UNIVERSIDADE ESTADUAL DE CAMPINAS

TEREZA CRISTINA SOUZA SPOSITO

Tamanho, forma, alometria e crescimento em algumas espécies de *cecropia (Cecropiaceae)* do Brasil

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Tem quatro teorias de árvore que eu conheço.

Primeira: que arbusto de monturo agüenta mais formiga.

Segunda: que uma planta de borra produz frutos ardentes.

Terceira: nas plantas que vingam por rachaduras lavra

um poder mais lúbrico de antros.

Quarta: que há nas árvores avulsas uma assimilação maior

de horizontes.

Manoel de Barros em "O guardador de águas"

RESUMO

Tamanho, forma, alometria e crescimento foram estudados em algumas espécies de *Cecropia*, da região Sudeste do Brasil e da Amazônia, e estão apresentados em três capítulos. Os padrões arquiteturais e relações alométricas de oito espécies de *Cecropia* estão descritos nos capítulos 1 e 2. Cinco espécies amazônicas, *C. concolor*, *C. palmata*, *C. purpurascens*, *C .ulei* e *C. sciadophylla*, foram estudadas em Manaus (AM). Três espécies do Sudeste do Brasil, *Cecropia glaziovii, C. pachystachya* e *C. hololeuca* foram estudadas em Linhares (ES). As espécies são mirmecófitas, com exceção de *C. hololeuca* e *C. sciadophylla*. Para o estudo da arquitetura das árvores foram tomadas as medidas de altura, diâmetro, altura da primeira ramificação, número de ramos e folhas, área foliar, comprimento do entrenó e taxa de ramificação. Tanto na Amazônia como no Sudeste, o tamanho e os padrões arquiteturais formam um gradiente de áreas abertas para florestas. *Cecropia hololeuca* e *C. sciadophylla*, as espécies de floresta, tiveram arquitetura similares, com altura em torno de 20-25 m, taxas de ramificação menores, e área foliar maior. *Cecropia concolor* e *C. pachystachya* tiveram até 13 m de altura, com área foliar menor, sendo típicas de habitats abertos. As outras espécies ocuparam as bordas de floresta e são intermediárias entre estes dois extremos. As relações alométricas entre diâmetro e altura, e características da copa e altura, foram analisadas através de regressões das variáveis transformadas em logaritmo. Foram testados três modelos de design mecânico ótimo: similaridade elástica, geométrica e estresse constante. As espécies de *Cecropia* estudadas estão mais próximas da similaridade geómetrica. As espécies diferiram nas relações diâmetro-altura considerando a amplitude total de alturas, mas a maioria delas não apresentou diferenças entre indivíduos ramificados e não ramificados. De maneira geral, as relações entre a copa e altura das árvores foram similares. O número de ramos e folhas tiveram alguma variação entre as espécies, relacionadas ao ínicio do processo de ramificação. A área foliar total apresentou uma relação alométrica constante, embora os interceptos das regressões tenham diferido de acordo com a área foliar das espécies. O crescimento e a longevidade foliar em plantas jovens das três espécies do Sudeste, e foi estudado em Nova Lima, MG, durante um ano. *Cecropia glaziovii* e *C. pachystachya* produziram mais entrenós durante o ano do que *C. hololeuca*. Os valores máximos do incremento em altura e diâmetro foram maiores nas duas espécies mirmecófilas do que em *C. hololeuca*, mas não houve diferença significativa entre as medianas das espécies. O número de entrenós produzidos no ano e o incremento em altura foram positivamente correlacionados com a pluviosidade mensal para todas as espécies. A taxa de emergência de folhas foi maior nas espécies mirmecófilas do que em *C. hololeuca*. A taxa de mortalidade foi maior para as folhas de *C. glaziovii* do que para as outras duas espécies. As folhas de *C. hololeuca* e *C. pachystachya* duraram mais tempo (± 7 meses) do que as folhas de *C. glaziovii* (± 4 meses). A análise da arquitetura e alometria das oito espécies de *Cecropia* mostrou que, mesmo num grupo de espécies consideradas tipicamente pioneiras, ocorrem variações morfológicas que estão relacionadas à ocorrência destas espécies em gradientes de luminosidade. As diferenças encontradas no estudo do crescimento e da produção de folhas das três espécies podem ter influência na ocorrência de formigas nestas espécies.

Palavras-chave: Alometria, arquitetura, área foliar, Brasil, *Cecropia*, crescimento, longevidade foliar, mirmecófitas, mutualismo, pioneiras, ramificação.

ABSTRACT

Size, form, allometry and growth were studied in some *Cecropia* species, from Amazonian and Southeastern Brazil. Architectural patterns and scaling of stem and crown was studied in five Amazonian species: *Cecropia concolor*, *C. palmata*, *C. purpurascens*, *C. ulei* and *C. sciadophylla*, in Manaus (AM); and in three Southeastern species *Cecropia glaziovii*, *C. hololeuca* and *C. pachystachya*, in Linhares (ES). The species are myrmecophytes except *C. hololeuca* and *C. sciadophylla*. Height, diameter, height of first branching, number of branches, number of leaves, total leaf area, internode length and bifurcation ratio were measured for undamaged trees. In both areas, size and architectural characters are displayed as a gradient from open habitats to forest. Forest-inhabiting *C. hololeuca* and *C. sciadophylla* had similar architectures, with low bifurcation ratios, and big leaves. *Cecropia concolor* and *C. pachystachya* measure up to 13 m in height with smaller leaves and occur typically in open habitats. The remaining species occupy forest margins and are intermediate between these two extremes. The scaling relationships were studied with log-transformed variables and regressed on height. Three models of optimal 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. Species differ significantly in diameter-height relationships. Most of species did not vary in diameter-height relationships between unbranched and branched individuals. The crown-height relationships of species studied were similar. 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 for species, although regression intercepts differed according to species leaf areas. The growth and leaf longevity of saplings of the three southeastern species was studied during one year, in Nova Lima, MG. *Cecropia glaziovii* and *C. pachystachya* produced more internodes.yr^{-1} than *C. hololeuca*. Maximum values of height and diameter increments were higher for the two myrmecophytes than the non-myrmecophyte *C. hololeuca*, but medians did not differed significantly. Internodes.yr^{-1} and height increment was positively correlated with monthly rainfall for the three species. Leaf emergence was higher in myrmecophytic species. Leaf mortality was higher for *C. glaziovii* leaves than for the other species. Leaf longevity of *C. hololeuca* and *C. pachystachya* was higher (±7 months) than that of *C. glaziovii* (± 4 months). Architectural and allometric analysis of the eight *Cecropia* species, showed that, although they are considered typical pioneer trees, morphological variation founded could be related to light gradient occupation of species. Differences found in growth and leaf longevity of the three species could influence ant occupation of species.

Key words: allometry, architecture, branching, Brazil, *Cecropia*, crown, growth, leaf area, leaf longevity, mutualism, myrmecophyte, pioneer

INTRODUÇÃO GERAL

Toda a morfologia das árvores reflete, de alguma forma, o ambiente que elas ocupam. A altura total, tamanho de folhas (White 1983), tamanho das copas (Hallé et al. 1978), crescimento (Clark & Clark 1992), investimento em defesa (McKey 1984; Coley et al. 1985) e longevidade foliar (Chabot & Hicks 1982) são características que variam conforme o ambiente disponha de mais ou menos luz e nutrientes. Algumas características associadas às plantas de sol incluem filotaxia espiralada, gemas apicais eretas e orientação das folhas também ereta (revisão em Givnish 1988). Espécies arbóreas tolerantes à sombra geralmente apresentam folhas maiores se comparadas com aquelas intolerantes (White 1983). Árvores que crescem em locais abertos apresentam uma copa mais baixa e mais esférica, enquanto árvores de floresta tendem a apresentar um tronco longo e uma copa mais estreita (Hallé et al. 1978). Nos estudos alométricos que relacionam caule e copa de árvores, as espécies de dossel, subdossel e pioneiras apresentam maior ou menor investimento em diâmetro, que, por sua vez, está relacionado ao tamanho da copa que o caule deve sustentar (King 1996).

As embaúbas, conhecidas espécies do gênero *Cecropia*, são plantas largamente associadas com áreas perturbadas e estágios iniciais de sucessão, em florestas tropicais da América. São árvores de pequeno a grande porte, de folhas grandes e peltadas, e caule e ramos ocos, marcados por nós que correspondem à cicatriz da estípula que protege a gema terminal (Berg 1978a; Joly 1977). As espécies de *Cecropia* são plantas heliófilas, de crescimento rápido, em geral consideradas tipicamente pioneiras (Swaine & Whitmore 1988; Whitmore 1989). Entretanto, alguns estudos começaram a separar grupos de espécies de *Cecropia* mais ou menos tolerantes à sombra (Davidson & Fisher 1991; Folgarait & Davidson 1994). Seria então muito provável que as características morfológicas associadas às plantas de sol e sombra estivessem, de alguma forma, representadas na morfologia de *Cecropia*, pois, muitas vezes, estas características representam respostas adaptativas das plantas ao ambiente em que elas vivem.

Espécies de *Cecropia* apresentam variações morfológicas em suas folhas (Berg 1978b) e no padrão de ramificação (Guillaumet 1984). Embora indivíduos de *Cecropia* sejam encontrados crescendo isoladamente, é comum a ocorrência de espécies associadas a florestas ou a ambientes mais abertos. O objetivo geral deste estudo foi analisar a variação morfológica de caracteres vegetativos e do crescimento de algumas espécies de *Cecropia*, para verificar se estes caracteres estão relacionados ao habitat em que as espécies ocorrem. Nesta tese, são analisados a arquitetura e as relações alométricas de oito espécies, cinco amazônicas e três do sudeste do Brasil. Os aspectos de tamanho, forma, alometria e crescimento serão abordados em três capítulos. O primeiro tem como objetivo analisar as diferenças e semelhanças morfológicas relacionadas ao padrão arquitetural de oito espécies de *Cecropia*, na Amazônia (Manaus, AM) e na região Sudeste (Linhares, ES). Se há alguma variação morfológica interespecífica, como ela estaria relacionada ao habitat? O segundo capítulo trata das relações alométricas do caule e da copa destas mesmas espécies. Existem diferenças interespecíficas nas relações alométricas, e será que elas apresentam alguma variação em relação ao habitat? Espécies de habitats abertos, mais ricos em luz geralmente apresentam altas taxas de crescimento (Coley et al. 1985) e longevidade foliar menor (Chabot & Hicks 1982, Reich et al. 1992). No terceiro capítulo, são analisados o crescimento e a longevidade foliar de plantas jovens de três espécies de *Cecropia*, na Mata do Jambreiro, em Minas Gerais, para verificar se existem diferenças entre duas espécies mirmecófilas, que ocorrem em locais mais abertos, e uma não mirmecófila, que ocupa o ambiente mais sombreado da floresta.

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Capítulo 1*

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. Forest-inhabiting *C. hololeuca* and *C. sciadophylla* 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, Brazil, *Cecropia*, crown, 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 adaptive responses of individuals to environmental conditions, although adaptive responses of 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 branchings 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 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 occuppied 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 Southeast region.

Brazilian *Cecropia* species show macro-morphological differences in branching patterns and leaf characteristics. Furthermore, although any *Cecropia* species grows isolated, typical forest and open habitats species are observed. To what extent are morphological differences associated with differences in habitat of these species? The purpose of this study was to compare size and form of eight *Cecropia* species in two regions of Brazil, emphasising aspects related to branching patterns, leaf area and branching ratio.

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, and Centro de Pesquisas Agro-florestais da Amazônia Ocidental (CPAA) (operated by the Empresa Brasileira de Pesquisa Agropecuária). The former, located inside the city of Manaus, has a 20-m tall forest. The latter are located on the Manaus - Itacotiara Road, 26 and 29 km north of the city (2° 51' S; 59° 52' W). The Reserva Ducke is characterized by a 30-40 m high canopy and the CPAA by a mosaic of pastures, fallow agricultural land and secondary forest. Between 1971 and 1993, annual rainfall averaged 2500 mm and mean temperature was approximately 25°C (CABRAL 1996). 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 more common in open fields and abandoned agricultural lands. *Cecropia palmata* and *C. purpurascens* occur in open habitats or forest borders. *Cecropia sciadophylla* occur in gaps and along forest borders, sometimes forming dense stands. Plants of *C. ulei* occur in forest gaps and edges, but some adults are found in subcanopy of secondary forests.

The study site in Southeast Brazil was the Reserva Florestal de Linhares, in North of Espírito Santo state (19° 06' S; 39° 45' W). The 218 km^2 is mostly high canopy forest, 20-25 m in height. The two other important vegetation types associated with sandy soils are "mussununga" forest, 10 - 15 m high, and grassy "nativo" fields with scattered shrubs and small trees forming thickets (JESUS 1988; PEIXOTO & GENTRY 1990). Annual mean rainfall and temperature were 1242 mm and 23°C respectively (1975-1993). *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 a 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 1-m stem segment between 1.5 and 2.5 m high and mean internode length was obtained by division. Plants less than 2.5 m tall did not have internodes measured. Number of first order branches and leaves was counted directly using 8 x 24 binoculars. Number of leaves per branch was estimated by division of total number of leaves per number of first-order branches. Branching pattern was drawn for each tree to compare architecture of species.

Most of the individuals had one leaf 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 (see Anexo I). 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. *Analysis*

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 box-plots diagrams of SYSTAT (1992).

3. Results

3.1 *Species characteristics*

Morphological characteristics of *Cecropia* species were summarized in Table 1. *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 1). *Cecropia concolor* and *C. pachystachya* 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 1), 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 1, Fig. 4).

Cecropia pachystachya and *C. glaziovii* had fewer first order branches than the other species (maximum 23-25 branches, Table 1, 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 1, Fig. 5). Other species showed maxima ranging from 46 to 78 branches (Table 1). *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 1, Fig. 5 and 6), because plants with fewer branches also have fewer leaves. Number of leaves per branch was significantly different among species (Table 1, $F = 16.4$; $P < 0.001$; $N = 7$); *Cecropia purpurascens* and *C. concolor* presented the lowest values (6.7 - 7.3), while the other species held 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 1, $F = 18.5$; $P < 0.001$; $N = 8$). *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 1), 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 1, $F = 30.19$; $P < 0.001$; $N = 7$). *Cecropia sciadophylla, C. glaziovii* and *C. hololeuca* had higher means values about 9-10 m (Table 1, Fig. 11), while the others species branched between 4 and 6 m in height. The height of first branching is about 58-77% of total height in species and these proportions (arcsine transformed) were not significantly different among species ($F = 0.416$, $P > 0.05$, $N = 7$).

3.2. *Architectural patterns of species*

The branching process of *Cecropia* species is represented in Fig. 12. When a plant begins its 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 others species, branch position tends to horizontal (Fig. 1 and 12). Pattern of emission of higher order branches was different among species. While *C. concolor*, *C. glaziovii*, *C. palmata* and *C. pachystachya* had more trees with second and third order branches, *C. hololeuca*, *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 remainder species (Table 1, Fig. 13), excepting *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 2); 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 $r = -0.56$, 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.

