. Juvenile allometries relating to mass: stem mass vs. total mass (A), leaf mass vs. total mass (B), and support mass vs. total mass (C) for *Pterospermum diversifolium* (●) and *P. javanicum* (○). Fitted lines used Eq. 1; continuous lines represent *P. diversifolium*, dashed lines represent *P. javanicum*. Support mass is defined as the sum of petiole and branch mass.

Fig. 8. Relationship between the degree of self-shading (DSS) and stem height. Each symbol represents one tree; ● = monoxial *Pterospermum diversifolium*, ○ = branched *P. javanicum*, and × = monoxial *P. javanicum*. The DSS value is defined as the proportion of the sum of overviews projection leaf area of all leaves within a crown to those of overlapped (shaded) by upper leaves; a crown without any leaves shaded by upper leaves would have a DSS value of 0%. See the text for more details.

King (1996) found that long-lived species showed a greater increase in crown diameter when they reached the upper end of their height range. Yamada et al. (2001) observed a switch from stem elongation to radial growth with increasing tree size in another tropical species in the Sterculiaceae (*Scaphium longiflorum* Ridley); small trees elongated rapidly but thickened less during rapid stem elongation, whereas large trees elongated relatively little but thickened rapidly to strengthen the stem’s mechanical stability. The relative importance of rapid height growth and stem stability for a tree would depend on tree size. An alternative explanation of the nonlinearity of the D–H relationship involves the relationship’s dependence on reproductive maturity (Thomas and Ickes, 1995; Thomas, 1996). The D–H relationship, leaf proliferation, and leaf size are all known to show pronounced allometric discontinuities associated with the onset of reproduction (Alvarez-Buylla and Martinez-Ramos, 1992; Thomas and Ickes, 1995; Thomas, 1996). More studies are needed to assess the allometric discontinuities related with reproductive onset and to identify the size at which reproductive onset occurs for various species.

*Pterospermum javanicum* continued height growth after reaching the continuous canopy layer and passed through this layer to become emergent. In contrast with D–H relationships, *P. javanicum* ceased crown expansion after reaching the canopy layer, although juveniles allocated considerable energy to expanding their crown area. The asymptotic maximum crown width for *P. javanicum*, estimated using a generalized allometry, was smaller than that of *P. diversifolium*. Thus, the allometric strategies adopted by juveniles appear to be largely

fit observed D–H relationships for whole-plant development (Aiba and Kohyama, 1996; Thomas, 1996). The maximum heights we estimated using a generalized allometry for D–H relationships were lower for *P. diversifolium* than for *P. javanicum*. This is because the architecture of juvenile *P. diversifolium* is suitable for rapid initial height growth, but height growth ceases when these trees reach the canopy layer and the trees rarely pass through the layer to become emergents.
in relation to understory light conditions. The study of whole-plant development trajectories is strongly recommended for researchers interested in clarifying the diverse growth strategies that may be adopted by tropical trees passing from the seedling stage to maturity.

**Coexistence mechanisms for two congeneric species within a community—Differentiation of growth strategies between** *P. diversifolium* and *P. javanicum*, assessed by means of tree architecture, can be expected to lead to equilibrium coexistence in a community if the two species differ in their regeneration niche as a function of understory light conditions. This is because each phenotype potentially provides competitive advantages, and these advantages depend on understory light conditions. In the competition for growth and survival between these two species, *P. diversifolium* is hypothesized to outperform *P. javanicum* in bright microsites because its architecture is better adapted to rapid height growth. In contrast, *P. javanicum* is hypothesized to outperform *P. diversifolium* in shaded microsites because its architecture is better adapted to light assimilation under those conditions. Therefore, we can expect that the spatial distribution of *P. diversifolium* in a forest community will be restricted to brighter microsites, whereas *P. javanicum* will be more widely distributed where understory light is limited. Furthermore, stem elongation by *P. diversifolium* in bright microsites is likely to be more rapid than that of *P. javanicum*. To verify these hypotheses, further comparative studies of spatial distribution, survival, and growth in relation to understory light conditions will be needed.

**LITERATURE CITED**


