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Architectural patterns of eight *Cecropia* (Cecropiaceae) species of Brazil

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Summary

Architectural patterns of eight *Cecropia* species were studied in Amazonian and Southeastern Brazil. Height, diameter, height of first branching, number of branches and leaves, leaf area, internode length and branching ratio were measured for undamaged trees. The Amazonian species *C. concolor, C. palmata, C. purpurascens, C. ulei* and *C. sciadophylla* were studied in Manaus. *Cecropia glaziovii, C. hololeuca* and *C. pachystachya* were studied in Linhares, Espírito Santo. All except *C. hololeuca* and *C. sciadophylla* are myrmecophytes. In both areas, size and architectural characters are displayed as a gradient from open habitats to forest. *Cecropia hololeuca* and *C. sciadophylla* are common in forests and had similar architectures, with low branching ratios, and a height of first branch of around 9 m, about 3 m higher than the other species. The branching pattern of both species and the maximum height recorded (≈ 20–25 m respectively) allow them to remain in the canopy longer than the other *Cecropia species. Cecropia concolor* and *C. pachystachya* measure up to 13 m in height and are typical of open habitats. The remaining species occupy forest margins and are intermediates between these two extremes.

Key words: branching ratio, myrmecophytes, pioneers, tropical forest.

1. Introduction

Comparative studies of plant morphology are useful tools to investigate ecological and evolutionary processes within and among related species. Size and form variations reflect the environmental conditions of the species habitat, although individuals are subjected to phylogenetic constraints which may limit the developmental possibilities available.

Particularly in trees, size, form and resulting canopy structure are directly associated with competitive ability and successional status. Horn (1971) proposed two extreme tree strategies, the monolayer and the multilayer, based on crown characters of temperate trees. Multilayer form is associated with early successional species, characterised by a number of overlapping leaves randomly distributed throughout the crown. Monolayer form characterizes later successional species, having leaves arranged in one or very few layers, with little self-shading. In this sense, branching pattern has important implications for leaf position and light interception by trees.

Branching patterns of trees can be quantified by the branching ratio or bifurcation ratio, the ratio of the number of terminal to proximal branches (Strahler 1957). The branching ratio was thought to be a species specific constant related to successional status, with lower branching ratios associated with monolayered, late successional trees, and high ratios with much-branched early successional trees (Whitney 1976). However, some studies found that the branching ratio could vary between individuals of the same species in contrasting light habitats, although plants growing in open habitats developed higher branching ratios than plants in shady habitats (Steingraeber et al. 1979; Pickett & Kempf 1980).

The crown size and form of trees may be an indicator of light conditions of plant growth. Plants growing in the open usually display low, spherical crowns, while forest trees tend to have shallow crowns and long trunks (Hallé et al. 1978; Torquebiau 1986). Branching height is a characteristic of species that varies as a function of light conditions. Moreover, branching height is a character directly associated with a definite forest

stratum (TORQUEBIAU 1986) and determines the space that a tree will occupy in the canopy.

In this study, we focus on patterns of variation in plant size and form of Brazilian *Cecropia* (Cecropiaceae) species. *Cecropia* is a genus of neotropical pioneer trees with hollow stems and branches, typically occupied by mutualistic ants (mainly *Azteca* sp., Formicidae, Dolichoderinae). They are fast-growing and are normally associated with initial phases of succession (WHITMORE 1989; ALVAREZ-BUYLLA & MARTINEZ-RAMOS 1992). Ants colonize myrmecophytic species earlier in life, when a velvet-like structure, termed trichilium, is produced at the base of each leaf petiole. Glycogen rich corpuscles (RICKSON 1971; 1976), called Müllerian bodies, are produced by the trichilia and harvested by ants as food. Trees benefit from ant association through protection against herbivores (SCHUPP 1986; DAVIDSON et al. 1991; ROCHA & BERGALLO 1992; VASCONCELOS & CASIMIRO 1997) and vine infestation (JANZEN 1969) (but see ANDRADE & CARAUTA 1982; PUTZ & HOLBROOK 1988; WETTERER 1997 for a counterview). Two Brazilian species, *Cecropia sciadophylla* and *C. hololeuca,* lack trichilia and are considered non myrmecophytes (BERG 1978; BENSON 1985), the former in Amazonia and the latter in the Southeast region.

Some *Cecropia* species show more tolerance to shade than others (DAVIDSON & FISHER 1991; FOLGARAIT & DAVIDSON 1994), and are more common near or within forests. Brazilian *Cecropia* species that occur in open or forest habitats show macromorphological differences in branching patterns and leaf characteristics. Therefore,

some of the morphological traits associated with sun or shade plants may be present in the Brazilian *Cecropia* species. The purpose of this study was to compare size and form of eight *Cecropia* species in two regions of Brazil, emphasizing aspects related to branching patterns, leaf area and branching ratio, and their occurrence in a gradient from open to forest habitats. Comparisons of the allometric relationships between crown and height complement the morphological analysis of these *Cecropia* species and can be found in SPOSITO & SANTOS (2001).

2. Materials and methods

2.1. Species and study areas

Eight *Cecropia* species were studied in disturbed or secondary forest habitats, in Brazilian Amazonia (5 spp.) and southeastern Brazil (3 spp.). Sites visited in Amazonas state were the Fundação Universidade do Amazonas (FUA), the Reserva Ducke, owned by the Instituto Nacional de Pesquisas da Amazônia (INPA), and the experimental area of Empresa Brasileira de Pesquisa Agropecuária – EMBRAPA – Amazônia Ocidental (Table 1). Species sampled were *Cecropia concolor* Will., *C. palmata* Will., *C. purpurascens* C. C. Berg, *C. ulei* Snethl. and *C. sciadophylla* Mart. (non-myrmecophyte) (Fig. 1). *Cecropia concolor* is commoner in open fields and abandoned agricultural lands. *Cecropia palmata* and *C. purpurascens* occur in open habitats or forest borders. *Cecropia sciadophylla* occurs in gaps and along forest borders, sometimes forming dense, monospecific edges between

Table 1. Site characteristics where the Brazilian *Cecropia* species were sampled.

