

## DIAMETER, HEIGHT, CROWN, AND AGE RELATIONSHIPS IN EIGHT NEOTROPICAL TREE SPECIES<sup>1</sup>

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**Abstract.** Diameter, height, crown shape, and crown area were measured on 23–42 trees ranging in size from saplings to large adults for each of eight common dicotyledonous tree species in a neotropical forest on Barro Colorado Island, Panama. Six species were canopy trees, one species was an emergent tree, and the remaining species was an understory tree. Crown areas and shapes were quantified by eight radii measured every 45° from the trunk to the vertically projected edge of the crown. Crown areas were calculated from the areas of circles with the average radius; crown shapes were measured by the coefficients of variation of the eight crown radii. Age-diameter relationships were estimated from diameter growth increments over an 8-yr period.

Observed height–diameter relationships were compared to expectations based on the theories of elastic similarity, constant stress, and geometric similarity. Slopes of log-transformed height–diameter relationships differed from the theoretically expected value of 2/3 for elastic similarity in three of eight species; two canopy species had higher slopes, but not as high as the expected value of 1.0 for geometric similarity; one canopy species was shorter, but the slope was greater than the slope of 0.5 predicted by the constant stress theory. The theory of elastic similarity also predicts that canopy mass to trunk mass ratio should remain constant during tree growth. Observed ratios based on proxy variables for the masses were constant in six of eight species—the two deviant species had heavier crowns in large trees than expected from their diameters. Crown shapes were much more variable in some species than others. The understory species had much lower  $r^2$  values for height–diameter and crown–diameter relationships, suggesting that these relationships may be more variable in trees that live in the less windy understory than in trees that reach the canopy.

The allometric relationships for the species in this study were not unique for each species, suggesting that it may be possible to model the allometric relationships of many species with fewer equations than species. If the primary adaptive forces acting on tree species in a diverse forest are their physical environment and the sum of competitive interactions with an ever-changing mix of neighbors, then different species may have similar resource allocation patterns. Thus, using the age-size relationships, we found three groups of species among the seven canopy species. Two groups had three species each and one species (*Ocotea whitei*) was in a group by itself. The understory species, *Faramaea occidentalis*, was also in a group by itself.

**Key words:** allometry; Barro Colorado Island; crown area; diameter at breast height; guilds; height; neotropical trees; Panama; structure.

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## INTRODUCTION

Arborescent terrestrial plants allocate carbon to stems to support their photosynthetic tissues and elevate their leaves above competitors and into the sunlight. In closed-canopy forests, plants compete for light with neighboring plants and who wins or loses is determined largely by who shades whom. This in turn depends on relative height and crown growth rates as a function of light intensity (Woods and Whittaker 1981, Tilman 1988). Therefore, to understand the structure and dynamics of forests and the competitive interactions among the tree species in them, one needs to understand the relationships among bole diameter, tree height, and crown area through ontogeny for each tree species (Shugart et al. 1981).

There is a cost assessed against growth rate whenever resources are allocated to nonphotosynthetic vs. photosynthetic tissues (Givnish 1982, 1984, Lawton 1984). Other things equal, in the race to the canopy, trees that allocate fewer resources to supporting stems and trunks per unit of height growth should grow faster than trees that allocate more (King 1981, Lawton 1984, Tilman 1988). The trade-off is in survival: self-supporting plants that allocate too little to stems may buckle under their own mass or break due to wind stress or other loads such as snow (King and Loucks 1978) or epiphytes (Putz 1983, Putz et al. 1983). According to Schniewind (1962), the ability to resist breakage from wind loads is a primary factor in tree survival. Mechanical constraints set lower limits to allocation to trunks for a given height achieved in self-supporting plants. McMahon (1973), advancing an earlier model of Greenhill (1881), investigated the theoretical buckling strength of tree trunks modeled as self-supporting, tapering columns. He argued that if trees are just thick enough to prevent buckling, then basal trunk diameter should scale as the  $3/2$  power of height, or alternatively, that height should scale as the  $2/3$  power of trunk diameter. If the scaling exponent ( $\beta$ ) between diameter and height is equal to 0.67 then the tree is said to maintain elastic similarity through ontogeny (Rich 1986, Rich et al. 1986; K. J. Niklas, *unpublished manuscript*). McMahon (1973) and McMahon and Kronauer (1976) also found that trees are generally about one-quarter of their predicted buckling height, thus most trees are over-built (see also Niklas 1992). Two alternative models of tree growth are geometric similarity (Rich 1986, Rich et al. 1986) and constant stress (Dean and Long 1986, Niklas 1992, *unpublished manuscript*). According to the geometric similarity model  $\beta$  should equal 1.0; this model is based on the proportions of the tree remaining constant through ontogeny. In the constant stress model,  $\beta = 0.5$ ; the model is based on the assumption that the trunks taper such that stress produced by wind pressure along the stem is equalized (Dean and Long 1986, K. J. Niklas, *unpublished manu-*

*script*). Niklas (1992) reports that the constant stress model is the most generally applicable model, assuming that the local environment is sufficiently windy. Norberg (1988) found that small growth forms, from mosses to small trees were described by geometric similarity, while the allometry of large arborescent growth forms was better described by elastic similarity.

McMahon and Kronauer (1976) and King and Loucks (1978) developed the elastic similarity model further to consider the support of branched tree crowns in forest-grown trees, and in particular the ratio of crown mass to trunk mass,  $R$ . Trees growing in closed-canopy forest tend to have smaller crowns concentrated at the top of the trunk, and are simpler structures to model than are open-grown trees. The earlier versions of the model did not include the mass of the crown and thus overestimated the potential height of the trees (see Niklas 1992 and Holbrook and Putz 1989). King and Loucks (1978) took  $R$  into account in their calculation of the minimum diameter,  $d_{\min}$ , that a tree could reach without buckling:

$$d_{\min} = 2\{w/CE\}^{1/2}h^{3/2}, \quad (1)$$

where  $w$  is wood density (mass/unit volume),  $h$  is total tree height,  $E$  is Young's modulus of elasticity for wood of the given species, and  $C$  is a constant of proportionality dependent on trunk taper and the ratio of crown mass to trunk mass (King 1981). King (1981) assumed that the rate of height growth would be jointly constrained by allocation to wood production and by shifts in allocation between crown and trunk. He showed that if trees retain a similar shape, i.e., exhibit a constant  $R$  (ratio of crown mass,  $W_c$ , to trunk mass,  $W_t$ ), then the maximum height growth rate should occur at an  $R$  of  $\approx 0.17$ . Thus, assuming forest-grown trees have been constrained by selection to maximize height growth subject to mechanical constraints of supporting their crown, then such trees should achieve the fastest extension growth when their crowns weigh approximately one-sixth as much as their trunks.

The value of  $R = 0.17$  was derived under simplifying assumptions that: (1) wood density and elasticity are uniform; (2) the crown is borne in the top 10% of the bole (i.e., forest-grown trees); (3) growth rate of above-ground biomass is proportional to crown area (photosynthetic area); (4) the crown mass is proportional to the square of crown area; and (5) that self-pruning of shaded branches occurs. Assumption (4), that crown mass is proportional to the square of crown area (area of the vertical projection of the tree crown on a horizontal plane), was tested by King and Loucks (1978) in a self-thinning stand of aspen. They obtained the fitted relationship,  $W_c = A_c^{1.7}$ , which did not differ significantly from the expected relationship,  $W_c = A_c^2$ , where  $W_c$  is the mass of the crown, and  $A_c$  is crown area.

In this paper, we report on the diameter-height re-

TABLE 1. Taxon, growth form, and age–height relationship in the eight study species on Barro Colorado Island, Panama. Canopy and emergent trees were defined as species whose average adult height is >20 m, the adult height of understory species were defined as 4–10 m (Hubbell and Foster 1990). Total abundance is the abundance of all stems  $\geq 1$  cm dbh in the given species in the first census of the 50-ha plot (1980–1982). Estimated ages were calculated as described in *Methods and data analysis*.

