

Allometry, adult stature and regeneration requirement of 65 tree species on Barro Colorado Island, Panama

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Abstract: This study provides a community-level analysis of how regeneration requirement and adult stature are related to tree allometry (diameter, height and crown size) throughout post-seedling ontogeny on Barro Colorado Island, Panama. Comparing 65 species, gap species are taller, have higher diameter growth rates and occupy more low-canopy sites (≤ 10 m canopy height) than shade species at small diameters (≤ 10 cm dbh). For trees > 10 cm dbh, diameter-height relationships and growth rates no longer differ between gap and shade species, but shade species have larger, particularly deeper, crowns than gap species. Species with tall adult stature have more slender stems with larger crowns compared with treelet and mid-canopy species starting at 5 cm dbh. From 10 to 40 cm dbh, diameter growth rate is also significantly greater for tall species. The consistent allometric differences between functional groups on a community level will, in part, determine vertical and horizontal stand structure.

Key Words: allometry, forest structure, functional groups, Panama, tree architecture

INTRODUCTION

Light resources in a forest vary both in space and time (Baldocchi & Collineau 1994, Parker 1995, Smith *et al.* 1992, Yoda *et al.* 1983). Horizontally, the forest can be divided into gaps, which have high light availability all the way to the forest floor, and closed canopy, where there is a strong vertical gradient of light availability. Differences in vertical light profiles between gaps and closed canopy are ephemeral; within a short period of time, gaps can close and develop a strong vertical light gradient, or trees fall to create new gaps (Canham *et al.* 1990, Valverde & Silvertown 1997).

The allometry of a tree species, here considered the relationship of trunk diameter to height and crown size, determines in part where its leaves are positioned in the light gradients of the forest (Horn 1971, Pearcy & Valladares 1999). For many species, allometry is not linear, rather it changes through ontogeny based on both current and anticipated future light environments

(King 1996, Sterck & Bongers 2001). A current high-light environment enables a tree to grow more rapidly and invest in height growth whereas low light availability encourages crown expansion, creating greater surface to capture low light (Claveau *et al.* 2002, Kohyama 1991, Takahashi *et al.* 2001). But allometric patterns are also determined by inherent carbon allocation strategies geared toward future light environments that species will experience. A tall, shade-tolerant species that germinates in the dark understorey can expect to be in the high light of the upper canopy eventually, and allometric shifts through ontogeny may help species achieve and adapt to these future light environments. The degree to which current light conditions versus inherent allocation strategy shapes allometry is not clear and varies for different species (Bonser & Aarssen 1994, Coomes & Grubb 1998, Poorter & Werger 1999).

Allometric differences among functional groups

Some of the variation in allometry among individual species may be explained by functional group identity (Chesson & Pantastico-Caldas 1994, Kohyama 1991).

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Both regeneration requirement (gap-dependent vs. shade-tolerant species, hereafter referred to as gap and shade species) and adult stature (tall vs. short species) relate to how species partition vertical and horizontal light resources, so it is not surprising that there is growing, yet incomplete, evidence that allometry is also part of the life history trade-offs associated with these functional groups (Aiba & Kohyama 1996, 1997; King 1996, Poorter *et al.* 2003, Thomas 1996a). However, most of these studies focus on a particular stage of ontogeny (Poorter *et al.* 2003) or on a small number of species (Claussen & Maycock 1995, Davies *et al.* 1998, King 1996, O'Brien *et al.* 1995, Sposito & Santos 2001, Sterck & Bongers 1998, 2001).

For regeneration requirement, most studies have focused on early stages of ontogeny, where we would expect gap species growing in high-light environments to have rapid height growth and shade-tolerant species growing in the dark understorey to have greater crown development (Claussen & Maycock 1995), although this is not always observed (Aiba & Kohyama 1997, King 1996, Sterck & Bongers 1998). Seedlings germinating in gaps and adjacent understorey areas experience increasing similar light conditions as gaps close. Gap and shade species may adjust to increasingly similar light conditions through their ontogeny by changing allocation to height versus crown development, resulting in more similar allometries in adult stages. The few studies of adult allometry comparing gap and shade species in tropical forests are equivocal (Aiba & Kohyama 1997, King 1996, Poorter *et al.* 2003, Sterck & Bongers 1998).

For allometric differences related to adult stature, differences in tree height and crown size between tall, mid-sized and understorey species have also not shown consistent patterns. Species of different stature, by definition, have different heights as mature trees, but at earlier stages of ontogeny, tall and subcanopy species do not necessarily have different diameter-height relationships. Several studies suggest that there are significant differences in diameter-height relationships as early as 5 cm dbh (King 1996, Thomas 1996a), but others do not (Alves & Santos 2002, Davies *et al.* 1998). Is there a concurrent trade-off between investment in height versus crown development throughout ontogeny for tall versus subcanopy species? Again there is a wide range of results on this question (Aiba & Kohyama 1997, Alves & Santos 2002, King 1996; Kohyama *et al.* 2003, Poorter *et al.* 2003, Sterck & Bongers 1998, Sterck *et al.* 2001).

Here we present allometric relationships throughout post-seedling ontogeny for a large number of species in a single forest. This study provides a synthesis of how regeneration requirement and adult stature are related to tree allometry throughout ontogeny on a community level. Two specific questions are addressed. As juveniles, do gap and shade species have different diameter-height

and diameter-crown size relationships, and do these juvenile allometric differences persist as adults? How early in ontogeny do species of different adult statures differ in diameter-height or diameter-crown size relationships? To do this, allometric relationships were developed for 65 species from the 50-ha permanent forest dynamics plot on Barro Colorado Island, Panama.

METHODS

Site information

The data for this study were collected on Barro Colorado Island (BCI) (9°09'N, 79°51'W), a 15-km² island covered with semi-deciduous lowland moist forest located in Lake Gatun in the Panama Canal (Dietrich *et al.* 1982). The old-growth forest on the island is believed to have been mostly free of agricultural clearing for the past 1500 y, and have a minimum age of 500 y (Piperno 1990). The island receives an average of 2650 mm y⁻¹ of rainfall, with a dry season that lasts usually from January to April.

Between 1980 and 1982, a 50-ha permanent plot was established in which every tree stem ≥ 1 cm diameter was mapped and identified to species, and its diameter was measured. Every 5 y since 1980, the diameters of all trees have been re-measured with recruitment to the 1-cm diameter class and mortality noted. In the 1995 census data used in this study, there were 301 species on the 50-ha plot. Detailed descriptions of BCI and the 50-ha plot can be found elsewhere (Condit 1998, Croat 1978, Hubbell & Foster 1983, Leigh 1999).