Study site	Geographic location	Vegetation	Rainfall Temperature
Amazonas state			
EMBRAPA – Amazônia Ocidental	Manaus – Itacoatiara road, 29 km north of Manaus (2° 51′ S; 59° 52′ W)	mosaic of pastures, fallow agricultural land and secondary forest	2500 mm* 25°C
Fundação Universidade do Amazonas – FUA	inside the city of Manaus	20–25 m tall forest	
Reserva Ducke – (INPA)	Manaus – Itacoatiara road, 26 km north of Manaus	30–40 m tall forest	
Espírito Santo state			
Reserva Florestal de Linhares	Linhares – São Mateus road, 30 km north of Linhares (19° 06′ S; 39° 45′ W)	20–25 tall forest; "mussununga" and "nativo"@	1242 mm# 23°C

@ Mussununga and nativo are vegetation types associated with sandy soils; the former is a 10–15 m high forest and the latter is formed by grassy fields with scattered shrubs and small trees forming thickets (JESUS 1988; PEIXOTO & GENTRY 1990)
* Mean annual rainfall and temperature between 1971 and 1993 (CABRAL 1996)
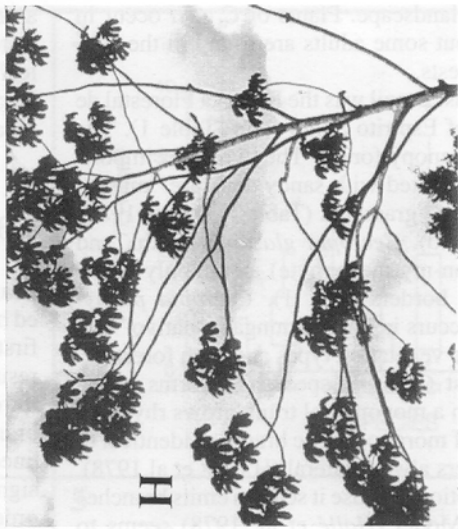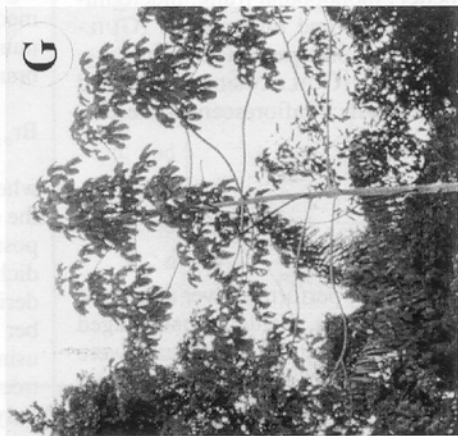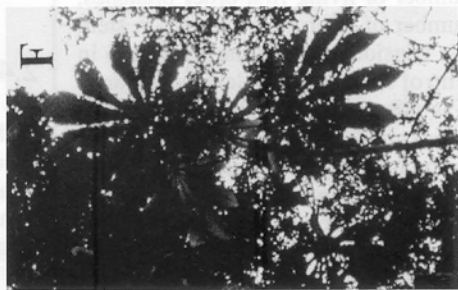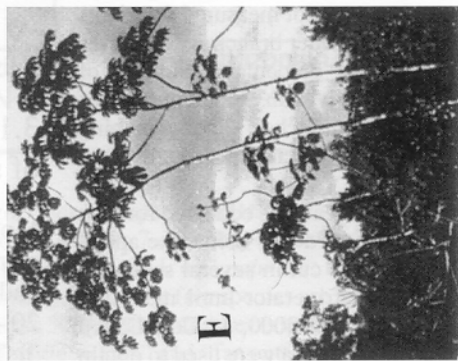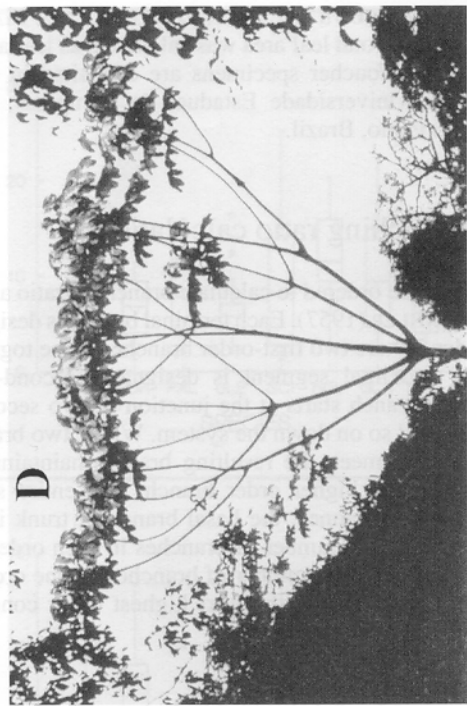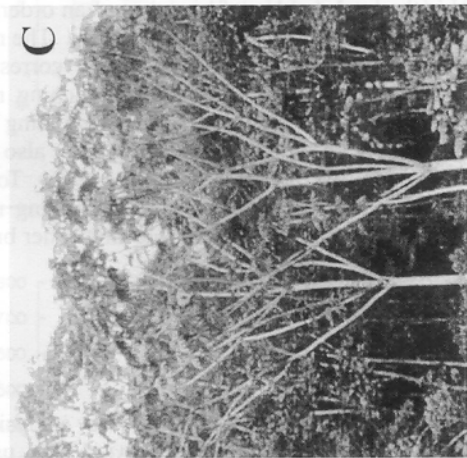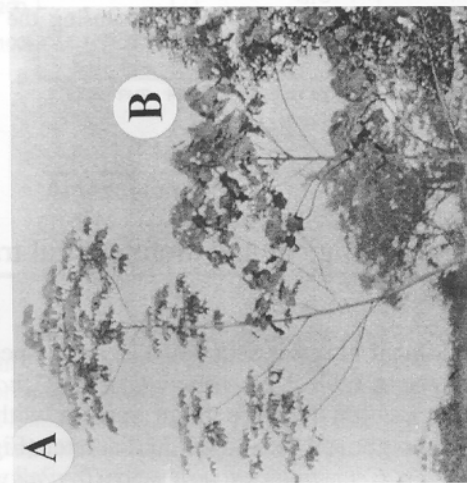# Mean annual rainfall and temperature between 1975 and 1993

Fig. 1. Brazilian *Cecropia* species studied. (A) *Cecropia concolor*; (B) *C. purpurascens*; (C) *C. sciadophylla*; (D) *C. hololeuca*; (E) *C. palmata*; (F) *C. ulei*; (G) *C. pachystachya*; (H) *C. glaziovii*.

the forest and the open landscape. Plants of *C. ulei* occur in forest gaps and edges, but some adults are found in the subcanopy of secondary forests.

