

The architecture and allometry of mangrove saplings

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Summary

1. The architecture and allometry of eight populations of mangrove tree saplings of seven species (1.5–3 m in height) were studied at Sungei Merbok, Kedah, Peninsular Malaysia. Three populations (*Bruguiera cylindrica*, *Bruguiera parviflora* and *Rhizophora apiculata*) were growing in shaded conditions, the other five (*Avicennia alba*, *Rhizophora apiculata*, *Rhizophora mucronata*, *Sonneratia alba* and *Xylocarpus granatum*) were in the open.

2. Comparisons were made between the population specific allometric regressions for dimension pairs of the form $\ln y = b_1 \ln x + b_0$. The bifurcation ratio (R_b) for the branching system of each sapling was calculated.

3. In the majority of the allometric regressions the populations differed significantly in b_0 but not b_1 , though some significant slope differences were found, particularly for regressions involving root dry weight.

4. The allometric analysis showed that for saplings of the same height, those growing in the shade had lower shoot dry weight and lower dry weight and area of leaves than the open-grown ones. The shaded saplings also exhibited a greater accumulation of foliage at the top of the plant.

5. *Xylocarpus granatum* was notable for a low investment in leaves, which was probably explained by recent flushing, and in roots, which may reflect the limited development of pneumatophores in this species. The shaded *Bruguiera* populations showed a relatively high root investment probably because of their abundant pneumatophore development.

6. When compared to published results of allometric analyses for shaded saplings from lowland tropical rain forest and warm temperate rain forest it was found that the shaded mangroves were consistently more similar to the unshaded mangroves than to the rain-forest saplings. This may be because the shaded mangroves were growing under higher average irradiances than those from the rain forests. It is argued, however, that mangrove species are inherently more likely to show an architecture better suited to high irradiance conditions than the majority of broad-leaved evergreen rain-forest trees.

Key-words: Allometry, bifurcation ratio, mangroves, shade, tree architecture

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Introduction

All autotrophic plant species have a requirement for the same set of resources for survival and growth. This includes light, water, carbon dioxide and a range of elements usually obtained from the soil. Despite these fundamental similarities plants show a tremendous diversity in form. Even within each life-form

group, such as trees, there is much variation, not just between species but frequently also between populations of the same species growing under different conditions. Clearly, no single plant form is optimal for all conditions and it is tempting to use adaptationist reasoning to explain environmentally related variations in plant morphology. The concept of form being governed by a whole series of evolutionary trade-offs between relative allocation of resources to different structures and physiological activities has become widely accepted in recent years (Bloom, Chapin & Mooney 1985; Givnish 1986, 1987; Küppers 1989).

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A number of different approaches to plant form have been used. In the study of tree morphology, these have included the classification of branching architecture (Hallé, Oldeman & Tomlinson 1978) and foliage arrangement (Horn 1971; Brüning 1976), the quantitative analysis of branching (Oohata & Shidei 1971; Ford 1985) and the comparison of allometric relationships between the weights or sizes of various tree parts (Kohyama 1987; King 1990). The latter has the advantage of being a more dynamic approach because the allometric relationship summarizes the development pattern of a particular population.

In this paper we present an analysis of the above- and below-ground form of juvenile mangrove trees growing in Malaysia. The mangrove forests of the world are morphologically monotonous (Tomlinson 1986), containing a very restricted range of both tree and leaf form, particularly when compared to inland tropical forests. The low species diversity of the mangrove flora may explain this uniformity, yet there is convergence on a typical mangrove tree morphology from phylogenetically diverse taxa (Tomlinson 1986). By studying the architecture and allometric relationships of the mangrove saplings we aimed to see if significant differences in form existed both between species within the mangrove, and between mangroves and other evergreen forest types for which data have been published (Kohyama 1987; Kohyama & Hotta 1990).

Materials and methods

The mangrove saplings studied were all growing along the banks of the estuary of the Sungei Merbok (5°30'N, 100°25'E), Kedah, Peninsular Malaysia. The estuary and its fringing mangroves have been intensively studied (Ong, Gong & Wong 1980; Ong *et al.* 1991). The mangrove forest is dominated by *Rhizophora apiculata* and *Bruguiera parviflora* which are managed for pole and charcoal production. *Rhizophora mucronata* and a number of other species, including those studied for this research, tend to grow at the fringes of the stands of the dominants.