Data set

The allometry data set consists of 494 individuals from 65 species and was collected in two different years by the authors (Table 1). The first part of the data (referred to as 'O'Brien' throughout the paper) was collected by S. O'Brien in the dry season of 1993 and focused on 47 species that had the greatest stem density in the plot (O'Brien 1994). He measured 5–8 individuals per species, selecting at least one tree in each doubling diameter class (1–2 cm, 2–4 cm, 4–8 cm, etc.), thus concentrating the measurements at smaller diameters. The second part of

Table 1. Number of species in each adult stature and regeneration-requirement category for which allometry was compared on Barro Colorado Island, Panama.

	Gap	Shade
Tall	10	26
Subcanopy		
Mid-sized	2	15
Treelet	1	11

the data was collected by S. Bohlman in the dry season of 1997 (referred to as 'Bohlman' throughout the paper). The main goal of this data-collection effort was to predict canopy structure of the 50-ha plot so larger individuals of the 28 species studied by O'Brien (1994) were measured and 18 new species, all canopy species, were added. For the new species added by Bohlman, each species' diameter range in the plot was divided into five equal intervals and one or two randomly chosen trees in each interval were measured. Small sample sizes (5–10 individuals per species) were chosen in order to include as many species as possible. O'Brien (1994) found this number adequate to derive highly significant allometric relationships with good fits. Because the goals for our studies differed, the two data sets were not distributed evenly across the different categories of regeneration requirement and adult stature. The methods of Bohlman and O'Brien are described below and differences between the two discussed. More details on the methods by O'Brien are found in O'Brien (1994) and O'Brien *et al.* (1995).

Tree measurements

For all trees, dbh (at ~1.3 m), overall tree height, height to crown base and crown radius were measured by both Bohlman and O'Brien. We focused on the diameter range of 1–50 cm. Throughout this paper we refer to allometric differences that occur 'throughout ontogeny', recognizing that we are not including the seedling stage (<1 cm dbh) nor for tall trees, large diameters (>50 cm dbh). Trees in which a significant part of the crown had broken off or whose crown was indistinguishable from lianas or other crowns were not measured. If there was a trunk anomaly at 1.3 m, such as buttressing, the stem diameter measurement was taken directly above the anomaly. When stem diameter could not be obtained in the field due to irregular trunks or buttressing, diameters from the 1995 census were used. Because the average diameter growth rate for most species is less than 10 mm over the 2-y period between this study and the 1995 census (Condit *et al.* 1993), the use of the 1995 data likely did not add serious error to the analysis (O'Brien 1994).

For the data collected by Bohlman, tree heights and crown radii were measured using a laser rangefinder (Advantage Laser Rangefinder Model # 1095-02, Norcross, GA). In most cases, tree height was measured from directly beneath the crown. The upper part of the crown was visible in most tree crowns because foliage density is depressed in the dry season. The highest foliage, or branches in the case of deciduous trees, was determined by choosing the highest of at least five measurements of upper crown foliage.

For trees measured by Bohlman where dense foliage obscured a clear view of the upper crown, and for all trees

measured by O'Brien, an angle and distance method was used to determine tree height. Height was calculated by multiplying the distance between the observer and the tree by the tangent of the angle to the top of the tree. The angle to the top of the tree was measured with a clinometer. The horizontal distance from the observer to the tree was measured using a rangefinder by Bohlman and measuring tape by O'Brien, with the distance between the observer and tree approximately equal to the tree's height. The height to eye level of the observer was added to all tree height calculations.

The height to crown base measurements followed the procedure for tree height with a vertical laser rangefinder measurement used by Bohlman, and distance and angle methods used by O'Brien. The location of the crown base was defined differently in the two studies. Bohlman used the lowest level of foliage that was part of the vertically continuous crown. If the lowest edge of the crown was uneven, several measurements of the crown base were averaged. O'Brien used the height of the first main crotch in the trunk or the height of the lowest branch that formed part of the crown. Crown depth was calculated by subtracting the height to crown base from the overall tree height.

Crown radius, defined as the distance from the crown edge to the trunk base, was measured at each of eight compass directions in 45° increments for both Bohlman and O'Brien. A clinometer was used to find the position directly beneath the crown's edge, then the distance to the trunk was measured with the laser rangefinder for Bohlman and with a measuring tape for O'Brien. For leaning trees where the trunk base did not coincide with the centre of the crown, a point at the centre of the crown was established and used as the centre point for the crown radius measurements. The eight measurements per crown were averaged.

Observer differences

There were several differences in methods between the two observers (Bohlman and O'Brien) that may have led to systematic differences in the measurements and necessitated careful consideration of observer in the data analysis. For tree height, O'Brien used a distance and angle method while Bohlman used mostly direct vertical measurements using a rangefinder. There were significant differences in tree height due to observer (Figures 1 and 2), but the magnitude of the differences was small (Figure 1). For the height to the crown base, O'Brien (1994) used the height of the first main crotch in the trunk or the height of the lowest branch that formed part of the crown. For Bohlman's measurements, the lowest point of the continuous canopy was used, which tends to be higher in the tree than the height to the first main crotch. Height

