SCALING OF STEM AND CROWN IN EIGHT *CECROPIA* (CECROPIACEAE) SPECIES OF BRAZIL[1]

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The scaling of stem and crown was studied in eight *Cecropia* species in Amazonian and southeastern forests of Brazil. The Amazonian species, *C. concolor, C. palmata, C. purpurascens, C. sciadophylla,* and *C. ulei* were studied in Manaus, Amazonas, Brazil. The southeastern species, *C. glaziovii, C. hololeuca,* and *C. pachystachya* were studied in Linhares, Espírito Santo, Brazil. Measures of diameter, height, number of branches, number of leaves, and total leaf area were log transformed and regressed on height. Three models of mechanical designs of trees, elastic, constant stress, and geometric similarity, were tested for *Cecropia.* None of the models can totally describe *Cecropia,* but geometric similarity was a close approximation. Most of the species did not vary in diameter–height relationships between unbranched and branched individuals. Safety factors diminished with height in most species studied. The crown–height relationships were similar for all species. Numbers of branches and leaves showed some variation among species and are related to height of first branching. Total leaf area had a constant allometric relationship among species, although regression intercepts differed according to species leaf areas. The scaling relationships of stem and crown in *Cecropia* varied with adult size of the studied species.

Key words: allometry; Brazil; *Cecropia*; Cecropiaceae; myrmecophyte; pioneer; tropical tree.

The relationship between size and shape in trees is important for understanding adaptive differences among species, competitive interactions, and the structure and dynamics of forests. Differences in allocation between trunks and crowns enable distinct strategies of space occupation in forests (King, 1990; Kohyama and Hotta, 1990). Early successional trees are able to invade open areas in high densities and grow quickly; this ability may be closely related to the height and extension of the foliage (King, 1981). However, to attain a given height, a tree requires a minimum diameter to avoid buckling due to its own mass (McMahon, 1973) and to resist breakage from wind action (Dean and Long, 1986). Natural selection favors trees that have a height–diameter relationship that permits height growth without compromising mechanical stability.

Three models have been proposed to describe the mechanical design of trees. The *elastic similarity model* considers tree trunks as self-supporting tapering columns. To resist buckling under their own mass, basal trunk diameter (D) should scale at 3/2 power of height (H), or alternatively, $H \propto D^{2/3}$ (McMahon, 1973). The *constant stress model* is based on the assumption that trunks taper such that stress produced by wind pressure along the stem is equalized; in this model, $H \propto D^{1/2}$ or $D \propto H^{2}$ (Dean and Long, 1986). The *geometric similarity model* assumes the scaling exponent equals 1.0, i.e., trunk diameter will scale in direct proportion to diameter (Norberg, 1988). These three models assume that wood properties do not change with tree size (Niklas, 1994).

McMahon (1973) plotted height vs. trunk diameter for the largest known living specimens of North American dicotyledonous and gymnosperm tree species and found the scaling

relation to conform to that predicted by the elastic similarity model. However, this conclusion was criticized since the data were not examined statistically to determine the scaling exponent for H vs. D (La Barbera, 1989; Niklas, 1994).

The elastic similarity model is based on Euler's buckling formula (McMahon, 1973) and predicts the critical height to resist buckling (H_{crit}) by the formula

$$H_{\mathrm{crit}} = C\ (E/\rho)^{1/3}\ D^{2/3}$$

where C is a constant of proportionality, E is Young's modulus of elasticity, ρ is the density of stem wood, and D is the trunk diameter. The constant $C = 0.792$ when the force is distributed over the full extent of the member (Greenhill, 1881; cited in Niklas, 1994). McMahon (1973) assumed $C = 0.792$ and E/ρ as a constant ratio for the species he examined. However, specific density of wood in trees is not constant (Wiemann and Williamson, 1989; Rueda and Williamson, 1992; Castro et al., 1993). Furthermore, the modulus of elasticity ($E = 1.05 \times 10^5$ kg/m^2) given in McMahon (1973) was considered too low by Niklas (1994), since E for most of species of wood is on the order of 10^8 kg/m^2.

Niklas (1994) reevaluated the relation between tree height and trunk diameter as well as that between buckling critical height and diameter. According to his analysis, dicotyledonous trees conform to the elastic similarity model, and geometric similarity was not rejected for gymnosperm trees. For dicotyledonous and gymnosperm pooled data, both stress similarity and elastic similarity models appear inappropriate to describe the allometric relation between height and diameter. Moreover, scaling relationships are not constant during tree ontogeny (Dean and Long, 1986; Niklas, 1994, 1995; Sterck and Bongers, 1998). Scaling of trunk diameter is size dependent for the temperate tree *Robinia pseudoacacia* (Niklas, 1995). In this plant, height and trunk taper progressively change, complying with geometric similarity for young plants and subsequently giving the appearance of elastic or stress similarity as plants get older and larger. Similar changes in scaling exponents of diameter–height relationships with size were found in different height ranges of tropical trees (King, 1996).

Studies of tropical tree allometry found exponents close to

TABLE 1. Sample characteristics of the Brazilian *Cecropia* species included in this study. In parentheses are shown corresponding abbreviations used in the figures.

Species	Height range (m)	N	Location	Mutualism with ants	Habitat
C. concolor Will. (CON)	1.3–13.1	38	Manaus	present	open
C. palmata Will. (PAL)	1.9–16.0	30	Manaus	present	open forest border
C. purpurascens C. C. Berg (PUR)	1.1–14.3	31	Manaus	present	open forest border
C. sciadophylla Mart. (SCI)	1.2–25.2	34	Manaus	absent	forest gaps forest border
C. ulei Snethl. (ULE)	1.8–16.4	21	Manaus	present	forest gaps understory
C. glaziovii Snethl. (GLA)	1.7–22.3	37	Linhares	present	forest border riparian forest
C. hololeuca Miq. (HOL)	2.7–20.2	29	Linhares	absent	forest gaps forest border
C. pachystachya Tréc. (PAC)	1.3–12.0	29	Linhares	present	open

1 for saplings of canopy and understory trees (King, 1990, 1996; Kohyama and Hotta, 1990) and for species of initial successional phases (Alvarez-Buylla and Martinez-Ramos, 1992; Claussen and Maycock, 1995); adult canopy trees or emergents showed exponents equal to or greater than that of the elastic similarity model (Farnsworth and Niklas, 1995; O'Brien et al., 1995; King, 1996). Shade-intolerant, pioneer species, with short life spans, invest more in height growth than in strength and longevity. Low safety margins facilitate rapid height growth by lowering the biomass needed to achieve a certain height (King, 1981; Alvarez-Buylla and Martinez-Ramos, 1992). When in the sapling stage, canopy and emergent trees show exponents closer to the geometric similarity model, but when they become adults, their diameter conforms to elastic or stress similarity models, with higher safety factors, since stability and survival may be favored over rapid height growth in adult trees (King, 1996).