Species	Family	Growth form	Total abundance	Sam-ple size	Modulus of elasticity*	Estimated age (yr) at given height			
						5 m	10 m	20 m	30 m
<i>Alseis blackiana</i>	Rubiaceae	Canopy	7587	30	41 022	31	71	144	195
<i>Beilschmiedia pendula</i>	Lauraceae	Canopy	2387	34	121 884	28	67	122	152
<i>Fareamea occidentalis</i>	Rubiaceae	Understory	23 465	23	NA	26	70	194	...
<i>Ocotea whitei</i>	Lauraceae	Canopy	1149	39	NA	11	29	66	88
<i>Prioria copaifera</i>	Leguminosae	Emergent	1357	38	NA	17	44	130	150
<i>Quararibea asterolepis</i>	Bombacaceae	Canopy	2402	42	103 383	26	68	133	169
<i>Tetragastris panamensis</i>	Burseraceae	Canopy	3233	40	158 683	21	55	141	195
<i>Trichilia tuberculata</i>	Meliaceae	Canopy	12 942	42	81 580	34	84	161	205

\* Data from Putz (1984) in kg/cm<sup>2</sup>, NA = not available.

relationships and diameter–crown area relationships in eight neotropical tree species growing in a closed-canopy forest. We also estimate the size–age relationships of these tree species based on size-specific diameter increments over an 8-yr period (S. P. Hubbell et al., unpublished data). The main questions posed are: (1) What model of tree allometry, elastic, geometric, or constant stress, do the species follow? (2) Is  $R$ , the ratio of “crown mass” to “trunk mass,” constant through ontogeny from saplings to large canopy adults? (3) Finally, do the growth and allocation patterns among the species cluster into a reduced number of life history guilds of similar species?

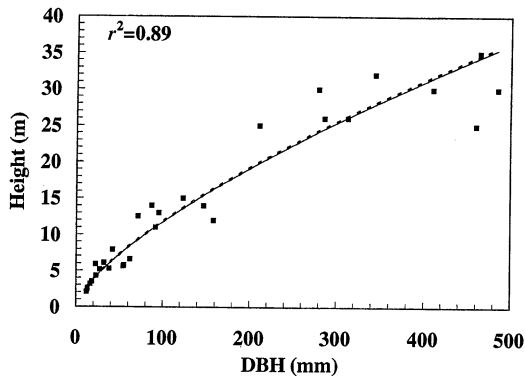
The data for this study were collected nondestructively by measuring living trees and saplings. Consequently, we do not have mass data for crowns and trunks, and we have only limited data on wood densities and values of  $E$ , Young's modulus (Table 1). With simple field measurements of tree dimensions, we can determine the scaling exponent ( $\beta$ ) for diameter–height relationship in each species and whether the assumption of a developmentally constant ratio of allocation to trunk vs. crown biomass is correct. In Eq. 1, the specific wood density and Young's modulus of the given tree species are assumed constant through ontogeny. In the case of parameter  $C$ , constancy depends on  $R$  having a fixed value (King 1981). If the value of  $R$  changes during tree growth, Eq. 1 may still be valid, but  $C$  will no longer be a constant and the allometric relationship between diameter and height may change. de Castro et al. (1993), Putz (1984), Rueda and Wil-

liamson (1992), and Wiemann and Williamson (1989) provide examples of species in which wood specific densities are not constant. Variable wood density is found particularly strongly in fast growing pioneer species (Whitmore 1973, Wiemann and Williamson 1988, 1989). None of the species in this study is a pioneer.

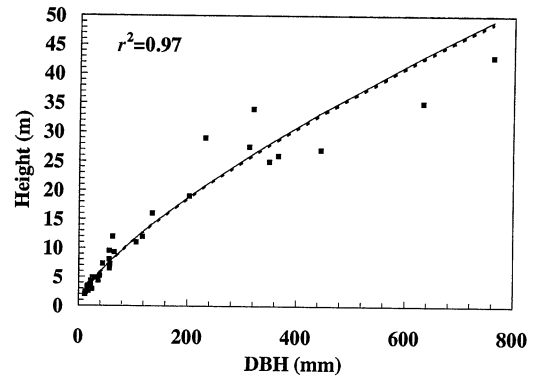
These questions about tree dimensions have been asked about eight species in a well-known tropical forest, the old-growth forest on Barro Colorado Island (BCI), Panama, as part of an ongoing study of the dynamics of the BCI forest. The principal organizing question for this long-term project has been to explain the maintenance of the >300 species of trees and shrubs in the forest. One potential explanation for species richness lies in niche differentiation among species in the patterns of growth and allocation to trunks and crowns, and how these allocation patterns dictate and respond to competition for light. The importance of growth and allocation to understanding forest dynamics and competitive interactions among trees has led to many studies in tropical forests that consider the correlation between bole diameter and plant height, crown size, tree age, biomass, and leaf area index. These studies (Davis and Richards 1933, Heinsdijk 1957, 1958, Dawkins 1963, Shinozaki et al. 1964, Kira and Shidei 1967, Ovington and Olson 1970, Perez 1970, Misra et al. 1974, Kira 1976, Rich 1986, Rich et al. 1986, Yamakura et al. 1986, Brown et al. 1989, Scatena et al. 1993, O'Brien 1994) found strong correlations both within and across species, suggesting that many species have similar allocation patterns. Many of these studies

FIG. 1.  $\log_{10}$ height— $\log_{10}$ diameter regressions for the eight study species and their  $r^2$  values. The data are shown on a linear scale with the transformed best fit line calculated from the logarithmically transformed data. This presentation of the data highlights the relative increase in stem diameter compared to height at large diameters compared to small diameters. The thin solid line shows the least squares best fit line, the heavy dashed line gives the bias-corrected best fit line. The squares are the measured data. The corresponding regression statistics are given in Table 2. The effect of the inherent negative bias of back-transformed predictions can be seen most clearly in *Fareamea occidentalis*—the least squares prediction underestimates the heights of the taller trees. In general, however, the correction for the bias in the diameter–height regressions was generally unimportant (see Table 3).