Populations of saplings of various tree species were sought, with individuals in the range 1.5–3 m in height. Seven species (listed in Table 1) were sampled in areas of roughly similar salinity and tidal regime. However, the sapling populations differed in the degree of shading under which they grew. *Avicennia alba*, *R. apiculata*, *R. mucronata*, *Sonneratia alba* and *Xylocarpus granatum* were found in the open. *A. Bruguiera cylindrica*, and a separate *R. apiculata*, population were growing under a continuous canopy and *B. parviflora* under a discontinuous canopy that partially shaded the saplings. Only apparently undamaged saplings were utilized in a destructive analysis of architecture and allometry.

The following variables were measured for each

Table 1. Attributes of the eight populations of mangrove sapling studied at Sungei Merbok. *n* = number of individuals sampled

Species	Family	Growth conditions	Architectural model*	<i>n</i> (<i>n</i> roots)	Mean nearest neighbour distance (cm)	Height range (cm)	SLA† (cm ² g ⁻¹)	Mean leaf area‡ (cm ²)	Mean bifurcation ratio (R _b)‡
<i>Avicennia alba</i> Blume	Avicenniaceae	open	Attms	9(0)	76	141–219	90.6 ± 2.9 ^c	25.4 ± 1.0 ^u	5.8 ^{ab}
<i>Bruguiera cylindrica</i> (L.) Blume	Rhizophoraceae	shade	Attms	10(9)	38	164–270	143 ± 6.7 ^c	40.5 ± 2.0 ^b	11.8 ^a
<i>Bruguiera parviflora</i> (Roxb.) Wight & Arn. ex Griff.	Rhizophoraceae	semi-shade	Attms	10(9)	46	130–246	94.8 ± 2.7 ^c	37.1 ± 1.4 ^b	6.8 ^{ab}
<i>Rhizophora apiculata</i> Blume	Rhizophoraceae	open	Attms	10(10)	139	137–253	64.4 ± 1.9 ^{ab}	34.7 ± 1.5 ^b	6.5 ^{bc}
<i>Rhizophora apiculata</i>	Rhizophoraceae	shade	Attms	10(4)	33	190–285	81.1 ± 2.5 ^c	39.0 ± 1.6 ^b	6.2 ^{abc}
<i>Rhizophora mucronata</i> Poir.	Rhizophoraceae	open	Attms	10(6)	68	174–265	59.0 ± 2.2 ^a	71.1 ± 3.0 ^c	4.9 ^{abc}
<i>Sonneratia alba</i> J.J.Sm.	Lythraceae	open	Pettit	10(5)	150	160–240	81.4 ± 6.0 ^{bc}	20.6 ± 1.1 ^a	3.8 ^{bc}
<i>Xylocarpus granatum</i> Koen.	Meliaceae	open	Rauh	10(10)	97	150–244	111 ± 6.0 ^d	26.1 ± 2.5 ^a	3.4 ^c

* Information gathered from Tomlinson (1986). † Mean values in the column are significantly different if they do not share the same letter according to a multiple range test based on 95% confidence intervals. ‡ Mean values in the column are significantly different if they do not share the same letter according to a multiple range test based on Kruskal–Wallis ANOVA by ranks.

sapling before root excavation was begun: distance to the nearest neighbouring larger individual, height (from substrate surface to shoot tip), two orthogonal crown diameters, the average of which was used to calculate crown area; and main stem diameter at 1.3 m from the substrate surface (dbh) (the mean of two orthogonal estimates made using vernier calipers). The mangrove mud was then carefully dug away from the sapling root systems by hand, assisted by a low pressure water jet from a pump and the incoming tide. Care was taken to retrieve as much of the root system as possible from the mud. Despite a large team of workers there was not time to excavate the root systems of all the saplings, though *A. alba* was the only species for which no data on roots are available. The species growing in the shade were particularly difficult to extract because of the many roots from neighbouring trees growing among the root system of the chosen sapling. Once free of the substrate the saplings were transported by boat to our field laboratory where the leaves (including petioles) were plucked off the saplings. These were counted in 50 cm strata from the sapling base. The leaves (and stipules if present) were kept for drying. A subsample of 20 leaves taken from different heights within the crown was traced onto paper. These leaf outlines were cut out and measured on an area machine (Delta-T Devices, Cambridge, UK) and a mean leaf area calculated for each sapling. The defoliated sapling was then sketched to give an accurate sideview of its system of branching. The sketch was subsequently used to calculate the bifurcation ratio (R_b) of each sapling using the formula of Steingraeber, Kascht & Franck (1979). The shoot and roots were then separated and each part cut up and placed into plastic bags for transportation to the laboratory where each fraction was dried in an oven at 105 °C until a constant dry weight was achieved. The 20-leaf subsample was separated into petiole and lamina fractions so that an estimate of specific leaf area (SLA, lamina area per unit dry weight) could be made, and also a conversion factor between lamina area and lamina plus petiole dry mass which was used in calculating total leaf area for each sapling from its total foliage dry weight. The above-ground parts of