Most comparisons of tree allometry have treated unrelated species or groups of species with similar habitats. In this study, we examined scaling relationships for eight congeneric species of *Cecropia* (Cecropiaceae) in Brazil. *Cecropia* is a neotropical genus of pioneer, fast-growing trees, normally associated with initial phases of succession (Whitmore, 1989; Alvarez-Buylla and Martinez-Ramos, 1992). These eight *Cecropia* species increase in adult size along a habitat gradient from open habitats to forest (Sposito, 1999). Leaf size of species increases in the same direction, and species that occur in forest gaps or in forest edge had the largest leaves, when compared to species that occur in open habitats (Sposito, 1999). It could be expected that regression coefficients of allometric relationships increase, following the gradient from open habitats to forest, since allometry and habitat are related (Rich et al., 1986; King, 1990, 1996; Kohyama and Hotta, 1990; Claussen and Maycock, 1995). We address four questions: (1) Do allometric relationships between diameter and height differ among Brazilian species of the genus *Cecropia*? (2) Which model of tree allometry, elastic, geometric, or constant stress, do the species most closely follow? Are there differences related to open-forest gradient for the species? (3) Do the scaling exponents of diameter–height relationships differ between unbranched and branched trees? (4) Do crown–height relationships differ among species?

MATERIALS AND METHODS

Species and study areas—Eight *Cecropia* species were studied in disturbed or secondary forests in two areas: Brazilian Amazonia and southeastern Brazil (Table 1). The study sites in Amazonas state were Fundação Universidade do Amazonas (FUA) inside Manaus, Reserva Ducke, and the experimental area of Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA), Amazônia

Ocidental on the Manaus–Itacotiara road, 26–29 km north of Manaus (2°51′ S, 59°52′ W). The FUA and Reserva Ducke are medium (20 m tall) and high canopy (30–40 m tall) forests, respectively. The area of EMBRAPA consists of pasture and fallow agricultural land with a mosaic of secondary forest and open cultivated areas. Annual mean rainfall and mean temperature at the EMBRAPA site were 2500 mm and 25°C between 1971 and 1993 (Cabral, 1996).

Most *Cecropia* species form mutualistic relationships with ants: trees benefit from ant association through protection against vines and herbivores (Janzen, 1969; Schupp, 1986; Rocha and Bergallo, 1992; Vasconcelos and Casimiro, 1997; but see Andrade and Carauta, 1982; Putz and Holbrook, 1988; and Wetterer, 1997, for different views). Myrmecophytic *Cecropia* possess structures termed trichilia, at the base of each petiole, that produce glycogen-rich Müllerian bodies (Rickson, 1971, 1976) fed upon by ants. Two Brazilian species, *Cecropia sciadophylla* and *C. hololeuca,* lack trichilia and are not myrmecophytes (Berg, 1978; Benson, 1985).

Amazonian species sampled were *Cecropia concolor* Will., *C. palmata* Will., *C. purpurascens* C. C. Berg, *C. ulei* Snethl., and *C. sciadophylla* Mart. (nonmyrmecophytic) (Table 1). Of these, *C. concolor* is more common in open fields and abandoned agricultural lands, *C. palmata* and *C. purpurascens* occur in open habitats or forest borders, and *C. sciadophylla* occurs in gaps and forest borders, at times forming dense stands. Plants of *C. ulei* occur in forest gaps, but some adults occur in the subcanopy of secondary forest.

In southeastern Brazil, the study site was Reserva Florestal de Linhares, located north of Espírito Santo state (19°06′ S, 39°45′ W). The area is a mosaic of tall forest (20–25 m in height), low forest ("mussununga," 10–15 m high) and savanna scrub called "nativo" on progressively sandier soils (Jesus, 1988; Peixoto and Gentry, 1990). Annual mean rainfall and temperature were 1242 mm and 23°C, respectively (1975–1993). *Cecropia glaziovii* Snethl. and *C. hololeuca* Miq. (nonmyrmecophytic) occur along forest borders, whereas *Cecropia pachystachya* Trécul grows in "mussununga," "nativo," and transition between these and high forest.

Measurements of plant size—Measurements of height, diameter at breast height (dbh, breast height = 1.3 m above soil surface), number of live first-order branches, and number of leaves were recorded for plants over a range of heights, from ~1 m tall saplings to large adults ($N \geq 30$ individuals per species, except $N = 29$ for *Cecropia pachystachya* and $N = 21$ for *C. ulei*). Total height was defined as the top of the crown in branching trees and the height of tree apical stipule in pole plants. Diameter was measured at the last internode in plants <1.3 m. If stilt roots were present, diameter was measured ~30 cm above the highest roots. Number of first-order branches and number of leaves were counted directly using binoculars. Number of leaves per branch was estimated by dividing the total number of leaves by the number of first-order branches.

We collected one leaf per plant (typically the leaf at the third internode below the apical meristem) for area measurements using a LI-COR area meter (Model LI-3000, LI-COR, Lincoln, Nebraska, USA). We used the method of Alvarez-Buylla and Martinez-Ramos (1992) to measure crown size: number of branches, number of leaves, and total leaf area, calculated as leaf area multiplied by number of leaves. Voucher specimens are in the Herbarium of the Universidade Estadual de Campinas, São Paulo, Brazil (UEC).

Analysis—The variables used in our study were stem diameter (in centimetres), tree height (in metres), number of branches, number of leaves, and total leaf area (in square metres). The allometric equation is described as $Y = aX^b$ or the correspondent log-transformed equation, $\log Y = \log a + b \log X$, where X is the independent variable, Y the dependent variable, and a (Y intercept) and b (slope of regression) are parameters obtained by regression analyses. Log$_{10}$-transformed measures were regressed on log height because height influences the light environment and space available for plant growth (King, 1981, 1996). Least squares (LS) regression of the transformed data was used to determine the allometric (scaling) relationships, because it is appropriate when the objective is to compare the standard dispersion statistics obtained from two or more data sets (see Niklas, 1994). Moreover, our data become comparable to other previous studies with tropical species.

Regression lines were compared using standard methods (Zar, 1984). First, homogeneity of slopes was tested. If no difference was found among slopes, an analysis of covariance was conduced to test for differences among adjusted means. When F was significant, the Scheffé multiple comparison test was used to identify significant ($P < 0.05$) differences among the means (Huitema, 1980). When comparing LS regressions, differences can occur in either a (Y intercept) or b (regression slope). If b differs among species, species with larger b will show greater increase of Y per increment of X. If a differs but b does not, species with larger a will have a consistently larger amount of Y at any X (Kohyama and Hotta, 1990). Nonsignificant regressions were not included in multiple comparisons.

To test for agreement with each of the three models of tree development, we computed the 95% confidence limits for the LS slopes of each species and determined whether the limits bracketed the expected slopes when log$_{10}$ diameter was plotted against log$_{10}$ height (after O'Brien et al., 1995). Safety factors of species were calculated as $d/d_{\min}$ (King, 1981) where d is the actual stem diameter and $d_{\min}$ is the theoretical minimum buckling diameter calculated using the formula, $0.1\ h^{3/2}$ (d in centimetres), which was derived from McMahon's (1973) buckling equation, that is an approximation of a more accurate specification of McMahon's buckling limit, as shown in his figure, where $d = 0.0011\ h^{3/2}$ (d and h both in metres; King, 1996).