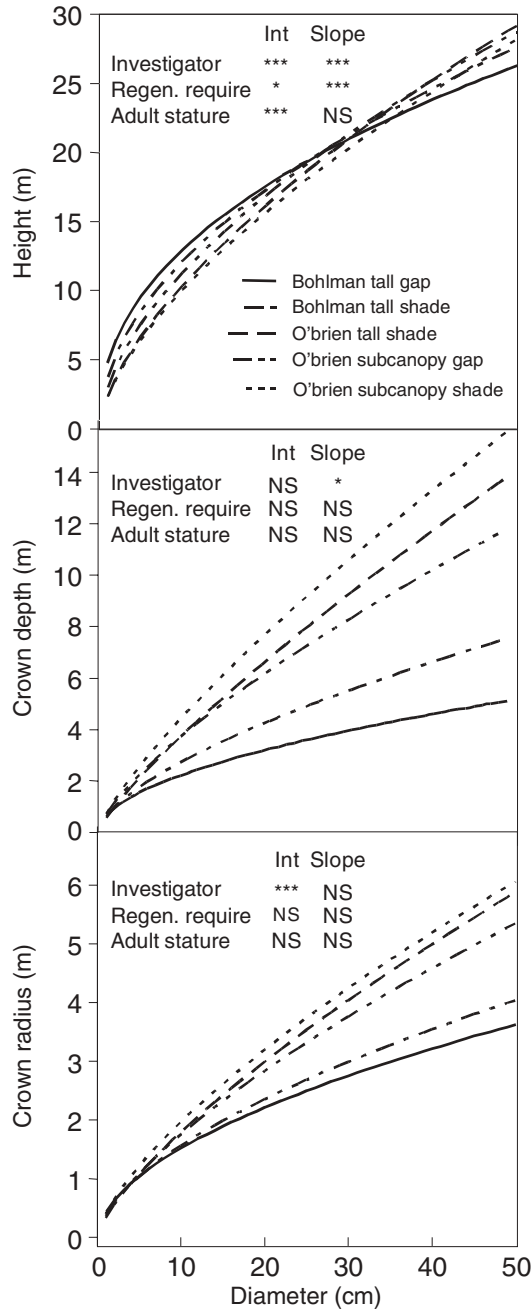


Figure 1. Log-log regressions between crown dimensions and diameter for different investigators, regeneration requirements, and adult statures. The lines represent the predicted patterns determined from all trees in each group. Insets indicate the P-values from an analysis of variance of slopes and intercepts. Significant differences are indicated by *** $P < 0.005$, * $P < 0.05$, NS not significant.

to crown base was significantly smaller and crown depth significantly greater for O'Brien (Figure 1). O'Brien also had significantly larger crown radius measurements than Bohlman (Figure 1). Measuring the base and edges of a tree crown is difficult because the observer must 'smooth' between branches to define the perimeter and base of the

crown, which increases subjectivity of this measurement. Especially for taller trees, it can also be difficult to separate interlaced branches of different species. The differences in all these tree dimensions among observers may also be related to uncharacterized life history traits that differ between the two sets of species measured in each study.

Data analysis

For each species, ordinary least squares regression was used to develop a linear fit between diameter and tree height, crown depth, and crown radius. Reduced axis regression (RMA) was not used because the error in the independent variable (diameter) was much less than in the dependent variables. Both diameter and the tree characteristics were first log-transformed. To reduce the effect of the potential asymptotic behaviour of tree height and crown dimensions at large diameters, only data from 1–50 cm dbh were used. In all cases, stem diameter was the independent variable.

The fitted allometric equations were used to estimate tree height and crown dimensions at five diameters (2, 5, 10, 20 and 40 cm dbh) for each species. Crown volume was calculated at each diameter using the estimated crown radius and crown depth and assuming a half-ellipsoid crown shape. Height and crown dimensions were predicted only within the observed diameter range of each species. About 40% of the species had maximum diameters less than 50 cm. Within these diameter ranges (either 1 cm to 50 cm or 1 cm to the maximum diameter), log-log or power function fits were nearly identical to fits using non-linear asymptotic equations (Chave *et al.* 2003). Within the diameter ranges of individual species, significant deviations from power function fits occurred mainly for tall species at diameters greater than 50 cm. We excluded four species that had poor fits or asymptotic behaviour within the target diameter ranges as determined by the r^2 values and visual inspection of the allometric fits.

Diameter growth rates

The 1990 and 1995 BCI forest inventory data were used to calculate the average annual diameter growth rates of each species. Trees were excluded if the point of measurement on the tree changed between 1990 and 1995. They were also considered to have measurement error and excluded if annual growth rate was greater than 7.5 cm y^{-1} or relative annual growth rate was $< -5\% \text{ y}^{-1}$ (Condit *et al.* 1993, 1999). Growth rates for each species were averaged within five doubling diameter classes (1.4–3.2, 3.3–7.0, 7.1–14.0, 14.1–28.0, and

28.1–56.0 cm) centred on the diameters for which allometry was estimated (2, 5, 10, 20 and 40 cm).

Surrounding canopy height

We used a previously collected data set on maximum canopy height as an indicator of the average light environments of each species at different heights. These data, collected with a mechanical rangefinder every 1–2 y since 1983, provide maximum canopy height, placed in six height categories: 0–2 m, 2–5 m, 5–10 m, 10–20 m, 20–30 m, and >30 m, at every stake in the 5-m-interval grid that covers the 50-ha plot (Hubbell & Foster 1987, Welden *et al.* 1991). The 1995 data were used. We used the maximum canopy height of the grid point closest to the tree as an indicator of its surrounding canopy height (Welden *et al.* 1991). For the 65 species in this study, surrounding canopy heights were determined for every tree on the plot. Then for each species, the percentage of surrounding canopy height in each canopy height category was determined for each doubling diameter class (1.4–3.2, 3.3–7.0 and 7.1–14.0; the same divisions as for diameter growth rates). Surrounding canopy heights were not calculated for the two largest diameter classes, 14.1–28.0 and 28.1–56.0 cm, because the nearest grid point was likely to include the target tree's crown and thus not represent the height of neighbouring trees. Trees growing with surrounding canopy heights less than 10 m were considered to occur in low-canopy sites (Welden *et al.* 1991). High-canopy sites were ≥ 10 m height.

Comparing allometry among species

The predicted allometry of each species was compared to continuous and categorical measures of regeneration requirement and adult stature. The continuous variable for adult stature was maximum height as determined from the allometry data set. We also considered using maximum diameter as determined from the full 1995 stem census data, but maximum height gave similar results and provided a stronger relationship with the allometry data. For categorical variables, we used the definitions from Condit *et al.* (1996): U, treelets (< 10 m), M, mid-sized trees (10–20 m), and, T, tall trees (20 m). For some of the analyses, mid-sized (M) and treelets (U) were combined to form a subcanopy (SC) category.

For regeneration requirement, species were categorized as gap (G) or shade (S) based on at least one of two factors, sapling recruitment to low canopy sites (the colonizing index) and a principal components analysis (PCA) strongly related to growth rate at small diameters (Condit *et al.* 1996, Welden *et al.* 1991). Gap species had greater than 30% of saplings recruit to low-canopy sites

(Welden *et al.* 1991) and scored greater than (–0.35) on the first PCA axis reported by Condit *et al.* (1996). The categorical variable was used for the main part of the analysis rather than either the colonizing index or PCA output because these two continuous variables had many missing values for the species in our data set. The data were also analysed by grouping species into combined shade-tolerance and adult-stature categories: tall gap species (T-G), subcanopy gap species (SC-G), tall shade species (T-S) and subcanopy shade species (SC-S).