stilt roots of the *Rhizophora* species were treated as stems. The above-ground parts of the pneumatophores of the other species were included in the below-ground root system dry weight.

The sapling dimensions (Table 2) were used to derive allometric relationships of the form

$$\ln y = b_0 + b_1 \ln x \quad \text{eqn 1}$$

between dimension pairs for each species. Statistical comparisons of allometric relationships between sapling populations were conducted in a similar way to those reported by Kohyama & Hotta (1990) and Kohyama & Grubb (1994). Analysis of variance was used to compare the allometric regressions between the populations. It was also employed to compare intercepts (b_0) assuming identical slopes (common b_1). A good fit to this model of a series of parallel lines for the allometric regressions for a particular parameter pair allows the prediction of a population's relative allocation to y for any given x . Correlation analysis was used to compare pairs of allometric relationships across the populations to search for consistent differences in allometry between populations.

A similar analysis for that performed on the data from the Merbok mangroves was used to compare the allometries for these saplings with data for the above-ground parts of saplings from lowland tropical rain forest of Sumatra, Indonesia (Kohyama & Hotta 1990) and warm temperate rain forest on Yakushima Island, Japan (Kohyama 1987).

Results

The two shaded sapling populations (*B. cylindrica* and *R. apiculata*) had, on average, closer neighbours than the other populations (Table 1). The *B. cylindrica* saplings had the highest SLA and that of the shaded *R. apiculata* saplings was significantly higher than that of the open-grown conspecifics. Surprisingly, the SLA of *X. granatum* in the open was higher than that of *R. apiculata* in the shade. The mean leaf size of the shaded and unshaded *R. apiculata* populations was not significantly different (Table 1).

Shading appears to have had an effect on the distribution of foliage on the saplings. Using the data on numbers of leaves in 50 cm height bands on each sapling, curves of cumulative leaf number against relative height were drawn for each species using a third order polynomial regression fitted through the data available for all individuals of each population (Fig. 1). A good fit was obtained in all cases with r^2 ranging 0.753 – 0.937, though the negative gradient occurring on part of the *B. parviflora* curve (the least good fit) is impossible by definition. However, the figure does illustrate some important points. If the leaves were uniformly distributed up the height of the sapling the plot should fall across the diagonal of the figure. The clear deviation by all the species above

Table 2. List of the dimensions measured and used for allometric analysis of mangrove saplings including the abbreviations and units of measurement

Height	H	cm
Diameter at breast height (dbh)	D	cm
Projected crown area	A_c	cm ²
Total leaf area	A_l	cm ²
Dry mass of leaves	W_l	g
Dry mass of stems	W_s	g
Dry mass of roots	W_r	g
Dry mass of shoot	W_{sl}	g
Total sapling dry mass	W_{slr}	g

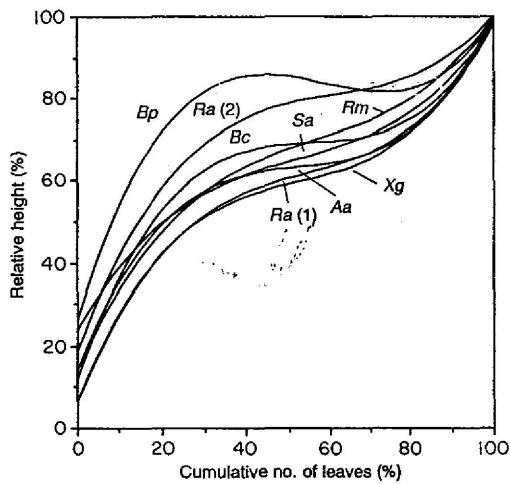


Fig. 1. Foliage distribution by height on mangrove saplings from Sungei Merbok. Curves represent third order polynomial regressions fitted to the data for all the saplings from any one population. Aa, *Avicennia alba*; Bc, *Bruguiera cylindrica*; Bp, *Bruguiera parviflora*; Ra (1), *Rhizophora apiculata* (open-grown population); Ra (2), *Rhizophora apiculata* (shaded population); Rm, *Rhizophora mucronata*, Sa, *Sonneratia alba*; Xg, *Xylocarpus granatum*.