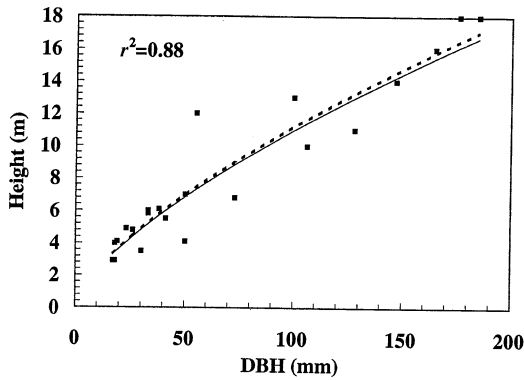
*Alseis blackiana*



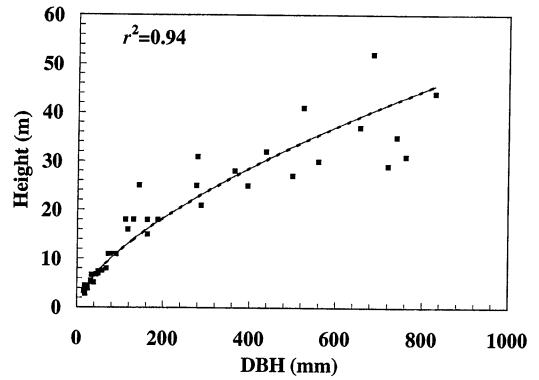
*Beilschmiedia pendula*



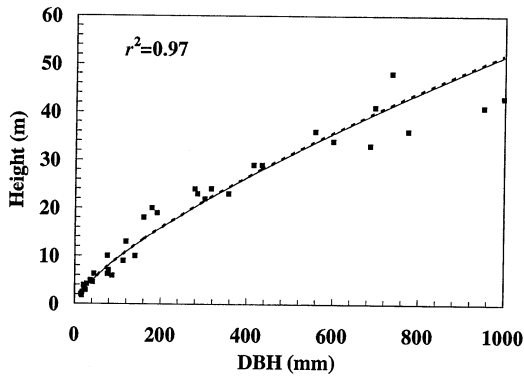
*Faramea occidentalis*



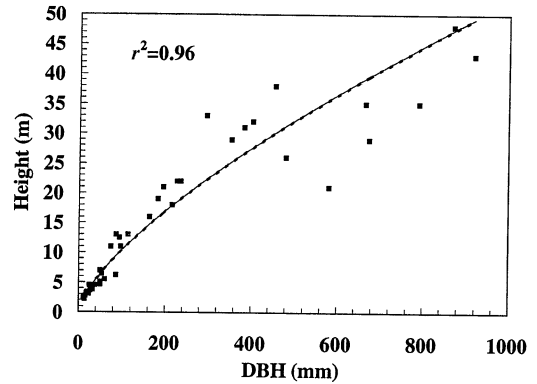
*Ocotea whitei*



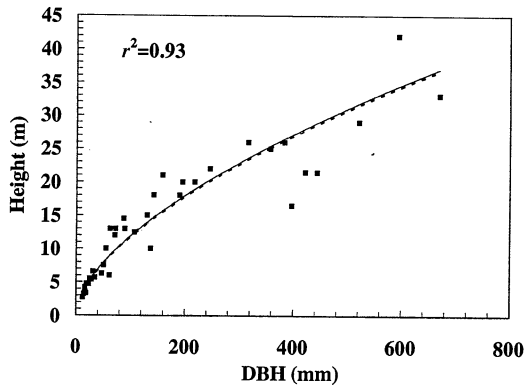
*Prioria copaifera*



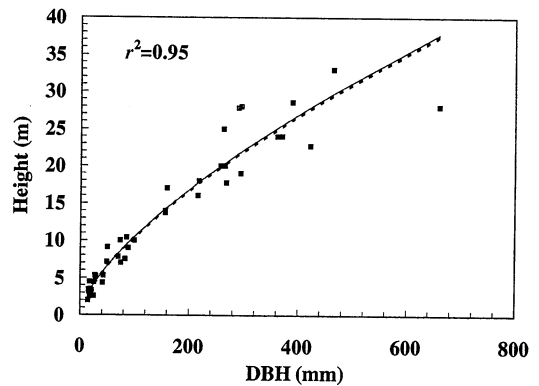
*Quararibea asterolepis*



*Tetragastris panamensis*



*Trichilia tuberculata*



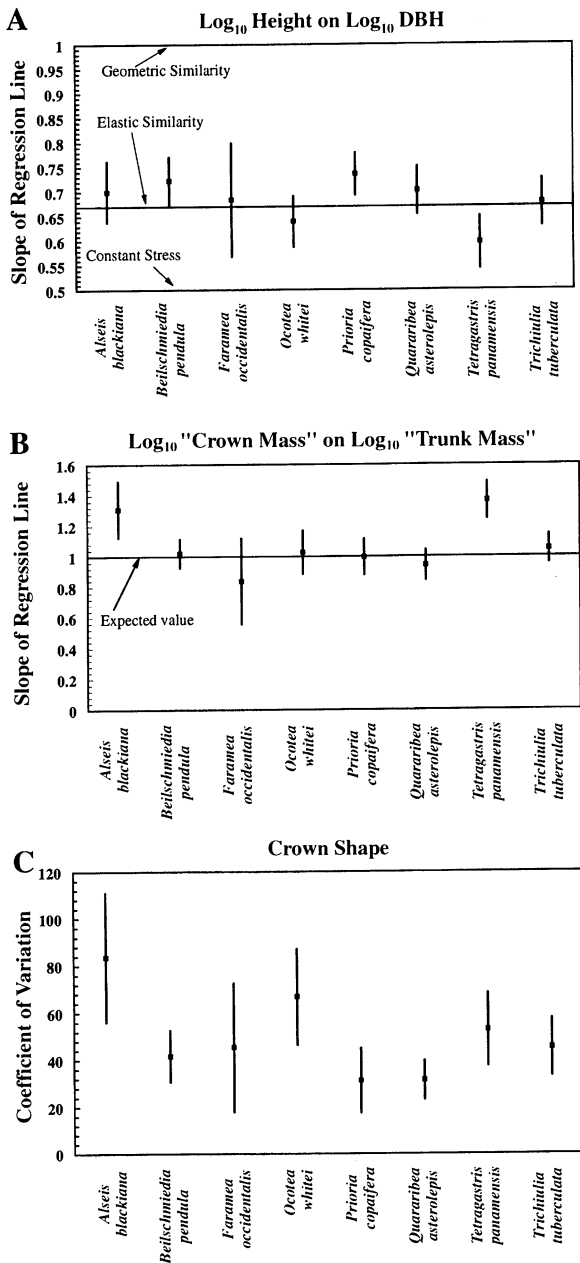


FIG. 2. (A) The mean and 95% confidence intervals on the slopes of the regressions of  $\log_{10}$  height on  $\log_{10}$  diameter for the eight study species. The expected values of  $\beta$  (0.5, 0.67 and 1.0) for the three models of tree structure are indicated in the figure. Although three species confidence intervals do not overlap the expected value for elastic similarity, their values are much closer to the expected value for elastic similarity than to the expected values for geometric similarity or the constant stress models. (B) The mean and 95% confidence limits on the slopes of the regressions of  $\log_{10}$  crown mass [proxy variable: (crown area)<sup>2</sup>] on  $\log_{10}$  trunk mass [proxy variable: (dbh<sup>2</sup>)h] for the eight study species. The confidence intervals for two species, *Alseis blackiana* and *Tetragastris panamensis*, did not overlap the expected value of 1.0; both species had "heavier" crowns than expected. (C) The mean and coefficients of variation of square-root transformed crown radii, and their 95% confidence limits for the eight study species. The corresponding statistics are given in Table 5.

(Heinsdijk 1957, 1958, Ovington and Olson 1970, Perez 1970, Kira and Shidei 1967, Yamakura et al. 1986, Brown et al. 1989, Scatena et al. 1993) lump many species together, making the tacit assumption that the species have the same allocation patterns.

The eight species used in this investigation are among the most common species in the BCI forest, and consequently they are expected to play a large role in structuring the tree community (Hubbell and Foster 1990). If significant differences in allocation patterns are found, then these differences should be examined in greater detail to assess the potential role of allocation patterns in maintaining tree diversity in the BCI forest. If, on the other hand, these species show little evidence of differentiation in allocation patterns, explanations for coexistence should be sought elsewhere. It may well be, for example, that there are broad ecological guilds of species with similar allocation patterns and similar functional relationships between height, diameter, and crown area. It would be useful if measuring a small sample of trees in a forest were sufficient to construct general predictive equations relating diameter at breast height (dbh) to height and crown area for more than one species. Ideally it would then only be necessary to measure a subset of species carefully and accurately. From these measurements, a reduced number of general equations relating dbh to tree height and crown area could be computed, eliminating the necessity to measure each species and every tree. For example, perhaps a small number of equations will suffice for mature-phase, canopy tree species whereas understory trees may require a separate set of equations.

METHODS AND DATA ANALYSIS

The trees measured in this study were located in a 50-ha forest permanent plot established in 1980 on Barro Colorado Island, Panama (Hubbell and Foster 1983). The forest on BCI is a semideciduous moist tropical forest (Leigh et al. 1982, Hubbell and Foster 1983), which receives  $\approx 2600$  mm of rain every year (50-yr average [Rand and Rand 1982]). Wind speeds on BCI are generally highest in the dry season (late December to the end of April [Dietrich et al. 1982]) and range from  $\approx 5$  km/h to just over 9 km/h and are predominantly from the north. Wet-season wind speeds are generally lower, ranging from  $\approx 1$  km/h to 4.5 km/h; wind direction in the wet season is more variable than in the dry season (Windsor 1990). In 1982 all stems of free-standing woody plants  $> 1$  cm dbh (1.3 m) were identified in the 50-ha plot, measured for dbh and mapped. In 1985 (Hubbell and Foster 1990) and again in 1990 (Condit et al. 1992), the plot was recensused, all new plants  $\geq 1$  cm dbh were incorporated, preexisting plants were remeasured, and mortality was recorded.