3.3. Plant size and habitat

An overview of vegetative characters comparison 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 forests 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 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).

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 limited and suggest that pioneer-climax framework should be view as a means of identifying the extremes of a continuum of tree life histories. Morphological variation of 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 assigned to shade-tolerant trees. *Cecropia hololeuca* and *C. sciadophylla* were different from the other species on architectural traits. Mean values of branching ratio of both species are comparable to values found for plants growing in shade (WHITNEY 1976; STEINGRAEBER 1979; PICKETT & KEMPF 1980). The crown pattern of both species was similar to monolayer form and they had the larger leaf size among species. 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*. Furthermore, the two forest *Cecropia* species had first branches broken less frequently 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 branches more vertical (HORN 1971). Stilt roots are very common in *Cecropia* and this was also 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). Corner's rule predicts that "the greater the ramification, the smaller become the branches and their appendages" (e.g. leaves) (HALLÉ 1978, 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.

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; chap.3 of this thesis). 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 the 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, until now, 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.

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Table 1 - Morphological characteristics of eight *Cecropia* species of Brasil. *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 (m^2)*	Height 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
N	38	38	21	38	21	37	21	26	20	(AM)
cv	-	-	-	-	22.8	56.0	23.8	40.4	55.5	
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
N	30	30	18	30	18	30	18	24	17	(AM)
cv	-	-	-	-	20.3	81.1	14.9	37.9	52.7	
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
N	31	31	20	31	20	29	20	25	15	(AM)
cv	-	-	-	-	21.4	61	30	39.8	43.8	
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
N	34	34	17	34	17	31	17	24	14	(AM)
cv	-	-	-	-	17.3	75.7	26.1	41.6	29.4	

Minimum and maximum values observed * Mean ± 1 SD

Table 1- Continued

SPECIES	Height (m)	Diameter (cm)	Number of branches	Number of leaves	Number of leaves / branch	Leaf area (m^2)	Height of first branch (m)	Mean internode length (cm)	Branching ratio	Location
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
N	21	21	2	21	-	21	-	16	-	(AM)
cv	-	-	-	-	-	74.2	-	45.9	-	
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^{c}	3.8 ± 1.6^{a}	7.2 ± 3.8^{b}	Linhares
N	38	37	18	38	18	31	18	35	15	(ES)
cv	-	-	-	-	17.7	74.6	19.4	42.1	52.1	
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
N	32	31	23	32	23	24	22	29	18	(ES)
cv	-	-	-	-	16.2	64.6	22.9	43.8	28.4	
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
N	29	29	11	29	11	28	11	25	8	(ES)
cv	-	-	-	-	25.2	73.3	30	42.9	36.9	

Table 2 - 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. palmata	-0.07	0.02	17
C. purpurascens	0.25	-0.75*	15
C. sciadophylla	-0.35	-0.56*	14
C. glaziovii	0.33	0.27	14
C. hololeuca	0.04	0.14	17
C. pachystachya	0.06	-0.22	8

* $P < 0.05$

Figure Legends

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

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 three later are of southeastern Brazil. In a box-plot graph, the box comprises 50% of 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).

Fig. 8. Variation of individual leaf area (m^2) in function of height (m), of eight *Cecropia* species in Brazil. Circles represent unbranched individuals and asterisks represent branched individuals. Equations are for log-transformed variables.

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.

Fig. 12. Branching patterns of three *Cecropia* species of Brazil, deduced trough observation of developmental phases of species. Arrows represent indeterminate growth. *Cecropia sciadophylla* shows the same model of *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.*

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

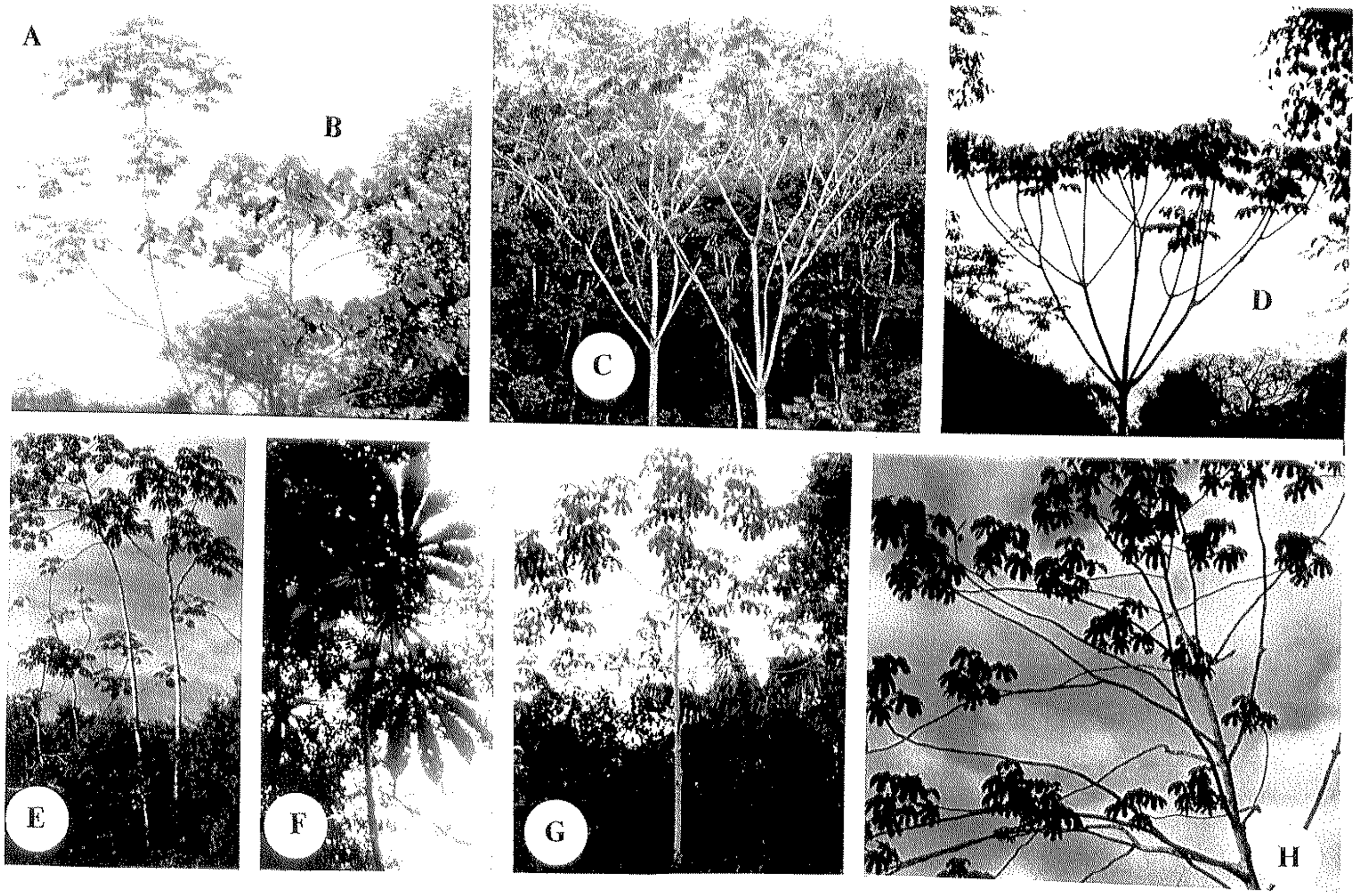
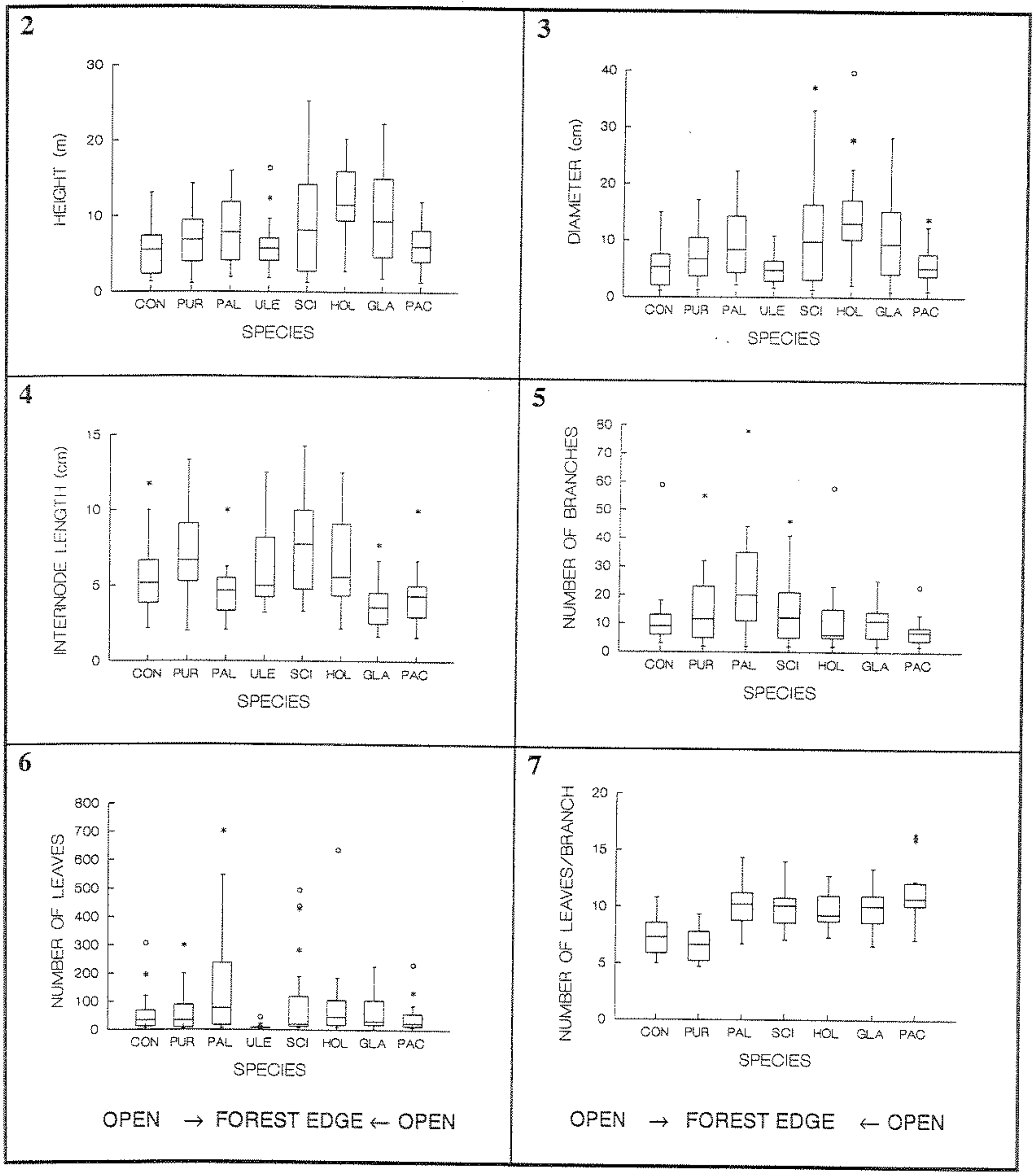


FIGURE 1

FIGURE 2 - 7


2
HEIGHT (m)
0
10
20
30
CON PUR PAL ULE SCI HOL GLA PAC
SPECIES
3
DIAMETER (cm)
0
10
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40
CON PUR PAL ULE SCI HOL GLA PAC
SPECIES
4
INTERNODE LENGTH (cm)
0
5
10
15
CON PUR PAL ULE SCI HOL GLA PAC
SPECIES
5
NUMBER OF BRANCHES
0
10
20
30
40
50
60
70
80
CON PUR PAL SCI HOL GLA PAC
SPECIES
6
NUMBER OF LEAVES
0
100
200
300
400
500
600
700
800
CON PUR PAL ULE SCI HOL GLA PAC
SPECIES
OPEN → FOREST EDGE ← OPEN
7
NUMBER OF LEAVES/BRANCH
0
5
10
15
20
CON PUR PAL SCI HOL GLA PAC
SPECIES
OPEN → FOREST EDGE ← OPEN

FIGURE 8

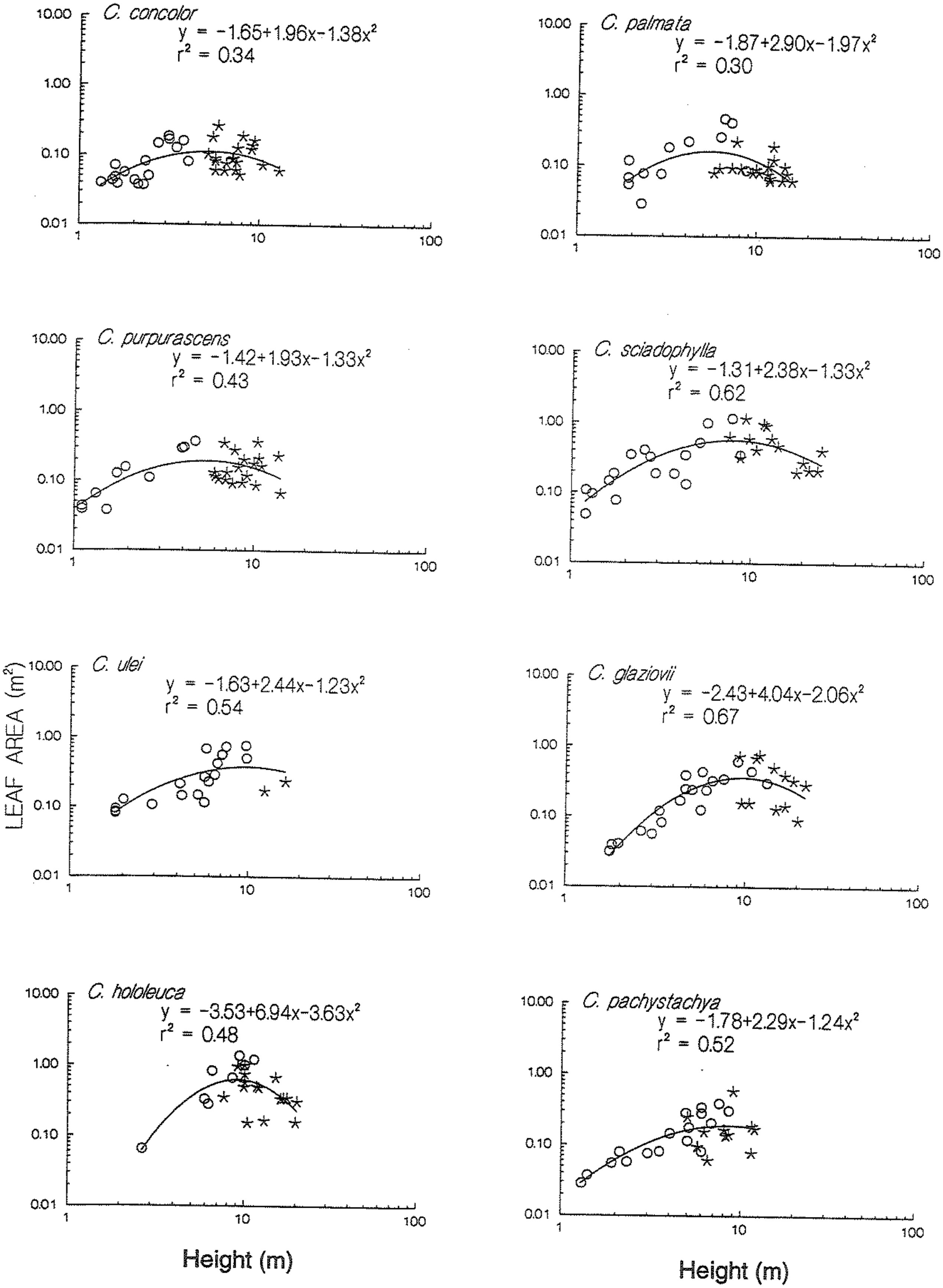

C. concolor
y = −1.65+1.96x−1.38x²
r² = 0.34
C. palmata
y = −1.87+2.90x−1.97x²
r² = 0.30
C. purpurascens
y = −1.42+1.93x−1.33x²
r² = 0.43
C. sciadophylla
y = −1.31+2.38x−1.33x²
r² = 0.62
C. ulei
y = −1.63+2.44x−1.23x²
r² = 0.54
C. glaziovii
y = −2.43+4.04x−2.06x²
r² = 0.67
C. hololeuca
y = −3.53+6.94x−3.63x²
r² = 0.48
C. pachystachya
y = −1.78+2.29x−1.24x²
r² = 0.52
LEAF AREA (m²)
10.00
1.00
0.10
0.01
1
10
100
Height (m)
Height (m)