the diagonal from the origin indicates a tendency for the leaves to be accumulated at the top of the plant. This relative absence of leaves at the base of the sapling is clearly more pronounced in the shaded populations.

Significant differences between the sapling populations occurred in nearly all the allometric regressions investigated (Table 3). These differences were largely the result of differences in the intercepts (b_0) of the allometric equations ($P < 0.001$ in nearly all cases), though some significant differences in slope (b_1) were also found. Nearly all the allometric relationships involving W_r showed slope but not intercept differences. All the allometries, except those involving W_r , showed very good fits ($P < 0.001$) to the common slope model (Table 3) indicating that the differences between populations in intercept (b_0) indicate directly the relative allocation in y for any given x .

There was a close correlation between many of the allometries in terms of the more important factor of b_0 allowing the use of relatively few relationships to summarize the results of the analysis (Fig. 2). The striking feature of Fig. 2 is the impact of shade. The three shaded populations, *B. cylindrica*, *B. parviflora* and *R. apiculata*, generally showed negative deviations from the common intercept, while the open-grown population showed positive ones. This pattern was reinforced by the consistently clear intraspecific difference of *R. apiculata*. The unshaded plants had greater mass and crown size for a given height than shaded ones and more leaves for a given crown area. *Xylocarpus granatum* provided the major anomaly

among the sun populations by having a low investment in leaves. This species frequently showed the lowest intercept for allometries against leaf area, weight or crown area.

The allometric relationships involving root dry weight differed from the rest in having significant slope differences between populations. Leaf, stem and shoot dry weight against root dry weight showed strongly correlated deviations from the mean regression slope for the sapling populations. These population differences can be summarized in Fig. 3. For a given shoot dry weight, the two *Bruguiera* species showed a proportionately higher root weight than the other species. There was little difference between the three *Rhizophora* populations in this allometric relationship. *Xylocarpus granatum* had the lowest root

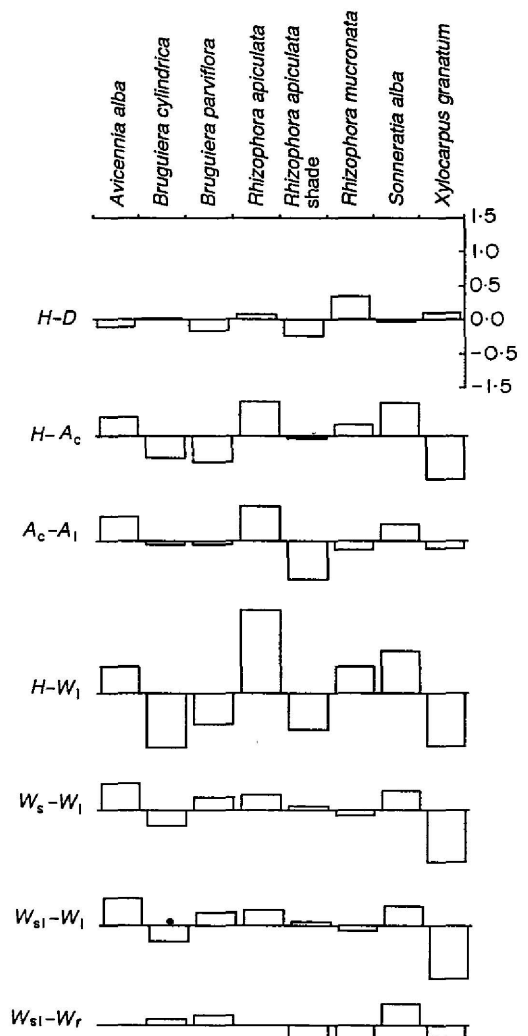


Fig. 2. Deviation in population b_0 value from the overall mean b_0 value with a fixed slope (common b_1) for some of the allometric relationships ($x - y$) for the eight mangrove sapling populations from Sungei Merbok. A positive deviation indicates a greater investment than average by that species in y for a given value of x . Dimension abbreviations are explained in Table 2. No data were obtained for W_r for *Avicennia alba*.