From this data set, eight common species ( $> 20$  individuals per ha) were chosen for study, including one emergent species, six canopy species, and one understory species (Table 1) (Hubbell and Foster 1990). Very

TABLE 2. Regression of  $\log_{10}$  height in metres on  $\log_{10}$  diameter in millimetres for eight neotropical tree species from BCI including the 95% confidence limits are for the slopes of the regression equations and the  $r^2$ s. The ratio is the bias correction ratio described in *Methods and data analysis*, see also Fig. 1.

Species	Intercept	Slope	95% confidence limits for slope		$r^2$	Ratio
			Lower	Upper		
<i>Alseis blackiana</i>	-0.331	0.700	0.639	0.762	0.951	1.01
<i>Beilschmiedia pendula</i>	-0.392	0.723	0.674	0.771	0.966	0.99
<i>Faramea occidentalis</i>	-0.327	0.684	0.568	0.799	0.878	0.96
<i>Ocotea whitei</i>	-0.209	0.640	0.588	0.691	0.945	1.00
<i>Prioria copaifera</i>	-0.492	0.736	0.693	0.779	0.972	0.99
<i>Quararibea asterolepis</i>	-0.390	0.703	0.654	0.751	0.956	1.00
<i>Tetragastris panamensis</i>	-0.121	0.597	0.543	0.650	0.931	1.01
<i>Trichilia tuberculata</i>	-0.339	0.678	0.630	0.726	0.953	1.01

common species were chosen because they control much of the space in the forest, and therefore coexistence among these species must be explained. If tree dimensions and growth allocation patterns are an important axis of niche differentiation promoting coexistence, then such differentiation should be evident among these abundant species. *Trichilia tuberculata* (Meliaceae) and *Alseis blackiana* (Rubiaceae) were the two most abundant mature-phase, canopy tree species in the 50-ha plot and the understory tree *Faramea occidentalis* (Rubiaceae) was the most abundant species in its physiognomic class. Collectively, the eight species (Table 1) constituted more than one-fifth (22.5%) of all free-standing woody plants  $\geq 1$  cm dbh in the 50-ha plot.

Measurements on each species were performed over a range of diameters, from  $\approx 1$  cm dbh up to large adults. All trees were forest grown in a mixed-species, natural forest stand having  $\approx 4800$  stems per ha  $\geq 1$  cm dbh and  $\approx 410$  stems per ha  $\geq 10$  cm dbh (Hubbell and Foster 1990). Since we anticipated computing regressions of log height on log diameter, we selected approximately equal numbers of sample plants in a stratified random sample of each species by doubling diameter class (1–1.9 cm dbh, 2–3.9 cm dbh, etc.). Total height of each tree was measured using a clinometer and tape measure, except for plants less than  $\approx 3$  m tall, which were measured directly with measuring rods. Crown shape was estimated by measuring the

horizontal distance from the trunk to the vertical projection of the edge of the canopy in eight compass directions  $45^\circ$  apart starting with north. Crown area, the vertical projection of the crown on a horizontal plane beneath the tree, was calculated as a circle with a radius equal to the average of the eight radii (O'Brien 1994). To reduce the correlation between variance and the mean, we computed the coefficient of variation of the square root transformed radii for each tree (Sokal and Rohlf 1981).

Data analysis consisted of calculating least squares linear regressions for  $\log_{10}$  height in metres on  $\log_{10}$  dbh in millimetres, and  $\log_{10}$  crown area in square metres on  $\log_{10}$  dbh in millimetres, for each species. Since we were interested in predicting tree height and crown area from dbh, we chose to treat dbh as the independent variable in these regressions. To test for agreement with the three models of tree development, we computed the 95% confidence limits for the slopes in each species, and determined whether the limits bracketed the expected slopes when  $\log_{10}$  height was plotted against  $\log_{10}$  diameter. We indirectly tested for changes in  $R$ , by computing the ratio  $W_c$  to  $W_r$ . Given our nondestructive measurements, we assumed that  $W_r \propto (\text{dbh})^2 h$  and that  $W_c \propto A_c^2$  (King and Loucks 1978, King 1981), where  $h$  is total tree height and  $A_c$  is crown area. If  $R$  is constant, as expected by King (1981), then a regression of  $\log_{10} A_c^2$  on  $\log_{10} (\text{dbh})^2 h$  as proxy variables for crown mass and trunk mass, respectively, should have a slope

TABLE 3. Regression of  $\log_{10}$  crown area in square metres on  $\log_{10}$  diameter in millimetres, the 95% confidence limits for the slope, the  $r^2$ s for the regressions, and the bias correction ratio (described in *Methods and data analysis*).

Species	Intercept	Slope	95% confidence limits for slope		$r^2$	Ratio
			Lower	Upper		
<i>Alseis blackiana</i>	-2.941	1.755	1.920	2.019	0.869	1.12
<i>Beilschmiedia pendula</i>	-1.947	1.393	1.268	1.518	0.942	1.04
<i>Faramea occidentalis</i>	-1.422	1.133	0.757	1.509	0.652	1.27
<i>Ocotea whitei</i>	-1.991	1.346	1.149	1.542	0.839	1.05
<i>Prioria copaifera</i>	-1853	1.368	1.211	1.525	0.896	1.05
<i>Quararibea asterolepis</i>	-1.697	1.274	1.137	1.411	0.898	1.01
<i>Tetragastris panamensis</i>	-2.684	1.768	1.602	1.933	0.925	1.01
<i>Trichilia tuberculata</i>	-1.916	1.409	1.284	1.533	0.929	1.13

TABLE 4. Regression of crown mass (proxy variable:  $\log_{10}$  crown area in square metres) on trunk mass [proxy variable:  $\log_{10}(\text{diameter}^2 \text{ in square metres})(\text{height in metres})$ ] for eight neotropical tree species on Barro Colorado Island, the 95% confidence limits for the slopes and the  $r^2$ s for the regressions. The slopes for two of the eight species differed significantly from unity. Both species, *Alseis blackiana* and *Tetragastris panamensis*, had crowns that were significantly heavier than expected for their diameters.

Species	Intercept	Slope	95% confidence limits for slope		$r^2$	Ratio
			Lower	Upper		
<i>Alseis blackiana</i>	2.361	1.310	1.127	1.492	0.885	1.39
<i>Beilschmiedia pendula</i>	2.643	1.021	0.927	1.114	0.939	1.15
<i>Faramea occidentalis</i>	2.489	0.839	0.559	1.119	0.649	2.15
<i>Ocotea whitei</i>	2.355	1.027	0.886	1.169	0.854	1.14
<i>Prioria copaifera</i>	2.786	0.997	0.881	1.114	0.894	1.23
<i>Quararibea asterolepis</i>	2.631	0.943	0.844	1.043	0.902	1.12
<i>Tetragastris panamensis</i>	2.969	1.365	1.245	1.484	0.933	1.11
<i>Trichilia tuberculata</i>	2.834	1.050	0.957	1.143	0.928	1.45

not significantly different from unity. Unfortunately, we cannot test whether the value of  $R$  is  $\approx 0.17$  without additional data on wood densities and elastic moduli for all of the species. In all the regressions using  $\log_{10}$  transformed data we applied the bias correction method outlined in Snowdon (1991) to remove the inherent negative bias in back-transformed logarithmic regressions (Snowdon 1991, O'Brien 1994).

Data on growth rates for each tree species were derived from diameter-specific growth increments measured on individual plants over the census intervals, 1982–1985 and 1985–1990. Growth rates were calculated for doubling diameter classes, 1–1.9 cm dbh, 2–3.9 cm dbh, up to  $\geq 32$  cm dbh. Between the two census intervals, growth rates were autocorrelated, particularly in plants larger than the 1–1.9 cm dbh size class (Condit et al. 1995). Moreover, faster growing plants had higher survival rates, and the probability of mor-

tality decreased approximately exponentially with increasing diameter growth rate (S. P. Hubbell et al., unpublished data). The growth rates of plants which survived all 8 yr averaged  $\approx 1$  SD above mean growth rates of all plants of a given diameter class in either shorter census, regardless of species. Therefore, for present purposes, to project diameter as a function of age, we used growth rates that were 1 SD above the size-class mean, eliminating most slow-growing suppressed plants that were destined to die before reaching maturity. Ages for a given diameter were estimated by calculating the time required to grow through each doubling size class from the size class specific growth rates (S. P. Hubbell et al., unpublished data). Age was then correlated with height to estimate the length of time required by each species to reach the canopy of the forest, or adult stature in the case of the understory species.