RESULTS

Diameter–height relationships—Linear regressions best described the *Cecropia* allometric relationships. Linear regressions slopes for log–log diameter–height relationships differ among the *Cecropia* species studied ($F = 2.85$, $P = 0.007$, df = 7, $N = 242$; Fig. 1). The regression slope of *Cecropia ulei* was significantly lower than that of *C. glaziovii* and *C. concolor* (Fig. 2). The *Cecropia glaziovii* regression slope was significantly larger than that of *C. purpurascens*. The remaining species did not differ on slopes, but significant differences were found for the adjusted Y intercepts among them ($F = 5.57$, $P < 0.001$, df = 5, $N = 191$), showing that diameter is larger in the *C. hololeuca* species compared with *C. pachystachya* for a given height.

As a group, southeastern Brazilian species do not show significant differences in slopes (Fig. 2). Among the Amazonian species, *C. concolor* differed from *C. ulei,* but the other species did not show significant differences (Fig. 2). The Amazonian species tended to be thicker ($\log a = -0.0130 \pm 0.0294$) than the southeastern species ($\log a = -0.1557 \pm 0.0305$) at the low end of the height range (plants 1 m tall), with the two groups converging at greater heights ($\log a$ for plants 10 m tall: Amazonian species = 1.0066 ± 0.0382; southeastern species = 1.0037 ± 0.0251).

Diameter–height relationships of most *Cecropia* species do not conform to elastic ($b = 3/2$) or stress similarity models ($b = 2$) (Table 2, Fig. 2). In six species, 95% confidence limits of slopes bracketed the geometric similarity model ($b = 1$). Only in *C. concolor* and *C. glaziovii* did confidence intervals

fall between $b = 1.0$ and $b = 1.5$. The slope of *Cecropia* spp. (pooled data) bracketed none of the expected values, but it is closest to the line of geometric similarity.

Most of the species did not vary in diameter–height relationships between unbranched and branched individuals (F values range 0.004–1.031; $P > 0.05$, Table 2), except for *Cecropia palmata* ($F = 6.42$, $P = 0.02$, df = 1, $N = 30$). For all species, coefficients of determination of regressions for total number of individuals were larger than those obtained when the unbranched and branched individuals were regressed separately (Table 2) because of the larger range in height for the combined data.

Safety factors ($d/d_{\min}$) decreased significantly with height in most *Cecropia* species (Fig. 3). Plants showed diminishing safety factors across the range in height. In most species, taller trees approach the elastic buckling limit but do not surpass it. A power function model best described the changes in safety factor (Fig. 3). The safety factor of *Cecropia hololeuca* did not show the same pattern of the other species during ontogeny, but this could be a consequence of lacking individuals <2 m in height in the sample. Exponents of the relationship between safety factor and height were significantly different among species ($F = 2.85$, $P = 0.007$, df = 7, $N = 235$). A plot of the 95% confidence intervals of the slopes shows that *C. ulei* and *C. purpurascens* had a fast decreasing of safety factor in comparison to the remaining species (Fig. 4).

Crown–height relationships—Slopes of linear regressions between number of first-order branches and height did not differ significantly among species (excluding *C. ulei*, which was mostly unbranched, and species with no significant regressions) ($F = 0.74$, $P = 0.57$, df = 4, $N = 95$, Table 3). Intercepts were significantly different ($F = 17.28$, $P < 0.001$, df = 4, $N = 95$); *C. sciadophylla, C. hololeuca,* and *C. glaziovii* had adjusted intercepts significantly lower than the other species (Table 3), showing that number of branches is lower in these species compared with other species at the same height. This result is a consequence of differences in the height of first branching of species. In *C. sciadophylla, C. hololeuca,* and *C. glaziovii*, branching begins when plants reach ∼9–10 m in height, whereas the remaining species branch at ∼4–6 m (mean values in Sposito, 1999).

For unbranched individuals, most species did not show significant relationships between number of leaves and height (Table 4, Fig. 5) and coefficients of determination were low. *Cecropia concolor, C. pachystachya,* and *C. glaziovii* showed significant slopes and a positive relationship between number of leaves and height, but did not differ in regression slopes ($F = 1.87$, $P = 0.16$, df = 2, $N = 53$) nor intercepts ($F = 0.498$, $P = 0.62$, df = 2, $N = 53$).

Number of leaves increased significantly with height for branched individuals in most species (Table 4, Fig. 5). Slopes did not differ significantly among species (excluding *C. ulei* and species with no significant regressions) ($F = 0.33$, $P = 0.86$, df = 4, $N = 95$) but intercepts differed ($F = 15.52$, $P < 0.001$, df = 4, $N = 95$). In *C. sciadophylla, C. hololeuca,* and *C. glaziovii,* the number of leaves is low compared with other species at the same height, because of the differences in height of first branching among species.

The number of first-order branches and number of leaves in branched trees increased, but not significantly, with height in *Cecropia pachystachya* and *C. purpurascens* (Tables 3 and 4). However, considering diameter instead of height, the regres-
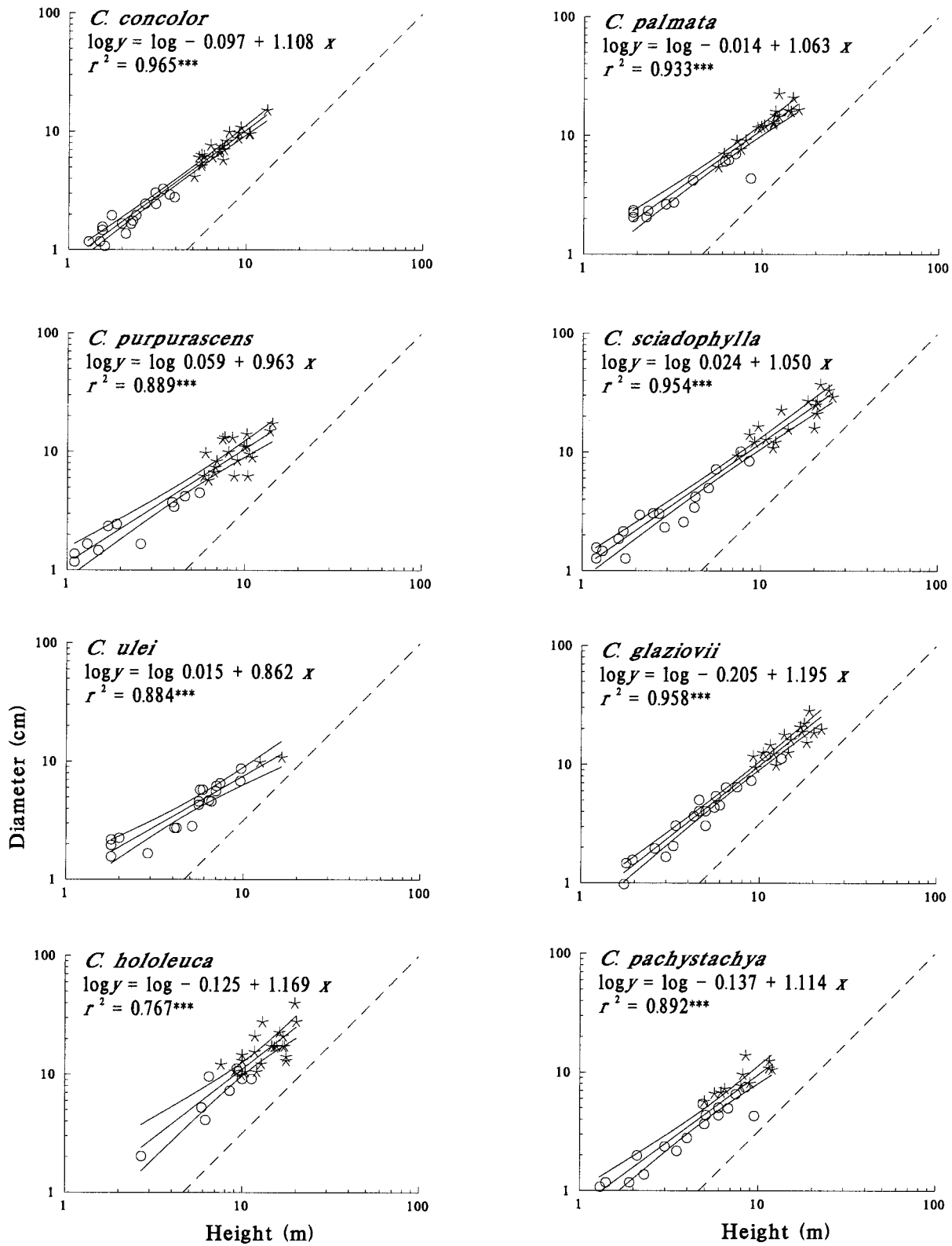
C. concolor
$\log y = \log -0.097 + 1.108\ x$
$r^2 = 0.965^{***}$