Table 3. Comparisons among eight populations of mangrove saplings in allometric relationships of the form $\ln y = b_1 \ln x + b_0$. For each pair of dimensions (x, y), the b_1 and b_0 values for the overall regression including all (n) individual saplings are given, with the Pearson product-moment correlation coefficient (r) for that regression. The results of ANOVA to test for significant differences between the populations in their respective b_1 and b_0 values are tabulated. The final two columns concern the common slope model. The common slope (common b_1), the average of the population specific b_1 values, is given with an indication of the significance of the fit of the common slope model to the data followed by the mean of the individual population b_0 values. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

x-y	n	Overall regression			Differences between populations		Common slope model	
		b_1	b_0	r	F for b_1	F for b_0	Common b_1	Mean b_0
H-D	79	1.94	-8.03	0.807	3.31	8.14***	2.06***	-8.68
H-A _c	76	1.29	2.04	0.344	2.35*	6.49***	1.91***	-1.22
H-A ₁	76	0.626	5.80	0.154	2.47*	9.22***	1.68***	0.227
A _c -A ₁	73	0.851	1.59	0.749	1.40	6.44***	0.762***	2.37
H-W ₁	76	0.400	2.59	0.085	1.87	14.7***	1.85***	-5.06
H-W _s	79	1.06	0.267	0.237	1.10	15.8***	2.61***	-7.90
H-W _{sl}	76	0.859	1.65	0.198	1.33	14.1***	2.38***	-6.36
A _c -W ₁	73	1.00	-4.15	0.761	1.25	11.3***	0.812***	-2.45
A _c -W _s	76	0.747	-0.689	0.621	0.432	11.8***	0.813***	-1.28
A ₁ -W ₁	76	1.07	-5.05	0.922	3.23**	11.8***	0.973***	-4.15
A ₁ -W _s	76	0.803	-1.44	0.732	1.88	11.7***	0.888***	-2.21
W _s -W ₁	76	0.821	-0.120	0.775	1.36	17.9***	0.815***	-0.080
W _{sl} -W ₁	76	0.929	-1.04	0.855	1.14	17.0***	0.889***	-0.786
H-W _r	52	0.307	3.59	0.009	0.670	4.62***	1.22*	-1.20
A _c -W _r	52	0.431	1.43	0.701	1.01	1.92	0.332*	2.29
A ₁ -W _r	52	0.577	-0.057	0.701	3.47**	0.406	0.555***	0.140
W ₁ -W _r	53	0.460	3.05	0.671	4.36**	0.976	0.517***	2.78
W _s -W _r	53	0.509	2.18	0.655	2.55*	1.91	0.504***	2.21
W _{sl} -W _r	52	0.539	1.85	0.685	2.98*	1.32	0.532***	1.90
H-W _{slr}	53	0.546	3.69	0.144	1.03	15.4***	2.32***	-5.67

weight for a given shoot weight. *Bruguiera parviflora* and *Sonneratia alba* had regression slopes of about 1.0 indicating that the root:shoot ratio changed little over the range of sapling size studied. That of *Bruguiera cylindrica* tended to increase whereas that

of the other four populations decreased as the saplings got bigger. Total leaf area against root dry weight showed a similar pattern among the populations (Fig. 3) except that *Rhizophora mucronata* and *S. alba* joined the *Bruguiera* species at the high slope end of the range.

There were significant differences in the branching patterns of the sapling populations as indicated by a Kruskal-Wallis one-way analysis by ranks of the bifurcation ratios ($KW = 40.9, P = 8 \times 10^{-7}$). The variances of the R_b values for the populations were too heterogeneous for a parametric analysis. Only in the *A. alba*, *S. alba* and the sun *R. apiculata* populations did the majority of individuals have four or more orders of branching. The shade population of *R. apiculata* had a mean R_b value very similar to the unshaded population (Table 1). Pinnate-leaved *X. granatum* had the lowest R_b value. Oohata & Shidei (1971) reported that the intercept of the branch order against \ln branch number regression was an accurate predictor of leaf number for some Japanese gymnosperms but underestimated leaf number for broad-leaved trees. This regression was tested for the Merbok mangrove saplings. The intercept strongly underestimated total leaf number but was a highly significant correlate to it ($r^2 = 0.63, P < 0.0001$, regression equation $y = 1.5x + 193$).

