Tree architecture in a Bornean lowland rain forest: intraspecific and interspecific patterns

Frank J. Sterck[1,2], Frans Bongers[1] & David M. Newbery[2]
[1]*Silviculture and Forest Ecology Group, Department of Environmental Sciences, Wageningen University, P.O. Box 342, 6700 AH Wageningen, the Netherlands (E-mail: f.j.sterck@bio.uu.nl; frans.bongers@btbo.bosb.wau.nl);* [2]*Geobotanical Institute, Bern University, Altenbergrain 21, 3013 Bern, Switzerland (E-mail: david.newbery@ips.unibe.ch)*

Abstract

Intraspecific and interspecific architectural patterns were studied for eight tree species of a Bornean rain forest. Trees 5–19 m tall in two 4-ha permanent sample plots in primary forest were selected, and three light descriptors and seven architectural traits for each tree were measured. Two general predictions were made: (1) Slow growing individuals (or short ones) encounter lower light, and have flatter crowns, fewer leaf layers, and thinner stems, than do fast growing individuals (or tall ones). (2) Species with higher shade-tolerance receive less light and have flatter crowns, fewer leaf layers, and thinner stems, than do species with lower shade-tolerance. Shade-tolerance is assumed to decrease with maximum growth rate, mortality rate, and adult stature of a species.

Two light descriptors (crown position index and available space, but not canopy height) indicated higher light conditions for trees with more rapid growth, and for trees of greater height. Light levels were higher for species with high maximum growth rates and with greater adult stature.

Most intraspecific architectural patterns conformed to the predictions: total leaf area and the number of leaf layers increased with increasing height and higher growth rates, and crown length/tree height ratio and stem slenderness respectively increased and decreased with growth rate. Yet, crown width/tree height ratio and relative crown length did not change with tree height, nor did they with previous growth. Slow growing (and short) trees may not have the reserves to invest in further horizontal crown growth, and to avoid leaf self-shading sufficiently within their relatively narrow crowns.

Predictions on interspecific architectural patterns were not supported by the data. Species that were expected to be more shade-tolerant (lower maximum growth, lower mortality, and shorter stature) had deeper crowns, greater leaf areas, and more leaf layers, than did less shade-tolerant species. These patterns may be explained by lower loss rates of branches and leaves of the more shade-tolerant species. These species avoid leaf self-shading by distributing their leaves at the crown periphery. The role of lateral light appears to be more important than hitherto realized. The crown width/height ratio and height/dbh ratio were negatively correlated, both intraspecifically and interspecifically. It is suggested that trees co-ordinate their crown and stem growth so that they maintain their stability at small safety margins in the forest understorey.

Introduction

Trees of tropical rain forest vary greatly in their architectural characters. These characters depend upon genetic constraints, previous growth, and tree size (Hallé et al. 1978; Bongers & Sterck 1998). Light plays a major determining role in the architectural patterns of tropical rain forest trees because (i) it is the main resource limiting growth in the forest understorey (Chazdon & Fetcher 1984; Fetcher et al. 1994), (ii) species have differing light requirements (Veneklaas & Poorter 1998) and their individuals encounter different light environments during their life-

times (Clark & Clark 1992; Sterck et al. 1999), and (iii) architectural form determines the way light is intercepted and determines tree stability mechanically, both of which finally affect tree performance (Chazdon 1986; Pearcy & Yang 1996; Valladares 1999). Several hypotheses have been put forward to explain the relationships between intraspecific and interspecific architectural patterns and light environment, but rarely have they been tested explicitly (Horn 1971; Oldeman & Van Dijk 1989; Valladares 1999).

We believe that there is no *a priori* reason to distinguish between hypotheses of intraspecific architectural patterns, and those of interspecific patterns. If we pool patterns within and between species, and compare all trees in low-light environments with those in high-light environments, the following conflicting views emerge from the literature: (1a) Trees in low-light environments (further referred to as 'low-light trees') invest proportionally more of their acquired resources in horizontal crown growth than in vertical crown growth, while trees of high-light environments ('high-light trees') do the opposite (Kohyama & Hotta 1990; Aiba & Kohyama 1997). Low-light trees spread their leaves over a larger horizontal plane and thus reduce leaf self-shading (Horn 1971; Ashton 1978), and in this way they increase their chances of encountering high-light patches (Shukla & Ramakrishnan 1986; O'Brien et al. 1995). (1b) Other studies, however, have suggested that low-light trees grow more slowly than high-light ones, and cause increased self-shading by packing their leaves more densely in their smaller crowns (Shukla & Ramakrishnan 1986; Küppers 1994). (2a) Low-light trees have longer leaf longevity and higher leaf allocation (King 1991; Reich et al. 1992), and greater leaf area, than do high-light trees. (2b) Alternatively, low-light trees face a reduction in leaf area because of their slow growth, and of their slow rate of leaf production in particular (King 1994; Sterck 1999). (3) Low-light trees have thinner stems than high-light trees because the former produce generally denser wood, which gives a mechanical stability to the stem equivalent to the thicker, less-dense wood of the latter, at a given tree height and stem diameter (Putz et al. 1983; Sterck & Bongers 1998). In this last respect there is general agreement. We now extend and reformulate these views to predict, first, intraspecific architectural patterns in relation to growth and size, and, second, interspecific patterns in relation to shade-tolerance, and light requirements of the species.