C. palmata
$\log y = \log -0.014 + 1.063\ x$
$r^2 = 0.933^{***}$

C. purpurascens
$\log y = \log 0.059 + 0.963\ x$
$r^2 = 0.889^{***}$

C. sciadophylla
$\log y = \log 0.024 + 1.050\ x$
$r^2 = 0.954^{***}$

C. ulei
$\log y = \log 0.015 + 0.862\ x$
$r^2 = 0.884^{***}$

C. glaziovii
$\log y = \log -0.205 + 1.195\ x$
$r^2 = 0.958^{***}$

C. hololeuca
$\log y = \log -0.125 + 1.169\ x$
$r^2 = 0.767^{***}$

C. pachystachya
$\log y = \log -0.137 + 1.114\ x$
$r^2 = 0.892^{***}$

Diameter (cm)

Height (m)

Fig. 1. Least squares regressions between diameter (*D*) and height (*H*) of eight *Cecropia* species of Brazil ($\log_{10}D = \log_{10} a + b \log_{10} H$), with 95% confidence limits of slopes. Circles represent unbranched and asterisks represent branched individuals. Dashed lines indicate the minimum diameter to prevent buckling in wooden columns, calculated as McMahon (1973).
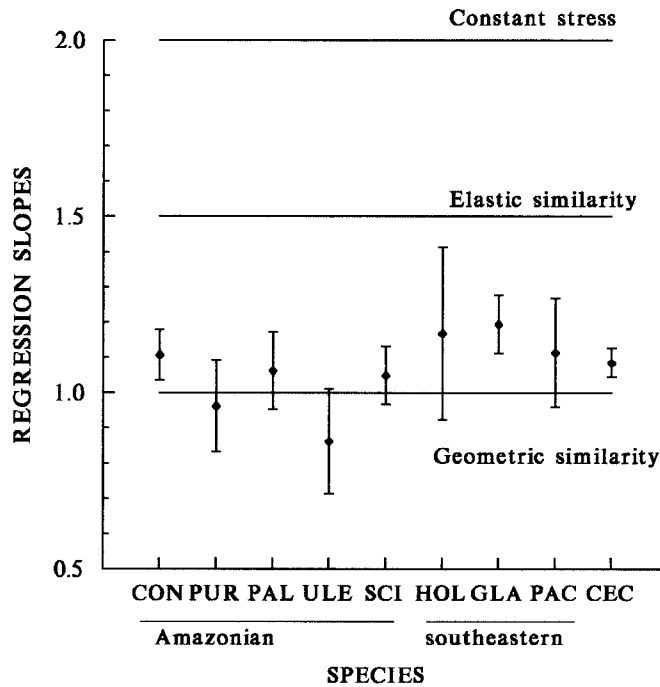
Fig. 2. Least squares regression slopes and respective 95% confidence intervals of the regressions of $\log_{10}$ diameter on $\log_{10}$ height for eight Brazilian *Cecropia* species. The first five species are from Amazonia and the latter three are from southeastern Brazil. CEC = *Cecropia* spp. (pooled data). The expected values of slopes for the three models of tree structure are indicated in the figure. Species abbreviation may be found in Table 1.

sions were significant. For number of first-order branches, r^2 = 0.53 and 0.88, respectively ($P < 0.01$ and $P < 0.001$); and for number of leaves, r^2 = 0.80 and 0.48, respectively ($P < 0.001$ and $P < 0.01$), indicating that, in both species, the number of leaves and branches are more closely related to trunk diameter than to tree height. The nonsignificance of the regressions with height could be due to limited height growth of both species, which decreases the range of the x variable.

Slopes of the linear regressions between number of leaves and number of branches differ significantly among species (F = 18.24, $P < 0.001$, df = 6, N = 128; Table 5, Fig. 6). In *C. concolor* and *C. purpurascens*, the number of leaves increases more slowly with number of branches than in the other species, because they have a lower number of leaves/branch (Sposito, 1999). The latter species did not show heterogeneity

in slopes (F = 1.363, P = 0.254, df = 4, N = 87) nor intercepts (F = 0.221, P = 0.924, df = 4, N = 87).

Total leaf area (in square metres) and height were positively related and slopes were not significantly different among species (F = 1.68, P = 0.11, df = 7, N = 231; Table 6, Fig. 7). Adjusted intercepts, however, were significantly different (F = 8.92, $P < 0.001$, df = 7, N = 231) and *C. sciadophylla* and *C. hololeuca* showed the largest total leaf areas at a given height (Table 6). These intercepts differences are related to the large leaves of both species, when compared to the remaining species studied (Sposito, 1999).

DISCUSSION

Stem allometry—The analysis of scaling relationships of stem in *Cecropia* showed that the species grow nearly isometrically (Fig. 2). With respect to slopes of diameter–height relationships, the 95% confidence intervals for two of the eight species did not bracket the geometric similarity model. These species, *C. concolor* and *C. glaziovii*, had larger exponents than were predicted by the geometric similarity model, but the exponents were not high enough to conform to predictions of the elastic similarity or stress similarity models. *Cecropia* spp. (pooled data) showed a slope significantly greater than one, but do not conform to the elastic similarity model. Therefore, none of the models can totally describe *Cecropia* spp., but geometric similarity is a close approximation.

Size-dependent changes in scaling exponents of diameter–height relationships were not found for most *Cecropia* studied. Although physical changes occur with tree development, these changes do not seem to significantly alter the scaling exponent during *Cecropia* ontogeny. However, safety factors diminish with height in most *Cecropia* species studied, and taller trees approach, but do not surpass, the estimated elastic buckling limit. For maintenance of a high growth rate, low safety factors are expected in shade-intolerant species (King, 1981; Rich et al., 1986; Alvarez-Buylla and Martinez-Ramos, 1992; Claussen and Maycock, 1995). In contrast, certain other shade-intolerant canopy species have high safety margins at larger size (King, 1996; Sterck and Bongers, 1998), which is similar to later successional species. Low safety factors may not be a rule for light-demanding trees.