FIGURE 9 - 11

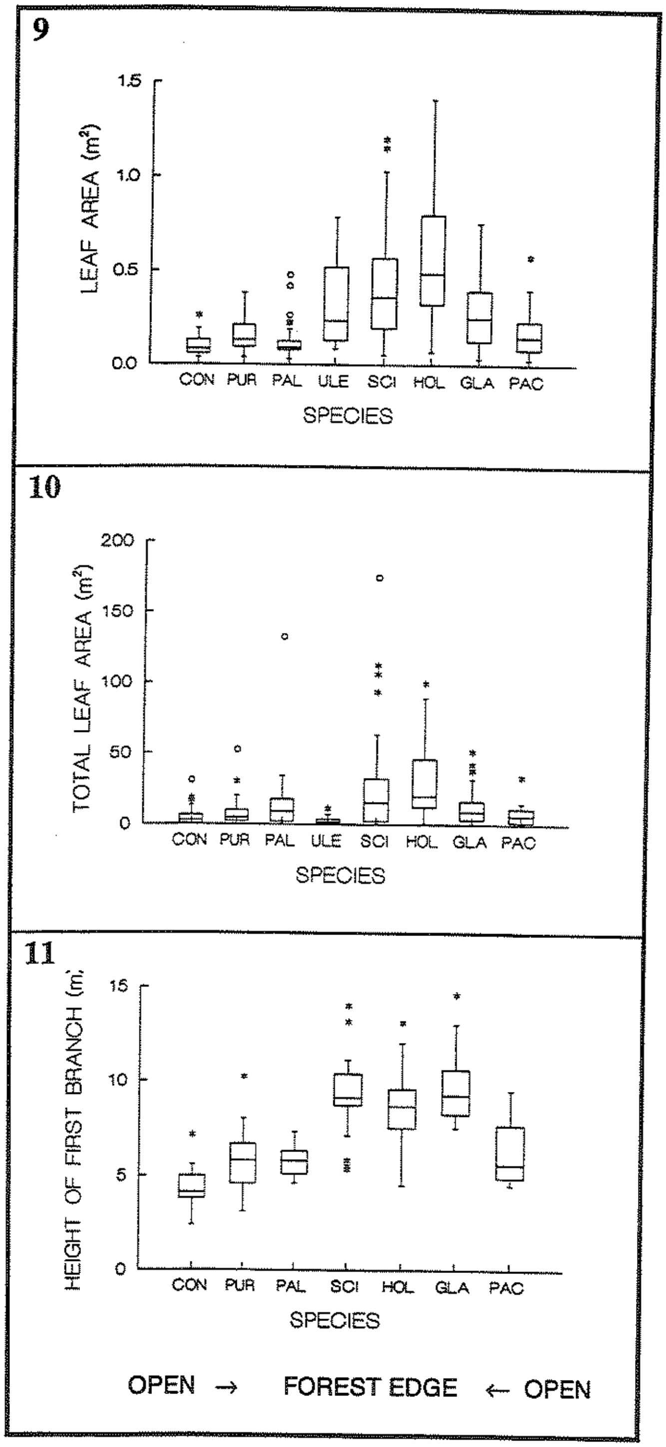
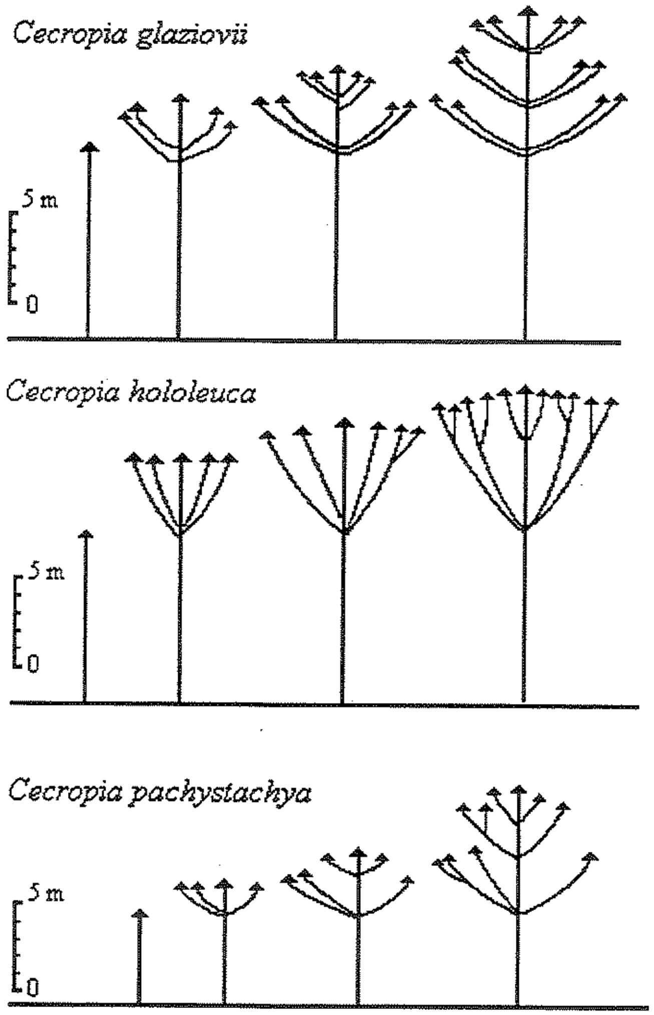

9
LEAF AREA (m²)
1.5
1.0
0.5
0.0
CON PUR PAL ULE SCI HOL GLA PAC
SPECIES
10
TOTAL LEAF AREA (m²)
200
150
100
50
0
CON PUR PAL ULE SCI HOL GLA PAC
SPECIES
11
HEIGHT OF FIRST BRANCH (m)
15
10
5
0
CON PUR PAL SCI HOL GLA PAC
SPECIES
OPEN → FOREST EDGE ← OPEN

FIGURE 12

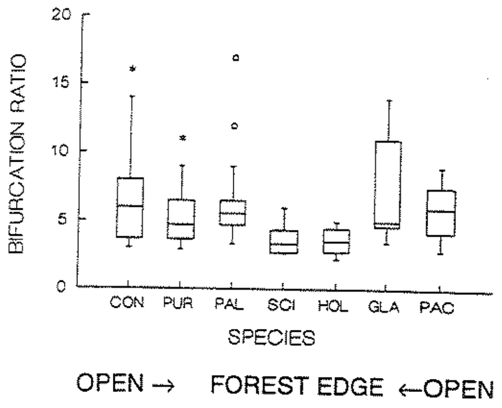


Cecropia glaziovii

Cecropia hololeuca

Cecropia pachystachya

FIGURE 13


BIFURCATION RATIO
20
15
10
5
0
CON
PUR
PAL
SCI
HOL
GLA
PAC
SPECIES
OPEN →
FOREST EDGE
←OPEN

Capítulo 2*

SPOSITO AND SANTOS-SCALING OF STEM AND CROWN IN CECROPIA

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

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ABSTRACT

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. ulei and C. sciadophylla, were studied in Manaus. Cecropia glaziovii, C. hololeuca and C. pachystachya were studied in Linhares. The species are myrmecophytes except C. hololeuca and C. sciadophylla. Measures of diameter, height, number of branches, number of leaves and total leaf area were log-transformed and regressed on height. Three models of optimal 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. Species differ significantly in diameter-height relationships. Most of the species did not vary in diameter-height relationships between unbranched and branched individuals. Safety factors diminish with height in most species studied. The crown-height relationships of species studied were similar. Numbers of branches and leaves showed some variation among species and are related to height of branching beginning. Total leaf area had a constant allometric relationship for species, although regression intercepts differed according to species leaf areas. The scaling relationships of stem and crown in Cecropia reflected the differences in size of studied species.

Key words: allometry, Brazil, Cecropia, myrmecophyte, pioneer, tropical tree

The relationship between size and shape in trees is important in understanding the structure and dynamics of forests and competitive interactions among species. Differences in allocation between trunks and crowns reflect strategies of space occupation in forests (King, 1990; Koyhama and Hotta, 1990). Successional trees are able to invade open areas in high densities and grow fast, and this ability may be closely related to foliage height and growth rate (King, 1981). However, to attain a given height, a tree first needs to achieve a minimum diameter to avoid buckling due to its own weight (McMahon, 1973) and to resist breakage from wind action (Dean and Long, 1986). Therefore, trees should have a height-diameter relationship that permits height growth without compromising mechanical stability.

Three models have been proposed to describe the optimal 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).

McMahon (1973) plotted height versus trunk diameter for the largest known living specimens of North American dicotiledonous and gymnosperm tree species, and found the scaling relation to conform to that predicted by the elastic similarity model. However, this conclusion is criticized since the data were not examined statistically to determine the scaling exponent for H versus 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:

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

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, apud 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, dicotiledonous trees conformed to the elastic similarity model, and geometric similarity was not rejected for gymnosperm trees. For dicotiledonous 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 changes, 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 1 for saplings of canopy and understory trees (Kohyama and Hotta, 1990; King, 1990, 1996), and for species of initial successional phases (Alvarez-Buylla and Martinez-Ramos, 1992; Claussen and Maycock, 1995); adult canopy trees or emergents showed exponents that conform to elastic similarity model (O'Brien et al., 1995; King, 1996). Shade intolerant, pioneer species, with short life spans, invest more in height growth rather than in strength and longevity, and an allometric design with low safety margins facilitates 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 geometric similarity model, but when they become adults, their scale diameter conforms to elastic or stress models, with higher safety factors, since stability and survival should not be compromised by rapid height growth (King, 1996).

Comparisons of allometric relationships have treated unrelated species or groups of species with similar habits. In this study, we looked at 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). Increasing size of these eight Cecropia species is associated with habitat gradient from open habitats to forest (Sposito and Santos, unpublished). It could be expected that regression coefficients of allometric relationships increase, following the gradient from open habitats to forest, since allometry and habitat occupation are related (Rich et al., 1986; King, 1990, 1995; Koyhama and Hotta, 1990; Claussen and Maycock, 1995). The main questions of this study are: 1) Do allometric relationships differ among Brazilian species of the genus Cecropia? 2) Which model of tree allometry, elastic, geometric or constant stress, do the species 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). Sites visited in Amazonas state were Fundação Universidade do Amazonas (FUA) inside Manaus, and Reserva Ducke and Centro de Pesquisas Agro-florestais da Amazônia Ocidental (CPAA) (owned by Embrapa - Empresa Brasileira de Pesquisa Agropecuária) on the Manaus - Itacotiara road, 26 - 29 km north of Manaus (2° 51' S, 59° 52' W). FUA and Reserva Ducke are medium (20 m-tall) to high canopy (30-40 m-tall) forests, respectively. CPAA consists of pasture and fallow agricultural land with a mosaic of secondary forest and open cultivated areas. Annual mean rainfall and mean temperature 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 which 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 mirmecophytes (Benson, 1985; Berg, 1978).

Amazonian species sampled were Cecropia concolor Will., C. palmata Will., C. purpurascens C. C. Berg, C. ulei Snethl. and C. sciadophylla Mart. (non-myrmecophytic) (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 in 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. (non-myrmecophytic) occur along forest borders, whereas Cecropia pachystachya Trécul grows in 'mussununga', 'nativo' and transition between these and high forest.

Measurements of plant size - Measurements were performed on plants over a range of heights, from ≈1 m tall saplings to large adults. Accessible undamaged individuals were selected for measurement. At least 30 individuals were measured per species, except Cecropia pachystachya with 29 individuals and C. ulei with 21. For each tree we recorded height, circumference at 1.3 m above the soil (to obtain diameter), number of live first-order branches and number of leaves. Total height was defined as the top of the crown in branching trees, or the height of tree apical stipule in pole plants. Height was recorded with tapes, rods or clinometer, depending on height. Trunk circumference was measured at the last internode in plants shorter than 1.3 m. If stilt roots were present, circumference was measured ≈ 30 cm above them. 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 number of first-order branches.

Most of the individuals had one leaf per plant collected for area measurement. When possible, the leaf on the third internode bellow the apical meristem was chosen for measurement. Each leaf was cut into several pieces and kept in a plastic bag in a refrigerator until it could be measured. Leaf area was measured using a Li-Cor area meter (Model LI-3000, Li-Cor, 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 (cm), tree height (m), number of branches, number of leaves and total leaf area (m^2). The allometric equation is described as $Y = aX^b$ or the correspondent log transformed equation $\log Y = \log \underline{a} + \underline{b} \log X$, 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. Whether *F* was significant, 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 differ 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 (Koyhama and Hotta, 1990). Non-significant regressions were not included on multiple comparisons.

To test for agreement with 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 $\underline{d/d_{min}}$ (King, 1981) where $\underline{d}$ is the actual stem diameter and $\underline{d_{min}}$

is the theoretical minimum buckling diameter calculated using the formula, $0.1\ h^{3/2}$, which was derived from McMahon's (1973) buckling equation (see Anexo II).

RESULTS

Diameter-height relationships - Linear regressions slopes for log-log diameter-height relationships differ among the Cecropia species studied ($F = 2.85$; $P = 0.007$; df = 7, $N = 242$, Table 2, 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 Y-intercepts ($F = 5.57$; $P < 0.001$; df = 5; $N = 191$) in C. hololeuca and C. pachystachya (Table 2), showing that diameter is larger in the former species compared with the latter at the same height.