The effects of growth and size on intraspecific architectural patterns may actually be determined by the carbon budget. In the case of growth effects, trees with higher carbon budgets have more carbon available for growth and can allocate this carbon in various ways. They generally produce relatively thicker stems (Holbrook & Putz 1989), have higher (net) production rates for leaves, shoots, roots, and branches, and they are thus able to produce deeper crowns with more leaves (Sterck 1999). In the tropical forest understorey, particularly, carbon budgets and growth rates of trees generally reflect the availability of light (Fetcher et al. 1994). The role of the carbon budget in the effects of size is still not well understood (Cannell & Dewar 1994). On the one hand, trees will generally receive more light as they become taller (Bongers & Sterck 1998, although the opposite pattern may occur, temporarily, over short time scales – Clark et al. 1993; Sterck et al. 1999) and, accordingly, they increase their maximal photosynthetic rates (Kitajima 1996). As a consequence, trees may achieve higher net carbon budgets and change their architecture with height in a similar way as they would when responding to a range of light levels at a given size. On the other hand, taller trees have to maintain an increasing woody body and root structure, i.e., greater respiration costs to be maintained by a relatively small leaf area (Givnish 1986). This will reduce their net carbon budget and could result in changes in architecture with tree height that correspond to those that occur across decreasing light levels. In the literature there is still little evidence for either of these two possible effects of size on tree architecture and leaf display (Sterck 1997).

Interspecific architectural patterns are also related to the degree of shade-tolerance characteristic to the species. Tree species with low shade-tolerance generally grow fast and only survive at high levels of light (Ackerly 1996). In comparison, species with high shade-tolerance grow more slowly, and persist for longer time periods at low light levels. Tropical forest tree species appear to show a general trade-off between the growth rate when resources do not limit growth (maximum rate of growth) and the ability to survive in shade (Veneklaas & Poorter 1998). This is also reflected in the positive interspecific correlation between growth rate and mortality rate in forest saplings (Kobe 1996). Species with high growth and mortality rates are thus expected to exhibit architectural characteristics that are selected under high light, while species with lower rates exhibit those that are selected under low light environments (Fig-
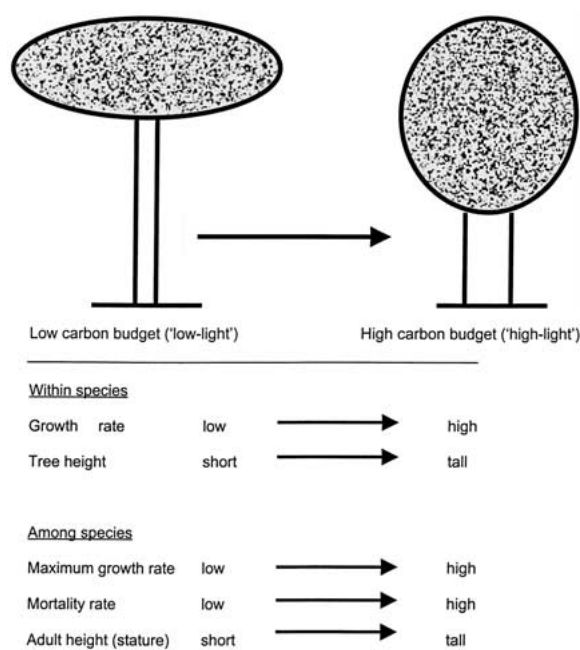
Figure 1. Predictions for intraspecific and interspecific architectural patterns. The arrows indicate the predicted directions of change with improved carbon budget (or increased light availability).

ure 1). Patterns may, furthermore, be correlated with adult stature. Successful individuals of species with tall adult stature spend a considerable part of their lives in the highly lit overstorey and may therefore show high-light features there. In contrast, individuals of most species of short adult stature spend their lives in the shaded understorey and would thus benefit from low-light features.

The hypothesized patterns remain unsolved because empirical studies have not distinguished between the effects of growth (as the outcome of light affecting carbon budget) and tree height (Coleman et al. 1994). Most studies have been confined to seedlings or very small saplings, and usually considered only a few species (Veneklaas & Poorter 1998). Our study concerns the architectural patterns in the large sapling to small tree size range, which is typical of understorey conditions, and compares these patterns among eight tree species of a Bornean rain forest. Referring to Figure 1, the following questions were addressed: (1) Do individuals within species with slow growth (or of short stature) encounter low-light environments, and do they have flatter crowns, fewer leaf layers, and thinner stems, than individuals with faster growth (or of taller stature) encountering high-light environments? (2) Do species with low maximum growth rates (and short adult stature) encounter low-light environments,

and do they have also flatter crowns, fewer leaf layers, and thinner stems, than species with higher maximum growth rates (and taller adult stature) encountering high-light environments?

Methods

Site and species

Tree architectural characters were studied for eight co-existing species of a Bornean lowland rain forest near to the Danum Valley Field Centre, Sabah, Malaysia (4°58′ N, 117°48′ E, Marsh & Greer 1992). This site is characterized by humid warm climate with temperatures between 18 (morning) and 35 °C (afternoon), and with average annual rainfall of 2669 mm in 1985–1998 (Walsh & Newbery 1999). The forest was classified as a *Parashorea malaanonan* type following Fox (1972). Two 4-ha plots were used for this study. Both plots were inventoried in 1985–1986, and again in 1995–1996, and ca. 18.000 trees ≥ 10 cm girth at breast height (dbh ≥ 3.1 cm) were tagged, measured, sampled, and identified to species. The plots have been described for their structure, composition (Newbery et al. 1992), associated topography and soils (Newbery et al. 1996), and for their dynamics 1986-1996 (Newbery et al. 1999). The canopy dominants in the two

Table 1. Life-history traits for the eight study species using data of populations of each species from two 4-ha plots of a tropical rain forest, Danum Valley Field Centre, Sabah, Malaysia (Newbery et al. 1999). Maximum sizes were derived for the populations, and growth rates (dbh increments between 1986 and 1996) for all trees with a dbh between 3.1 and 19.0 cm. These dbh limits correspond with the height limit of 5–19 m (see method section). *n* is given for trees ≤ 19 m.