For the comparison between different forests the shaded and unshaded mangrove populations were

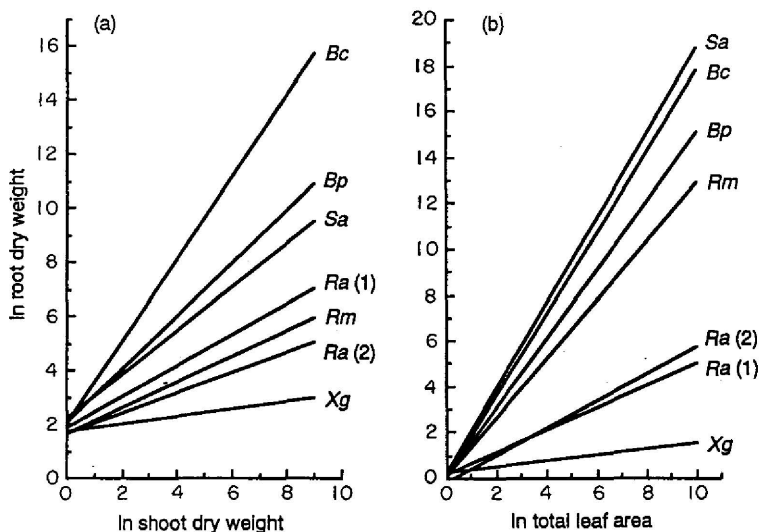


Fig. 3. The allometric regression of (a) shoot weight (g) and (b) total leaf area (cm^2) against root dry weight (g) for the eight mangrove sapling populations from Sungei Merbok. Aa, *Avicennia alba*; Bc, *Bruguiera cylindrica*; Bp, *Bruguiera parviflora*; Ra (1), *Rhizophora apiculata* (open-grown population); Ra (2), *Rhizophora apiculata* (shaded population); Rm, *Rhizophora mucronata*; Sa, *Sonneratia alba*; Xg, *Xylocarpus granatum*.

treated separately and compared with the tropical and warm temperate rain-forest datasets. In a majority of cases the differences in allometry between the different forest types lay in the intercept values rather than the slopes of the allometric regressions (Table 4), though dry-weight distribution among the major components did show significant slope differences as well. In most cases the parallel straight lines model

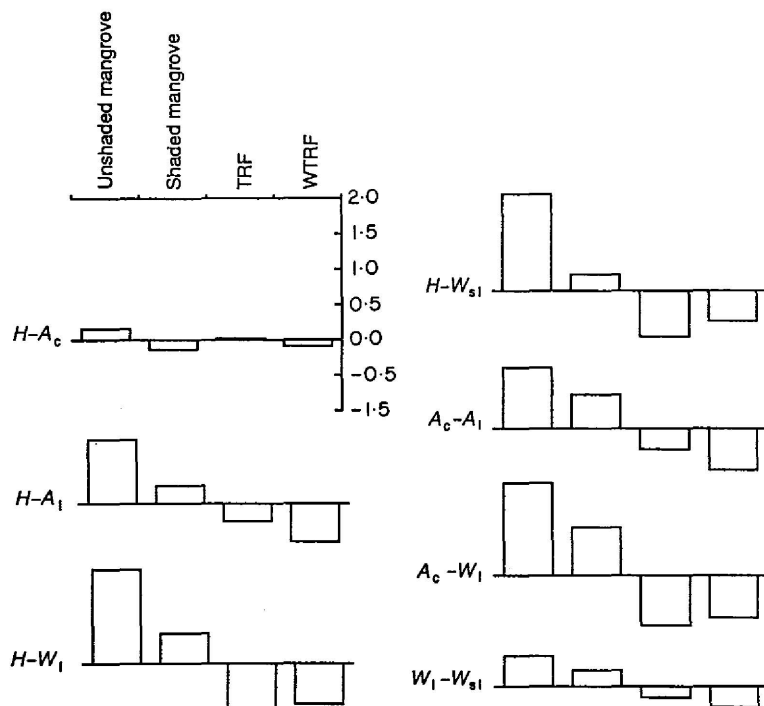


Fig 4. Deviation in b_0 among the four forest types from the overall mean b_0 to common b_1 for a selection of allometric relationships. Abbreviations to dimensions are explained in Table 1. Shaded and unshaded mangroves from Sungei Merbok are compared with shaded saplings from lowland tropical rain forest (TRF) in Sumatra (Kohyama & Hotta 1990) and warm temperate rain forest (WTRF) in Japan (Kohyama 1987).