Significant effects of adult stature and regeneration requirement on allometry were determined in two ways. First, the slopes and intercepts of the individual species' allometric relationships were compared to characterize differences in the rate of change between diameter and tree size over the entire size range examined (1–50 cm dbh). Second, to test for differences at individual size classes, the estimated tree heights and crown sizes at five doubling diameters were used. In both cases, analysis of variance was used to look for differences among species related to regeneration requirement and adult stature (S-Plus, Insightful Corp., Seattle, WA, USA). Because there were systematic differences in measurements by Bohlman and O'Brien, investigator was included as an independent variable in the regression model for the allometry analysis. To determine whether each factor was significant for all estimated diameters simultaneously, a sequential Bonferroni correction based on $P = 0.05$ was applied (Quinn & Keough 2002, Rice 1989). Tukey's honestly significant difference tests were used to determine the significance and magnitude of differences between regeneration requirement and adult stature categories. For the calculations of these differences, the categorical data for adult stature were used. The reported magnitude of differences between regeneration requirement and adult stature categories was corrected for differences in investigator.

RESULTS

Allometric relationships

For most of the species, a linear log-log relationship provided a good fit for the relationship between diameter and tree height for 1–50 cm dbh. For individual species, the r^2 values between diameter and tree height ranged from 0.53 to 1.00 with an average of 0.93. The relationships between diameter and crown depth and between diameter and crown radius were more variable within a species than the relationship between diameter and tree height. Values of r^2 for crown depth ranged from 0.00 to 0.99 with an average of 0.73 and for crown radius, from 0.43 to 0.99 with an average of 0.86. For functional groups, r^2 values only differed systematically

Table 2. Parameters of fitted linear relationships between diameter and four tree dimensions (tree height, crown depth, crown radius and crown volume) for different functional groups. Both the dependent and independent variables were log-transformed before analysis. Parameters were calculated for each species, then averaged over all species in each functional group.

Functional groups	Intercept	Slope	r ²	Estimated size(m) at dbh(cm)				
				2	5	10	20	40
Tree height (m)								
Gap	0.573	0.512	0.91	5.2	8.4	12.1	17.6	26.0
Shade	0.404	0.616	0.93	3.9	6.9	10.6	16.4	26.0
Tall	0.476	0.583	0.94	4.5	7.7	11.5	17.4	26.5
Subcanopy	0.391	0.610	0.91	3.8	6.6	10.2	15.7	23.2
Midstorey	0.404	0.617	0.91	3.9	6.9	10.5	16.2	23.2
Treelet	0.373	0.600	0.90	3.6	6.2	9.6	14.6	NA
Tall-Gap	0.599	0.496	0.93	5.4	8.7	12.4	18.0	26.1
Tall-Shade	0.428	0.617	0.95	4.2	7.3	11.2	17.2	26.6
Subcanopy-Shade	0.380	0.615	0.92	3.7	6.5	10.1	15.5	22.7
All	0.438	0.595	0.93	4.2	7.2	10.9	16.7	26.0
Crown depth (m)								
Gap	-0.108	0.527	0.46	1.0	1.7	2.6	4.1	5.9
Shade	-0.169	0.745	0.76	1.2	2.4	4.0	6.5	9.4
Tall	-0.169	0.637	0.63	1.1	1.9	3.0	4.9	8.1
Subcanopy	-0.142	0.782	0.79	1.3	2.6	4.4	7.3	10.5
Midstorey	-0.152	0.767	0.81	1.3	2.5	4.2	7.2	10.5
Treelet	-0.127	0.802	0.75	1.3	2.7	4.8	7.6	NA
Tall-Gap	-0.125	0.502	0.42	1.0	1.6	2.3	3.6	5.6
Tall-Shade	-0.185	0.689	0.71	1.2	2.1	3.3	5.4	9.1
Subcanopy-Shade	-0.152	0.801	0.81	1.3	2.6	4.5	7.5	10.8
All	-0.157	0.702	0.70	1.2	2.3	3.7	6.0	8.5
Crown radius (m)								
Gap	-0.424	0.599	0.84	0.60	1.0	1.5	2.3	3.2
Shade	-0.442	0.673	0.87	0.61	1.1	1.7	2.7	4.1
Tall	-0.471	0.643	0.87	0.56	1.0	1.5	2.4	3.7
Subcanopy	-0.397	0.678	0.86	0.68	1.2	1.9	3.0	4.5
Midstorey	-0.392	0.665	0.87	0.67	1.2	1.9	3.0	4.5
Treelet	-0.405	0.697	0.84	0.68	1.2	1.9	3.2	NA
Tall-Gap	-0.417	0.57	0.84	0.60	1.0	1.4	2.1	3.2
Tall-Shade	-0.483	0.671	0.88	0.53	1.0	1.5	2.4	3.9
Subcanopy-Shade	-0.391	0.676	0.86	0.69	1.2	1.9	3.1	4.7
All	-0.438	0.658	0.86	0.61	1.1	1.7	2.7	3.8
Crown volume (m ³)								
Gap	-0.638	1.70	0.85	0.99	4.3	13.6	46.7	134
Shade	-0.691	2.09	0.88	1.26	7.4	29.1	118	390
Tall	-0.766	1.94	0.86	0.93	4.9	17.9	70.0	290
Subcanopy	-0.596	2.10	0.90	1.49	8.8	34.8	143	456
Midstorey	-0.615	2.10	0.89	1.54	8.5	33.2	140	456
Treelet	-0.564	2.11	0.90	1.40	9.3	37.7	150	NA
Tall-Gap	-0.578	1.59	0.84	1.06	4.2	12.0	36.9	124
Tall-Shade	-0.846	2.08	0.87	0.87	5.2	20.4	84.0	361
Subcanopy-Shade	-0.573	2.10	0.89	1.55	9.1	36.0	148	504
All	-0.681	2.02	0.88	1.21	6.8	26.2	104	320

for the diameter-crown depth relationship (Table 2). The r² values were lower for gap species compared to shade species.

Regeneration requirement

The effects of regeneration requirement differed through ontogeny. Gap species had a significantly greater intercept but significantly flatter slope in the diameter-height

relationship than shade species (Figure 1), indicating that gap species started out taller than shade species as seedlings. But as adults, heights were more similar between the two functional types. This was confirmed by differences between gap and shade species at individual diameter classes (Table 2, Figure 2). Gap species maintained a height advantage of 0.8 to 1.1 m on average over shade species throughout ontogeny, but the difference was only significant up to 10 cm dbh.