The study site in Southeast Brazil was the Reserva Florestal de Linhares, in the North of Espírito Santo state (Table 1). The 218 km² is mostly high canopy forest. The two other important vegetation types associated with sandy soils are "mussununga" forest, and "nativo" grassland (Table 1) (JESUS 1988; PEIXOTO & GENTRY 1990). *Cecropia glaziovii* Snethl. and *C. hololeuca* Miq. (non-myrmecophyte) commonly grow along roads and forest borders (Fig. 1). *Cecropia pachystachya* Trécul (Fig.1) occurs in "mussununga", "nativo" and transitions between these vegetation types and high forest.

The architecture of most *Cecropia* species conforms to the Model of Rauh, in which a monopodial trunk grows rhythmically, developing rows of morphogenetic branches identical to the trunk and with flowers always lateral (HALLÉ et al.1978). *Cecropia ulei* is an exception because it seldom emits branches (Berg 1978). Corner's Model (*Hallé* et al. 1978) seems to describe its architecture better: monopodial trunk, indeterminate growth, lateral inflorescences and no branches (GUILLAUMET 1984). Reproduction is concurrent with branching, except for *C. concolor, C. ulei* (GUILLAUMET 1984) and *C. pachystachya* (pers. obs.) in which inflorescences are produced before branching.

2.2. Measurements of plant size

Measurements of each species were performed over a range of heights from ≈ 1 m tall to large adults, including undamaged individuals along forest trails. At least 30 individuals were measured per species, except *Cecropia pachystachya* with 29 individuals and *C. ulei* with 21. For each tree we registered height, circumference at 1.3 m high (to obtain diameter), height of first branch, number of living first-order branches, number of leaves and number of internodes in an 1-m stem segment. Total height was considered up to the crown top in branching trees, or to the tip of the apical stipule in pole plants. Height of first branch was measured even if the branch had died and fallen. Height was measured with a tape, pole or clinometer depending on plant height. Circumference was measured for the last internode in plants shorter than 1.3 m. If stilt roots were present, circumference was measured ≈ 30 cm above them.

Number of internodes was counted in an 1-m stem segment between 1.5 and 2.5 m high, and mean internode length was obtained by division. Internodes were not measured for plants less than 2.5 m tall. Number of first order branches and leaves was counted directly using 8 × 24 binoculars. Number of leaves per branch was estimated by division of total number of leaves per number of first-order branches. The branching pattern was drawn for each tree to compare species architecture.

From most of the individuals one leaf was collected for area measurement. When possible, the third leaf below the apical meristem was chosen. Each leaf was cut in several segments and stored in a plastic bag in a refrigerator until measured using a Li-Cor area meter (Model LI-3000, Li-Cor, USA). Branch and leaf number and total leaf area were used to obtain

an estimate of crown size (ALVAREZ-BUYLLA & MARTINEZ-RAMOS 1992). Total leaf area was calculated as leaf area times leaf number. Voucher specimens are deposited in the UEC Herbarium, Universidade Estadual de Campinas, in Campinas, São Paulo, Brazil.

2.3. Branching ratio calculation

Branches were ordered to calculate branching ratio as proposed by STRAHLER (1957). Each terminal branch is designated as first-order. Where two first-order branches come together, the resulting proximal segment is designated second-order. A third-order branch starts at the junction of two second-order branches, and so on down the system. Where two branches of unequal order meet, the resulting branch maintains the designation of the higher order branch. The entire system is ordered in this manner; the basal branch or trunk is thus of highest order. The number of branches in each order is summed. The ratio of the number of branches of one order to the number of branches of the next highest order constitutes a branching ratio (Br):

$$Br_{n:n+1} = N_n/N_{n+1},$$

where N is the total number of branches of an order, and n is the order number (STEINGRAEBER et al. 1979). The minimum possible value for this system is 2, which corresponds to dichotomous symmetry. In this study, branching ratio was derived as the antilog of the slope of the line relating log number of branches with order. Calculations may also be made using Motomura's formula (in WHITNEY 1976). To exclude trees beginning the branching process, branching ratio was only calculated for trees with 5 or more first-order branches.

2.4. Statistical analyses

Differences between means were assigned by analysis of variance (ANOVA) and the Tukey test (ZAR 1984), using log-transformed data (log_{10}) to obtain homoscedasticity. Data not transformed are summarized in figures using the box-plot diagrams of SYSTAT (1992).