## RESULTS

TABLE 5. Mean coefficient of variation in crown radii for eight neotropical tree species from Barro Colorado Island and the 95% confidence limits for variation in crown radii. The measure of crown shape was the coefficient of variation (CV) of the square-root transformed radii of the crown. Eight radii were measured for each tree at 45° intervals. The square-root transform was used to remove the correlation between the mean and the variance for trees of different sizes. Regressions of the CV on the square root of dbh had slopes not significantly different from zero, indicating that the transformation was successful at removing the correlation between the mean and variance for trees of different sizes ( $r^2$ s ranged from 0.001 to 0.226). The canopy tree, *Alseis blackiana*, had the most shape variation, while the emergent tree, *Prioria copaifera*, had the least.

Species	Mean CV of crown radii	95% confidence limits for slope	
		Lower	Upper
<i>Alseis blackiana</i>	83.71	56.31	111.11
<i>Beilschmiedia pendula</i>	41.81	30.81	52.67
<i>Faramea occidentalis</i>	45.6	17.94	72.68
<i>Ocotea whitei</i>	66.9	46.42	87.12
<i>Prioria copaifera</i>	31.36	17.53	45.01
<i>Quararibea asterolepis</i>	31.48	23.19	39.67
<i>Tetragastris panamensis</i>	52.99	37.48	68.31
<i>Trichilia tuberculata</i>	45.33	33.13	57.53

In five of eight species, the height-diameter relationships (Fig. 1) conformed to the expected  $\beta$  value of 2/3 expected in the elastic similarity model (Fig. 2A). Confidence limits at the 95% level bracketed the expected value of 2/3 for elastic similarity in the canopy trees, *Alseis*, *Ocotea*, *Quararibea*, and *Trichilia*, and in the understory tree, *Faramea* (Table 2). The slopes of  $\log_{10}$  height on  $\log_{10}$  dbh were greater than 2/3 in two species, *Beilschmiedia* and *Prioria*, but not as high as  $\beta = 1.0$  (geometric similarity); and were  $< 2/3$  in *Tetragastris*, but not as low as  $\beta = 0.5$  (constant stress). The coefficients of determination of the regressions,  $r^2$ , were greater than 0.88 in all species.

Crown area-diameter regressions were significant but at lower coefficients of determination than in the case of the height-diameter relationships (Table 3). Slopes of  $\log_{10} A_c$  vs.  $\log_{10}$  dbh ranged from a low of 1.21 in the understory species, *Faramea*, to a high of 1.74 in the canopy tree, *Tetragastris*. The coefficients of determination of the regressions ranged from a low of 0.61 in *Faramea* to a high of 0.93 in *Tetragastris*. Although the extremes of slope and  $r^2$  values were ob-

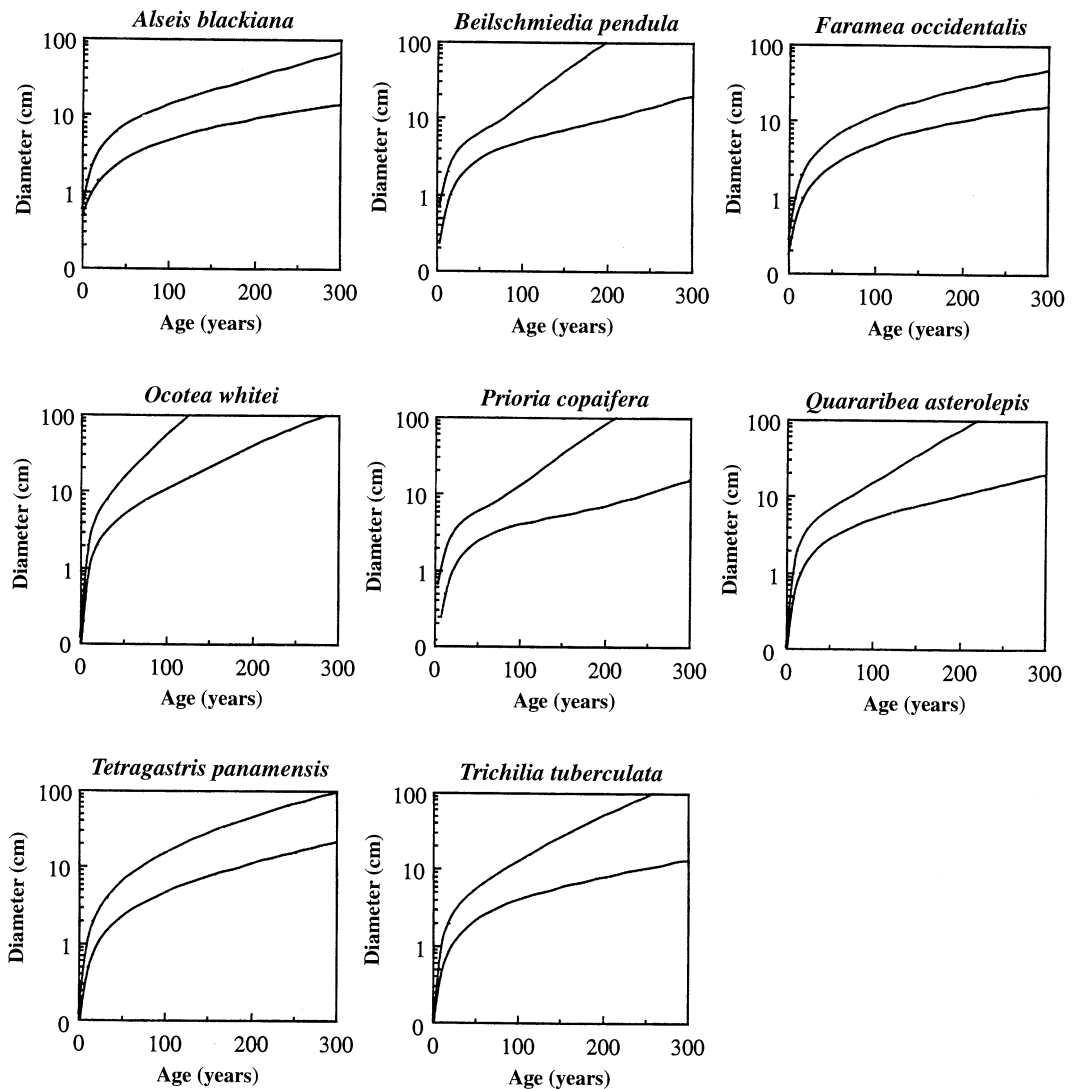


FIG. 3. Diameter growth with age for the eight study species. Two curves are displayed that are expected to bracket the possible values. The lower curve is based on mean diameter-specific growth rates. The upper curve is based on diameter-specific growth rates that are 1 SD above the mean. Because of temporally autocorrelated growth performance, the mean + 1 SD curve better characterizes the growth trajectory of trees that reach the canopy layer. The functions describing these curves are given in Table 6.

served in the same pair of species, there was no significant correlation between slope and coefficient of determination when all eight species were considered ( $r^2 = 0.16$ ,  $P > 0.3$ ).

The relationship between the proxy variables for crown mass and trunk mass,  $\log_{10}A_c^2$  and  $\log_{10}(\text{dbh})^2h$ , respectively, conformed to theoretical expectations in six of the eight species (Fig. 2B, Table 4). The 95% confidence limits on the slopes of the regressions bracketed the expected value of unity in all species but *Alseis* and *Tetragastris*. Both deviant species had crowns that were too heavy for their trunk masses. The greatest variability of all eight species in crown mass to trunk mass was observed in the understory species *Faramaea*.

Crown shapes were much more variable in some species than others (Table 5). The most variable crown shapes were found in *Alseis*, followed by *Ocotea* and then *Faramaea*. The least variable crowns were found in the emergent tree, *Prioria* (Fig. 2C).