Species	n	Stem[a]	Stature		Growth		Mortality[c]
			Dbh	Height	Median	95 Perc[b]	
			(cm)	(m)	(mm yr^{-1})	(mm yr^{-1})	(% yr^{-1})
Euphorbiaceae							
Baccaurea stipulata J. J. Sm.	205	P	37	18	0.41	1.37	1.07
Mallotus wrayi King ex. Hk. f.	1865	P	17	18	0.39	1.28	1.56
Mallotus penangensis Muell. Arg.	173	O	23	21	0.57	1.59	1.12
Aporosa falcifera Hook. f.	189	O	31	22	0.97	3.20	1.31
Dipterocarpaceae							
Parashorea malaanonan (Blco). Merr.	87	O	56	34	0.79	3.35	2.46
Shorea fallax Meij.	249	O	101	49	0.64	4.26	2.46
Shorea johorensis Foxw.	71	O	127	55	4.40	10.01	5.74
Shorea parvifolia Dyer	79	O	121	49	6.66	14.09	5.11

[a]P= plagiotropic, constructed by axes that cannot be distinguished from branches in the crown, O = orthotropic, clearly distinct from branches in the crown.
[b]95 percentile values are presented, thus correcting for outliers.
[c]Annualized mortality rate (Sheil et al. 1995, Newbery et al. 1999).

plots reach 60 m in height (Table 1), and the canopy surface is open and rough although ground level gaps are very scarce (Newbery et al. 1992).

The eight species studied belong to two families, and differ in adult stature, maximum growth rates, population mortality rate, and type of branch architecture (Table 1). The short adult stature species belong to the Euphorbiaceae, and the tall ones to the Dipterocarpaceae. These two plant families dominate, and are strongly representative of, the understorey and overstorey of the Danum Valley forest respectively (Newbery et al. 1992, 1996).

Selection of individuals and measurements

In October 1996, 5–19 m tall individuals were selected for each species (*n* = 31–51). Trees were selected from populations in both 4-ha plots, using a table of random numbers. Trees were excluded if they had an abrupt (>50%) decrease in stem diameter with height. Such a diameter change was most probably an indicator of recent heavy damage: to have retained such trees would have introduced a further complicating factor. Accordingly, 7–17% of individuals per species was excluded.

Tree height and the height of the lowest crown leaf were measured with a telescopic measuring pole (for trees ≤ 16 m) or range finder (for trees >16 m). Crown radii were measured in eight directions (N, NE, E,

etc.), using a clinometer (mean difference = 10 cm, 95% of the measurements with a precision of ±20 cm on the basis of independent 80 repeated measurements). The following traits were calculated: average crown width/tree height ratio, crown length/tree height ratio, relative crown length (crown length/average crown width ratio), and stem slenderness (height/dbh ratio).

The number of leaf layers was determined at five fixed locations, four of them halfway between the stem centre and crown edge at the four cardinal directions, and one above the stem. The telescoping measuring pole was pushed up through the foliage and the number of 'leaf hits' was counted. For trees taller than the pole (16–19 m) one leaf layer was added to compensate for the leaf layer(s) in the top of the crown that could not be reached. Internal crown cover was assessed visually by the vertical projection of the crown. Five classes were used: 1, 0 – 20% covered by leaves; 2, > 20 - 40%; 3, > 40 - 60%; 4, > 60 – 80%; and 5, > 80 – 100%.

For a sub-sample of trees (*n* = 10 per species) the number of leaves was counted and a sample of leaves (*n* = 30 per tree) was collected. Selected trees varied widely in their number of leaf layers and internal crown cover. Individual leaf areas were measured with a Delta Image Analysis System (Eijkelkamp 1991), and total leaf area per tree crown was calculated as the

Table 2. ANOVA-table representing the procedure to test for significant contributions to the model for species (dummy variables) and interaction terms (species × tree height, species × Previous annual growth). See Method section for explanation.

Model		SS	df	F	R^2	F change	p change
All variables included	Regression	1.26	23	7.6	0.41		
	Residuals	1.79	246				
	Total	3.05	269				
Remove height interactions	Regression	1.23	16	10.7	0.40	0.64	0.723
Remove growth interactions	Regression	1.23	16	10.7	0.40	0.60	0.754
Remove species	Regression	0.56	2	29.9	0.18	12.82	0.0001

Trait = constant + height + growth + species$_{1-7}$ + (species * height)$_{1-7}$ + (species * growth)$_{1-7}$.
Significance of the whole model: $p < 0.0001$.
Data are shown for the trait crown width – height ratio.

Table 3. Correlations between crown position and dbh growth (partial tau coefficients), and between tree height and three light descriptors (Spearman's rank correlations) for eight tree species of a Bornean lowland rain forest, Danum Valley, Sabah. Only trees 5–19 m tall are included. Dbh growth data for 1986–1996 (Newbery et al. 1999). Partial tau coefficients (τ) correct for associated changes in tree height, but significance levels cannot be calculated. See text for explanation of light descriptors.

	n	Crown position and Dbh growth τ	Tree height and		
			Crown position	Canopy height	Space available
Baccaurea stipulata	45	0.06	0.49***	−0.23	0.18
Mallotus wrayi	44	0.15	0.36**	−0.18	0.10
Mallotus penangensis	36	0.34	0.63***	−0.05	0.43**
Aporosa falcifera	41	0.22	0.66***	0.02	0.53***
Parashorea malaanonan	25	0.27	0.69***	−0.18	0.29*
Shorea fallax	39	0.35	0.79***	0.12	0.53***
Shorea johorensis	21	0.30	0.69***	0.04	0.68***
Shorea parvifolia	19	0.48	0.66***	−0.04	0.30*

*, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$.

product of the number of leaves and mean leaf area. This measured total leaf area was then regressed on an estimate, i.e., the product of the crown area, the number of leaf layers, and the internal crown cover. Using natural logarithms of both measured total leaf area and the mentioned product a linear relationship was fitted ($F = 206$, df = 72, $r^2 = 0.77$, $p < 0.0001$). This model, ln(total leaf area) = 0.70 ln(product), was then used to predict total leaf area for all individuals.