Table 4. Comparison of allometric relationships for above-ground dimensions for open-grown and shaded mangrove saplings with shaded saplings from lowland tropical rain forest and warm temperate rain forest. See Table 3 for further explanation

$x-y$	b_1	b_0	r	F for b_1	F for b_0	Common b_1	Mean b_0
$H-A_c$	1.43	1.30	0.750	1.60	2.08	1.36***	1.62
$H-A_1$	2.24	-3.00	0.817	0.066	33.5***	1.37***	1.22
$H-W_1$	2.66	-9.87	0.794	0.628	74.5***	1.48***	-4.09
$H-W_s$	3.27	-11.8	0.863	0.137	119***	2.32***	-7.20
$H-W_{s1}$	3.10	-10.7	0.852	0.280	122***	2.08***	-5.67
A_c-A_1	1.23	-2.22	0.853	1.47	85.2***	0.809***	1.25
A_c-W_1	1.44	-8.75	0.816	3.01*	190***	0.895***	-4.25
A_c-W_s	1.56	-8.76	0.784	1.63	166***	0.881***	-3.15
A_c-W_{s1}	1.52	-8.10	0.795	0.948	206***	0.871***	-2.73
A_1-W_1	1.19	-6.26	0.968	1.59	80.9***	1.02***	-4.93
A_1-W_s	1.27	-5.96	0.920	4.89**	36.9***	0.892***	-2.95
A_1-W_{s1}	1.25	-5.42	0.938	4.58**	50.2***	0.915***	-2.79
W_1-W_s	1.07	0.760	0.949	7.83***	8.48***	0.853***	1.44
W_1-W_{s1}	1.05	1.17	0.968	8.76***	9.25***	0.878***	1.71
W_s-W_{s1}	0.959	0.512	0.997	4.32**	5.57***	0.923***	0.661

showed a very good fit to the data. Only the $H-A_c$ allometry was without any significant difference between forest types in either intercept or slope. Many of the differences in allometries were correlated with each other. The intercept deviations for some of the regressions are plotted in Fig. 4. Unshaded mangrove tended to have large positive deviations in intercept but even shaded mangrove was always higher in intercept than the two dryland forests, for the allometries presented in Table 4. This indicates that for a given height mangroves had more leaf area and dry weight in all components than the shaded rain-forest saplings. For a given crown area, they had more leaf area and leaf dry weight, and a greater amount of support structure per weight of leaf.

Discussion

Shade plants generally have a higher SLA than sun plants, frequently a lower leaf-area index (LAI, area of leaf per unit of crown projected area) and a higher dry weight allocation to leaves but a lower allocation to roots than sun plants (Givnish 1988). The shaded mangrove saplings sampled did have higher SLAs than the open-grown ones, though *X. granatum* was anomalously high. This species periodically (annually at Sungei Merbok, J. E. Ong, personal observation) sheds all its leaves and flushes a new set immediately (Tomlinson 1986). The *Xylocarpus* saplings sampled appeared to have all recently flushed new leaves which presumably had not reached their mature SLA. The shaded saplings did exhibit a lower LAI than the sun plants, with the two populations of *R. apiculata* being particularly marked in their difference (Fig. 2).

There were clear and consistent differences in the morphology and allometry of the crown between the two classes of mangrove saplings. We ascribe these to the influence of shade but cannot entirely discount other environmental factors from being wholly or partially responsible for the differences. The shaded saplings had narrower crowns for a given height with fewer orders of branching and a greater concentration of the leaves at the top of the crown. Thus the mangroves tend to show the sun/shade divergence into multi-layered against monolayered crowns as propounded by Horn (1971) and observed in *Abies mariesii* by Kohyama (1980). Under shade conditions self-shading of foliage is minimized to maximize the total amount of light intercepted by the crown (Givnish 1988). In the open self-shading might become beneficial because the shaded leaves will be subjected to lower leaf temperatures and a reduced likelihood of photoinhibition. Sun leaves of two *Bruguiera* species in tropical Australia showed major reductions in assimilation rate after mid-morning on sunny days (Cheeseman *et al.* 1991). Givnish (1988) noted that in deep shade a relatively broad crown would make the most efficient photosynthetic returns