Diameter growth as a function of estimated age is shown in Fig. 3 and Table 6. The growth rates were size class specific and based on 8 yr of growth of between  $\approx 1000$  and 20 000 plants in each species. In the figure, two growth curves are displayed, one based on the mean growth rates (lower curve), the other based on positively autocorrelated growth in long-term survivors in which growth is sustained at 1 SD above the mean (upper curve). These two curves probably bound



TABLE 6. Diameter-age functions for the eight study species. Ages are derived from size-specific growth rates. Two functions are listed, one for mean growth rates and the other for rates that are 1 SD above the mean. Both functions are third-order polynomial fits to the means data. Let  $x$  = age (yr) and  $y$  = diameter (cm). Then  $y = a_0 + a_1x + a_2x^2 + a_3x^3$ . Coefficients

Species	Diameter-age function based on mean growth				Diameter-age function based on mean + 1 SD
	$a_0$	$a_1$	$a_2$	$a_3$	$a_0$
<i>Alseis blackiana</i>	$-4.400 \times 10^{-2}$	$3.131 \times 10^{-2}$	$-2.484 \times 10^{-5}$	$2.062 \times 10^{-7}$	$7.565 \times 10^{-1}$
<i>Beilschmiedia pendula</i>	$-5.431 \times 10^{-2}$	$7.214 \times 10^{-2}$	$-3.172 \times 10^{-4}$	$1.000 \times 10^{-6}$	$-5.993 \times 10^{-2}$
<i>Faramea occidentalis</i>	$1.710 \times 10^{-1}$	$4.620 \times 10^{-2}$	$1.795 \times 10^{-5}$	$6.155 \times 10^{-9}$	$2.658 \times 10^{-1}$
<i>Ocotea whitei</i>	$3.983 \times 10^{-2}$	$1.136 \times 10^{-1}$	$-5.185 \times 10^{-4}$	$4.661 \times 10^{-6}$	$1.185 \times 10^{-1}$
<i>Prioria copaifera</i>	$-2.790 \times 10^{-1}$	$7.031 \times 10^{-2}$	$-3.808 \times 10^{-4}$	$1.063 \times 10^{-6}$	$-8.457 \times 10^{-2}$
<i>Quararibea asterolepis</i>	$5.209 \times 10^{-2}$	$6.098 \times 10^{-2}$	$-1.670 \times 10^{-4}$	$6.151 \times 10^{-7}$	$8.387 \times 10^{-2}$
<i>Tetragastris panamensis</i>	$2.769 \times 10^{-2}$	$4.520 \times 10^{-2}$	$-2.937 \times 10^{-5}$	$3.856 \times 10^{-7}$	$1.134 \times 10^{-1}$
<i>Trichilia tuberculata</i>	$4.125 \times 10^{-2}$	$4.517 \times 10^{-2}$	$-8.705 \times 10^{-5}$	$2.785 \times 10^{-7}$	$4.200 \times 10^{-2}$

the actual long-term growth trajectories of these species. Based on these relationships, the species were grouped into four "guilds." The canopy tree *Ocotea* is the fastest growing species and is a group by itself; the understory tree *Faramea* is the slowest growing and is also the sole member of a group. A group of species with very similar growth trajectories, *Beilschmiedia*, *Prioria*, and *Quararibea*, were grouped together. These species grew more slowly than *Ocotea*. The last group of species has similar, but somewhat lower growth rates: *Alseis*, *Tetragastris*, and *Trichilia*.

Height growth as a function of estimated age is shown in Fig. 4 and Table 8 for the eight species. Again, two growth curves are displayed, one for mean growth (lower curve) and the other for growth sustained at 1 SD above the mean (upper curve). The same groupings in diameter growth were also evident in height growth. The species growing fastest in height was again *Ocotea*. Next came *Beilschmiedia*, *Prioria*, and *Quararibea* as a distinct group, followed by the group of *Alseis*, *Tetragastris*, and *Trichilia* (Fig. 3). *Faramea* was separated from the other species because it is an understory tree that very rarely reaches 30 m in height. Table 1 gives estimates of the ages of each species when they achieve a given height, assuming autocorrelated growth at 1 SD above mean growth. The groupings are evident

in the clustered ages at which the various species reach 30 m: group 1: *Ocotea* (88 yr); group 2: *Beilschmiedia*, *Prioria*, and *Quararibea* (group mean =  $157 \pm 10$  yr); group 3: *Alseis*, *Tetragastris*, and *Trichilia* (group mean =  $198 \pm 6$  yr); and group 4: *Faramea* (194 yr to reach 20 m, or 265 yr to reach 30 m). The understory tree *Faramea*, rarely, if ever, achieves a height of 30 m; a very small fraction of individuals (8 of 25 118 individuals in 1985) of this very abundant species reaches 20 cm dbh, or greater than  $\approx 23$  m in height. It was important to use the age-height relationship in determining guild membership because this relationship includes both the allometry of the species and their growth rates. Furthermore, the speed with which a tree reaches the canopy is more important than how quickly it reaches a given diameter.

#### DISCUSSION AND CONCLUSIONS

The three main questions posed in this study were: (1) Which model of tree development do the eight species studied in the BCI forest follow? (2) Is the ratio,  $R$ , of crown mass to trunk mass constant through ontogeny, as predicted by King and Loucks (1978) and King (1981)? (3) Are there differences that group the species into guilds based on growth and allocation patterns of the tree species?

TABLE 7. Height-age functions for the eight study species on Barro Colorado Island, Panama. Ages are derived from size-specific growth rates. Two functions are listed, one for mean growth rates and the other for rates that are 1 SD above the mean. Both functions are third-order polynomial fits to the means data. Diameters were first computed using the functions given in Table 6. Then heights were computed from these diameters. Let  $x$  = age (yr), and  $y$  = height (m). Then  $y =$

Species	Height-age function based on mean growth				Height-age function based on mean + 1 SD
	$a_0$	$a_1$	$a_2$	$a_3$	$a_0$
<i>Alseis blackiana</i>	$4.614 \times 10^{-1}$	$4.467 \times 10^{-2}$	$-3.257 \times 10^{-5}$	$1.052 \times 10^{-7}$	$5.680 \times 10^{-1}$
<i>Beilschmiedia pendula</i>	$6.172 \times 10^{-1}$	$6.768 \times 10^{-2}$	$-1.604 \times 10^{-4}$	$4.338 \times 10^{-7}$	$6.498 \times 10^{-1}$
<i>Faramea occidentalis</i>	$7.890 \times 10^{-1}$	$7.481 \times 10^{-2}$	$-1.350 \times 10^{-4}$	$1.387 \times 10^{-7}$	$9.264 \times 10^{-1}$
<i>Ocotea whitei</i>	$8.763 \times 10^{-1}$	$1.596 \times 10^{-1}$	$-7.310 \times 10^{-4}$	$3.105 \times 10^{-6}$	$9.391 \times 10^{-1}$
<i>Prioria copaifera</i>	$4.739 \times 10^{-1}$	$9.470 \times 10^{-2}$	$-3.151 \times 10^{-4}$	$8.362 \times 10^{-7}$	$7.885 \times 10^{-1}$
<i>Quararibea asterolepis</i>	$6.714 \times 10^{-1}$	$6.822 \times 10^{-2}$	$-1.495 \times 10^{-4}$	$3.403 \times 10^{-7}$	$7.629 \times 10^{-1}$
<i>Tetragastris panamensis</i>	$9.364 \times 10^{-1}$	$7.833 \times 10^{-2}$	$-1.640 \times 10^{-4}$	$3.197 \times 10^{-7}$	$1.002 \times 10^0$
<i>Trichilia tuberculata</i>	$7.256 \times 10^{-1}$	$5.136 \times 10^{-2}$	$-9.207 \times 10^{-5}$	$1.513 \times 10^{-7}$	$6.916 \times 10^{-1}$

of the polynomial are tabled below. Regressions all have  $r^2$ s  $> 0.99$ , however, close fits are expected because mean growth rates were computed for only six doubling diameter classes.