Three descriptors of the light environment were determined for each tree. Firstly, the crown position was estimated by two independent observers. Seven different classes of crown position were distinguished: 1, no direct light; 1.5, low lateral light; 2.0, medium lateral light; 2.5, high lateral light; 3, some overhead light; 4, full overhead light; 5, crown completely exposed (after Clark & Clark 1992). The classifications

of both observers were averaged to give one value per tree. Secondly, the amount of open space above each crown was determined, using the telescopic measuring pole and/or the range finder. For this measure trees were assigned to one of three classes : 1, < 1 m free space above at least half of the crown area; 2, 1–5 m free space above at least half of the crown area; 3, > 5 m free space above at least half of the crown area. Finally, the height of the forest canopy above each individual tree was determined, using the range finder. Because the upper canopy was often barely visible with the range finder, trees were assigned to five approximate canopy height classes: 1, < 10 m; 2, 10 - < 20 m; 3, 20 - < 30 m; 4, 30 - < 40 m; 5, ≥ 40 m.

Interspecific and intraspecific patterns in the light environment were tested. Since the three light descriptors were recorded on ordinal scales, non-parametric tests were used. The descriptors were thus compared among species using the Kruskall–Wallis test, and then the Dunnet test for pair-wise species' comparisons. Within species, each of the light descriptors was correlated with tree height, using Spearman's rank correlation (r_s) coefficient. Crown position was correlated with previous growth (dbh increment in 1986–1996), using Kendall's partial correlation (τ) which removed the correlation between previous growth and tree height.

The dependency of architectural traits on species, previous growth and tree height was explored using a separate multiple regression model for each trait. Each model included a number of independent variables; tree height, previous growth, species (codes as 'dummy variables'), and interaction terms for species × tree height and species × previous growth. Previous growth and tree height were independent, because trees were selected on the basis of their height at the end of the experiment in 1996. Prior to the analysis, the architectural traits were $\log_{10}$-transformed to normalize their variances.

Each regression model was simplified as far as possible in the following way (Table 2). The contributions of species' interaction terms to the regression were tested for their significance, and than the species effects. The full model first included tree height, previous growth, the species as seven 'dummy variables', and the interaction terms (species × height and species × previous growth). For all architectural traits a similar result was found: species had a significant effect ($p < 0.01$), but the two interactions terms did not ($P > 0.05$). The model could thus be simplified in all cases by removing the interaction terms, to allow the effects of height and previous growth to be tested irrespective of species. Analysis of covariance (ANCOVA) was then used to test for the predicted intraspecific and interspecific architectural patterns. The intraspecific patterns were based on the regression coefficients of the architectural trait on tree height or on previous growth, taking the other as a covariate. The interspecific patterns were based on differences in the intercepts of the ANCOVA model.

A further test was performed to test for interspecific architectural patterns. Species-specific maximum growth rates, mortality rates, and measures of adult statures (Table 1) were correlated with species-specific architectural traits (Pearson correlation, r). The intercepts in the ANCOVA analysis were taken as the specific architectural trait values. Interspecific differences in the intercept represent 'average' architectural trait differences between species, given that the effects of tree height and previous growth were similar for all species. Partial parametric correlation coefficients (r_p) were calculated in order to remove the phylogenetic effect of plant family.

Results

Light environment

The intraspecific architectural patterns were similar among species: crown position was positively correlated with the growth rate between 1986 and 1996 (Table 3). The correlations were weak, possibly because crown positions were determined after the period of growth. Crown position and space available above individuals increased with tree height for all species (Table 3). The correlations were weakest (crown position) or not significant (available space) for *B. stipulata* and *M. wrayi*. These weak correlations resulted from the low crown position values (≤ 2) across all heights for these two species. Forest canopy height did not change with tree height.

There were few interspecific differences in crown position and available space (Table 4). The *Shorea* spp. tended to have the highest crown positions and the largest space available above their crowns, in particular *S. johorensis* and *S. parvifolia*. There were no significant differences in crown position or available overhead space among the other species. The species also did not differ significantly in the forest canopy height over the individuals sampled.

Architecture: intraspecific variation

The effects of tree height and previous growth on architectural traits were significant, and did not statistically differ among species (Table 5). With increasing height, the crown width/tree height ratio decreased while the crown length/tree height ratio did not change. This pattern indicated an increase in relative crown length with height. The stem slenderness did not change significantly over the investigated height range. Traits of leafiness (total leaf area, internal crown cover, number of leaf layers) generally increased with tree height. The effects of previous

Table 4. Medians of three light descriptors compared between eight species of a Bornean lowland rain forest, Danum Valley, Sabah. Sample sizes are shown in Table 3. See text for explanation of light descriptors (crown position, canopy height, and space available).

Species	Crown position	Canopy height	Space available
Kruskall–Wallis, *P* =	0.003	0.33 n.s.	0.02
Baccaurea stipulata	2 a	5	2 a
Mallotus wrayi	2 ab	4	2 a
Mallotus penangensis	2 ab	4	2 ab
Aporosa falcifera	2 ab	5	2 ab
Parashorea malaanonan	1.75 a	4	2 ab
Shorea fallax	2 ab	3	3 ab
Shorea johorensis	2.5 b	4	3 ab
Shorea parvifolia	2.25 b	4	3 b

Species are different for a trait when the medians do not share any of the same letters (Dunnet T3 test).

growth on crown and stem dimensions differed from the effects of tree height. Trees with faster previous growth generally had larger crowns and less slender stems. Relative crown length was unaffected by previous growth (Table 5). The effect of previous growth on traits of leafiness was similar to the effect of tree height: leafiness increased with higher previous growth rates.