As a group, southeastern Brazilian species do not show significant differences on slopes (Fig. 2). On Amazonian species, C. concolor differed from C. ulei, but the other species did not show significant differences (Fig. 2). In a general way, Amazonian species tended to be more slender than southeastern species, since slopes tended to be lower in the former group.

Diameter-height relationships of most Cecropia species do not conform to elastic ($b = 3/2$) nor 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 species did not vary in diameter-height relationships between unbranched and branched individuals (F-value range 0.004 - 1.031; $P > 0.05$, Table 3), except for Cecropia palmata ($F = 6.42$, $P = 0.02$, df = 1, $N = 30$). However, 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 (Tables 2 and 3).

Safety factors (d/d_{min}) decrease with height in most Cecropia species (Fig. 3). Plants showed diminishing safety factors before branching and branched trees have low, fairly constant safety factor. In most species, taller trees approximate the elastic buckling limit but do not surpass it. An exponential 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 lower than 2 m in height in sample. Exponents of the relationship between safety factor and height were significantly different among species ($F = 2.85$ $P = 0.007$, df = 7, $N = 235$). 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 and species with no significant regressions) ($F = 0.74$, $P = 0.57$, df = 4, $N = 95$) (Table 4). Intercepts were significantly different ($F = 17.28$, $P < 0.001$, df = 4, $N = 95$); C. sciadophylla, C. hololeuca and C. glaziovii had intercepts significantly lower than the other species (Table 4), 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 around 9-10 m in height, whereas the remainding species branch at about 4 - 6 m (chap.1 of this thesis).

For unbranched individuals, most species did not show significant relationships between number of leaves and height (Table 5, 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 is positively related with height for branched individuals in most species (Table 5, 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 variation of number of first order branches and number of leaves in branched trees was not related with height in Cecropia pachystachya and C. purpurascens (Table 4 and 5). However, considering diameter instead of height, the regressions were significative. 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, increasing diameter is related to crown size increasing.

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 6, Fig. 6). In C. concolor and C. purpurascens the number of leaves increases more slowly with branching than in the other species, because they had a lower number of leaves/branch (chap. 1 of this thesis). 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 (m^2) and height were positively related and slopes were not significantly different among species ($F = 1.68$, $P = 0.11$, df = 7, $N = 231$, Table 7, Fig. 7). Intercepts however, were significantly different ($F = 8.92$, $P < 0.001$, df = 7, $N = 231$) and C. sciadophylla, C. hololeuca and C. palmata showed the largest total leaf areas with height being constant (Table 7).

DISCUSSION

Stem allometry - The analysis of scaling relationships of stem in Cecropia showed that species oscillate along the line of isometric growth. With respect to slopes of diameter-height relationships, two of the eight species did not bracket the geometric similarity model. These species, C. concolor and C. glaziovii, had larger diameters 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 different from one, but do not conform with 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 of Cecropia studied. Although physical changes occur with tree development, these changes do not seem alter significantly the scaling exponent during Cecropia ontogeny. However, safety factors diminish with height in most Cecropia species studied, and taller trees approximate, but do not surpass the 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, other shade-intolerant canopy species had high safety margins at larger size (King, 1996; Sterck and Bongers, 1998), which is similar to later sucessional species. Low safety factors may not be a rule for light demanding trees.

Safety factors of smaller trees of the Brazilian Cecropia species and of C. obtusifolia in Mexico (Alvarez-Buylla and Martinez-Ramos, 1992) are very large, if compared to other tropical species (Claussen and Maycock, 1995; Sterck and Bongers, 1998). A large diameter at the beginning of development seems to be common in Cecropia. However, the differences of exponents of the relationship 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 of Cecropia ulei and C. purpurascens. These two species showed a steeply decreasing safety factor in plants up to 6 m in height, which means that trees become slender at the sapling stage. In a general way, Amazonian species were more slender than the Southeastern species. This trend could be related to the high rainfall of Amazonia in contrast to Southeastern Brazil, since internode lengths and rainfall are correlated in some Cecropia species (Davis 1970; chap. 3 of this thesis).

Comparing values from our study with other Cecropiaceae (Table 8) similar exponents were found. The exception was Pourouma bicolor, in which the slope of regression between height and diameter of 6 to 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}) 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. decreases two orders of magnitude over the range of tree heights sampled (Fig. 8). Specific gravity of Cecropia wood is around 2.5-5.5 $\times 10^2$ kg m^{-3} (Bonsen and ter Welle, 1983). Cecropia glaziovii had a mean value of 3.6 $\times 10^2$ kg m^{-3} (A. Fidalgo, Universidade de São Paulo, pers. comm.), which is about 60% of the wood density value used in McMahon's (1973) minimum diameter calculation. Therefore, Cecropia species may be growing far from the theoretical buckling limit, and the physical properties of wood in the genus may explain why they grow with an exponent lower than 3/2. Nonetheless, this calculation should be viewed only as an approximation because Cecropia species have hollow stems. 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 permited 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 $\underline{E}$ and the second moment of area $\underline{I}$. 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 confered by the spatial distribution of materials in a representative cross-sectional, and depends on size, shape and geometry. Thus, flexural stiffness can be increased by using materials with large $\underline{E}$ or by increasing the second moment of area $\underline{I}$ (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, $\underline{I}$ values should be altered, once secondary growth of basal portions of stem modifies the stem geometry. Therefore, mechanical 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 diferences in branching height and with leaf size of each 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 had a positive and significative slope of regression between number of leaves on height, perhaps indicating a high leaf production rate. This is a relevant factor in myrmecophytic species because 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 unity of height and had few leaves at the apex when adult. This mechanical design may be formed 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 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 probably contributes to diminish the production of spadices, and consequentely of fruits and seeds, even if it could compensate with more spadices or more fruits per spadice.

All studied species had a positive relationship between total leaf area and height. Individual leaf size increases as plants grow and diminishes after branching (chap. 1 of this thesis) in Cecropia species studied. Total leaf area increases with height because number of leaves and number of branches increase with height, except for C. pachystachya and C. purpurascens. For both species, the results suggest that individual leaf size increases with height in branched trees, but it does not happen (chap. 1 of this thesis). The results found for C. pachystachya and C. purpurascens could be a consequence of limited height growth of both species, because when use diameter instead of height, the regressions were significant for number of branches and leaves. Number of branches and leaves increase during plant growth, but the height of these two species is limited, causing the non-significance of the regressions with height.

Habitat and allometry - Cecropia pachystachya and C. hololeuca, and C. concolor and C. sciadophylla are the two pairs of species that represent the extremes of open-forest habitats in both Brazilian regions. Comparing diameter-height regressions of these species, there were no significant differences on slopes. Significant differences were found for intercepts in the southeastern species and they are related to size. Thus, in a general way, the allometric relationships in Cecropia seem to represent a model, with different sizes for the species analysed. 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).

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Table 1 – Sample characteristics of the Brazilian Cecropia species included in this study. In parentheses, the correspondent abbreviation used in 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	open understorey
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

Table 2- Least squares regression of log diameter (cm) on log height (m) for eight Cecropia species of Amazonian and Southeastern Brazil ($\log_{10}$ diameter = $\log_{10}$a + b $\log_{10}$ height) and for pooled species (Cecropia spp.), 95% confidence limits of regression slopes and the coefficient of determination (r^2). Adjusted means were calculated with a common slope of b = 1.06, for species that did not have significant differences in slopes. Same letters indicate non-significant differences (ANCOVA and Test of Scheffé, $P < 0.05$). F values in text. N values as in table 1.

Species	Intercept (log a)	Slope (b)	95% confidence limits for slope		$r^{2\#}$	adjusted mean
			Lower	Upper		
C. concolor	-0.097	1.108^{ac}	1.037	1.179	0.965***	-0.066 ^{ab}
C. palmata	-0.014	1.063 ^{abc}	0.953	1.173	0.933***	-0.012 ^{ab}
C. purpurascens	0.059	0.963 ^{ab}	0.834	1.092	0.889***	-0.012 ^{ab}
C. sciadophylla	0.024	1.050 ^{abc}	0.967	1.133	0.954***	0.011 ^{ab}
C. ulei	0.015	0.862 ^{b}	0.713	1.011	0.884***	-
C. glaziovii	-0.205	1.195 ^{c}	1.112	1.278	0.958***	-
C. hololeuca	-0.125	1.169 ^{abc}	0.925	1.413	0.767***	0.016 ^{a}
C. pachystachya	-0.137	1.114 ^{abc}	0.960	1.268	0.892***	-0.098 ^{b}
Cecropia spp. ($N = 249$)	-0.067	1.086	1.045	1.127	0.918***	-

\# *** $P < 0.001$

Table 3- Least squares slopes of regression of log diameter (cm) on log height (m) for unbranched and branched individuals of Cecropia species of Amazonian and Southeastern regions of Brazil ($\log_{10}$ diameter = $\log_{10}\underline{a} + \underline{b}\log_{10}$ height), including 95% confidence limits of regression slopes and the coefficient of determination (r^2). Different letters in a row indicate significant differences.

	Unbranched			Branched		
Species	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

** $P < 0.01$, *** $P < 0.001$

Table 4- Regression of number of first order branches (B) as a function of height (m) for seven Cecropia species of Amazonian and Southeastern regions of Brazil ($\log_{10} \underline{B} = \log_{10}\underline{a} + \underline{b} \log_{10}$ height) and the coefficient of determination (r^2). Adjusted means were calculated with a common slope b = 1.741. Different letters indicate significant differences (ANCOVA and Scheffé Test, $P < 0.05$). *F* values in text. *N* values as in table 3.

Species	Intercept (log a)	Slope (b)	$r^{2\#}$	adjusted mean
C. concolor	-0.381	1.563	0.434**	-0.624^{a}
C. palmata	-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

Table 5 - Regression of number of leaves (L) on height (m) 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 means calculated with a common slope = 1.627, for branched individuals. *F* values are in text. Different letters in the same column indicate significant differences (ANCOVA and Scheffé Test, $P < 0,05$). *N* values as in table 3.

Species		Intercept (log a)	Slope (b)	$r^{2\#}$	adjusted mean
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}	-

\# * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns: not significant

Table 6 - Regression of number of leaves (L) on number of branches (B) of seven Cecropia species of Amazonian and Southeastern regions of Brazil (L = a + b B) and the coefficient of determination (r^2). Different letters indicate significant differences (ANCOVA and Scheffé Test, $P < 0.05$). *F* values are in text. *N* values as in table 3.

Species	Intercept (log a)	Slope (b)	$r^{2\#}$	common slope	common adjusted mean
C. concolor	21.169	5.250a	0.877***	-	-
C. palmata	11.352	9.131b	0.918***	8.432	-0.088
C. purpurascens	11.013	5.466a	0.949***	-	-
C. sciadophylla	-0.648	10.383b	0.965***		
C. glaziovii	2.347	9.705b	0.906***		
C. hololeuca	-9.987	10.472b	0.975***		
C. pachystachya	7.140	9.431b	0.952***		

\# *** $P < 0.001$

Table 7 - 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 (r^2). Adjusted means 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 are in text. *N* values as in table 1.

Species	Intercept (log a)	Slope (b)	$r^{2\#}$	adjusted mean
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}

*** $P < 0.001$

Table 8 - 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
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	-2.35*	1.24	0.956	1 - 35.0	50	Costa Rica (4)
Pourouma bicolor	-	0.77	-	1 - 6.0		Costa Rica (5)
Pourouma bicolor	-	1.68	-	6 - 24.0		Costa Rica (5)

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 meters); original manuscript cites P. aspera which is a synonym of P. bicolor (Berg et al., 1990) (5) King (1996) N for the two height classes = 43.

Figure Legends

Fig. 1 - Least squares regressions between diameter and height of eight Cecropia species of Brazil ($\log_{10}$diameter = $\log_{10}$ a + b $\log_{10}$height), with 95% confidence limits of slopes. Circles represent unbranched and asterisks branched individuals.

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 three latter 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 are in Table 1. Cecropia concolor, C. glaziovii and Cecropia spp. have intermediate values between the geometric and elastic similarity models. The confidence intervals for the other species overlapped the geometric similiarity model.

Fig. 3. Safety factor of stem diameter (d/d_{min}), 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. Circles represent unbranched and asterisks 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 $\log_{10}d/d_{min} = \log_{10} a - b \log_{10}$height, for eight Brazilian Cecropia species. Cecropia ulei slope differed from the other species, except for C. purpurascens. Cecropia purpurascens slope differed from C. concolor and from the three Southeastern species. *Cecropia glaziovii* slope differed of all the Amazonian species.

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

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 ($L = a + b B$).

Fig. 7. Fitted least squares regression lines of total leaf area (A) on height for eight Cecropia species of Amazonian and southeastern Brazil ($\log_{10} A = \log_{10} a + b \log_{10} \text{height}$).

Fig. 8. Comparison of least squares regressions of $\log_{10}$diameter on $\log_{10}$height. Solid line represents observed values of Cecropia species (pooled data) of this study; dashed line represents the buckling limit of McMahon (1973); dotted line is McMahon's buckling limit calculated with modulus of elasticity and density of Cecropia sp. wood (Mainieri and Chimelo, 1989).