3. Results

3.1. Morphological and architectural traits of species

Morphological characteristics of *Cecropia* species are summarized in Table 2. *Cecropia glaziovii, C. hololeuca* and *C. sciadophylla* were large species with adults 20–25 m height and 28–40 cm in diameter (Fig. 2 and 3, Table 2). *Cecropia concolor* and *C. pachystachya*
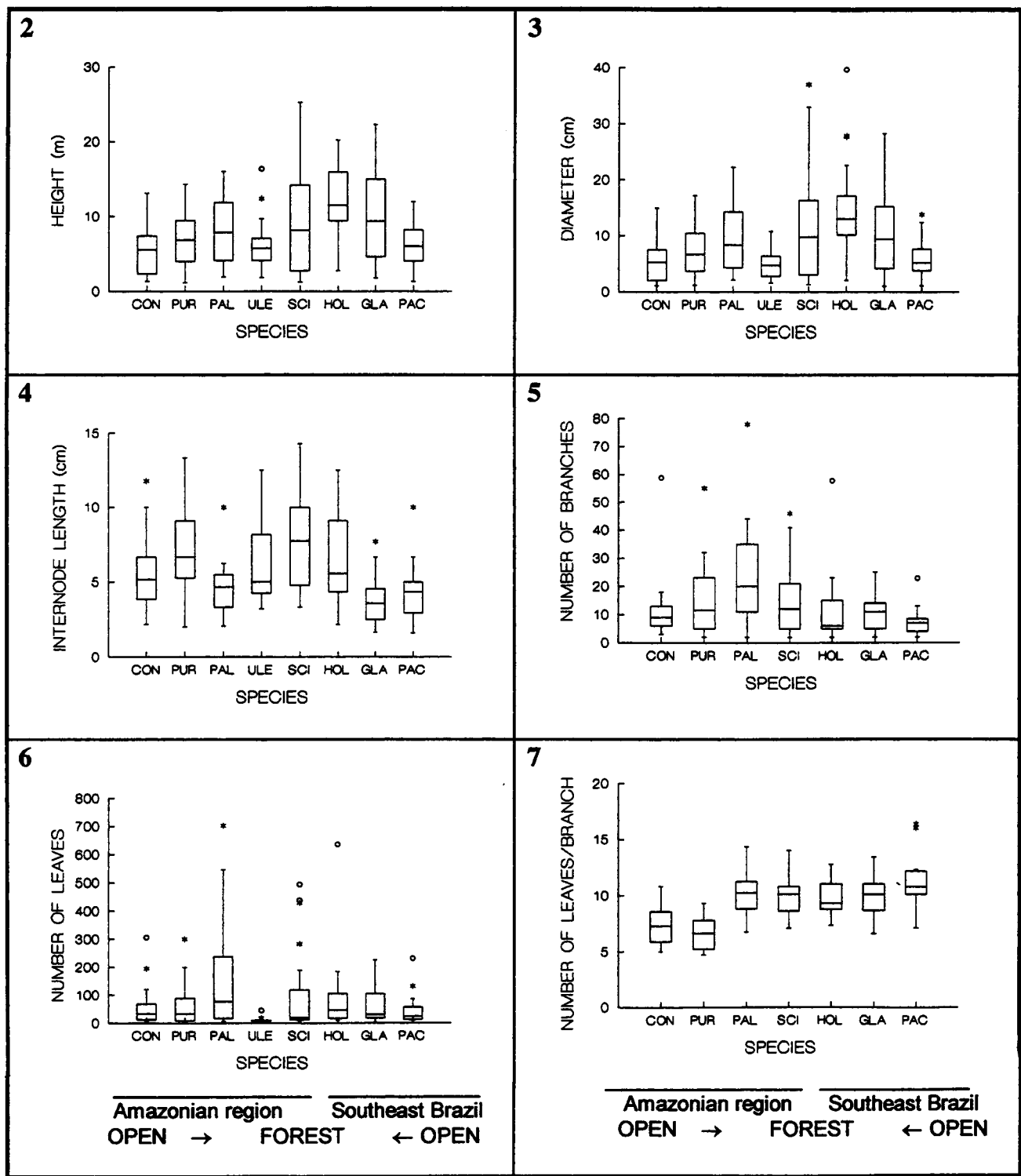
Fig. 2–7. Box-plots of morphological characteristics of eight *Cecropia* species in Brazil. 2. Height (m); 3. Diameter; 4. Internode length (cm); 5. Number of first order branches; 6. Number of leaves; 7. Number of leaves per branch. Species ordered from open to forest habitats are: CON = *C. concolor;* PUR = *C. purpurascens;* PAL = *C. palmata;* ULE = *C. ulei;* SCI = *C. sciadophylla;* HOL = *C. hololeuca;* GLA = *C. glaziovii;* PAC = *C. pachystachya.* The first five species are from Amazonia and the last three are from southeastern Brazil. In a box-plot graph, the box comprises 50% of the data; the central line marks the median. Inner and outer fences are defined by interquartile ranges. Asterisks are "outside values" and "far outside values" are circles (SYSTAT, 1992).

Table 2. Morphological characteristics of eight *Cecropia* species of Brazil. cv = coefficient of variation (%). Values within a column sharing the same letter do not differ significantly (ANOVA and Tukey test, $P < 0.05$). All tests were performed in log-transformed variables. *F* values are in text.

Species		Height# (m)	Diameter# (cm)	Number of branches#	Number of leaves#	Number of leaves/branch*	Leaf area (m²)*	Heigh of first branch (m)*	Mean internode length (cm)*	Branching ratio*	Location
C. concolor		1.3–13.1	1.1–15	3–59	6–308	7.3 ± 1.7^a	0.1 ± 0.05^a	4.3 ± 1.0^a	5.5 ± 2.2^{abc}	6.3 ± 3.5^b	Manaus (AM)
	N	38	38	21	38	21	37	21	26	20	
	cv	–	–	–	–	22.8	56.0	23.8	40.4	55.5	
C. purpurascens		1.1–14.3	1.2–17.2	2–55	4–300	6.7 ± 1.4^a	0.2 ± 0.1^{ab}	5.8 ± 1.7^b	7.2 ± 2.8^c	5.3 ± 2.3^{ab}	Manaus (AM)
	N	31	31	20	31	20	29	20	25	15	
	cv	–	–	–	–	21.4	61	30	39.8	43.8	
C. palmata		1.9–16.0	2.1–22.3	2–78	6–703	10.1 ± 2.0^b	0.1 ± 0.1^a	5.8 ± 0.9^b	4.6 ± 1.7^{abc}	6.5 ± 3.4^b	Manaus (AM)
	N	30	30	18	30	18	29	18	24	17	
	cv	–	–	–	–	20.3	61	14.9	37.9	52.7	
C. ulei		1.8–16.4	1.6–10.8	4–7	3–47	–	0.3 ± 0.2^{bcd}	–	6.4 ± 2.9^{bc}	–	Manaus (AM)
	N	21	21	2	21	–	21	–	16	–	
	cv	–	–	–	–	–	74.2	–	45.9	–	
C. sciadophylla		1.2–25.2	1.3–37	2–46	7–496	10.0 ± 1.7^b	0.4 ± 0.3^{cd}	9.2 ± 2.4^c	7.9 ± 3.3^c	3.6 ± 1.1^a	Manaus (AM)
	N	34	34	17	34	17	31	17	24	14	
	cv	–	–	–	–	17.3	75.7	26.1	41.6	29.4	
C. hololeuca		2.7–20.2	2.1–39.8	2–58	9–638	9.7 ± 1.6^b	0.6 ± 0.4^d	8.8 ± 2.0^c	6.7 ± 2.9^c	3.6 ± 1.0^a	Linhares (ES)
	N	32	31	23	32	23	24	22	29	18	
	cv	–	–	–	–	16.2	64.6	22.9	43.8	28.4	
C. glaziovii		1.75–22.3	1–28.3	2–25	2–225	9.9 ± 1.8^b	0.3 ± 0.2^{bc}	9.6 ± 1.9^b	3.8 ± 1.6^a	7.2 ± 3.8^b	Linhares (ES)
	N	38	37	18	38	18	31	18	35	15	
	cv	–	–	–	–	17.7	74.6	19.4	42.1	52.1	
C. pachystachya		1.3–12	1.1–13.8	2–23	8–233	11.3 ± 2.8^b	0.2 ± 0.1^{abc}	6.3 ± 1.9^b	4.3 ± 1.8^{ab}	5.9 ± 2.2^{ab}	Linhares (ES)
	N	29	29	11	29	11	28	11	25	8	
	cv	–	–	–	–	25.2	73.3	30	42.9	36.9	