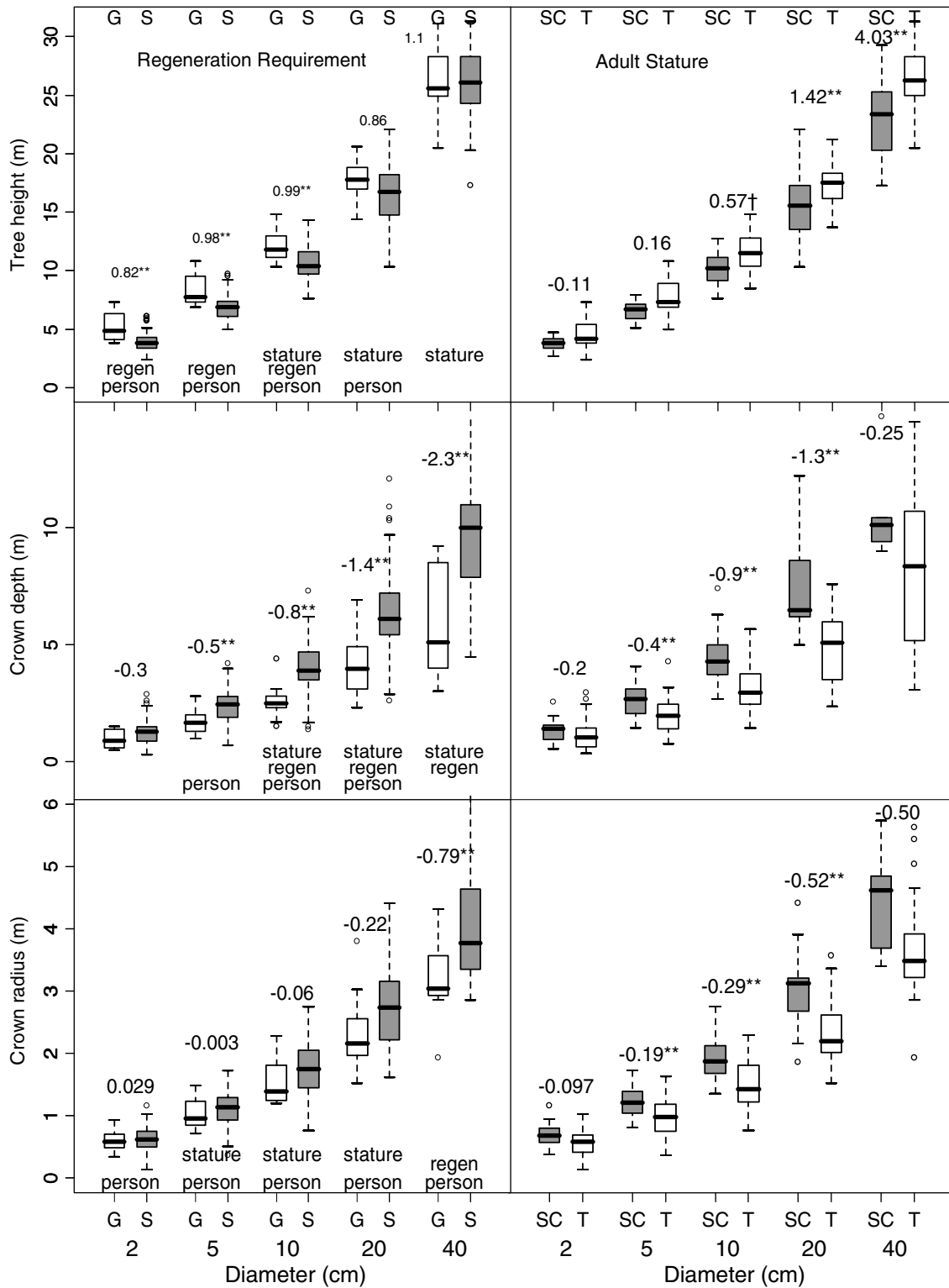


Figure 2. Boxplots describing allometric differences between regeneration and adult stature guilds. Median, quartiles and 95% confidence intervals are shown for regeneration groups on the left panel (G = gap and S = shade) and adult stature groups in the right panel (T = tall and SC = subcanopy). Note that differences in the means shown in Figure 1 are not always in the same direction as illustrated differences in the medians in this figure. In the left panels, the bottom of each graph shows the results of an analysis of variance with investigator (person), regeneration requirement (regen) and adult stature (stature) as factors. Factors that were significant at $P \leq 0.05$ after a Bonferroni correction are listed for each diameter. No significant interactions were found between the factors. No Bonferroni correction was used for growth rate because the data at different diameters were independent. Values above the boxplots are the mean differences between functional groups determined from Tukey's honestly significant difference tests, which adjust differences for other factors in the ANOVA. Asterisks indicate significant differences $P = 0.05$.

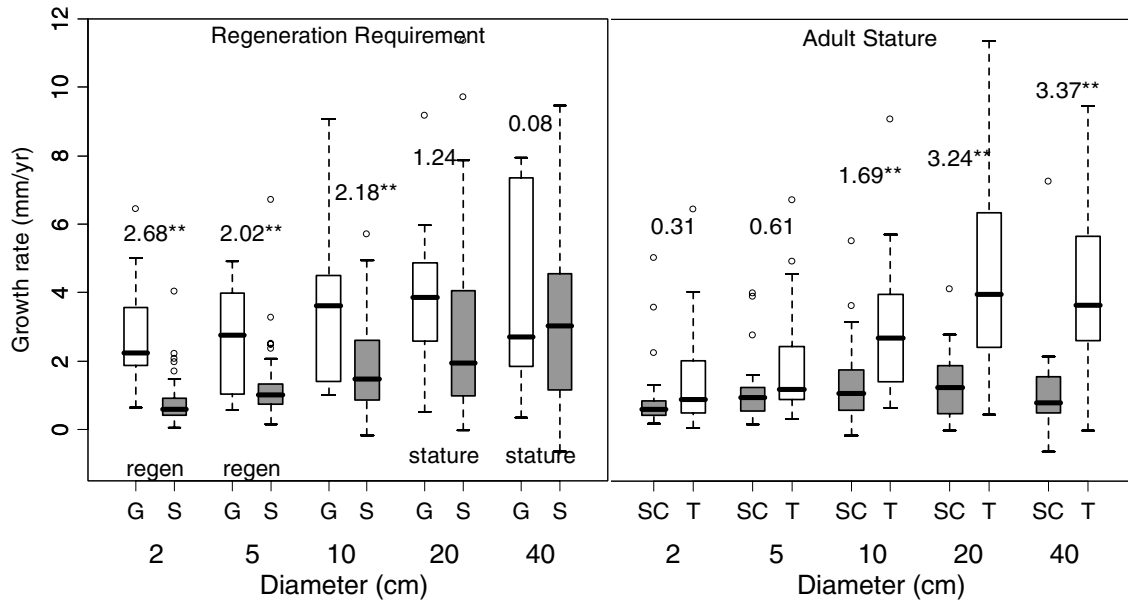


Figure 2. Continued

Regeneration requirement affected crown size mainly through crown depth and only at large diameters. There were no differences in the slopes and intercepts of the overall diameter-crown depth and diameter-crown radius relationships (Figure 1), but crown depth was significantly different between gap and shade species at some individual diameters. At 10 cm dbh and above, gap species had significantly shallower crowns than shade species by about 25% of the average crown depth (Table 2, Figure 2). There was also a weak, but not statistically significant, difference in crown radius, with shade species being wider than gap species at 20–40 cm dbh by 14–20% (Table 2, Figure 2). Overall, crown volume was greater for shade species by an average of 45–70% at 20 cm dbh and higher (Table 2).