FIGURE 1

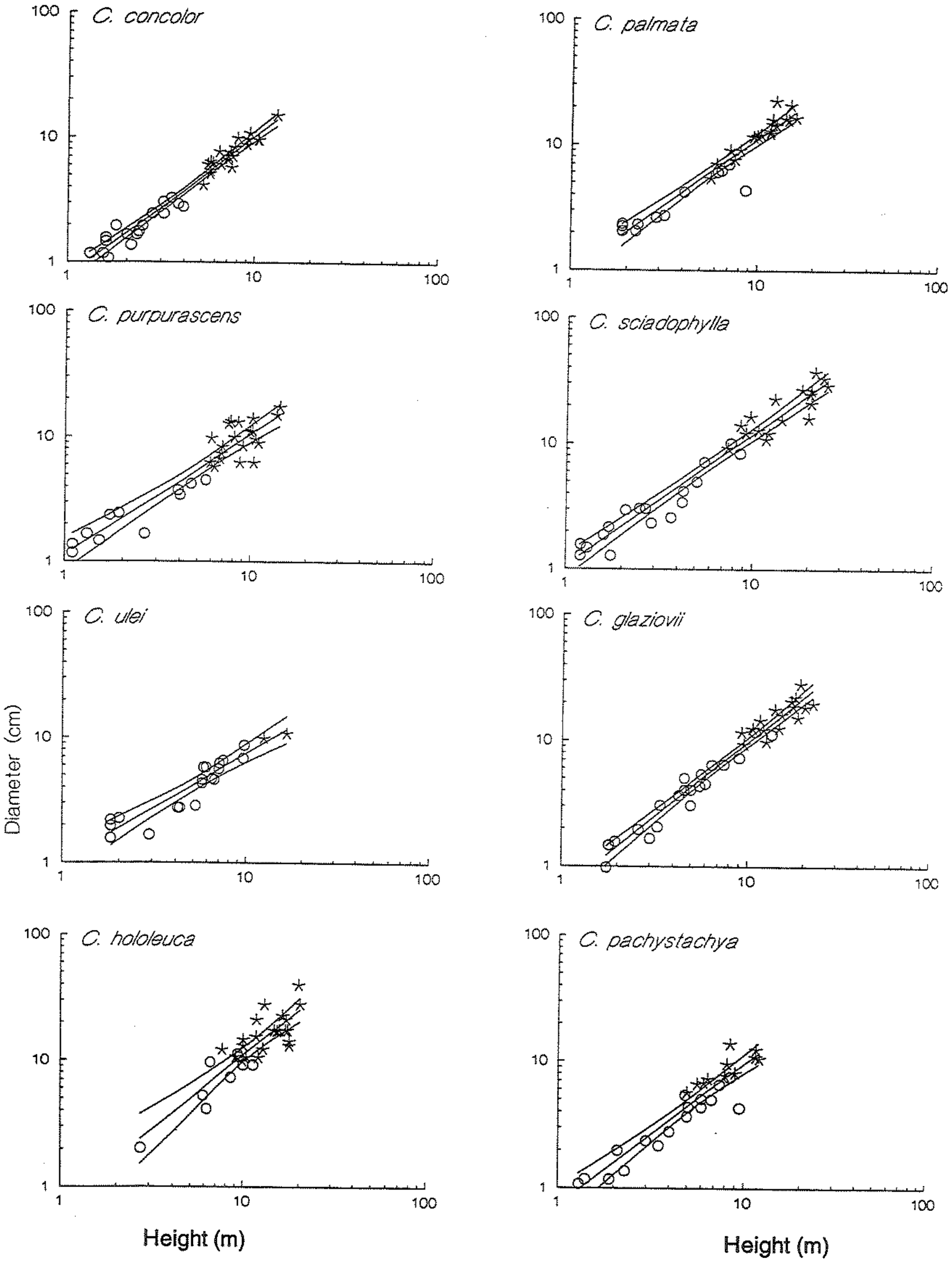
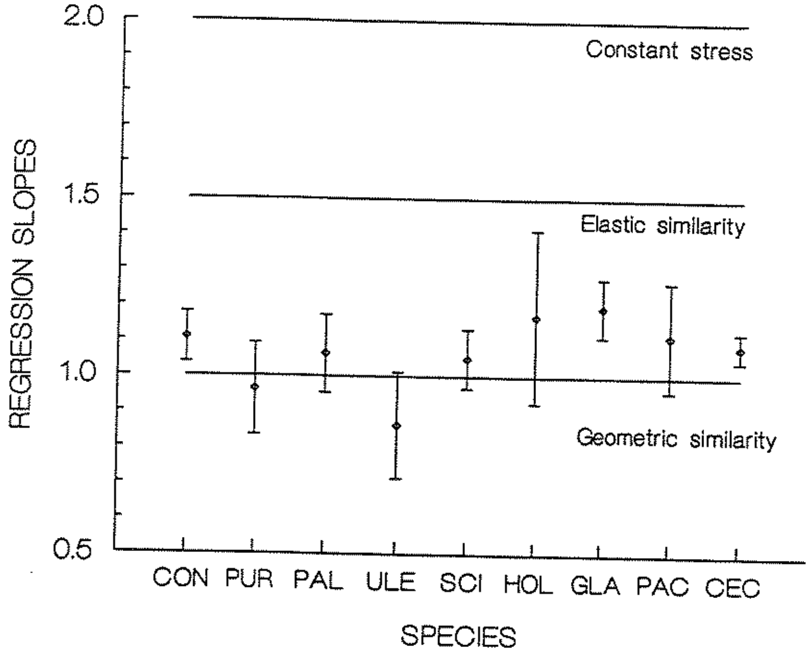
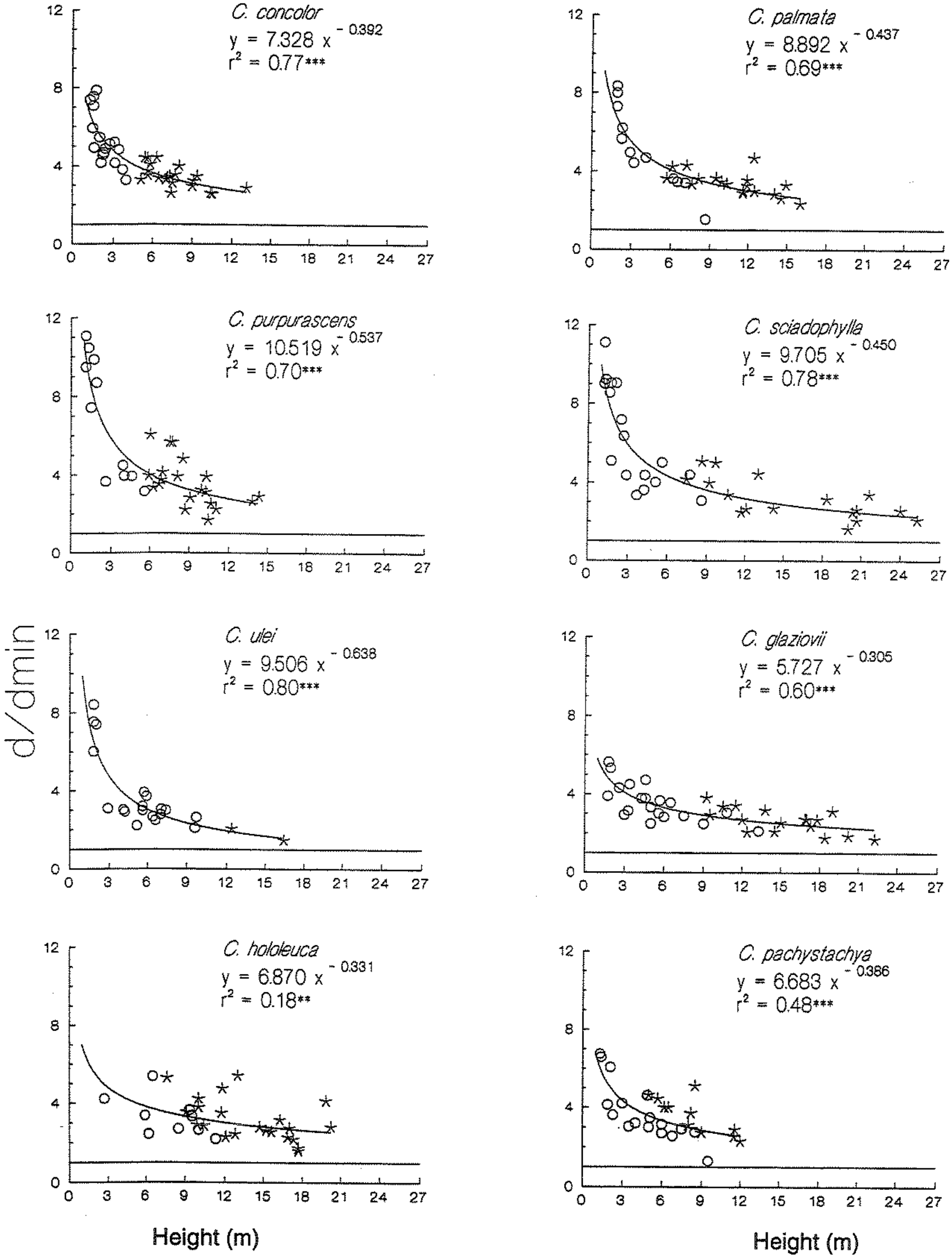

C. concolor
C. palmata
C. purpurascens
C. sciadophylla
C. ulei
C. glaziovii
C. hololeuca
C. pachystachya
Diameter (cm)
Height (m)
Height (m)
1
10
100

FIGURE 2



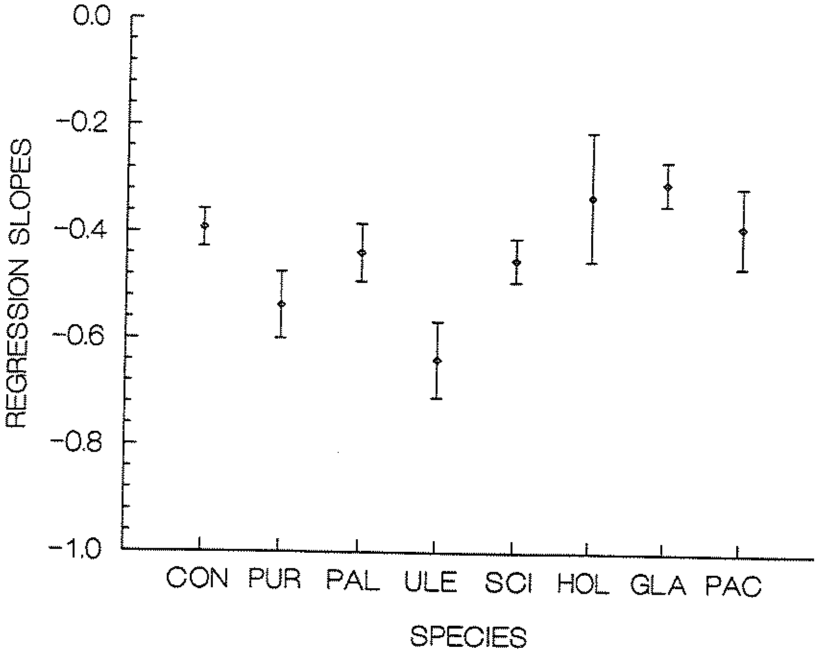
2.0
1.5
1.0
0.5
REGRESSION SLOPES
Constant stress
Elastic similarity
Geometric similarity
CON
PUR
PAL
ULE
SCI
HOL
GLA
PAC
CEC
SPECIES

FIGURE 3



C. concolor
y = 7.328 x - 0.392
r² = 0.77***
C. palmata
y = 8.892 x - 0.437
r² = 0.69***
C. purpurascens
y = 10.519 x - 0.537
r² = 0.70***
C. sciadophylla
y = 9.705 x - 0.450
r² = 0.78***
C. ulei
y = 9.506 x - 0.638
r² = 0.80***
C. glaziovii
y = 5.727 x - 0.305
r² = 0.60***
C. hololeuca
y = 6.870 x - 0.331
r² = 0.18**
C. pachystachya
y = 6.683 x - 0.386
r² = 0.48***
d/dmin
0
4
8
12
0
3
6
9
12
15
18
21
24
27
Height (m)
Height (m)

FIGURE 4



0.0
-0.2
-0.4
-0.6
-0.8
-1.0
REGRESSION SLOPES
CON
PUR
PAL
ULE
SCI
HOL
GLA
PAC
SPECIES

FIGURE 5

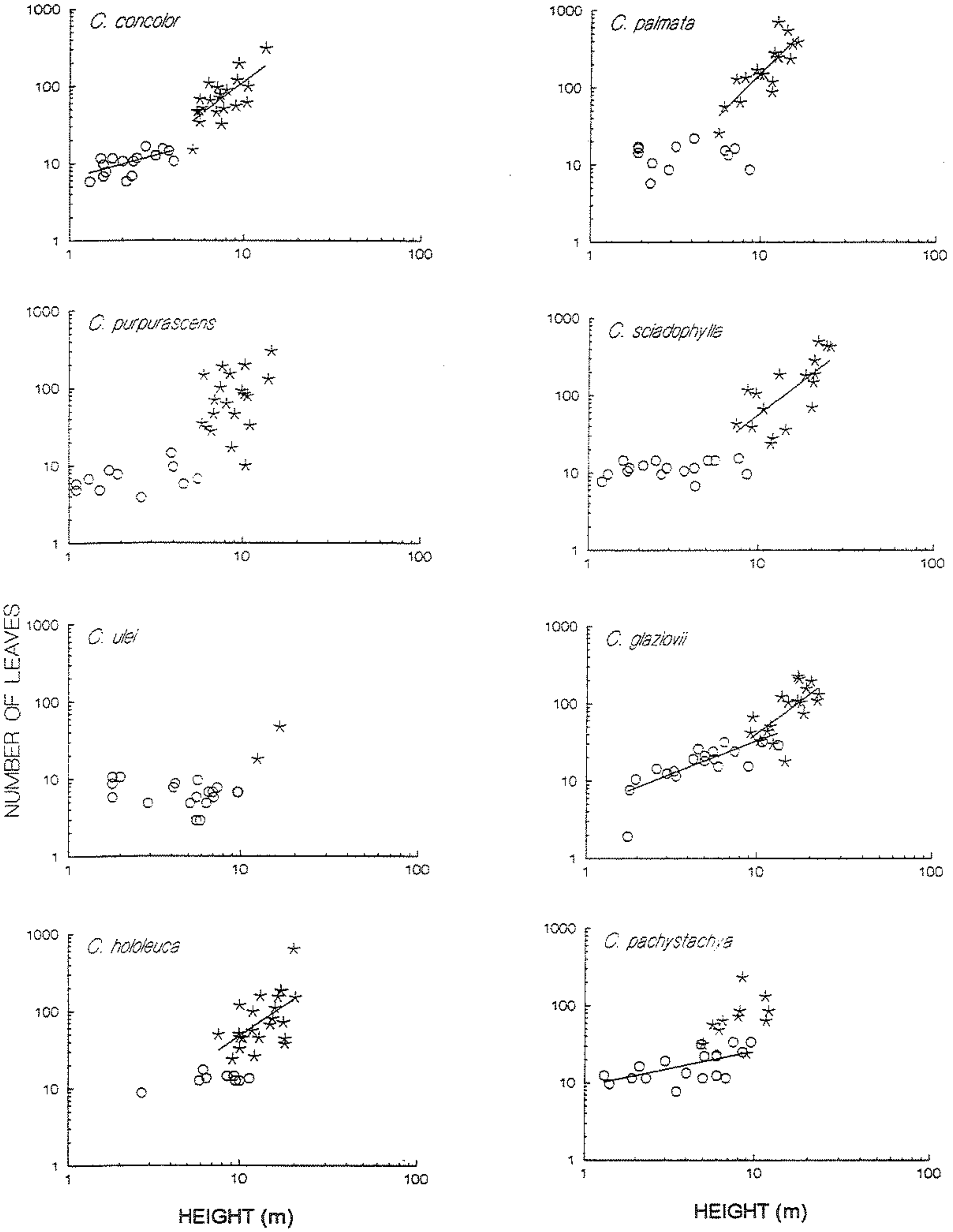
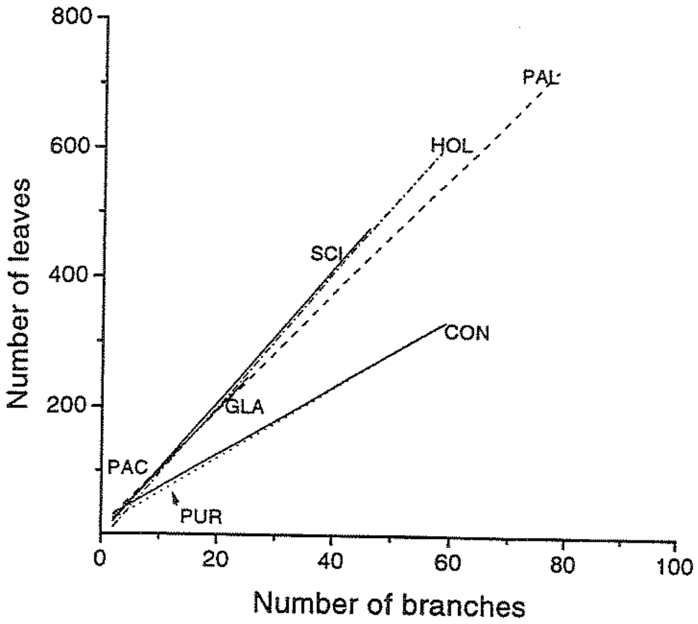