\# Minimun and maximum values observed   * Mean ±1 SD

C. concolor
$$\log y = -1.65 + 1.96x - 1.38x^2$$
$$r^2 = 0.34$$

C. palmata
$$\log y = -1.87 + 2.90x - 1.97x^2$$
$$r^2 = 0.30$$

C. purpurascens
$$\log y = -1.42 + 1.93x - 1.33x^2$$
$$r^2 = 0.43$$

C. sciadophylla
$$\log y = -1.31 + 2.38x - 1.33x^2$$
$$r^2 = 0.62$$

C. ulei
$$\log y = -1.63 + 2.44x - 1.23x^2$$
$$r^2 = 0.54$$

C. glaziovii
$$\log y = -2.43 + 4.04x - 2.06x^2$$
$$r^2 = 0.67$$

C. hololeuca
$$\log y = -3.53 + 6.94x - 3.63x^2$$
$$r^2 = 0.48$$

C. pachystachya
$$\log y = -1.78 + 2.29x - 1.24x^2$$
$$r^2 = 0.52$$

LEAF AREA (m²)
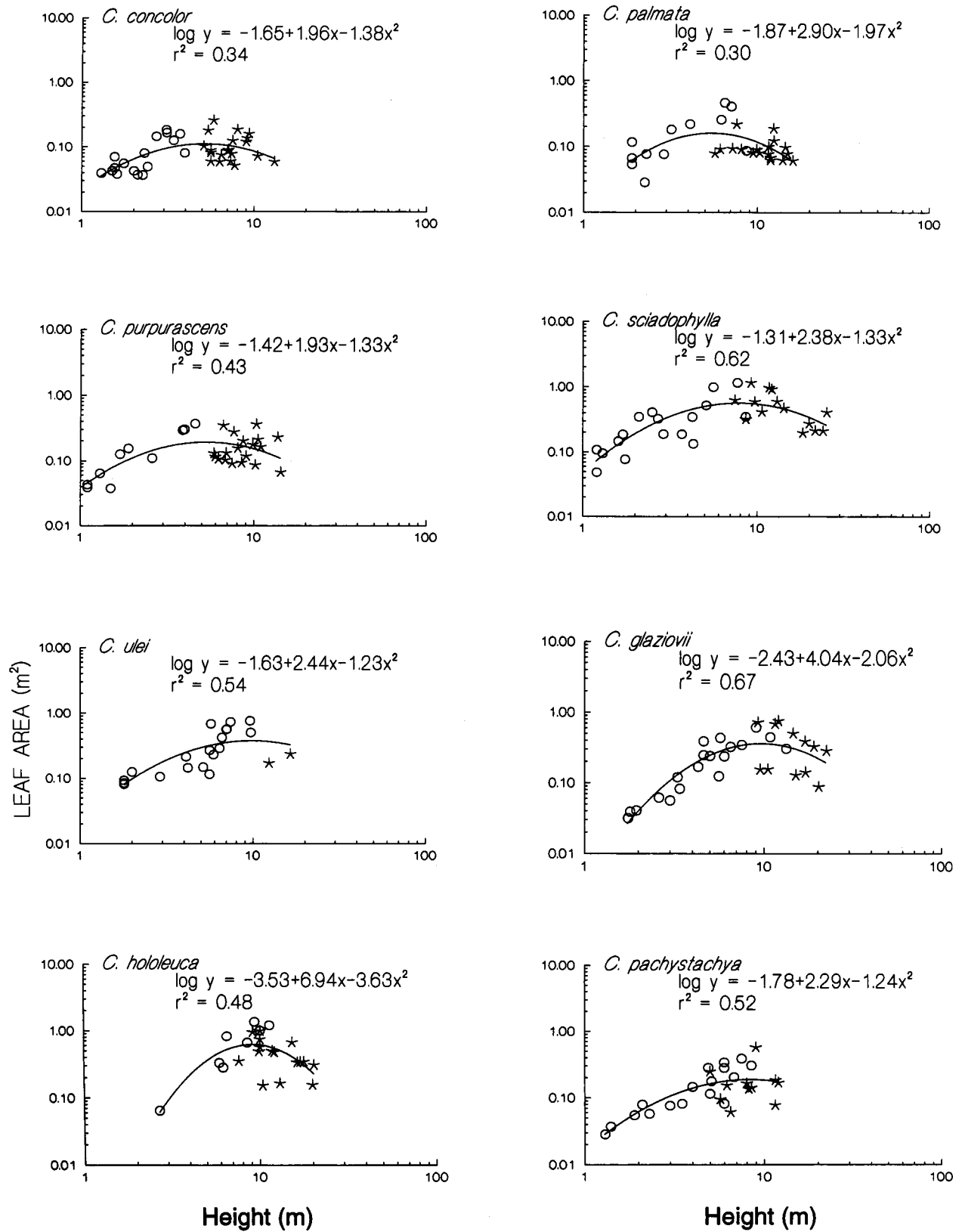
Height (m)   Height (m)

Fig. 8. Variation of individual leaf area (m²) as a function of height (m), in eight *Cecropia* species in Brazil. Circles represent unbranched individuals and asterisks represent branched individuals. Equations are for log-transformed variables.

were smaller, with maximum heights of about 13 m and diameters of 14–15 cm. *Cecropia purpurascens* and *C. palmata* showed a maximum height of 14 and 16 m, respectively, and were 17–22 cm in diameter. Two individuals of *C. ulei* measured 14–16.4 m in height, but these records represent "outlier" points in height range of this species. Most of the *C. ulei* trees did not surpass 10 m in height.