Architecture: interspecific variation

Tree species differed significantly for most architectural traits (Table 5). There were some general differences between the dipterocarps and the euphorbs: dipterocarps had shallower crowns and smaller total leaf areas than euphorbs. *S. parvifolia*, the fastest growing species, had the shallowest crown, the lowest internal crown cover, the lowest number of leaf layers, and the smallest total leaf area of all species. *S. parvifolia* was followed in these respects by *S. johorensis*, the second fastest growing species. *B. stipulata* and *M. wrayi* had the highest crown width/height ratio, two of the three highest crown length/height ratios and total leaf areas, and they tended to have the smallest stem slenderness ($p = 0.10$). Finally, *M. penangensis* differed strongly from all of the other species: it had the deepest and (relatively) narrowest crowns, with the highest number of leaf layers and greatest internal crown cover.

Several architectural traits were significantly correlated with the mortality rate (crown length/height

ratio, number of leaf layers) and the maximum growth rate (crown length/height ratio, stem slenderness, total leaf area, internal crown cover) of the species (Figure 2), but not with the two measures of adult stature (height and dbh, data not shown). Except for stem slenderness all relations with mortality rates and with maximum growth rates were negative (Figure 2). All patterns were significant when species were pooled, and most of them also held when the effect of plant family was partialled out.

Discussion

Intraspecific patterns for light descriptors

Light descriptors indicate that current light levels were higher for trees with the higher growth rates during the past 10 yr, as well as for trees of taller stature (Table 6). The consideration of growth as the outcome of light affecting carbon budget is supported by the correlation between light level and previous growth (Table 3). The correlation is weak, however, possibly due to light changes between 1986 and 1996 (see Rich et al. 1993; Sterck et al. 1999).

From the modest to strong correlation between our light descriptors and tree height we infer that trees may gradually receive more light as they get taller. At the same time trees face increased carbon sinks (e.g., maintenance of increasing woody parts and roots) as they get taller. The net effect for changes in the carbon balance with tree height therefore remains unclear.