C. concolor
C. palmata
C. purpurascens
C. sciadophylla
C. ulei
C. glaziovii
C. hololeuca
C. pachystachya
NUMBER OF LEAVES
HEIGHT (m)
HEIGHT (m)
1
10
100
1000
1
10
100

FIGURE 6



800
600
400
200
0
20
40
60
80
100
Number of leaves
Number of branches
PAL
HOL
SCI
CON
GLA
PAC
PUR

FIGURE 7

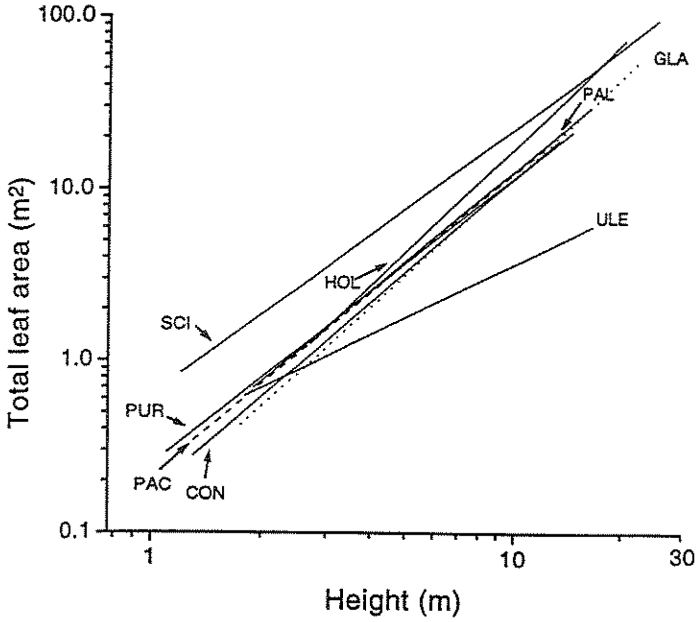
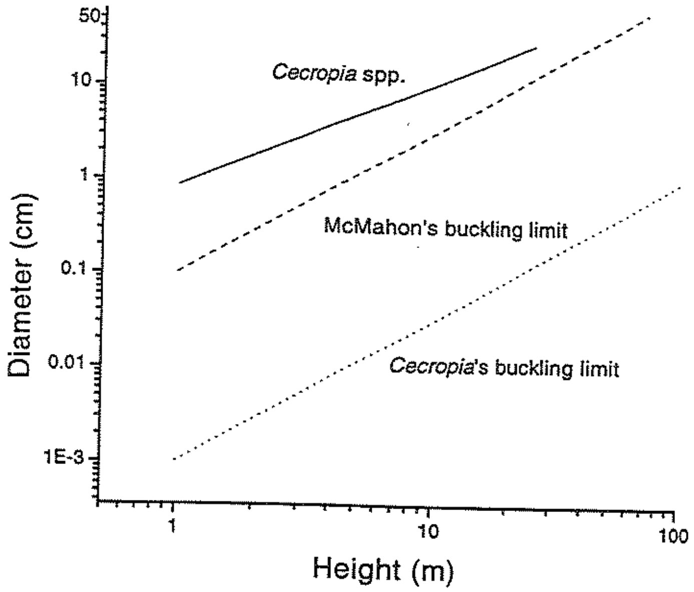

100.0
10.0
1.0
0.1
Total leaf area (m²)
1
10
30
Height (m)
GLA
PAL
ULE
HOL
SCI
PUR
PAC
CON

FIGURE 8



50
10
1
0.1
0.01
1E-3
Diameter (cm)
Cecropia spp.
McMahon's buckling limit
Cecropia's buckling limit
1
10
100
Height (m)

Capítulo 3

CRESCIMENTO E LONGEVIDADE FOLIAR EM JOVENS DE TRÊS ESPÉCIES DE *Cecropia* (CECROPIACEAE) DO SUDESTE DO BRASIL.

RESUMO

Cecropia glaziovii (Snethl.), *C. pachystachya* (Trécul) e *C. hololeuca* (Miq.) são espécies de embaúbas comuns nas florestas do Sudeste do Brasil. Dentre elas, somente *C. hololeuca* não é mirmecófila (não apresenta associação com formigas). O objetivo deste estudo foi acompanhar o crescimento em altura e diâmetro, a produção e longevidade das folhas das três espécies em plantas jovens (0,75 - 3,50 m de altura) para verificar possíveis diferenças entre as espécies mirmecófilas e não mirmecófilas. A área estudada localiza-se na Reserva Biológica da Mata do Jambreiro, Nova Lima, MG. Em abril de 1996 foram marcadas 14 a 16 plantas de cada espécie. Mensalmente foram anotadas a produção de novos entrenós e a produção e mortalidade de folhas. O crescimento das três espécies foi medido após 1 ano. As espécies mirmecófilas produziram mais entrenós durante o ano do que a não mirmecófila. Os valores máximos do incremento em altura e diâmetro foram maiores nas espécies mirmecófilas do que em *C. hololeuca*, mas não houve diferença significativa entre as medianas das espécies. O número de entrenós produzido no ano e o incremento em altura foram positivamente correlacionados com a pluviosidade mensal para todas as espécies. A taxa de emergência de folhas foi maior nas espécies mirmecófilas do que em *C. hololeuca*. A taxa de mortalidade foi maior para as folhas de *C. glaziovii* do que para as outras duas espécies. As folhas de *C. hololeuca* e *C. pachystachya* duraram mais tempo (± 7 meses) do que as folhas de *C. glaziovii* (± 4 meses).

Palavras-chave: Brasil, *Cecropia*, crescimento, longevidade foliar, mirmecófitas, mutualismo

ABSTRACT

Cecropia glaziovii (Snethl.), *C. pachystachya* (Trécul) and *C. hololeuca* (Miq.) are common pioneer species in Southeastern Brazil forests. Only *C. hololeuca* is non-myrmecophyte (no ant-association). The goal of this study was measure height and diameter growth, and leaf demography of the three species, in sapling trees (0,75 - 3,50 m height), to verify possible differences between myrmecophytic and non-myrmecophytic species. The study was conducted in Reserva Biológica da Mata do Jambreiro, Nova Lima, MG, Brazil. In April 1996, 14-16 plants of each species were marked. Internode production and the emergence and death of new leaves were recorded monthly. Height growth was measured after one year sampling. Myrmecophytic species produced more internodes than non-myrmecophyte. Maximum height increment values were higher in myrmecophytes than in *C. hololeuca*, but no significative differences were found among the species medians. Internodes.yr^{-1} and height increment were positive correlated with monthly rainfall in all species. Leaf emergence was higher in myrmecophytes than in *C. hololeuca*. Leaf death was higher for *C. glaziovii* leaves than for the other two species. Leaves of *C. hololeuca* and *C. pachystachya* (± 7 meses) lived longer than *C. glaziovii* leaves (± 4 meses).

Key-words: ant-plants, Brazil, *Cecropia*, growth, leaf longevity, mutualism,

INTRODUÇÃO

O gênero *Cecropia* (Cecropiaceae) é formado por árvores de pequeno a grande porte, de folhas grandes e peltadas, sendo o caule e ramos ocos, marcados por nós, que correspondem à cicatriz da estípula que protege a gema terminal (Berg 1978). As espécies de *Cecropia* são conhecidas por sua associação mutualística com formigas, principalmente do gênero *Azteca* (Formicidae, Dolichoderinae) (Berg 1978; Benson 1985). As formigas colonizam a planta logo nos primeiros estádios de desenvolvimento, quando surgem, na base do pecíolo das folhas, os triquílios, aglomerados de pêlos onde são produzidos os corpúsculos müllerianos, ricos em glicogênio (Rickson 1971), utilizados pelas formigas como alimento. Outra fonte de alimento utilizada pelas formigas são os "corpos perolados", pequenas gotículas encontradas na superfície abaxial de folhas novas (Folgarait & Davidson 1994). A maioria das espécies de *Cecropia* é mirmecófila, mas no Brasil ocorrem duas espécies que não possuem triquílios: *C. hololeuca* e *C. sciadophylla*, a primeira da região sudeste e a segunda da região amazônica (Berg 1978; Benson 1985).

Espécies de *Cecropia* mirmecófilas podem ser beneficiadas pela associação com formigas através da proteção contra herbívoros (Schupp 1986; Davidson et al. 1991; Rocha & Bergallo 1992; Vasconcelos & Casimiro 1997). Mas o custo associado com a manutenção de formigas parece ser alto, pois espécies mirmecófilas de *Cecropia*, que crescem em locais onde não existem as espécies de formigas mutualistas, tendem a não produzir triquílios ou corpúsculos müllerianos (Janzen 1973; Rickson 1977; Putz & Holbrook 1988). Por outro lado, as defesas químicas também devem ter custos altos, conforme sugere a correlação negativa entre a quantidade de taninos e taxa de produção de folhas observada em *C. peltata*, uma espécie mirmecófila da América Central (Coley 1986).

O tipo de defesa presente nas plantas parece ser influenciado pelas características de crescimento das espécies, principalmente a longevidade foliar (McKey 1984; Coley *et al.* 1985). Em ambientes pobres em luz e nutrientes, as plantas devem investir pesadamente em mecanismos de defesa e, consequentemente, apresentam folhas de alta longevidade e taxas de crescimento lentas (Coley et al. 1985). Folhas longevas, características de espécies de crescimento lento, favorecem a seleção para defesas "imóveis", como taninos e ligninas, que são metabolicamente inativos. Estas defesas têm altos custos de construção, mas não apresentam custos metabólicos contínuos de "turnover". Numa relação de custo-benefício, este tipo de defesa seria mais efetivo em folhas longevas, pois os custos de síntese poderiam ser amortizados por um período mais longo (McKey 1984). Folhas de vida curta favoreceriam a seleção para defesas móveis, os compostos de baixo peso molecular como alcalóides, glicosídeos cardíacos ou monoterpenos (Feeny 1976). Uma vez que estes compostos têm rápidas taxas de turnover, eles podem ser continuamente sintetizados (McKey 1984; Coley *et al.* 1985).

Em plantas mirmecófilas com folhas longevas, as folhas maduras seriam protegidas primariamente por defesas químicas ou mecânicas, como taninos e ligninas, pois este investimento seria mais econômico do que a manutenção de operárias, por um longo período de tempo. As operárias poderiam ser mantidas patrulhando exclusivamente as folhas novas. Por outro lado, em mirmecófilas de folhas de vida curta, as folhas maduras seriam patrulhadas em maior escala pelas formigas. Para estas plantas, taninos e ligninas representariam um alto custo porque a alta taxa de descarte de folhas levaria a uma grande perda de investimento nestes compostos. Ao invés disso, as operárias mantidas poderiam se transferir das folhas senescentes para o resto da planta (McKey 1984).

Além de fatores relacionados à defesa, a longevidade foliar também está associada ao crescimento. Em um levantamento abrangendo diversos ecossistemas, as taxas de crescimento relativo em plantas arbóreas jovens foram negativamente relacionadas com a longevidade foliar (Reich *et al.* 1992).

O objetivo deste estudo foi verificar a existência de diferenças na produção e longevidade das folhas, e no crescimento de três espécies de *Cecropia* que ocorrem no Sudeste do Brasil, uma delas não mirmecófila. *Cecropia pachystachya, C. glaziovii* e *C. hololeuca* ocupam um gradiente de áreas abertas para florestas (cap. 1 e 2 desta tese). De acordo com as teorias descritas, as espécies mirmecófilas e de ambientes abertos e mais ricos devem apresentar altas taxas de crescimento e longevidade foliar menor, quando comparadas com a espécie não mirmecófila, que ocupa o ambiente mais sombreado de floresta.

MATERIAL E MÉTODOS

Espécies

As espécies incluídas neste estudo foram *Cecropia glaziovii*, *C. pachystachya* e *C. hololeuca,* esta última não mirmecófila. *Cecropia glaziovii* e *C. hololeuca* alcançam por volta de 20-25 metros de altura e ocorrem, geralmente, em florestas e bordas de florestas na região sudeste do Brasil. *Cecropia glaziovii* ocorre tambem no Estado de Santa Catarina. *Cecropia pachystachya* apresenta um porte menor (ca. de 12 m) e uma distribuição mais ampla, ocorrendo no sul, sudeste e centro-oeste do Brasil, em áreas de cerrado, campos, ocupando lagoas em processo de assoreamento, matas de restinga e áreas degradadas.

Área de Estudo

O estudo foi realizado na Reserva Biológica da Mata do Jambreiro, localizada no município de Nova Lima, Minas Gerais, na vertente sul da Serra do Curral. A área pertence à MBR- Minerações Brasileiras Reunidas S. A. que explora minério de ferro na serra. A mata faz limite ao norte com a Mina de Águas Claras, tendo perdido 10 ha de área em função da construção da barragem de contenção de rejeitos. Nas porções sul e sudoeste ocorrem vários condomínios de casas que ainda mantém a vegetação de cerrado e floresta, fazendo contato com a Reserva. A pluviosidade anual média é de 1824 mm e a temperatura média anual é de 19°C, de acordo com os dados meteorológicos coletados na mina entre 1983 e 1990. As chuvas estão concentradas no período de outubro a março e durante os meses de inverno ocorre uma estação seca. O relevo é montanhoso e a vegetação da área é composta, em sua maior parte, por floresta estacional semidecidual submontana (Andrade 1992). Aparentemente, a floresta apresenta pouca caducifolia para um clima estacional. Ocorrem também manchas de cerrado e campos nos limites com a mata.

Os indivíduos de *Cecropia glaziovii* e *C. hololeuca* estavam nas bordas da floresta, ao longo das estradas de acesso à barragem. Os indivíduos de *C. pachystachya* ocorreram nas áreas de campo cerrado, ou de transição entre mata e campo cerrado, ou em áreas abertas e barrancos ao longo das estradas.