Between 2 and 20 cm dbh, absolute diameter growth rate varied among species with different regeneration requirements, with differences decreasing at larger diameters (Figure 2). At 2 cm dbh, the mean growth rate of gap species was three times greater than shade species, but the difference declined steeply. At 20 cm dbh, gap species had growth rates 37% greater than shade species and at 40 cm dbh, there was no difference.

The height of the surrounding canopy was significantly different throughout ontogeny for gap and shade species. From 2–10 cm dbh, gap species occurred at a significantly greater proportion of sites with low surrounding canopies (< 10 m height) than shade species (Table 3).

Adult stature

Differences in height, crown size and growth rate associated with adult stature occurred concurrently from

10–40 cm dbh with little or no effect at smaller sizes (Figure 2). The differences between tall and subcanopy species in diameter growth rate and height increased with diameter, but the differences in crown size remained proportionally constant at all diameters. Crown depth and crown radius were 15–20% greater in subcanopy versus tall species (Table 2). Tall species had a significantly steeper slope in the height-diameter relationship than subcanopy species (Figure 1), indicating tall species had increasingly greater height than subcanopy species. At individual diameter classes, species of different adult stature had significantly different tree heights starting at 10 cm dbh (Figure 2). From 10–20 cm dbh, there was a 10–15% difference in height between tall and treelet species (Table 2). Significant differences between tall and mid-sized species only occurred at diameters of 40 cm and above. There were no significant differences in tree height at any diameter between mid-sized and treelet species.

Crown dimensions were significantly different between tall and subcanopy species at a wide range of diameters. At individual diameter classes, subcanopy species had significantly wider and deeper crowns than tall species by 15–25%, starting at 10 cm dbh (Table 2, Figure 2). Crown volume of subcanopy species was greater by 50% on average than tall species from 10–40 cm dbh (Table 2). As with tree height, differences between tall and subcanopy trees in terms of crown size were driven by differences between tall and treelet species at diameters of 10–20 cm, and tall and mid-sized species at diameters of 20–40 cm. There were no significant differences between mid-sized and treelet species at any diameter. Despite the differences at individual diameters, neither the slope nor the intercept in the diameter-crown

Table 3. Maximum heights of the surrounding canopy for trees of different diameters and functional groups. Heights are expressed as a percentage, in each 10-m height category, of all trees for a given diameter and functional group. Distributions were calculated for each species, then averaged over all species in each functional group. Asterisks represent canopy height categories with significant differences between functional groups (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$).

Diameter of target tree (cm)	Surrounding canopy height (m)	Regeneration requirement			Adult stature		
		Gap	Shade	Difference	Tall	Subcanopy	Difference
2	0–10	20	10	– 10***	12	11	– 2
	10–20	29	24	– 5*	24	25	1
	20–30	33	36	2	35	36	1
	> 30	19	31	12***	29	30	1
5	0–10	17	9	– 7***	11	10	0
	10–20	31	26	– 5	26	27	0
	20–30	39	36	– 2	37	36	– 1
	> 30	14	29	15***	26	27	1
10	0–10	17	10	– 8***	11	11	0
	10–20	26	26	0	26	26	0
	20–30	41	38	– 3	39	36	– 3
	> 30	16	27	11***	23	27	4

depth and diameter-crown radius relationships were statistically different (Figure 1). The difference in the slope in the diameter-crown radius relationship was nearly significant, indicating that subcanopy species had a faster rate of increase in crown radius through ontogeny than tall species.

Diameter growth rate varied significantly among species of different adult statures only at larger diameters from 10–40 cm dbh (Figure 2). At these diameters, the mean diameter growth rate of tall species was 70–100% greater than that of subcanopy species (Figure 2). Tall and mid-sized species varied significantly from 20 to 40 cm, whereas tall and treelet species were significantly different from 10 to 20 cm dbh. The growth rates of mid-sized and treelet species did not differ significantly at any diameter.

The height of the surrounding canopy did not differ among species of different adult statures (Table 3). From 2 to 10 cm dbh, tall, mid-sized and treelet species had the same proportion of trees in each surrounding height category.

There did not appear to be a significant interaction between the stature and regeneration in terms of their relationship with allometry, although this was difficult to evaluate because the species were not evenly distributed among the different variables (Table 1). There were no significant interaction terms between adult stature and regeneration requirement in the analysis of variance for any of the allometry variables. When just tall species were compared, gap and shade species showed significant differences in diameter-height and diameter-crown depth relationships as well as growth rate throughout ontogeny. When just shade-tolerant species were compared, tall and subcanopy species showed significant differences in all allometric relationship as well as growth rates.

Figure 3 summarizes the allometry, growth rates and surrounding canopy heights through ontogeny for different combinations of regeneration requirement and adult stature. Overall, regeneration requirement and adult stature explained a substantial portion of the variance in tree height, crown radius or crown depth among species (Table 4). These functional groups explained 25–35% of the variation in tree height, crown depth, or crown radius (Table 4).

Other allometric relationships

Among species, there was no relationship between tree height and crown depth or tree height and crown radius within any diameter class, except a negative relationship between tree height and crown radius at 40 cm dbh (Table 5). There was no relationship between growth rate and either tree height, crown depth or crown radius at any individual diameter class. Crown radius and crown depth were strongly positively correlated among species within all diameter classes, such that species with a larger crown radius also tended to have a larger crown depth (Table 5). As a result, where crown size differences occurred between different functional groups, crown volume differences were much greater than either crown depth or crown radius differences (Table 2).