Diameter-age function based on mean + 1 SD		
a1	a2	a3
$9.401 \times 10^{-2}$	$1.072 \times 10^{-4}$	$2.118 \times 10^{-6}$
$2.072 \times 10^{-1}$	$-2.619 \times 10^{-3}$	$2.049 \times 10^{-5}$
$1.091 \times 10^{-1}$	$2.165 \times 10^{-5}$	$4.632 \times 10^{-7}$
$2.699 \times 10^{-1}$	$-1.693 \times 10^{-3}$	$4.529 \times 10^{-5}$
$1.995 \times 10^{-3}$	$-2.481 \times 10^{-3}$	$1.765 \times 10^{-5}$
$1.837 \times 10^{-1}$	$-1.622 \times 10^{-3}$	$1.262 \times 10^{-5}$
$1.103 \times 10^{-1}$	$2.877 \times 10^{-4}$	$1.337 \times 10^{-6}$
$1.210 \times 10^{-1}$	$-5.175 \times 10^{-4}$	$5.824 \times 10^{-6}$

Three species showed significant departures from the height-diameter relationship expected from the elastic similarity model, however, these species also did not agree with the predictions of the geometric similarity or constant stress models. Two of these species, *Beilschmiedia pendula* and *Prioria copaifera*, were taller for their diameters than was predicted by the elastic similarity model. Conversely, *Tetragastris panamensis* was shorter, suggesting a higher margin of safety against buckling in this species than in the other seven species. The wood of *Tetragastris* is relatively dense (Miller 1976), specific gravity = 0.77 (Anonymous 1988), and stiff, i.e., it has a high modulus of elasticity,  $E = 158\,633 \text{ kg/cm}^2$  (Putz 1984). The  $E$  for *Tetragastris* is the highest among the five species for which data were available (Table 1). When crown mass was considered, *Tetragastris* trees also had heavy crowns for their trunk mass, which may explain the stouter stature of this species. The heavier than expected crown in *Alseis blackiana*, whose height-diameter relationship did not depart significantly from elastic similarity, may be explained by the very dense wood of *Alseis* (F. Putz, *personal communication*). The wood of *Alseis* is denser than that of the other seven species. Thus *Alseis* may be more resistant to buckling than the other species in this investigation.

$a_0 + a_1x + a_2x^2 + a_3x^3$ . Coefficients of the polynomial are tabled below. Regressions all have  $r^2 > 0.99$ , but close fits are expected because mean growth rates were computed for only six doubling diameter classes.

Height-age function based on mean + 1 SD		
a1	a2	a3
$1.543 \times 10^{-2}$	$-4.685 \times 10^{-4}$	$2.313 \times 10^{-6}$
$1.841 \times 10^{-1}$	$-1.249 \times 10^{-3}$	$8.603 \times 10^{-6}$
$1.763 \times 10^{-1}$	$-8.113 \times 10^{-4}$	$2.117 \times 10^{-6}$
$4.167 \times 10^{-1}$	$-4.803 \times 10^{-3}$	$4.362 \times 10^{-5}$
$2.874 \times 10^{-1}$	$-2.382 \times 10^{-3}$	$1.474 \times 10^{-5}$
$1.903 \times 10^{-1}$	$-1.252 \times 10^{-4}$	$6.818 \times 10^{-6}$
$2.148 \times 10^{-1}$	$-1.168 \times 10^{-3}$	$4.248 \times 10^{-6}$
$1.461 \times 10^{-1}$	$-7.082 \times 10^{-4}$	$3.394 \times 10^{-6}$

King (1986) argued that high-density wood may provide the best combination of flexibility and strength needed to withstand high winds. Putz et al. (1983) examined the relationship between snapoff and tipup frequency among a number of BCI tree species and found a significant negative correlation between mortality rates and wood density. During the interval 1982–1985, of the eight species studied here, *Alseis* had the second lowest annual percent mortality rate of all species for trees  $> 32 \text{ cm dbh}$  (1.85%); *Prioria* had the lowest rate (0.94%) (S. P. Hubbell et al., *unpublished data*). The highest annual percent mortality of trees  $> 32 \text{ cm dbh}$  among these species was seen in the fastest growing species, *Ocotea* (6.67%) and in a slower growing species, *Quararibea* (9.41%). These mortality rates were probably elevated due to an intense drought that occurred during this interval (Hubbell and Foster 1990, Condit et al. 1992).

We were surprised that in an essentially random taxonomic draw of eight species from the BCI forest, i.e., random with respect to growth allometries, three of the eight species deviated from all three theoretical models. Two of the species' architectures were such as to reduce the margin of safety against mechanical failure. We suggest that the explanation may lie partly in the fact that canopy tree species in the forest of BCI can rely on neighboring trees for support. Trees may ricochet off their neighbors, which prevents them from swaying, and thus from buckling or tipping up (see also Holbrook and Putz 1989). Support for this idea comes from a recent study of the fate of BCI canopy trees that lose their neighbors. Young and Hubbell (1991) discovered that trees on the edge of treefall gaps are not only much more likely to fall or snap off, but that when they do, they are much more likely to fall into the gap, i.e., to fall in the direction of the lost neighbors. However, they also reported that trees on the edges of gaps have more asymmetrical crowns, and that the largest crown radii tend to develop on the sides facing the gaps. The mass imbalances created by these crown asymmetries probably partially explains the tendency of trees to fall into gaps. Furthermore, the combined effect of reduced wind load and lateral shade may stimulate trees to grow relatively taller for a given diameter compared with open-grown trees (e.g., Holbrook and Putz 1989).

The answer to the second question, whether the ratio,  $R$ , of  $W_c$  to  $W_t$  remains constant throughout ontogeny, was yes in six of eight species. The two species that departed from expectations, *Alseis blackiana* and *Tetragastris panamensis*, had crowns that were significantly heavier than expected ( $R > 1.0$ ). However, our analyses were based on the assumptions in King (1981), particularly that crown masses are proportional to the square of crown areas. If this assumption is false, then our analysis will fail until more complete data are available on wood densities and actual crown and trunk masses. We think that the assumption is probably reasonably accurate, however, because it would be un-