Safety factors of smaller saplings of the Brazilian *Cecropia* species and of *C. obtusifolia* in Mexico (Alvarez-Buylla and Martinez-Ramos, 1992) are large compared to other tropical species (Claussen and Maycock, 1995; Sterck and Bongers, 1998). A large diameter at the beginning of development

TABLE 2. Least squares slopes of regression of log diameter (in centimeters) on log height (in meters) for unbranched and branched individuals of *Cecropia* species of Amazonian and southeastern regions of Brazil ($\log_{10}$ diameter = $\log_{10} a + b \log_{10}$ height), including 95% confidence limits of regression slopes and the coefficient of determination (r^2). Different letters within a row indicate significant differences.

| Species	Unbranched			Branched		
	Slope	r^2	N	Slope	r^2	N
C. concolor	0.930[a]	0.823***	17	1.066[a]	0.828***	21
C. palmata	0.755[a]	0.855***	12	1.140[b]	0.869***	18
C. purpurascens	0.749[a]	0.858***	11	0.734[a]	0.330**	20
C. sciadophylla	0.946[a]	0.886***	17	0.904[a]	0.720***	17
C. glaziovii	1.060[a]	0.791***	19	0.908[a]	0.644***	18
C. hololeuca	1.171[a]	0.820***	6	0.853[a]	0.420***	23
C. pachystachya	0.840[a]	0.773***	18	0.789[a]	0.688**	11
Cecropia spp.	0.962[a]	0.844***	100	1.084[a]	0.724***	128

** $P < 0.01$, *** $P < 0.001$.
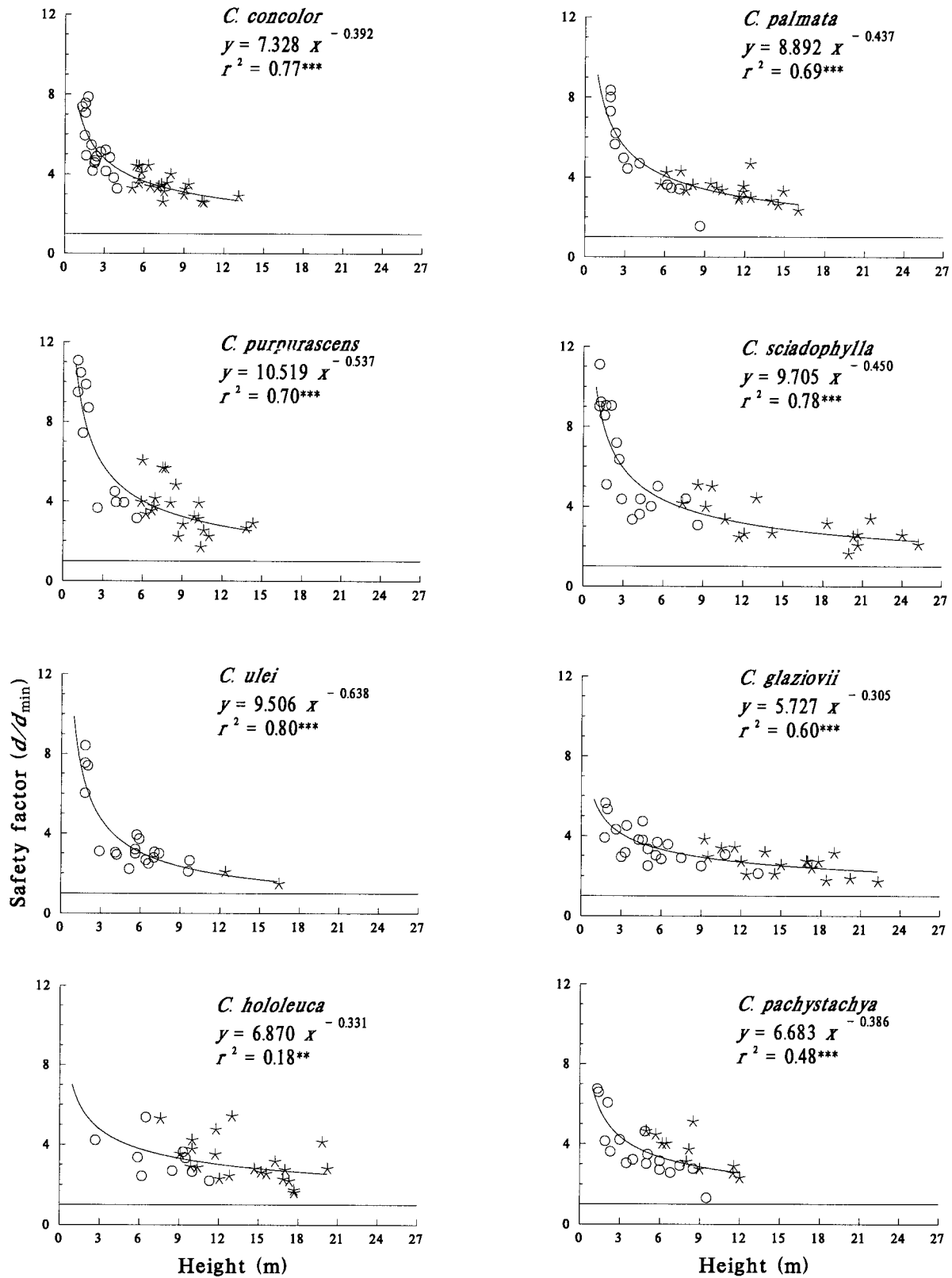
Fig. 3. Safety factor of stem diameter (d/d_{min}) as a function of height (H), where d is the actual stem diameter and d_{min} is the theoretical minimum diameter of elastic buckling (McMahon, 1973) of eight Brazilian *Cecropia* species ($\log_{10} d/d_{min} = \log_{10} a - b \log_{10} H$). Circles represent unbranched and asterisks represent branched individuals. Horizontal lines show $d = d_{min}$. Significance of fitted lines: ** $P < 0.01$, *** $P < 0.001$.
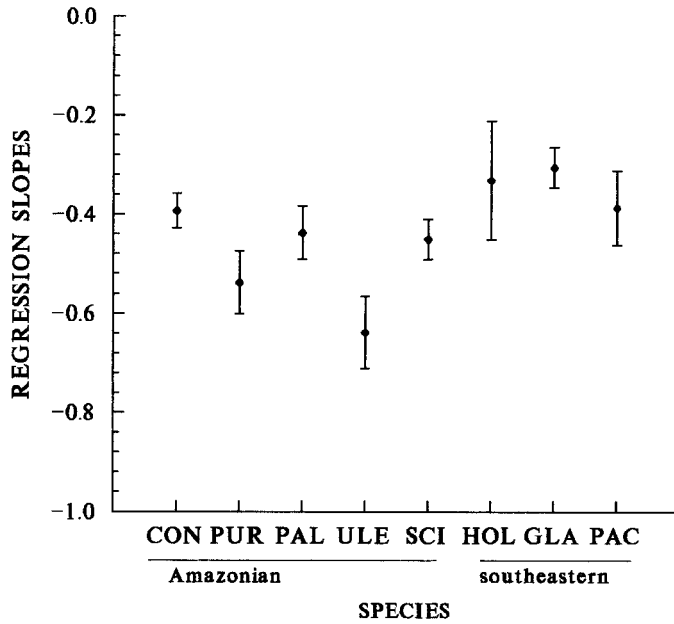
Fig. 4. Regression slopes and respective 95% confidence intervals of $\log_{10} d/d_{\min} = \log_{10} a - b \log_{10} H$, for eight Brazilian *Cecropia* species. Species abbreviations may be found in Table 1.