Internode length, despite the large intraspecific variation (*cv* about 40%; Table 2), differed significantly among the eight *Cecropia* species ($F = 10.23$; $P < 0.001$; $N = 8$). *Cecropia concolor, C. palmata, C. glaziovii,* and *C. pachystachya* had mean internode lengths between 3.8 and 5.5 cm, and the other species had means of 6–8 cm (Table 2, Fig. 4).

Cecropia pachystachya and *C. glaziovii* had fewer first order branches than the other species (maximum 23–25 branches, Table 2, Fig. 5). *Cecropia hololeuca* and *C. concolor* showed maximum of 58 and 59 branches, respectively, but most of the branching trees of these species had about 25 branches (Table 2, Fig. 5). Other species showed maxima ranging from 46 to 78 branches (Table 2). *Cecropia ulei* seldom branches (BERG 1978), although two very large individuals were found with 4 and 7 branches. Distribution of number of branches and leaves follows approximately the same pattern (Table 2, Fig. 5 and 6), because plants with fewer branches also have fewer leaves. Number of leaves per branch was significantly different among species (Table 2, $F = 16.4$; $P < 0.001$; $N = 7$); *Cecropia purpurascens* and *C. concolor* presented the lowest values (6.7–7.3), while the other species had 9.7–11.3 leaves per branch (Fig. 7).

Leaf area varies as a function of tree height, increasing as plants grow and diminishing after branching (Fig. 8). The curved patterns of leaf area variation and height were described by a quadratic regression model and explained between 30–67% of the variation of leaf area (Fig. 8). Leaf area was significantly different among species (Table 2, $F = 18.5$; $P < 0.001$; $N = 8$). *Cecropia sciadophylla, C. ulei, C. glaziovii* and *C. hololeuca* had leaves larger than those of other species (Fig. 9). All species showed high intraspecific coefficients of variation (Table 2), because of leaf area differences related to increasing height and high variation of leaf area between plants of similar height (Fig. 8). Total leaf area was larger for *C. sciadophylla* and *C. hololeuca* and smaller for *C. ulei* since it is seldom branched (Fig. 10).

The *Cecropia* species studied showed significant differences in height of first branching (Table 2, $F = 30.19$; $P < 0.001$; $N = 7$). *Cecropia sciadophylla, C. glaziovii* and *C. hololeuca* had higher means values about 9–10 m (Table 2, Fig. 11), while the others species branched between 4 and 6 m in height. The height of
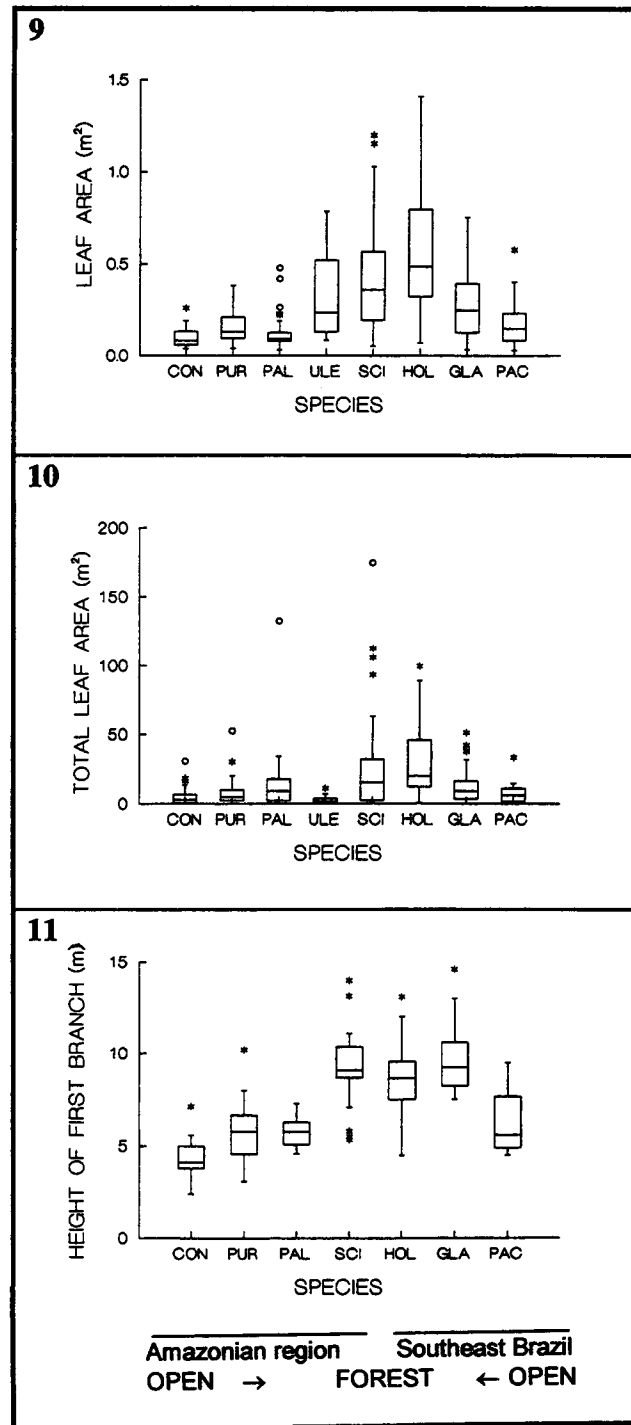

Fig. 9–11. Box-plots of morphological characteristics of eight *Cecropia* species in Brazil. 9. Leaf area (m^2); 10. Total leaf area (m^2); 11. Height of first branch. Species legends as in Fig. 2.

first branching is about 58–77% of total height in species and these proportions (arcsine transformed) were not significantly different among species ($F = 0.416, P > 0.05, N = 7$).