Intraspecific patterns for architectural traits

Trees with slow previous growth were predicted to have flatter crowns, fewer leaf layers, and thinner stems than did trees with faster previous growth. These predictions are only partly supported by the data (Table 6). Slow growers indeed had less leaf area and fewer leaf layers than did fast growers, but they did not have shallower crowns. These patterns are similar to differences between shade trees and trees grown in the open: shade trees reduced their leafiness considerably because their long leaf life-span did not compensate for their slower leaf production rates (Sterck 1999). The result was that the shade trees had lower numbers of leaf layers, just as our slow growing trees at Danum. There seems little need for reducing self-shading by investments in further horizontal crown (i.e., branch) extension. In addition, the low carbon
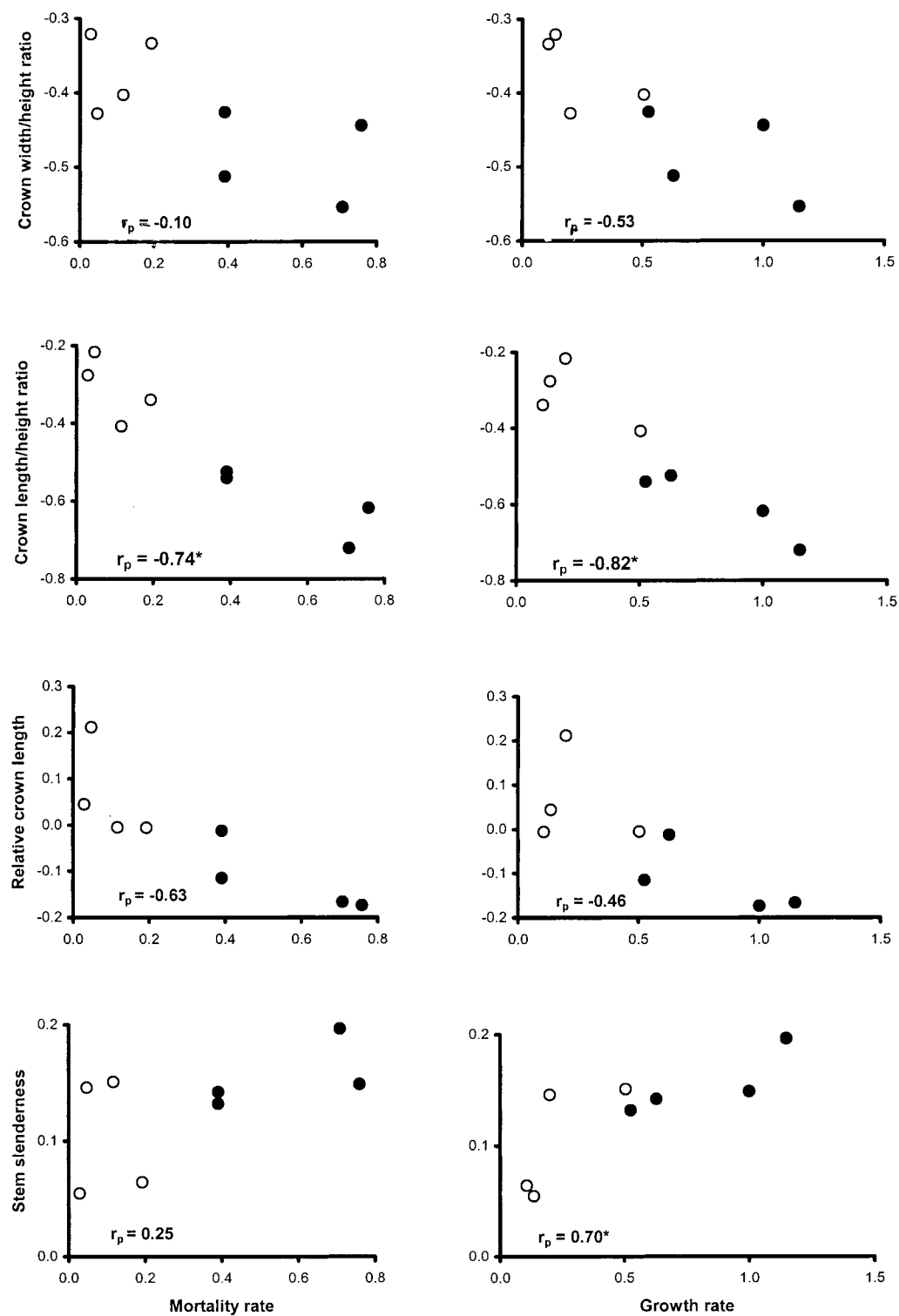
Figure 2. Scatter plots for interspecific patterns between architectural traits and life-history traits for eight tree species of Bornean rain forest at Danum Valley, Sabah. Architectural trait values are the ($\log_{10}$-transformed) intercept values of each species in the ANCOVA analysis (see Table 5 for the back transformed intercept values). These values may be negative because of the $\log_{10}$-transformation. The life-history traits were mortality rates and the maximum growth rates, calculated as the 95% percentile values of the population rates (see Table 1), and they were also $\log_{10}$-transformed. Partial correlation coefficients (r_p) were calculated between architectural traits and life-history traits, to correct for the effect of plant family (df = 5, *, $p \leq 0.05$, (*), $p \leq 0.10$). Euphorbs are represented as open circles and dipterocarps as closed circles.
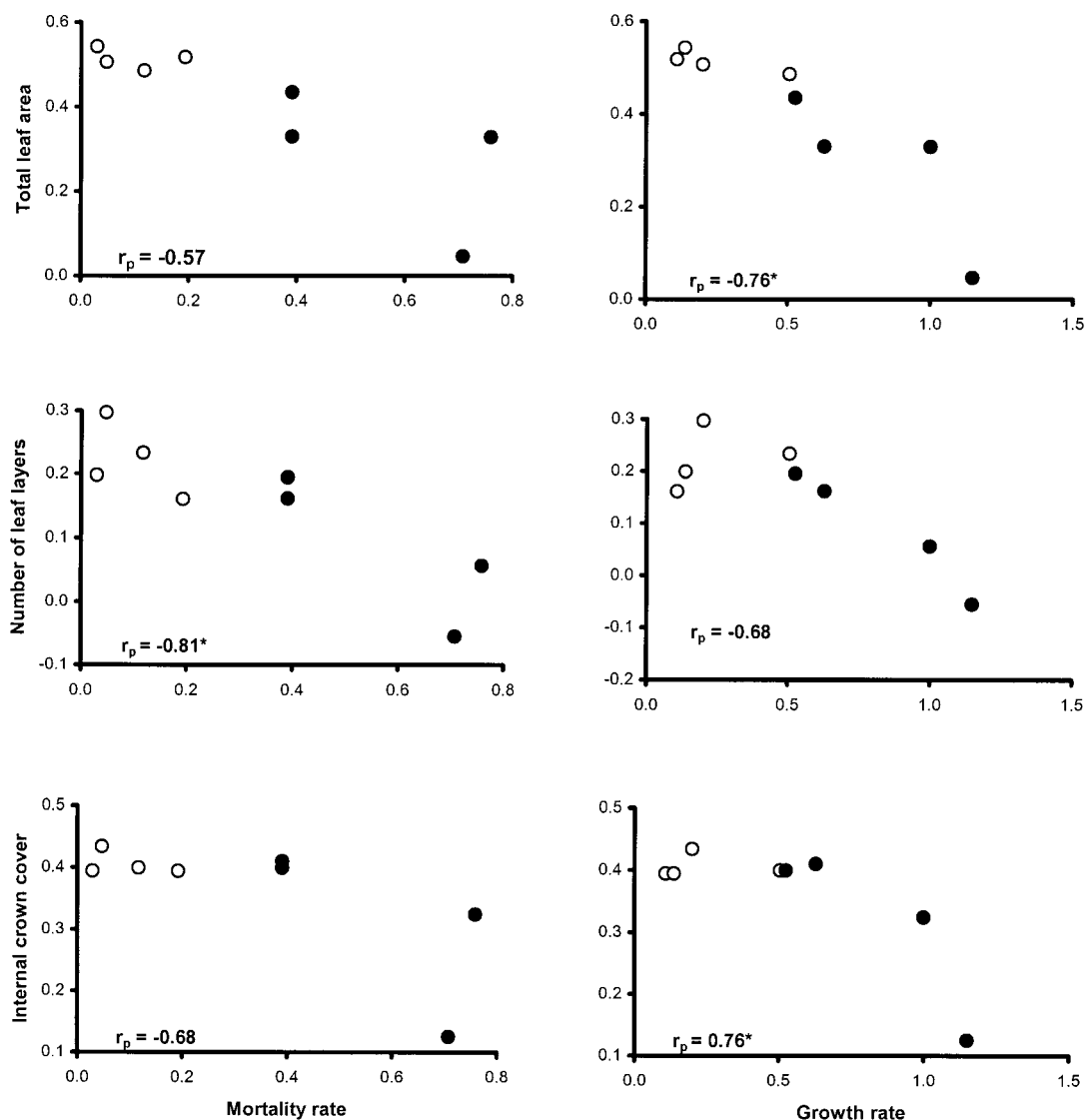
Figure 2. Continued.

budgets of shade trees may limit their crown extension, in both horizontal and vertical direction.

The slow growers had thinner stems (higher stem slenderness) at a given tree height than fast growers (Table 5). Slow growers may have had thin stems due to relatively large investments in crown development and leaf area, and may thus have enhanced their probability of survival in the shade under a limited carbon budget (e.g., King 1994; Veneklaas & Poorter 1998). Additionally, their thin stems may reflect a mechanical (thigmomorphogenic) response to lower load and bending stresses owing to their relatively small crowns (e.g., Mattheck & Kubler 1997). These two al-

ternative explanations, based on the data here, remain hypothetical.