seems to be common in *Cecropia.* However, the differences of safety factor and height indicate that safety factors of some species decrease faster than others. In other words, height growth investment could be high in some species at the initial phases of tree development. This is the case for *Cecropia ulei* and *C. purpurascens.* These two species showed steeply decreasing safety factors in plants up to 6 m in height associated with their low diameter–height exponents. The Amazonian species were thicker than the southeastern species comparing 1–2 m tall individuals. This trend could be related to the high rainfall of Amazonia in contrast to southeastern Brazil, since internode lengths are correlated with rainfall in some *Cecropia* species (Davis, 1970; Sposito, 1999).

In comparisons of values from our study with other Cecropiaceae (Table 7), similar exponents were found. The exception was *Pourouma bicolor,* in which the slope of regression between height and diameter of 6–24 m tall trees conforms to the elastic similarity model (King, 1996). However, a previous study considering another height range of the species (1–35 m) found the regression slope for *P. bicolor* to be significantly lower than that predicted by the elastic similarity model (Rich et al., 1986).

Although *Cecropia* species do not conform to elastic similarity model, we used modulus of elasticity ($E = 8.5 \times 10^8$ kg/m^2) and density ($\rho = 4.1 \times 10^2$ kg/m^3; green wood density) of *Cecropia* sp. wood (Mainieri and Chimelo, 1989) to calculate theoretical minimum buckling diameter as in McMahon (1973). Using these values, the buckling limit for *Cecropia* spp. ($0.001 \ h^{3/2}$; d and h in metres) is very close to McMahon's buckling limit. Specific gravity of *Cecropia* wood is ~2.5–5.5 $\times 10^2$ kg/m^3 (Bonsen and ter Welle, 1983). *Cecropia glaziovii* had a mean value of 3.6×10^2 kg/m^3 (A. Fidalgo, Universidade de São Paulo, personal communication). Calculations of safety factors should be viewed only as an approximation because *Cecropia* species have hollow stems with the hollow increasing in diameter with height in the lower part of the

TABLE 3. Regression of number of first-order branches (*B*) as a function of height (in meters) for seven *Cecropia* species of Amazonian and southeastern regions of Brazil ($\log_{10} B = \log_{10} a + b \log_{10}$ height) and the coefficient of determination (r^2). Adjusted intercepts were calculated with a common slope $b = 1.741$. Different letters indicate significant differences (ANCOVA and Scheffé test, $P < 0.05$). *F* values may be found in the text. *N* values as in Table 2.

Species	Intercept (log *a*)	Slope (*b*)	r^2	Adjusted intercept
C. concolor	−0.381	1.563	0.434**	−0.624[a]
C. plamata	−1.366	2.561	0.752***	−0.636[a]
C. purpurascens	−0.347	1.447	0.156[NS]	—
C. sciadophylla	−0.963	1.728	0.469*	−1.098[b]
C. glaziovii	−1.033	1.663	0.438**	−1.246[b]
C. hololeuca	−1.002	1.691	0.334**	−1.172[b]
C. pachystachya	−0.301	1.205	0.228[NS]	—

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS: not significant.

stem. Evaluating the effect of hollow stems in mechanical support of *Cecropia* requires destructive measures and it was not the aim of our study, since tree cutting is rarely permitted in biological reserves. However, one of the consequences of having a hollow stem is related to the flexural stiffness, i.e., the ability of any mechanical support member to resist bending (Niklas, 1994). Flexural stiffness is the product of Young's modulus of elasticity *E* and the second moment of area *I*. Young's modulus is the ratio of stress to strain measured for an elastic material within its proportional limits of loading. The second moment of area mathematically quantifies the ability of a support member to resist deformation and depends on size, shape, and geometry. Thus, flexural stiffness can be increased by using materials with large *E* or by increasing the

TABLE 4. Regression of number of leaves (*L*) on height (in meters) for eight *Cecropia* species of Amazonian and southeastern regions of Brazil ($\log_{10} L = \log_{10} a + b \log_{10}$ height). Regressions of unbranched individuals were not compared. Adjusted intercepts calculated with a common slope $= 1.627$, for branched individuals. *F* values may be found in the text. Different letters in the same column indicate significant differences (ANCOVA and Scheffé test, $P < 0.05$). *N* values are as in Table 2.

Species	Intercept (log *a*)	Slope (*b*)	r^2	Adjusted intercept
C. concolor				
unbranched	0.815	0.588[a]	0.384**	—
branched	0.314	1.748[b]	0.477***	0.255[a]
C. palmata				
unbranched	1.115	0.032	0.002[NS]	—
branched	−0.081	2.276[b]	0.700***	0.387[a]
C. purpurascens				
unbranched	0.762	0.231	0.139[NS]	—
branched	0.987	0.896	0.069[NS]	—
C. sciadophylla				
unbranched	1.001	0.129	0.109[NS]	—
branched	−0.008	1.762[b]	0.496**	−0.071[b]
C. ulei				
unbranched	0.965	−0.219	0.111[NS]	—
C. glaziovii				
unbranched	0.670	0.847[a]	0.572**	—
branched	−0.113	1.722[b]	0.430**	−0.223[b]
C. hololeuca				
unbranched	0.908	0.261	0.375[NS]	—
branched	0.098	1.585[b]	0.320**	−0.161[b]
C. pachystachya				
unbranched	0.965	0.449[a]	0.366**	—
branched	1.028	0.890	0.181[NS]	—