on investment in support structures but as soon as similar-sized competitors are present the advantages of extra height become paramount. This probably explains why the shaded mangrove saplings invested strongly in height growth with relatively narrow crowns at the top of the plant supported by few orders of branching. The shaded mangrove saplings appeared neotenic and etiolated when compared with open-grown saplings of the same height. Internode elongation had allowed them to gain height with less crown development.

The similarity of bifurcation ratio between the sun and shade *R. apiculata* saplings indicates that there had been no digression from the typical architecture of the species. This seems to reinforce Tomlinson's (1986) recognition of mangrove trees as being notably model conforming. While a number of species have been found to have R_b unaffected by shade, for example, *Quercus phylliraeoides* (Oohata & Shidei 1971), *Fraxinus americana* (Whitney 1976), others exhibit a lower R_b when shade-grown, for example, *Acer saccharum* (Steingraeber *et al.* 1979), *Populus deltoides* (Borchert & Slade 1981) and a variety of trees and shrubs from sub-tropical north India (Shukla & Ramakrishnan 1986).

There was no strong evidence that the shaded mangroves invested relatively more dry mass in leaves, a trend reported for shade-tolerant lowland tropical rain-forest species (King 1991). *Avicennia alba* had the highest leaf weight per unit stem weight, which may reflect its lower wood density than the other mangroves, 9–38% lower according to the data provided by Desch (1954). Again presumably because of recent flushing, *X. granatum* showed a low investment in leaves.

The relatively high allocation of dry weight to roots by the *Bruguiera* species is not what would be expected in shaded plants (cf. Givnish 1988). An explanation for this may be found in the inclusion of the pneumatophores in the root system dry weight. The three species with relatively high allocation to roots, the *Bruguiera* species and *S. alba*, have many pneumatophores which are likely to increase the dry weight of the root system. The stilt roots of the *Rhizophora* species were included as stem dry weight because they serve as supports, as well as channels for gas exchange to the root system. This factor confounds any investigation of the effect of shade, though *R. apiculata* did show a lower allocation of dry weight to roots in the shade, as would be generally expected (Givnish 1988). *Xylocarpus granatum* had the lowest root weight for a given shoot weight. This was not expected because its low leaf weight, owing to recent flushing, would tend to push the allocation ratio the other way. The absence of pneumatophores in the saplings of this species (Tomlinson 1986) may explain this result. The allometric analysis confirmed that several of the mangrove species studied had very similar architecture and allometry, notably the open-

grown *A. alba*, *R. apiculata*, *R. mucronata* and *S. alba*.

The comparison of the Merbok mangroves with the data on Japanese warm temperate rain forest and Sumatran lowland tropical rain forest showed the mangrove saplings to be consistently different from the rain forest ones. The mangroves, regardless of growth conditions, had allometries of a less shade-adapted type than the rain-forest saplings. One obvious reason for this may be that the mangroves were under less shade than the saplings in the rain forests and were, therefore, less extreme in their morphology. However, there do appear to be valid reasons to expect such a difference. Mangrove trees are specialists at colonizing newly deposited, littoral substrates and, unlike the majority of rain-forest tree species (Whitmore 1984), have not been noted for their shade tolerance. The investment of relatively less dry matter in leaves by the shaded mangrove saplings than the open-grown ones may also reflect the relatively low degree of shade tolerance in this community, which in turn may be a part explanation for the consistent crown morphology of the mangrove species. Many of the most shade-tolerant rain-forest saplings have crowns of plagiotropic branches supporting flat sprays of leaves. These pessimists (*sensu* Kohyama 1987) are absent from the true mangrove where most of the species are markedly orthotropic, at least as juveniles (Tomlinson 1986). Possible reasons for this absence, other than phylogenetic constraints concerning the evolution of salt tolerance, include the physiological impracticality of persistence in deep shade (the pessimist strategy) on a salty and anoxic soil (Janzen 1985; Lugo 1986) and the competitive inferiority of plagiotropism to orthotropism under better illumination.

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