DISCUSSION

Regeneration requirement

This study supported that the functional group identity of a species can indicate its allometric trajectory through

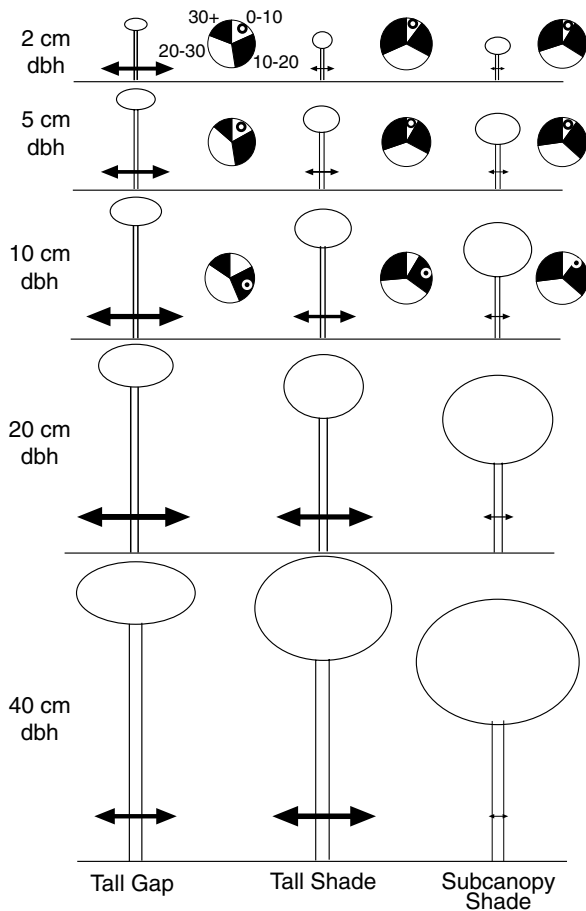


Figure 3. Tree allometry, diameter growth rates and height of surrounding canopy for species of different functional groups through ontogeny. Tree height, crown depth and crown radius of the tree diagrams are proportional to predicted allometry for each functional group at the five diameters. The size of the arrows on the trunks is proportional to absolute diameter growth rates. The pie charts give the proportion of trees at the given diameter growing with a surrounding maximum canopy of 0–10 m, 10–20 m, 20–30 m, and 30+ m height. The bull's-eye within the pie chart represents the predicted mean tree height for the functional group at the given diameter and shows in which canopy height class the predicted height falls. Blocks of the pie chart clockwise from the bull's-eye represent the percentage of trees where the surrounding canopy is taller than the target tree.

a wide range of size classes. For species of different regeneration requirements, differences in height versus crown size occurred in separate size classes. At small diameters, when gap species occurred in a greater proportion of high-light microsites than shade species, gap species were taller with higher growth rates than shade species, although crown sizes did not differ. Above 10 cm diameter, however, all size dimensions of gap species started to decline relative to shade species. The height advantage of gap species over shade species declined rapidly from 2 to 10 cm until there was no statistical difference in height between gap and shade species at

20 cm dbh. After 80 cm dbh, gap species actually tended to be slightly shorter at the same diameter than shade species (S. Bohlman, unpubl. data). Crown size, especially crown depth, was less for gap species by up to 25% starting at 10 cm dbh. At 50 cm and above, the mean growth rate of all gap species on the BCI plot was actually less than all the shade species combined, although the difference was not statistically significant (S. Lao, pers. comm.).

The nearly concurrent decline in the growth rate and size of gap species relative to shade species after 10 cm dbh may be caused by several factors. First, the difference in light availability between gap and shade species decreases through ontogeny (Valverde & Silvertown 1997, van der Meer *et al.* 1998). Increasingly stout stems, lower diameter growth rates, and smaller crowns of gap species through ontogeny may be important to avoid breakage or treefall as the trees get larger. Indeed, the mortality rate of gap species drops at larger size classes (Condit *et al.* 1995). In general, gap species may have greater production of sun foliage than shade foliage and thus be physiologically limited in generating the layers of shade foliage that create a deep crown (Ellsworth & Reich 1996, Strauss-Debenedetti & Bazzaz 1996). Gap species may allocate carbon to reproduction over growth earlier in ontogeny than shade species (Davies & Ashton 1999). Finally, there may be an interaction between allometric trajectories and plant defence for gap and shade species. In general, gap species allocate fewer resources to plant defence (Coley & Barone 1996). This may accommodate greater height and diameter growth at small diameters, but may have the long-term consequence of increased herbivory and pathogen damage through time, leading to decreased growth and size dimensions.

Adult stature

For species of contrasting adult statures, differences in size and growth began early in ontogeny and increased as the trees grew larger. Small differences early in ontogeny may reflect the fact that tall species and most of the subcanopy species are pre-reproductive below 5 cm dbh and have a similar strategy of allocating to height growth at this stage. However, even a small height advantage in the shaded understorey can provide an increase in light levels that, although small in absolute terms, can be significant to carbon uptake (Montgomery & Chazdon 2001, 2002; Mulkey *et al.* 1993, Oberbauer *et al.* 1993). The investment in height growth then may be a positive feedback as height growth increases access to light, and higher light allows greater height and diameter growth, leading to increasing differentiation in height between species of different adult statures. Limited height growth for smaller-statured species may also reflect the strategy of subcanopy species to persist in shaded conditions through

Table 4. Coefficients of determination (r^2 values) for the relationship between characteristics of species at individual diameter classes and both the colonizing index and maximum height (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$). Colonizing index, which is the per cent mortality for trees ≤ 4 cm dbh at low-canopy sites (less than 10 m in height) is a measure of regeneration requirement. Maximum height is a measure of adult stature.

	Diameter class (cm)				
	2	5	10	20	40
Colonizing index					
Tree height	0.31***	0.29***	0.16**	0.01	-0.03
Crown depth	-0.01	0.07*	0.17**	0.20***	0.28**
Crown radius	-0.02	-0.01	0.00	0.01	0.06
Diameter growth rate	0.41***	0.42***	0.35***	0.19***	0.01
% low canopy site	0.56***	0.54***	0.30***		
Maximum height (m)					
Tree height	0.14***	0.26***	0.32***	0.29***	0.33***
Crown depth	0.00	-0.17***	-0.35***	-0.31***	-0.15*
Crown radius	-0.08*	-0.16***	-0.21***	-0.27***	-0.10*
Diameter growth rate	0.00	0.01	0.07*	0.23***	0.23***
% low canopy site	0.00	-0.01	-0.02		

Table 5. Coefficient of determination (r^2 values) for the relationship between pairs of allometric variables and diameter growth rate at individual diameter classes (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$).