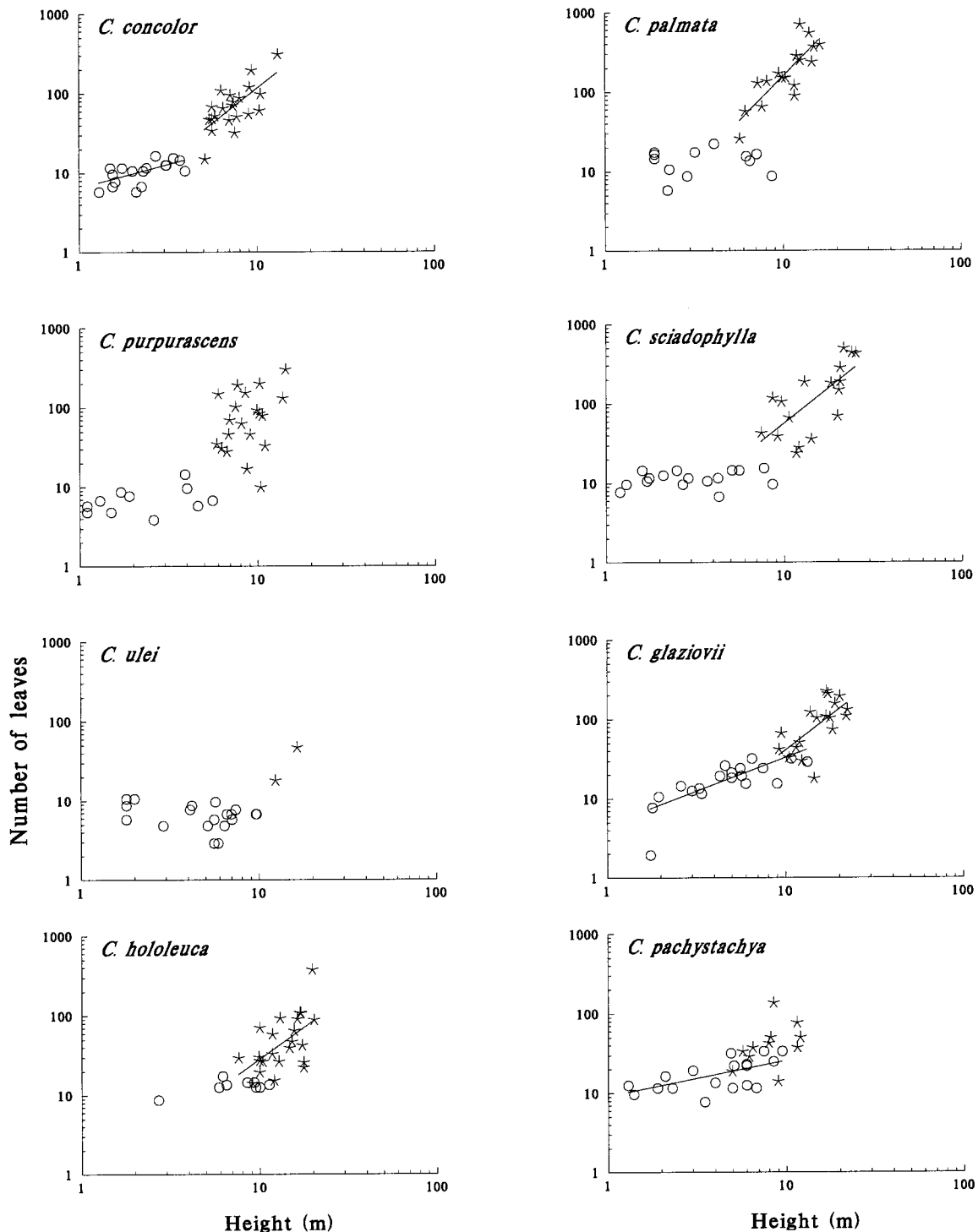** $P < 0.01$, *** $P < 0.001$, NS: not significant.

Fig. 5. Least squares regressions of number of leaves (*L*) on height (*H*) for eight *Cecropia* species of Amazonian and southeastern Brazil ($\log_{10} L = \log_{10} a + b \log_{10} H$). Circles represent unbranched individuals and asterisks represent branched individuals.

second moment of area *I* (Niklas, 1994). The effect of having a hollow stem can be evaluated by comparing the critical buckling length of hollow and solid columns, with equivalent external radii. Considering the same moduli of elasticity, a hollow beam can be extended in length by 26% the length of a solid counterpart with the same diameter before it reaches its critical length (Niklas, 1992, p. 154). The comparison with

beams could be extended to cylindrical stems. During ontogeny, however, *I* values should be altered, once secondary growth of basal portions of stem modifies the stem geometry. Possible changes in *E,* green wood density, stem taper, and ratio of crown mass to stem mass could also result in some ontogenetic changes in safety factor other than those inferred from the diameter–height exponents. Therefore, mechanical

TABLE 5. Regression of number of leaves (*L*) on number of branches (*B*) of seven *Cecropia* species of Amazonian and southeastern regions of Brazil (*L* = *a* + *bB*) and the coefficient of determination (*r²*). Different letters indicate significant differences (ANCOVA and Scheffé test, *P* < 0.05). *F* values may be found in the text. *N* values are as in Table 2. Common slope = 8.432 and common adjusted intercept = −0.088 for species that did not have different slopes.

Species	Intercept (*a*)	Slope (*b*)	*r²*
C. concolor	21.169	5.250[a]	0.877***
C. palmata	11.352	9.131[b]	0.918***
C. purpurascens	11.013	5.466[a]	0.949***
C. sciadophylla	−0.648	10.383[b]	0.965***
C. glaziovii	2.347	9.705[b]	0.906***
C. hololeuca	−9.987	10.472[b]	0.975***
C. pachystachya	7.140	9.431[b]	0.952***

*** *P* < 0.001.

TABLE 6. Regression of total leaf area (*A*) on height for eight *Cecropia* species of Amazonian and southeastern regions of Brazil ($\log_{10} A = \log_{10} a + b \log_{10}$ height) and the coefficients of determination (*r²*). Adjusted intercepts were calculated with a common slope = 1.695. Different letters in the same column indicate significant differences (ANCOVA and Scheffé test, *P* < 0.05). *F* values may be found in the text. *N* values are as in Table 1.

Species	Intercept (log *a*)	Slope (*b*)	*r²*	Adjusted intercept
C. concolor	−0.765	1.838	0.810***	−0.676[ab]
C. palmata	−0.650	1.766	0.701***	−0.591[bc]
C. purpurascens	−0.607	1.683	0.777***	−0.615[ab]
C. sciadophylla	−0.197	1.557	0.796***	−0.302[c]
C. ulei	−0.469	1.037	0.471***	−0.938[a]
C. glaziovii	−0.840	1.921	0.804***	−0.648[ab]
C. hololeuca	−0.782	2.031	0.675***	−0.440[bc]
C. pachystachya	−0.664	1.769	0.752***	−0.611[ab]

*** *P* < 0.001.

support in *Cecropia* needs a further approach that considers the particularities of the stem geometry and ontogenic changes.

Crown allometry—The relationships between height and crown characteristics of the *Cecropia* species studied were very similar. In general, differences of regression intercepts were related to differences in branching height and leaf size of species. The allometry of the eight *Cecropia* species of the two regions of Brazil is broadly similar to that of *C. obtusifolia* in México (Alvarez-Buylla and Martinez-Ramos, 1992). Nonetheless, some crown features should be emphasized. The differences found in number of leaves per branch in *C. concolor* and *C. purpurascens* suggest differences in birth and mortality rates of leaves among species. More evidence for difference in leaf life span of species was found for unbranched *C. concolor, C. glaziovii,* and *C.pachystachya* trees. These individuals showed a significant increase in number of leaves with height, perhaps indicating a high leaf production rate. This is a relevant factor in myrmecophytic species be-

cause the production rate of Müllerian bodies in *Cecropia* declines rapidly and regularly as leaves age (Folgarait and Davidson, 1994). If *Cecropia* species have differences in their leaf production rate, this will have a direct consequence on the mutualistic relationship with ants, because plants that produce more leaves will be a better resource for ants.