Cecropia glaziovii

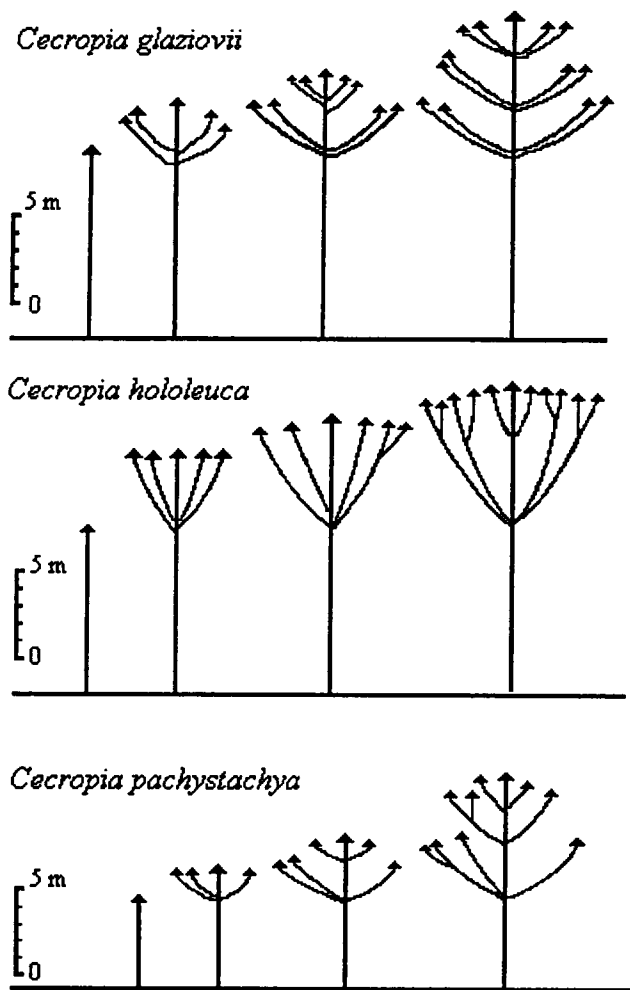*Cecropia hololeuca*

Cecropia pachystachya

Fig. 12. Branching patterns of three *Cecropia* species of Brazil, deduced through observation of developmental phases of species. Arrows represent indeterminate growth. *Cecropia sciadophylla* shows the same model as *C. hololeuca*, with orthotropic branches more vertical than the other species. *Cecropia palmata* is similar to *C. glaziovii* and *C. concolor* is similar to *C. pachystachya*. *Cecropia ulei* was not represented because it seldom branches.

The branching processes of the *Cecropia* species are represented in Fig. 12. When a plant begins branching, it typically emits 3–5 branches (range 1–6) from one or more neighboring nodes. After ≈1 m height growth by the major stem, 3–5 additional branches are produced, and so on. Branch orientation is orthotropic in the species studied, however *C. sciadophylla* and *C. hololeuca* have their orthotropic branches almost vertical while in the other species, branch position tends to horizontal (Fig. 1 and 12). The pattern of emission of higher order branches differed among the species. While *C. concolor*, *C. glaziovii*, *C. palmata* and *C. pachystachya* had more trees with second and third order branches, *C. holo-*

Table 3. Spearman coefficients of correlation between branching ratio and height and diameter of *Cecropia* spp. for branched individuals with at least 5 branches in Amazonian and Southeastern regions of Brazil.

Branching ratio			
Species	vs. Height	vs. Diameter	N
C. concolor	−0.01	−0.15	20
C. purpurascens	0.25	−0.75*	15
C. palmata	−0.07	0.02	17
C. sciadophylla	−0.35	−0.56*	14
C. hololeuca	0.04	0.14	17
C. glaziovii	0.33	0.27	14
C. pachystachya	0.06	−0.22	8

* $P < 0.05$

leuca, *C. sciadophylla* and *C. purpurascens* had individuals with fourth or fifth order branches. Consequently, branching ratios were significantly different among species ($F = 6.06$, $P < 0.001$, $N = 7$, Table 1). *Cecropia sciadophylla* and *C. hololeuca* showed branching ratios significantly lower than the remaining species (Table 2, Fig. 13), except *C. pachystachya* and *C. purpurascens*, which did not show significant differences with any species.

Cecropia species show different trends when branching ratio and tree size are related. Correlations between branching ratio and height were not significant for any species (Table 3); however, *Cecropia purpurascens* and *C. sciadophylla* showed significant correlations between branching ratio and tree diameter (Spearman rank correlation, $r_S = -0.74$, $P < 0.05$ and $r = -0.56$,
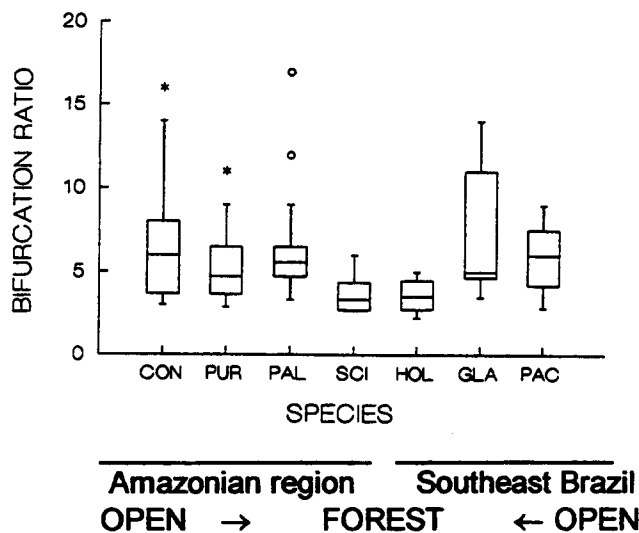

Fig. 13. Box-plots of branching ratio of eight *Cecropia* species of Brazil. Species legends as in Fig. 2.

$P < 0.05$ respectively). Branching ratios tended to diminish as diameter increases, i.e. more bifurcated trees had thicker stems in both species. The remaining species did not show significant correlations between branching ratio and diameter.