Coleta de dados

No final de abril de 1996 foram marcados 20 indivíduos de cada uma das três espécies de *Cecropia*, mas nem todos sobreviveram. Alguns indivíduos foram perdidos por causa da forte chuva de janeiro de 1997, que provocou desabamentos nas estradas levando algumas plantas marcadas. Outras foram cortadas pela MBR na limpeza da estrada, apesar de todos os apelos e contatos feitos com a empresa. Por esta razão, o número final de indivíduos ficou entre 14 e 16 para cada espécie.

O tamanho inicial da planta e seu crescimento foram positivamente correlacionados em estudos feitos com algumas espécies tropicais arbóreas (Swaine et al. 1987; Clark & Clark 1992, Sposito e Santos, não publicado). Sendo assim, para possibilitar uma comparação entre as espécies, a altura das plantas foi limitada dentro da faixa de 0,75 - 3,50 m, (Fig. 1). Os indivíduos de *C. hololeuca* apresentaram diâmetros menores, se comparados às outras duas espécies, mas a maior parte dos indivíduos estava na faixa de 1 - 4 cm (Fig. 1).

O último entrenó de cada planta foi marcado com tinta para tecido de cor branca. O diâmetro (a 1,30 m do solo ou no último entrenó), altura e número de folhas dos indivíduos foram registrados. A contagem de folhas e entrenós foi feita a cada 30 dias, em doze amostragens. A emergência de uma folha foi considerada quando ela estava fora da estípula, mesmo que não estivesse ainda totalmente expandida. A folha foi considerada morta quando não se encontrava mais presa ao caule, ou quando não havia nenhum tecido verde, mesmo que ela ainda estivesse presa à planta Não foram incluídas na contagem as folhas acidentalmente danificadas pelo manuseio das plantas, e as folhas que nasceram e morreram no mesmo mês. Este critério foi adotado pois o objetivo do estudo foi acompanhar a longevidade foliar e não a demografia das folhas. O crescimento foi medido ao final de 360 dias, usando fita métrica e paquímetro. Os entrenós de cada planta foram medidos sempre do lado direito de uma cicatriz foliar. Este procedimento padronizou as medidas, uma vez que os entrenós são irregulares. O diâmetro foi medido no mesmo local marcado no início do trabalho.

Análise de dados

As medidas de crescimento foram analisadas comparando-se os intervalos de confiança (95%) das medianas dos parâmetros analisados, usando a opção gráfica "notch", do programa SYSTAT (1992). Se os intervalos em torno de duas medianas não se sobrepõem, pode-se concluir que as medianas das duas populações são diferentes (McGill *et al.* 1978). O coeficiente de correlação de Spearman foi usado para comparar o crescimento mensal e a pluviosidade do local, e outros parâmetros relacionados às folhas.

Para o cálculo da idade das folhas, considerei todas as folhas nascidas no mesmo mês com a mesma idade. As taxas de emergência e mortalidade das folhas foram estimadas pelo número de folhas novas e mortas de cada mês. As taxas de recrutamento foram estimadas pela diferença entre as taxas de emergência e mortalidade das folhas. A taxa de "turnover" das folhas foi estimada pela divisão da taxa de emergência pela taxa de mortalidade, e indica o tempo de renovação das folhas. A comparação entre as espécies foi feita através da comparação dos intervalos de confiança das medianas.

A meia-vida das folhas (em dias) foi estimada usando a fórmula (Watkinson 1986):

meia-vida = $(t \ln 2)(\ln N_0 - \ln N_t)^{-1}$, onde t = longevidade máxima em dias, N = número de folhas.

As curvas de sobrevivência das folhas das três espécies foram calculadas e comparadas pelo teste de Peto e Peto (valor crítico denominado *LR*) (Pyke & Thompson 1986). As curvas foram calculadas somente para as folhas nascidas no mês de maio de 1996. Nos meses seguintes não houve número de folhas suficiente para análise, devido aos efeitos da sazonalidade e longevidade alta das folhas de algumas espécies.

RESULTADOS

Crescimento

O crescimento foi diferente entre as espécies mirmecófilas e a não mirmecófila (Tab. 1). *Cecropia glaziovii* e *C. pachystachya* produziram mais entrenós durante o ano (mediana = 27 e 21,5 entrenós respectivamente) do que *C. hololeuca* (mediana = 13 entrenós) (Fig. 2a). Os valores máximos do incremento em altura e em diâmetro foram maiores nas espécies mirmecófilas do que em *C. hololeuca*, mas não houve diferença significativa entre os intervalos de confiança (95%) dos valores das medianas das espécies (Tab. 1; Fig. 2b e c). O comprimento dos entrenós não diferiu significativamente entre as espécies (Tab. 1; Fig. 2d).

O número de entrenós produzido no ano e o incremento em altura foram positivamente correlacionados com a pluviosidade mensal para todas as espécies (Tab. 2, Fig. 3). O comprimento dos entrenós também apresentou correlacão positiva com a pluviosidade, exceto para *C. hololeuca*, cujo coeficiente de correlação não foi significativo (Tab. 2, Fig. 3). No mês de julho, que foi um dos mais secos do ano, 75% das plantas amostradas de *C. hololeuca* não produziram entrenós, contra 21% de *C. glaziovii* e 28% em *C. pachystachya*.

Produção de folhas e longevidade foliar

A taxa de emergência de folhas foi maior em *Cecropia glaziovii* e *C. pachystachya* (medianas = 26,5 e 21,5, respectivamente) do que em *C. hololeuca* (mediana = 13) (Tab. 3; Fig. 4a). A taxa de mortalidade foi maior para as folhas de *C. glaziovii* (mediana = 15) do que para as outras duas espécies (medianas = 3 e 5,5 para *C. hololeuca* e *C. pachystachya* respectivamente) (Tab. 3, Fig. 4b), sendo que para um indivíduo de *C. pachystachya* não houve registro de morte de folhas no período amostrado. As folhas de *C. hololeuca* e *C. pachystachya* duraram mais tempo (em torno de 7 meses) do que as folhas de *C. glaziovii* (em torno de 4 meses) (Tab. 3; Fig. 4c). Não foram encontradas diferenças significativas interespecíficas entre as taxas de recrutamento, (Tab. 3, Fig. 5a). Entretanto, houve uma variação maior nas espécies mirmecófilas, que também apresentaram as maiores taxas de recrutamento de folhas (Fig. 5a). A taxa de "turnover" de folhas foi maior em *C. pachystachya* (mediana = 4,13) e *C. hololeuca* (mediana = 4) (Tab. 3, Fig. 5b), indicando que nestas duas espécies a renovação das folhas foi mais lenta do que em *C. glaziovii*, cujo "turnover" foi menor (mediana = 1,77). O número de folhas total produzido durante o ano foi correlacionado com o número de folhas inicial da planta em *C. glaziovii* (r_S = 0,881; P < 0,001; n=14) e *C. pachystachya* (r_S = 0,618; P < 0,05; n=14), mas não para *C. hololeuca* (r_S = 0,391; 0,2 < P < 0,1; n=16).

As curvas de sobrevivência das folhas nascidas em maio de 1996 diferiram entre *C. glaziovii* e *C. hololeuca* (*LR* = 30,05; *P* < 0,001), e *C. glaziovii* e *C. pachystachya* (*LR* = 20,44; *P* < 0,001), mas não entre *C. hololeuca* e *C. pachystachya* (*LR* = 0,02; *P* > 0,05) (Fig. 6). A meia-vida das folhas foi estimada em 52, 97 e 92 dias para *C. glaziovii, C. hololeuca* e *C. pachystachya* respectivamente.

DISCUSSÃO

Embora o crescimento não tenha apresentado diferenças significativas entre as espécies, foram observados valores maiores de crescimento em altura e diâmetro nas espécies mirmecófilas. Este resultado está de acordo com a tendência já observada em outros estudos sobre os possíveis benefícios da presença ou ausência de formigas. Plantas mirmecófilas que cresceram sem formigas apresentaram crescimento menor quando comparadas com plantas ocupadas, tanto em espécies de *Cecropia* (Schupp 1986; Vasconcelos e Casimiro 1997), como em *Tachigali mirmecophila* (Fabaceae) (Fonseca 1994). Segundo alguns estudos, os benefícios viriam principalmente da defesa contra herbívoros que as formigas proporcionam (Janzen 1969; Schupp 1986; Rocha & Bergallo 1992; Fonseca 1994; Vasconcelos & Casimiro 1997). Mas também é possível que as espécies mirmecófilas possam absorver nutrientes de rejeitos dos ninhos ou das próprias formigas (ver Rickson 1979; Luizão & Carvalho 1981). Entretanto, é importante ressaltar que a tendência a um crescimento maior não significa, necessariamente, que este seja um benefício direto da mirmecofilia, pois neste estudo não foi medido o nível de herbivoria e sua relação com a presença de formigas.

O efeito da pluviosidade no comprimento dos entrenós foi observado em duas espécies de *Cecropia* da Costa Rica e relacionado à ocorrência das estações seca e chuvosa (Davis 1970). A alternância de entrenós curtos e longos poderia ser usada para estimar o crescimento passado em *Cecropia*, como sugere Davis (1970). Crescimento e pluviosidade foram altamente correlacionados nas três espécies estudadas, mas em *C. hololeuca* não houve correlação significativa para o comprimento dos entrenós. Portanto, nesta espécie não seria possível usar o tamanho dos entrenós como indicação de ocorrência de uma estação seca ou chuvosa, pelo menos na região estudada. Além disso, um número menor de entrenós produzidos no ano também dificultaria uma estimativa. No presente estudo, *C. hololeuca* produziu no máximo dois entrenós por mês, sendo que nos meses mais secos, muitas plantas não produziram entrenós. Entretanto, comprimento e número de entrenós devem variar entre as áreas de ocorrência da espécie, e resultados diferentes podem ser encontrados (Santos, não publicado).

A longevidade foliar das espécies estudadas está de acordo com o valor médio encontrado para espécies pioneiras, cerca de 6,9 ± 3,9 meses (Coley & Aide 1991). *Cecropia hololeuca* apresentou, neste estudo, folhas mais longevas do que no Rio de Janeiro (média de 95,33 dias; Santos, não publicado), mas a longevidade das folhas de *C. glaziovii* foi semelhante nos dois locais (média de 112,8 dias, Santos não publicado). Comparadas com outras espécies do gênero (todas mirmecófilas), *C. pachystachya* e *C. hololeuca*, na Mata do Jambreiro, apresentaram folhas mais longevas: *C. obtusifolia* (máximo de 120 dias; Núñez-Farfán & Dirzo 1989), *C. peltata* (12 semanas; Coley 1986) *C. obtusifolia* e *C. insignis* (4 - 4.7 meses respectivamente; Coley 1988) *C. ficifolia*, *C. polystachya*, *C. membranacea*, *C. engleriana* e duas espécies não descritas (A e B) (18 a 22 semanas; Folgarait & Davidson 1994). Com exceção de *Acacia cornigera*, cuja longevidade foliar está entre 6 - 9 meses (Janzen 1967 *apud* Fonseca 1994), outras espécies mirmecófilas apresentam longevidade foliar bem mais alta do que *Cecropia*: *Leonardoxa africana* (+ de 25 meses; McKey 1984), *Ocotea atirrensis* (24 meses; Bentley 1979) e *Tachigali myrmecophila* (30,7 - 81 meses, Fonseca 1994).

Os dados de crescimento e longevidade foliar das espécies estudadas, comparados com os dados da literatura mostraram que *C. glaziovii* encaixa-se perfeitamente no que seria esperado para uma típica espécie mirmecófila e pioneira, segundo as hipóteses de longevidade foliar e de disponibilidade de recursos (McKey 1984; Coley *et al.* 1985). Dentre as espécies de *Cecropia*, ela apresentou baixa longevidade foliar e altas taxas de crescimento, se comparada com *C. hololeuca*, cujo crescimento foi lento e cujas folhas tiveram longa durabilidade, com ausência de defesa por formigas. Ambas habitam florestas, mas *C. hololeuca* é uma espécie mais encontrada em ambientes sombreados do que *C. glaziovii*, que ocorre em muitas clareiras, e portanto, com menor limitação de luz. *Cecropia pachystachya* apresentou uma taxa de crescimento semelhante a de *C. glaziovii*, mas uma alta longevidade foliar para uma espécie mirmecófila do gênero *Cecropia*. A diferença em relação à *C. pachystachya* deve estar relacionada ao ambiente em que esta espécie ocorre, que em geral são locais muito iluminados, porém com solos menos ricos em nutrientes do que os solos de floresta.

Apesar das diferenças encontradas na longevidade foliar entre as espécies mirmecófilas, ambas produziram mais folhas e entrenós do que *C. hololeuca*, o que permite a manutenção de um suprimento mais constante de alimento para as formigas, pois a produção de corpúsculos müllerianos é maior nas folhas novas e decresce com a idade das folhas (Folgarait & Davidson 1994; Folgarait *et al.* 1994). Ainda, a taxa de "turnover" de folhas de *C. glaziovii* mostrou que esta espécie tem um tempo de renovação de folhas menor do que *C. pachystachya*, o que faz com que a primeira seja um recurso mais atrativo para as formigas. Uma vez que existe diferença na agressividade das espécies de *Azteca* (Longino, 1991), as duas espécies mais comuns do Sudeste (*A. alfari* e *A. muelleri*) podem competir pelas espécies de *Cecropia*. Poucos estudos existem sobre especialização de espécies de formigas e suas hospedeiras, mas é comum encontrar *Azteca* *muelleri*, que é geralmente mais ativa que *A. alfari* (obs. pessoal), habitando *C. glaziovii*[1] (Harada & Benson, 1988).

Embora os dados aqui apresentados corroborem, em sua maior parte, as relações sobre crescimento, longevidade foliar e defesa por formigas, existe uma grande probabilidade de haver variação dentro da amplitude geográfica da ocorrência das espécies estudadas. É importante saber primeiro se há alguma uniformidade na produção e mortalidade de folhas, pois já foram encontrados variações para *C. hololeuca*, no estado do Rio de Janeiro (Santos, não publicado). Além disso, dados sobre crescimento, produção e longevidade de folhas em outras espécies não mirmecófilas não existem até o momento.

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[1] *Azteca muelleri* foi encontrada com frequência em *Cecropia adenopus* (Harada & Benson 1988) que é sinônimo de *C. glaziovii*.

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Tabela 1 - Parâmetros de crescimento de três espécies de *Cecropia* da Região Sudeste do Brasil. A altura e o diâmetro correspondem às distribuições de tamanho inicial das plantas.

			Crescimento							
Espécie	Altura (m)	Diâmetro (cm)	Nº entrenós/ano		Altura (cm/ano)		Diâmetro (cm/ano)		Comprimento do entrenó (cm)	
	(Mín-Máx)	(Mín-Máx)	Mediana	Máx	Mediana	Máx	Mediana	Máx	Mediana	Máx
C. glaziovii	1,3 - 3,1	0,7 - 3,9	27,0	53	53,5	256	0,60	3,7	2,2	7,1
C. hololeuca	1,2 - 2,9	0,6 - 2,7	13,0	15	33,0	91	0,45	0,83	2,4	9,1
C. pachystachya	0,75 - 3,4	1,1 - 2,8	21,5	34	51,0	187	0,50	2,3	2,5	8,2

Tabela 2 - Coeficientes de correlação de Spearman entre a pluviosidade mensal e valores de crescimento médio das espécies de *Cecropia*, na Mata do Jambreiro, MG.