Cecropia ulei differs from the other species in that it seldom branches. Based on the regression analysis, it was the species that showed the lowest increment in diameter per unit of height and had few leaves at the apex when adult. This mechanical design may be found in understory plants protected from strong winds (Holbrook and Putz, 1989). The species could have limited growth because of its small total leaf area and low light levels in the understory. Furthermore, continued growth in height without increasing diameter would increase the likelihood of breakage. Although mechanical features of *Cecropia* wood apparently permit growing with low safety factors, *C. ulei* adults are rare in open windy habitats, which could help explain why *C. ulei* is less frequent than other
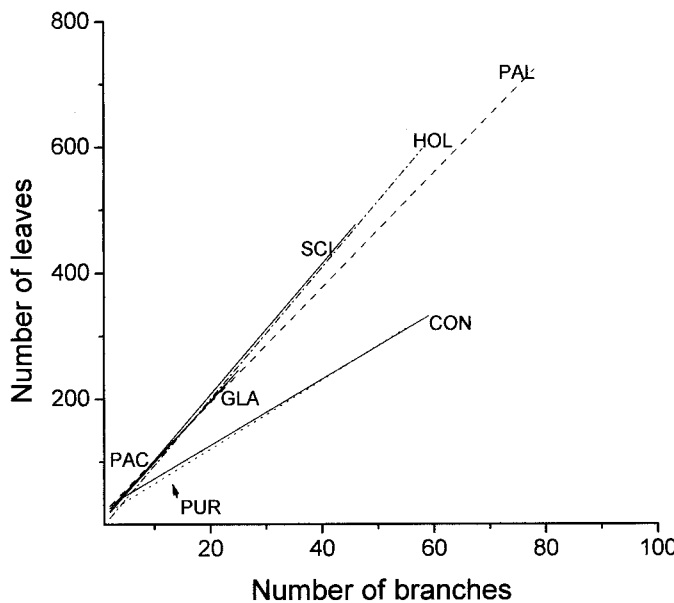

Fig. 6. Fitted least squares regression lines of number of leaves (*L*) on number of branches (*B*) of seven *Cecropia* species of Amazonian and southeastern Brazil (*L* = *a* + *b B*). Species abbreviations may be found in Table 1.
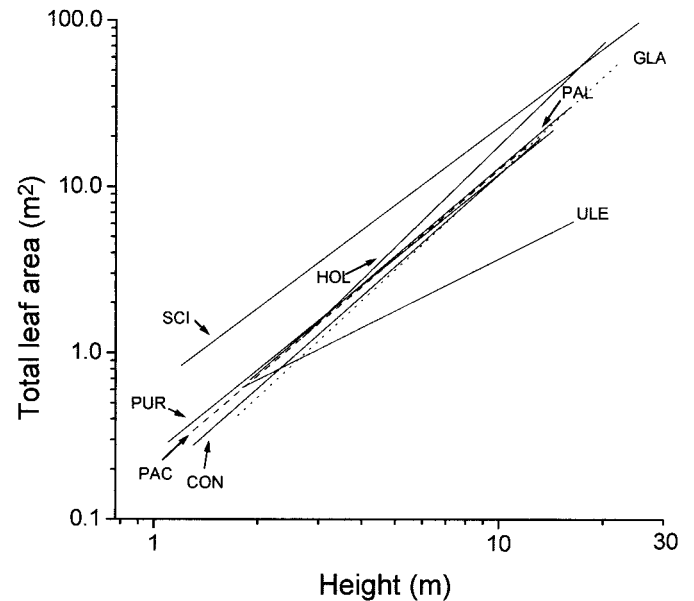

Fig. 7. Fitted least squares regression lines of total leaf area (*A*) on height (*H*) for eight *Cecropia* species of Amazonian and southeastern Brazil ($\log_{10} A = \log_{10} a + b \log_{10} H$). Species abbreviations may be found in Table 1.

TABLE 7. Parameters of least squares linear regressions between log diameter and log height of some species of Cecropiaceae ($\log_{10}$ diameter = $\log_{10} a + b \log_{10}$ height) and coefficients of determination (r^2). N = sample size.

Species	Intercept	Slope	r^2	Height range (m)	N	Location[a]
C. sciadophylla	−0.018	0.906	0.810	1–9.7	91	Manaus/Brazil (1)
C. obtusa	−0.075	0.894	0.820	1–5.0	71	Carajás/Brazil (2)
C. obtusifolia	−0.018	1.069	0.953	1–35.0	142	México (3)
Pourouma bicolor	−0.35	1.24	0.956	1–35.0	50	Costa Rica (4)
Pourouma bicolor	—	0.77	—	1–6.0	—[b]	Costa Rica (5)
Pourouma bicolor	—	1.68	—	6–24.0	—[b]	Costa Rica (5)

[a] References: (1) Hay (1982) (recalculated); (2) F. A. M. Santos and J. D. Hay (unpublished data); (3) Alvarez-Buylla and Martinez-Ramos (1992); (4) Rich et al. (1986) [diameter in metres in the manuscript; convert to centimetres by subtracting 2, i.e., −log(100)], original manuscript cites *P. aspera*, which is a synonym of *P. bicolor* (Berg, Akkermans, and Van Heusden, 1990); (5) King (1996).

[b] N for the two height classes together = 43.

Amazonian *Cecropia* species. Moreover, since number of spadices and number of branches are positively related (Alvarez-Buylla and Martinez-Ramos, 1992), the absence of branches may reduce the production of spadices, and consequently of fruits and seeds, even if it could compensate with more spadices or more fruits per spadice.

Habitat and allometry—*Cecropia pachystachya*–*C. hololeuca* and *C. concolor*–*C. sciadophylla* are the two pairs of species that represent the extremes of open and forested habitats in both Brazilian regions. Comparing diameter–height regressions of these species, we found there were no significant differences on slopes. Significant differences were found for the intercepts which were related to adult size. Thus, in a general way, the allometric relationships in different species of *Cecropia* seem to follow the same model, with some variations associated with adult sizes. Whether the scaling relationships were phylogenetically constrained or evolved independently remains to be studied. Another aspect that should be investigated is related to intraspecific variation in trunk allometry, with respect to wind stress, when plants grow in open and protected sites. Diameter–height relationships could change when plants are growing in dense stands, protected from wind effects (Holbrook and Putz, 1989).

Life span and allometry—A relationship between tree allometry and short life span was suggested by Alvarez-Buylla and Martinez-Ramos (1992) for *Cecropia obtusifolia*. According to these authors, if *Cecropia* continue to grow with the same allometric pattern, it would eventually reach the buckling limit. The incapacity to alter the relationship between diameter and height growth would promote tree senility. King (1996) found that longer-lived species showed greater increase in crown width and trunk diameter with increasing height, over the upper end of the height range, than did shorter-lived species. It is probable that studied *Cecropia* species would have differences in their life spans. Life span would increase in a gradient from open to forest habitats, and taller species with larger leaf area would be the longer lived. Further comparative studies are needed to determine the life span of the *Cecropia* species and its relationship with tree allometry. Differences of some crown characters of *Cecropia* could be more than "variations on a theme" and could be the determinants of the life history traits of these species.

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