Trees were predicted to have deeper crowns, more leaf layers, and relatively thicker stems (decreasing stem slenderness) as they got taller. Taller trees had relatively deeper crowns because, whilst the crown length/tree height ratio did not change with tree height, the crown width/tree height ratio decreased. This is consistent with relative crown length patterns found in a number of Neotropical rain forest trees (King 1996; Sterck & Bongers 1998). Taller trees also had larger total leaf areas and more leaf layers, but did not have lower stem slenderness. From other studies it appears

Table 5. Architecture of 5–19 m tall trees compared among eight species of a Bornean rain forest, Danum Valley, Sabah. Variables were $\log_{10}$-transformed. ANCOVA was used with species as the main factor. Because the effects of height and annual growth on the independent variables were not significantly different between species, differences between species are indicated by the intercept values (back-transformed intercept values are presented, and values with different letters are significantly different, $p < 0.05$). The effects of previous annual growth and tree height were the same for all species and are given. Sample sizes are shown in Table 3.

Species	Crown width/ height (m/m)	Crown length/ height (m/m)	Relative crown length (m/m)	Stem slenderness (m/cm)	Total leaf area (m²)	Internal crown cover (class values)	Number of leaf layers
Baccaurea stipulata	0.48 c	0.53 de	1.11 bc	1.13 a	3.49 c	2.48 b	1.58 bc
Mallotus wrayi	0.46 c	0.46 de	0.99 b	1.16 a	3.29 bc	2.48 b	1.45 bc
Mallotus penangensis	0.37 b	0.61 e	1.63 c	1.40 ab	3.21 bc	2.72 b	1.98 c
Aporosa falcifera	0.40 b	0.39 cd	0.99 b	1.42 ab	3.06 bc	2.51 b	1.71 bc
Parashorea malaanonan	0.37 b	0.29 bc	0.77 ab	1.35 a	2.72 bc	2.51 b	1.57 bc
Shorea fallax	0.31 ab	0.30 bc	0.97 b	1.39 ab	2.14 b	2.52 b	1.45 bc
Shorea johorensis	0.36 b	0.24 b	0.67 a	1.41 ab	2.13 b	2.11 b	1.14 b
Shorea parvifolia	0.28 a	0.19 a	0.68 a	1.57 b	1.11 a	1.33 a	0.88 a
Height (m) $\times 10^{-2}$	−1.59 ***	ns	1.10 **	ns	4.43 ***	1.05 ***	2.75 ***
Annual growth (cm yr^{-1}) $\times 10^{-2}$	8.85 ***	8.76 ***	ns	−3.61 **	16.16 ***	7.60 ***	6.48 **

that species differ for their stem slenderness patterns with tree height (Rich et al. 1986; Alvarez-Buylla & Martinez-Ramos 1992; Claussen & Maycock 1995; Sterck & Bongers 1998). A reduction in the ratio at maturity seemed to be typical for shade-tolerant tree species (e.g., Kira 1978; Rich et al. 1986), but was not found for our ('shade tolerant') understorey species.

In our study we were able to separate the effects of tree height from the effects of previous growth on architectural traits. However, the underlying causes of changes in architectural traits with tree height remain complicated. The effects of tree height may be driven by the correlated carbon budget, (light) resource levels, and/or bio-mechanics.

Interspecific patterns for light descriptors

The results indicated interspecific differences in light habitat. The *Shorea* species received more light and had more available free space for upward growth. This was most strongly the case for *S. johorensis* and *S. parvifolia*, the species that had the highest maximum growth rates, and the highest mortality rates. From this we suggest that these species experienced higher mortality due to light suppression than did the other species, while they could outgrow the other species in high-light environment and with more space availability. This is consistent with the idea of a trade-off between high maximum growth rates and high mortal-

ity rates due to light limitation in less shade-tolerant species (Kobe 1996; Veneklaas & Poorter 1998).

The other interspecific pattern amongst the light descriptors is related to height: while most species had more light and space available as they grew taller, *B. stipulata* and *M. wrayi* did not. These latter two species differed in a number of characters from the other species: they had the lowest maximum growth rates, achieved their maximal (adult) height, and became reproductive in the studied height range (F.J. Sterck pers. obs.). They may be more frequently overgrown by neighbouring trees than the other species that still expand vertically in this height range. The two species also differed from the other species in their stem development. The stem did not differ from the branches (all plagiotropic), while those of the other species did (orthotropic stem and plagiotropic branches). It remains unclear how these growth patterns relate to the observed pattern in light descriptors. In general, these results support our prediction that species with lower maximum growth rates, lower mortality rates, and smaller adult stature, experience lower light levels.

Interspecific patterns for architectural traits

We predicted that species with lower maximum growth rates, lower mortality rates, and shorter stature would have flatter crowns, fewer leaf layers, and thinner stems. Some of the observed patterns were op-

Table 6. Predictions for environmental and architectural patterns and the factual evidence for these patterns. Symbols indicate an increase (+), an decrease (−), or no change (0) of an environmental or architectural variable. Predictions refer to intraspecific and interspecific variation.

	Predictions	Evidence			
		Intraspecific		Interspecific	
		Height	Growth	Stature	Growth[c]
Environment[a]					
Crown position	+	+	+	+	+
Space available	+	+	nt	+	+
Canopy height	−	0	nt	0	0
Allometry[b]					
Crown width/height	−	−	+	−	0
Crown length/height	+	0	+	−	−
Relative crown length	+	+	0	−	−
Stem slenderness	−	0	−	0	0
Leaf display[b]					
Total leaf area	+	+	+	−	−
Internal crown cover	+	+	+	0	−
Number of leaf layers	+	+	+	0	−

nt = not tested.
[a] See Tables 3 and 4.
[b] See Table 5, Figure 2.
[c] Maximum growth, the same pattern applies to mortality rate m (Table 1).

posite to these predictions. Dipterocarps had shallower crowns, smaller total leaf areas, and fewer leaf layers than euphorbs (Table 5). This was particularly true for two dipterocarp species, *S. parvifolia* and *S. johorensis*. In general, these patterns seemed to be unrelated to the adult stature of the species, while they were related to the maximum growth rates and mortality rates of the species. A similar broad conclusion was drawn by Aiba & Kohyama (1997) for trees in of a Japanese warm-temperate rain forest. In more detail, relative crown length, total leaf area, the number of leaf layers, and internal crown cover in our study decreased with the increasing mortality rate and increasing maximum growth rate of the species, although not always significantly (Figure 2). Across species stem slenderness increased with maximum growth rate, indicating that fast growing species, especially dipterocarps, put on more height per unit dbh than slow growing species (euphorbs). The patterns were strongest when species were pooled, but also held when the effect of plant family was removed.