Variable 1	Variable 2	Diameter (cm) class				
		2	5	10	20	40
Crown radius	Crown depth	0.02	0.15***	0.22***	0.23***	0.22***
Tree height	Crown depth	0.00	0.02	0.08*	-0.01	-0.03
Tree height	Crown radius	-0.01	0.02	0.05	0.07*	0.00
Tree height	Diameter growth rate	0.15***	0.05*	0.07*	0.04	0.17***
Crown depth	Diameter growth rate	-0.02	0.05	0.10*	0.18***	-0.03
Crown radius	Diameter growth rate	-0.02	-0.02	-0.02	-0.01	-0.03

investing in lateral crown development rather than height growth.

Crown size showed a constant proportional difference between tall and subcanopy species of 20–25% through ontogeny. The larger crown size of subcanopy species versus tall species when both functional groups are small and living in a shaded understorey should lead to subcanopy species having higher net carbon gain than tall species. If so, increased resources could be detected through increased diameter growth, greater survival and/or reproduction. Diameter growth rates of subcanopy species were not greater than tall species early in ontogeny, but survival was greater for subcanopy species compared to tall species from 1 to 30 cm dbh (S. Lao, pers. comm.). Stout stems may allow subcanopy species to withstand a high rate of damage or mortality from falling debris in the understorey (Clark & Clark 1991, Koestel & Rankin-de Merona 1998, Paciorek *et al.* 2000). Increased carbon uptake may also be allocated to earlier reproduction for small-statured species, which occurs in Malaysian forests (Thomas 1996b) but not necessarily on BCI (Wright *et al.* 2005).

Comparison with other studies – gap preference

The lack of a standard measure of a species' regeneration requirement makes it difficult to compare the effects of regeneration requirement on allometry among studies. Both categorical and continuous variables have been used to define a species' regeneration requirement or gap preference, although categorical variables are more commonly used because what we perceive as gap and shade species results from a suite of interrelated life history characteristics, rather than a single quantifiable variable. Also, differences in light availability may be measured at different stages of ontogeny, not just for early stages of ontogeny. Therefore, the term 'gap preference' will be used in comparing these studies because it can refer to light preferences at any stage of ontogeny rather than the term 'regeneration requirement', used throughout this paper.

Surprisingly, analysis of data presented in several of these studies showed no relationship between height-diameter allometry and gap preference at small diameters (Aiba & Kohyama 1997, King 1996, Sterck & Bongers

1998, except Claussen & Maycock 1995). This contrasts to our study where we found strong and significant differences in the relationship between diameter and height, with gap species being taller at diameters less than 10 cm. At larger diameters (10–20 cm dbh), both Aiba & Kohyama (1997) and Poorter *et al.* (2003) found that species with a greater crown position index, and thus greater light availability, were taller. In this study, we found greater height for gap species at 10 cm but not by 20 cm dbh. Similarly, there were conflicting results about the relationship between gap preference and crown size. This study and Aiba & Kohyama (1997) found that gap species have a smaller crown size than shade species through much of ontogeny, but Poorter *et al.* (2003) found no relationship and King (1996) and Sterck & Bongers (1998) actually found the opposite result.

The fact that neither height nor crown size had a consistent relationship with gap preference suggests that there is not a height versus crown size trade-off for gap versus shade species. However, the conflicting observations may also be a result of the inconsistent definition and insufficient quantification of regeneration requirement and light demand. Also, Claussen & Maycock (1995) and Sterck & Bongers (1998) included fewer than five species in their analysis. The results in this study show that despite community-level trends, there is wide variation in allometry among functional groups, such that choosing only a couple of species from each functional group might not demonstrate the community-level trends.

Comparison with other studies – adult stature

The relationship between adult stature and allometry was more consistent among studies. Aiba & Kohyama (1997), King (1990, 1996), Kohyama *et al.* (2003) and Thomas (1996a) observed that tall species begin growing taller and more slender than subcanopy trees early in ontogeny, starting at around 5 cm dbh. Only two studies (Alves & Santos 2002, Davies *et al.* 1998), both of which included a small number of species, recorded the opposite result. Aiba & Kohyama (1997) and Kohyama *et al.* (2003) also found that diameter growth rate was greater for tall species starting at 12 cm dbh. The majority of studies also reported an effect of adult stature on crown size. King (1990, 1996), Kohyama *et al.* (2003), Poorter *et al.* (2003), Sterck & Bongers (1998) and Sterck *et al.* (2001) found that at the same diameter, the crowns of short species were wider and/or deeper than tall species and the difference began early in ontogeny. Again there were a few exceptions (Aiba & Kohyama 1997, Alves & Santos 2002).

Compared to gap preference, adult stature had consistent results that show a clear trade-off between

investment in height and crown size. The results may be more consistent because adult stature is more easily quantified. Also, by definition, species of different adult statures have different sizes as mature trees. Small species could, in principle, follow the same allometric trajectories as large species, but simply die or stop growing at a certain size. But it is more likely that some difference in diameter-height relationship contributes to the differences in adult size, which defines these functional groups. Furthermore, the steep vertical light gradient that drives the trade-off between height and crown size in tall versus subcanopy species occurs in most broadleaf, closed forests (Parker 1995, Parker *et al.* 2001). The variation in horizontal light environment that determines gap versus shade environments is much more variable spatially and temporally (S. Bohlman, unpubl. data) so that even consistent and quantitative definitions of gap preference may show a weaker relationship with allometry than adult stature.

Effect of allometric differences on stand structure

The differences in allometry between gap and shade species should translate into predictable spatial variation in canopy structure of a forest stand. Clearly, new gaps have different spatial structure than surrounding tall forest. But, size differences continue between gap and shade species through ontogeny (Figure 3) such that even as old gaps grow to the same height as the surrounding forest, structural differences will persist. As adults, gap species had shallower and somewhat narrower crowns, which may lead to increased light transmission to, and high growth rates for, the midstorey and understorey levels of the old gap versus surrounding forest. In some temperate broadleaf and conifer forests, light transmission was lowest for more shade-tolerant species (Canham *et al.* 1994, 1999), which also appears to be the case for tropical tree species on Barro Colorado Island (H. Muller-Landau, pers. comm).

In the shade portions of the forest, the allometric differences between gap versus shade species still come into play. While gap and shade species established at different sites to some degree, it is important to note that only 18% of individuals with < 5 cm dbh belonging to gap species occurred in low-canopy sites (Table 3). The rest were found at shaded, high-canopy sites, as were most of the small trees of the shade species. For gap and shade species occurring at the same sites, the greater investment in height growth by gap species may give them more access to light, but at the expense of lower investment in canopy development. Their more slender stems and lower wood density may contribute to their relatively low survival rate in both high- and low-canopy sites early in ontogeny (Condit *et al.* 1995, Welden *et al.* 1991).

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