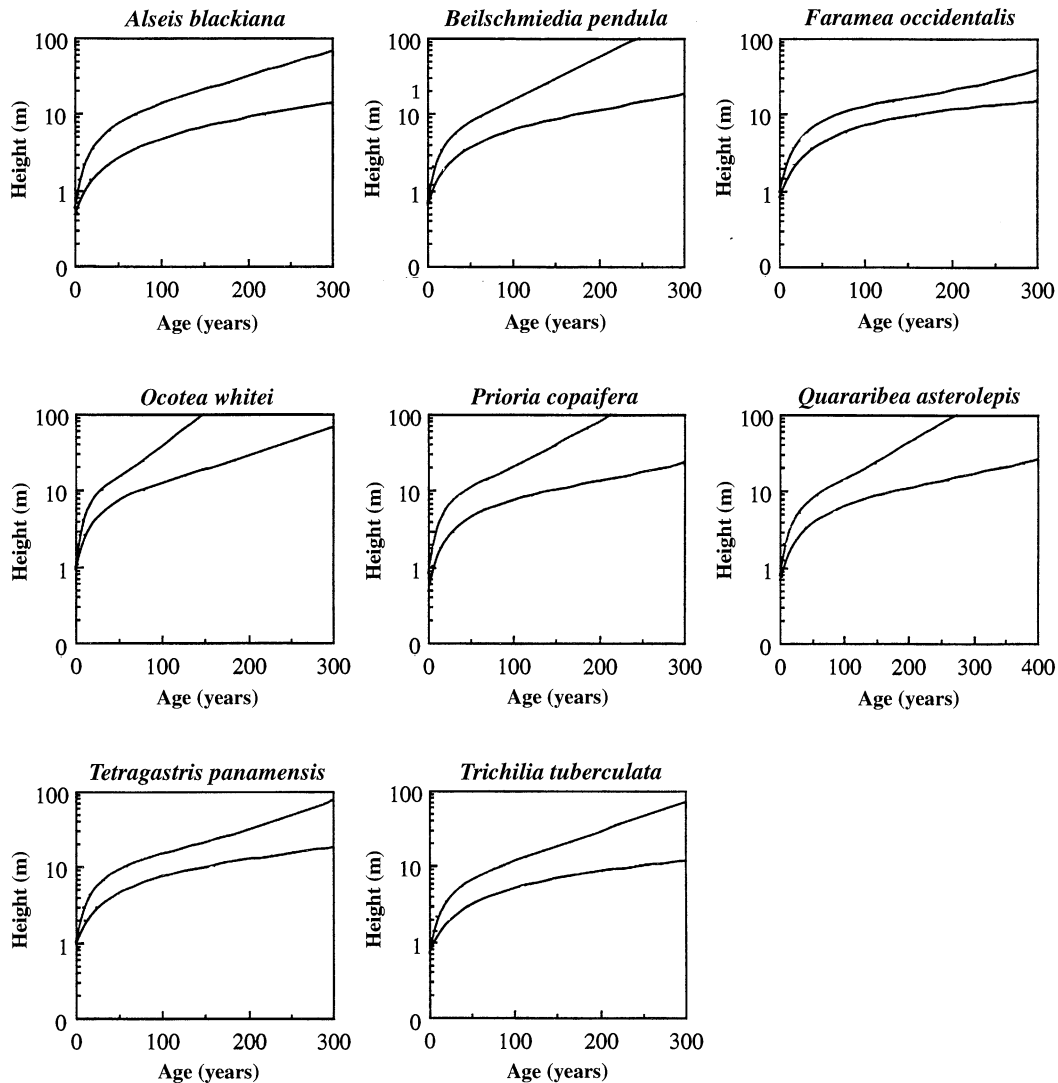


FIG. 4. Height growth with age for the eight species. Two curves are displayed that are expected to bracket the possible values. The lower curve is based on mean diameter-specific growth rates. The upper curve is based on diameter-specific growth rates that are 1 SD above the mean. Because of temporally autocorrelated growth performance, the mean + 1 SD curve better characterizes the growth trajectory of trees that reach the canopy layer. The functions describing these curves are given in Table 7. The tree heights used in this figure were predicted from diameters; therefore, uncertainty in the prediction of height must be considered when examining this figure. Diameter did account for 88–97% of the variance in height; thus, the height predictions are expected to be fairly accurate if the diameter-age relationships are accurate.

likely that the  $R$  would otherwise be so close to unity in so many species.

Crown shapes were analyzed by the coefficient of variation of the square-root-transformed crown radii. The results were interesting in that the species with the most variable crown, *Alseis blackiana*, also exhibited strong departures in the  $W_c$  to  $W_r$  ratio. Having high wood density may increase tolerance for more asymmetrical crown shapes in this species. In contrast, *Prioria copaifera* exhibited a very symmetrical crown. *Prioria* is the only emergent tree among the eight species surveyed and as such may have greater exposure to damaging winds that could break off more asym-

metrical crowns. Emergent trees might also have more rounded crowns because in the absence of competition for space, open-grown trees will tend to grow round, or spherical, crowns. We therefore expected that the understory species *Faramea occidentalis*, presumably less exposed to wind and having greater needs to “forage” horizontally for light in the understory, should exhibit more crown variability than the other species. *Faramea* exhibited the widest confidence limits on the slopes of the height–diameter and crown area–diameter regressions. In addition, *Faramea* was the third most variable species in crown shape. This is consistent with the hypothesis that selection has imposed different con-

ditions on geometric relationships in understory species than in canopy and emergent trees. This may be because understory plants are generally protected from strong winds, less subject to winds, and are less likely to be felled by wind. O'Brien (1994) found no relationship between wind direction and crown shape among 56 species growing on BCI. Furthermore, plants growing in the understory may forage for light; thus, their crowns may become very irregular. On the other hand, saplings of species that eventually reach the canopy cannot grow irregularly at small sizes because they may become unstable at large sizes. For example, *Ocotea* had the second highest variability in crown shape and had the highest growth and mortality rates among the species in this study (Condit et al., *in press*). *Ocotea*'s crown shape irregularity and tendency to lean (S. P. Hubbell, *personal observation*) may be because *Ocotea* is a more light-demanding species and is foraging for light. Testing these hypotheses must await a larger sample of understory and canopy species.

As expected, crown radii were generally small in comparison to height in these forest-grown tree species (Table 8). The mean radii for trees in the main canopy layer (>30 m) was between 3 and 6 m, although radii occasionally exceeded 10 m in some very asymmetrical crowns.

On the final question of the existence of life history guilds as revealed by growth patterns, there were four distinguishable groups based on diameter-age and height-age relationships (Tables 6 and 7, Figs. 3 and 4). Two extreme groups were represented by one species each: first, the relatively fast-growing species *Ocotea whitei*, which reached 30 m in an estimated 88 yr; and second, the slow-growing understory tree *Faramea occidentalis*, which in the rare event of reaching 30 m would be nearly 300 yr old. In between these extremes were two groups of three species each, with nearly identical growth rates and allometries. The faster growing group contained *Beilschmiedia pendula*, *Prioria copaifera*, and *Quararibea asterolepis*. This group reached the main canopy (30 m) in an estimated 157 yr (mean + 1 SD growth rate). *Alseis blackiana*, *Tetragastris panamensis*, and *Trichilia tuberculata* comprised the slow growing group, which are estimated to require nearly two centuries to reach the main canopy (198 yr).

To find four "guilds" among eight species might seem to discourage the search for a small number of general equations to describe the growth characteristics of the 310 BCI tree and shrub species in the 50-ha plot. *Faramea occidentalis* was the only understory species included in this investigation. Therefore, it might be expected that it would not be in a guild with the species that reach the canopy. In fact, three-quarters of the species measured (six of eight, or six of seven canopy and emergent species) fell into just two guilds. It is premature to conclude how many guilds might be evident when a larger fraction of the species have been

TABLE 8. Diameter, crown area, and crown radius through ontogeny to 30 m height for six main canopy neotropical tree species, up to 40 m in the emergent species, *Prioria*, and to 20 m in the understory species, *Faramea*.

Species	Height (m)	dbh (cm)	Crown area (m <sup>2</sup> )	Crown radius (m)
<i>Alseis blackiana</i>	2	0.9	0.06	0.14
	5	3.1	0.52	0.41
	10	8.2	2.70	0.93
	20	21.9	14.12	2.12
	30	38.8	37.15	3.44
<i>Beilschmiedia pendula</i>	2	1.0	0.23	0.27
	5	3.4	1.42	0.67
	10	9.0	5.54	1.33
	20	23.2	21.67	2.63
	30	40.6	48.05	3.91
<i>Faramea occidentalis</i>	2	0.8	0.29	0.31
	5	3.1	1.54	0.70
	10	8.7	5.31	1.30
	20	24.3	18.35	2.42
<i>Ocotea whitei</i>	2	0.7	0.13	0.20
	5	2.7	0.90	0.54
	10	7.9	3.94	1.12
	20	22.9	17.17	2.34
	30	42.9	40.75	3.60
<i>Prioria copaifera</i>	2	1.2	0.46	0.38
	5	4.3	2.36	0.87
	10	10.8	8.21	1.62
	20	27.4	28.53	3.01
	30	47.2	59.05	4.34
<i>Quararibea asterolepis</i>	2	1.0	0.35	0.33
	5	3.5	1.83	0.76
	10	9.5	6.47	1.43
	20	25.4	22.86	2.70
	30	45.3	47.80	3.90
<i>Tetragastris panamensis</i>	2	0.5	0.05	0.12
	5	2.4	0.64	0.45
	10	7.7	4.72	1.23
	20	24.3	34.91	3.33
<i>Trichilia tuberculata</i>	2	0.9	0.28	0.30
	5	3.6	1.92	0.78
	10	10.4	8.21	1.62
	20	29.9	35.06	3.34
	30	55.5	81.97	5.11

analyzed. Nonetheless, the similarity among species within each of the two larger guilds is quite close. This suggests that a reduction in the physiognomic dimensionality of this species-rich tropical tree community into a smaller set of functionally equivalent species is likely to occur. This reduction in the physiognomic complexity of the forest may greatly facilitate understanding of the structure of tropical forests.

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