How to explain these patterns? In general, species that are less shade-tolerant (and require more light) produce leaves, branches, and stem length at a higher rate than more shade-tolerant species (Shukla & Ra-makrishnan 1986; King 1994). If this is applied to our species, the less shade-tolerant species should have high rates of leaf and branch shedding at the base of the crown, to produce shallow crowns with few leaf layers and little leaf area. In terms of the carbon balance physiology, there seems no direct advantage in such a produce-and-discard strategy for the high light environment in which they usually live. Moreover, these trees would suffer from light suppression, as a reduced carbon budget would not allow them to produce enough new leaves and branches to compensate for the leaf and branch loss (King 1994). These arguments accord with the high mortality rates of less shade-tolerant species, and also with their reduced crown sizes under slower growth.

Interestingly, an alternative ecological explanation has been proposed by Campbell & Newbery (1993). They studied the same species and mentioned that shallow crowns, owing to rapid branch shedding rates, allow dipterocarps to reduce liana colonization from the ground (see also Putz 1984). They found, for a given stem dbh, that dipterocarps had lower liana loads than euphorbs. Moreover, liana colonization was lowest for the two faster growing species (with the shallowest crowns), *S. johorensis* and *S. parvifolia*.

Our results are consistent with the idea that these dipterocarps, and in particular the fast growing ones, may reduce liana colonization through fast growth rates and rapid branch (and leaf) turnover rates.

Euphorbs had deeper crowns, more leaf layers, and lived at lower levels of light availability than did the dipterocarps. *M. penangensis* showed the strongest pattern in this respect: it had the deepest and narrowest crown with the highest number of leaf layers, since it kept its leaf-supporting plagiotropic branches attached for long stretches of the stem. It formed a crown with a more or less hollow cylinder of foliage, with the leaves distributed over the crown periphery only (F. J. Sterck, unpubl. data). While trees of *M. penangensis* might experience high leaf self-shading when light comes mainly from above, they increase their light interception and minimize leaf self-shading when light comes more from the side. Analogously, deep crowns are typically found at higher latitudes where light comes more from the side than from directly above (Kuuluvainen 1992). Strikingly, diurnal light fluctuations showed relative high peaks in light halfway through the morning and the afternoon in a Neotropical forest (Oberbauer et al. 1988). Unfortunately, there are no such data for the Danum forest, or for any other Asian forest. In response to lateral light, tropical trees seem to adjust leaf distributions and leaf angles to maximize light interception (Ackerly & Bazzaz 1995; Pearcy & Yang 1996). Finally, the development pattern of *M. penangensis* seems to be associated with low branch (and leaf) loss rates, which permits this species to keep its crown in shape at relatively low growth rates in the understorey. In general, the same arguments might hold for the crown shape and leaf distribution of the other euphorb species, but more observations are needed. That the forest at Danum is still aggrading and is quite open and rough at mid-height plus the plots being largely located on ridge slopes suggests that lateral light might be of more importance compared to overhead light than previously realized. Tree architecture at Danum point to this notion.

B. stipulata and *M. wrayi* had the highest crown width/height ratios. As mentioned earlier, these two species differ from the other species in a number of properties: their low maximum growth rates, their short maximal (adult and reproductive) height, and their stem development. Possibly, the development of a wide crown at an early stage of their life helps these trees to shade shorter neighbours, and to establish their adult crown in a stratum that is usually very crowded with competing tree crowns (Lieberman & Lieberman
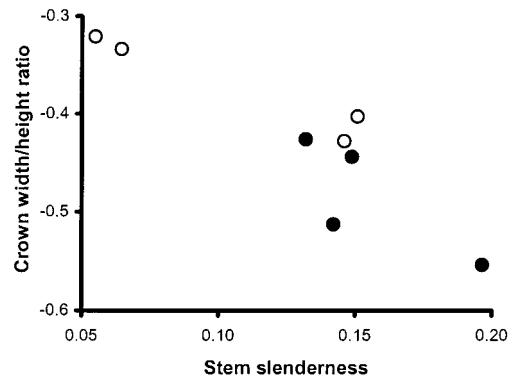

Figure 3. A species comparison for crown and stem dimensions for eight tree species of Bornean rain forest at Danum Valley, Sabah. The partial correlation coefficient r_p corrects for the effect of plant family ($r_p = 0.86$, df = 5, $p \leq 0.01$, two-tailed). Architectural trait values are the ($\log_{10}$-transformed) intercept values of each species in the ANCOVA analysis. These values may be negative because of the $\log_{10}$-transformation. Euphorbs are represented as open and dipterocarps as closed circles.

1994). In other forests, species of short adult stature also had wider crowns than species of tall adult stature (Aiba & Kohyama 1997; Sterck & Bongers 1998). At the same time, *B. stipulata* and *M. wrayi* had thicker stems for a given height than the other species. Apparently, the species with the wider crowns have thicker stems (Figure 3), which may reflect a thigmomorphogenic response to compensate for increased load and bending stresses (Mattheck & Kubler 1997). The generally small safety margins of trees in the forest understorey (Claussen & Maycock 1995; Sterck & Bongers 1998) suggest that responses are crucial to resist increased loading and bending stresses (imposed by growing crowns). This interspecific pattern is also reflected within species, and seems a general feature of trees world-wide (Mattheck 1991).

Acknowledgements

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