3.2. Plant architecture and habitats

An overview of vegetative character comparisons in the species studied indicates a gradient of size related to habitat. The same gradient occurs in Amazonia and southeastern Brazil. Plant size determined two extremes: small species of open habitats (*C. concolor* and *C. pachystachya*) and large secondary forest species (*C. sciadophylla* and *C. hololeuca*) (Fig. 2, 3). Leaf area and total leaf area showed a gradient of size as well, increasing from open to forest habitats (Fig. 9, 10). *Cecropia ulei* was not included in the gradient analysis because it can be found in both habitats and because it seldom branches. However, it was placed near the forest species because of its large leaf area. The remaining species could be considered intermediate, with different combinations of features between these two extremes. Internode length was longer in forest species than in open-area species (Fig. 4). Number of first order branches (Fig. 5) was higher in species that branch at lower heights (Fig. 13). Branching ratio decreases from open to forest habitats (Fig. 13).

Cecropia hololeuca and *C. sciadophylla* are described here as forest species. However, they are not invariably forest-inhabiting. Both species can grow as isolated individuals in open habitats, as can the other *Cecropia* species. *Cecropia sciadophylla* has a different situation in Amazonia. Near Manaus, in the experimental area of Biological Dynamics of Forest Fragments Project (BDFFP), maintained by INPA and Smithsonian Institution (SI,Washington, DC, USA), the existence of dense, monospecific edges of *C. sciadophylla* between the forest and open landscape is common (BIERRE-GAARD & STOUFFER 1997). We did not have the opportunity to observe these edges in our study areas. These monospecific edges could be an effect of large deforested areas opening, resulting from pasture and agricultural land formation. In Southeastern Brazil, *C. hololeuca* can occur in high density in burned forest areas, but other species grow together with it and it was not restricted to edges. *Cecropia pachystachya* can grow in monospecific stands when it invades silted-up lakes or any kind of land that was flooded and subsequently dried out. Because of the variation in *Cecropia* species habitats, we did not use a rigid classification of habitats, but suggest a size gradient related to occupation from open to forest habitats for these pioneer trees.

4. Discussion

Two life-history types in tropical trees have been distinguished: light-demanding pioneers that germinate, establish and grow to maturity only in gaps; and climax (persistent) species that germinate and establish in the shade and often attain maturity when juveniles are released from suppression (SWAINE & WHITMORE 1988). However, ALVAREZ-BUYLLA & MARTINEZ-RAMOS (1992) argued that a dichotomous classification to assign species to one of two life-history types is too limited and suggest that pioneer-climax framework should be viewed only as a means of identifying the extremes of a continuum of tree life histories. Morphological variation in architectural patterns of *Cecropia* corroborates previous studies that emphasize ecological and evolutionary diversity existing within broadly defined categories, such as pioneers and persistent trees. Although *Cecropia* species are described as typical pioneer trees, some species showed traits associated with shade-tolerant trees. *Cecropia hololeuca* and *C. sciadophylla* differed from the other species in architectural traits. Mean values of branching ratio of both species are comparable to values found for plants growing in shade (WHITNEY 1976; STEIN-GRAEBER 1979; PICKETT & KEMPF 1980). The crown pattern of both species was similar to monolayer form and they had the largest leaf size among the species studied. Leaf size is thought to be larger for late-successional, shade tolerant species compared to early successional tree species (NICOLA & PICKETT 1983; WHITE 1983).

Cecropia hololeuca and *C. sciadophylla* begin crown expansion about 10 m in height and reach about 20–25 m in height. These architectural traits may help maintain both species in the canopy. A pioneer tree which branches at a lower height and spreads horizontally may have its branches shaded by other trees, causing reduced productivity and eventual branch shed. Higher, more vertical branches may help optimize crown form in forest *Cecropia* species. Furthermore, the two forest *Cecropia* species had less frequently broken first branches than *C. glaziovii* and *C. palmata* (pers. obs., T. C. Sposito). Branches of forest *Cecropia* species are more vertical whereas other species tend to produce long horizontal branches more subject to breakage by wind and debris. Horizontal branches support their weight against a gravitational force greater than that for more vertical branches (HORN 1971). Stilt roots are very common in *Cecropia* and this has also been related to mechanical support (JENÍK 1978).

Leaf size of all species increased with plant height before branching and decreased afterwards. The same pattern was found in *Cecropia obtusifolia* in Mexico (ALVAREZ-BUYLLA & MARTINEZ-RAMOS 1992). Cor-

ner's rule predicts that "the greater the ramification, the smaller become the branches and their appendages" (e.g. leaves) (HALLÉ 1978 et al., p.82). Decreasing leaf size may be related to the difficulty in supporting big leaves on the relatively thinner branches. It could also be related to reiteration in which tree branches tend to repeat their initial seedling architecture with a reduced size and lobing. On the other hand, small leaves could be advantageous for a tree to minimize the risk of loosing a large part of its canopy, since branch breaking is common for some *Cecropia* species.

Interspecific differences in internode size could suggest differences in growth among species, because height growth rates are determined by number and length of internodes produced. Internode length is a feature directly influenced by environmental factors; rainfall and internode length are correlated in some *Cecropia* species (DAVIS 1970; SPOSITO 1999). The longer internodes of most *Cecropia* species from Manaus compared to southeastern species (Fig. 4) could be an effect of the high rainfall of Amazonia.

The two non-myrmecophytes, *Cecropia hololeuca* and *C. sciadophylla*, coincided in architectural patterns and size, but according to preliminary studies on *Cecropia* phylogeny including other species not studied here, they belong to a group of species with or without ants; therefore, at present, myrmecophily does not seem of phylogenetic value (Pilar Franco, pers. comm). However, there is evidence that habitat-related morphological changes and myrmecophily may have marched together in the evolution of *Cecropia* (HARADA & BENSON 1988; DAVIDSON & FISHER 1991; DAVIDSON et al. 1991; SCHUPP & FEENER 1991; FOLGARAIT & DAVIDSON 1994). Results found here could indicate that changes in plant size and form in *Cecropia* species may have facilitated adaptive radiation in different light conditions. Tentative hypotheses on the adaptive radiation of *Cecropia* should consider ecological variation and architectural patterns of species.

Acknowledgements

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