Espécie	Coeficiente de correlação de Spearman		
	Número de entrenós	Incremento em altura (cm)	Comprimento do entrenó (cm)
C. glaziovii	0,834**	0,839**	0,775*
C. hololeuca	0,916***	0,818**	$0,462^{n.s.}$
C. pachystachya	0,796*	0,930***	0,844**

* $P < 0,005$** $P < 0,002$ *** $P < 0,001$

Tabela 3 - Longevidade foliar, taxas de emergência, mortalidade, recrutamento e turnover de folhas das três espécies de *Cecropia* que ocorrem na região Sudeste. Valores mínimos (Mín), máximos (Máx) e mediana (Med). Na coluna de longevidade foliar o valor de N corresponde ao número de folhas; nas colunas restantes N corresponde ao número de plantas.

	Longevidade (meses)			Taxa de emergência			Taxa de mortalidade			Recrutamento			Turnover		
Espécie	Mín - Máx	Med	N	Mín - Máx	Med	N	Mín - Máx	Med	N	Mín - Máx	Med	N	Mín - Máx	Med	N
C. glaziovii	1 - 8	4	240	15 - 53	26,5	14	4 - 31	15	14	-8 - 27	14	14	0,65 - 4,75	1,77	14
C. hololeuca	2 - 11	7	65	11 - 15	13	16	0 - 6	3	16	5 - 15	10	16	1,83 - 11	4	14
C. pachystachya	1 - 12	7	103	5 - 34	21,5	14	0 - 10	5,5	14	5 - 34	16	14	1,5 - 3,0	4,13	13

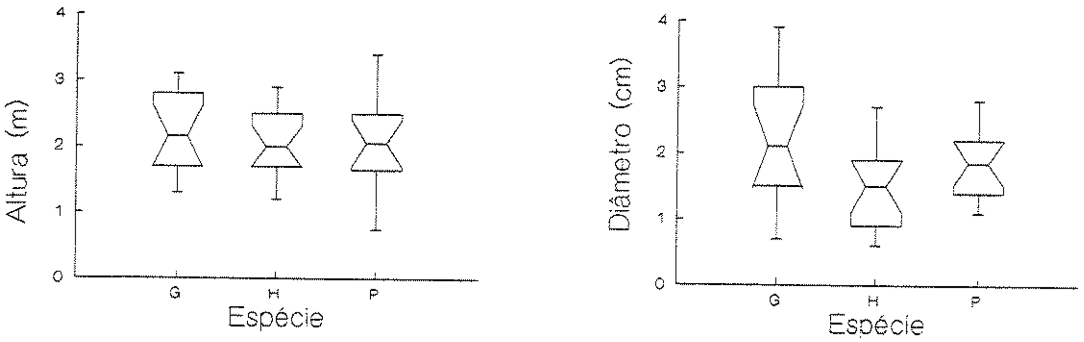


Fig. 1 - "Box-plots" das medidas de altura e diâmetro das espécies de *Cecropia* na Mata do Jambreiro, MG. O retângulo delimita 50% das observações e o traço central marca a mediana. As barras indicam a amplitude total da distribuição, exceto os pontos extremos ("outliers"), que são representados por asteriscos e aqueles muitos extremos que são os círculos (aparecem nas outras figuras). A porção afunilada do retângulo representa o intervalo de confiança (95%) da mediana. G = *C. glaziovii*; H = *C. hololeuca*; P = *C. pachystachya*.

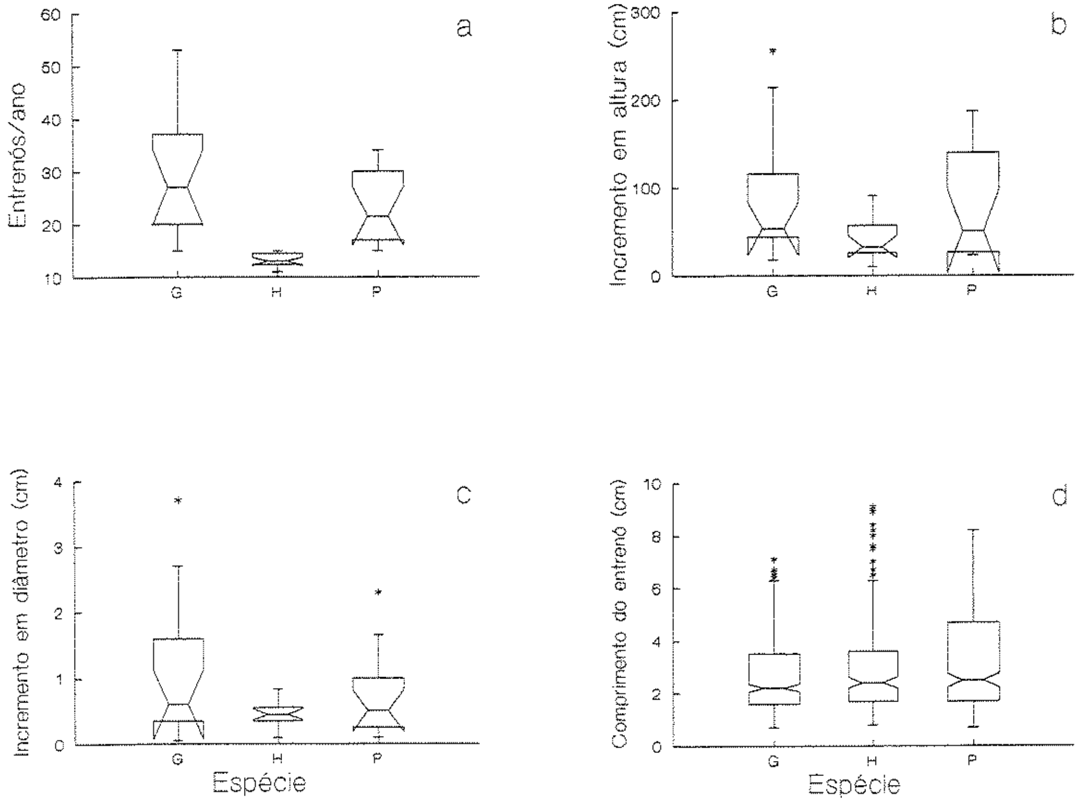
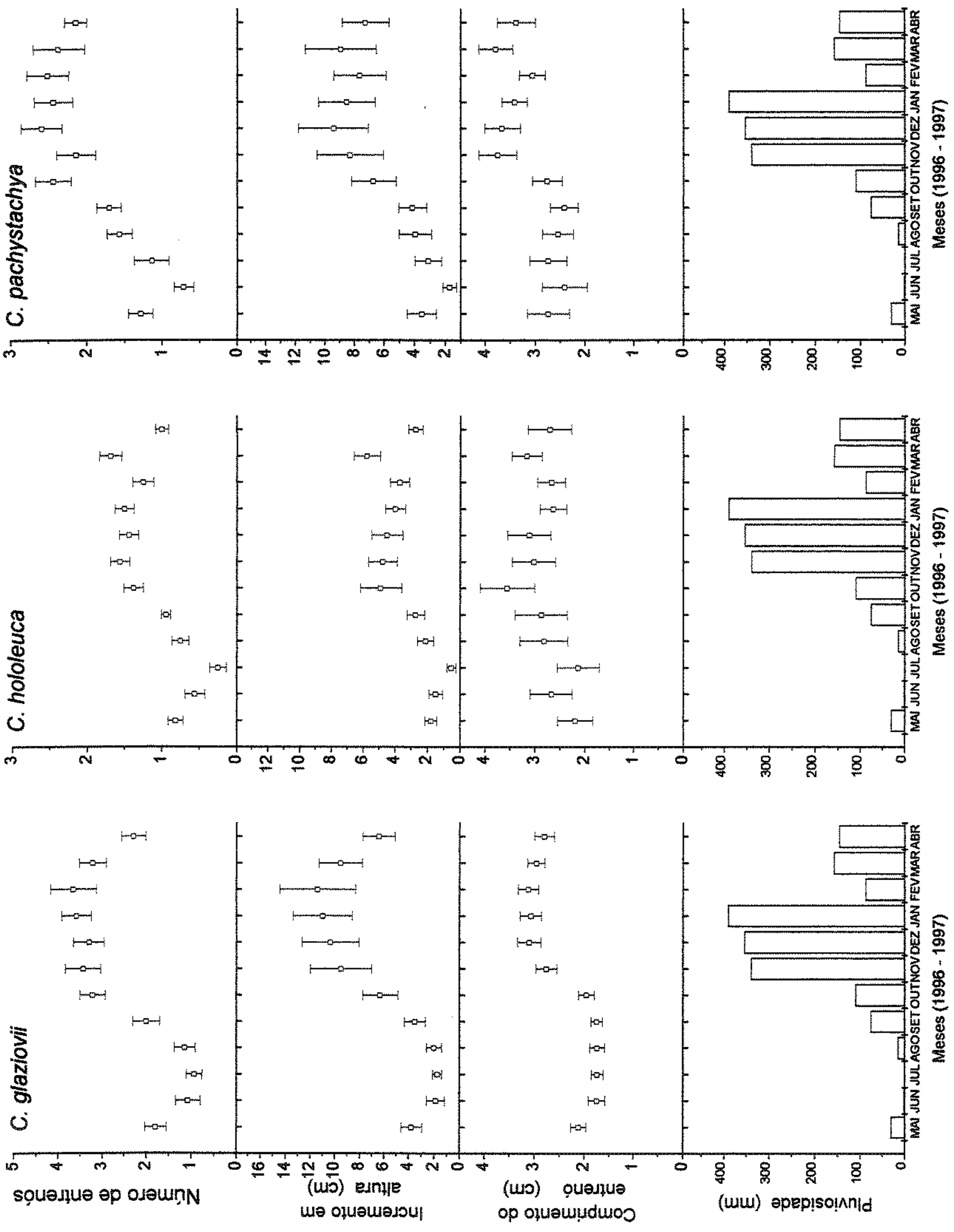


Fig. 2 - "Box-plots" dos parâmetros de crescimento das três espécies de *Cecropia* da Mata do Jambreiro - MG. a) número de entrenós produzidos no ano; b) incremento em altura (cm); c) incremento em diâmetro (cm) e d) comprimento do entrenó (cm). G = *C. glaziovii*; H = *C. hololeuca*; P = *C. pachystachya*.

Fig. 3 - Valores mensais do crescimento de três espécies de *Cecropia* e da pluviosidade mensal na Mata do Jambreiro, Nova Lima, MG. Média ± 1 erro padrão do número de entrenós, incremento em altura, comprimento do entrenó.


C. glaziovii
C. hololeuca
C. pachystachya
Número de entrenós
Incremento em altura (cm)
Comprimento do entrenó (cm)
Pluviosidade (mm)
MAI JUN JUL AGO SET OUT NOV DEZ JAN FEV MAR ABR
Meses (1996 - 1997)
0
1
2
3
4
5
6
8
10
12
14
16
100
200
300
400

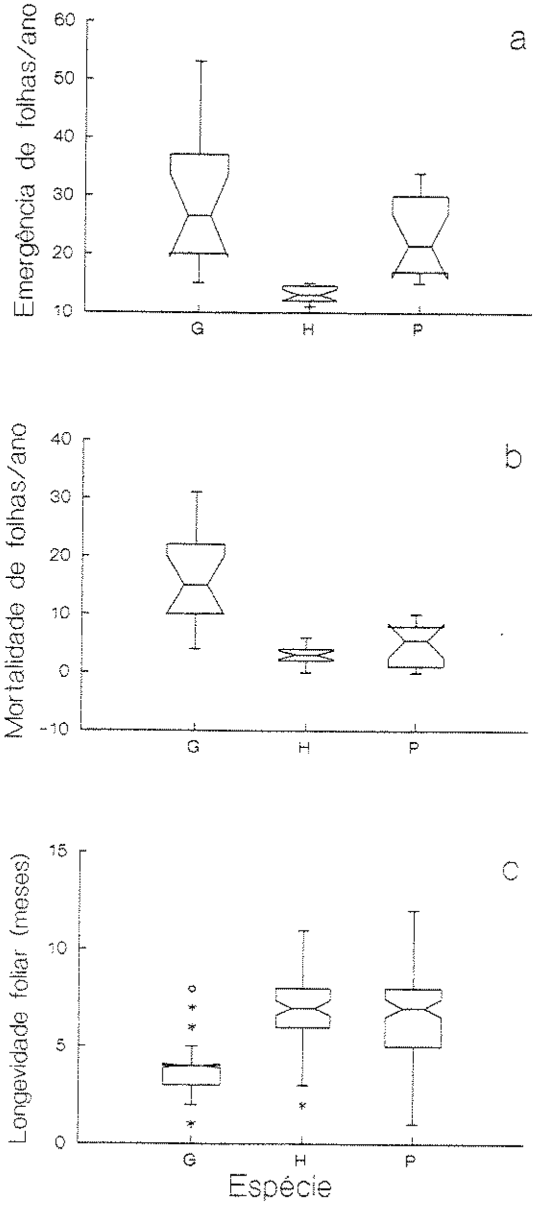


Fig. 4 - "Box-plots" dos parâmetros de produção e longevidade foliar das três espécies de *Cecropia*. a) emergência de folhas (ano^{-1}); b) mortalidade das folhas (ano^{-1}) e c) longevidade foliar (meses). G = *C. glaziovii*; H = *C. hololeuca*; P = *C. pachystachya*

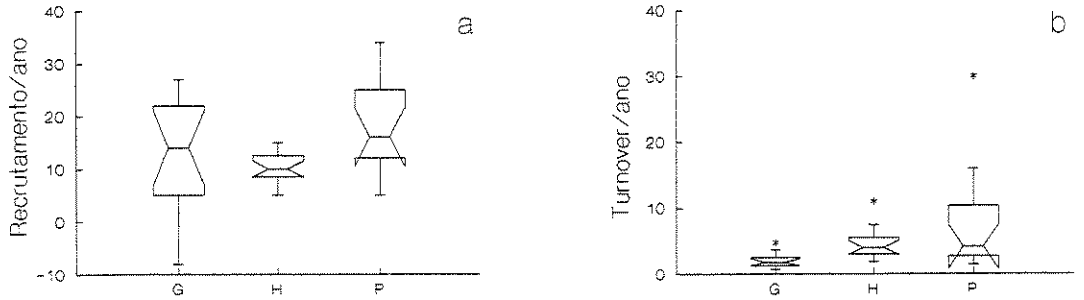


Fig. 5 - Taxas de recrutamento (ano^{-1}) (a) e "turnover" (ano^{-1}) (b) de folhas das três espécies de *Cecropia*. G = *C. glaziovii*; H = *C. hololeuca*; P = *C. pachystachya*

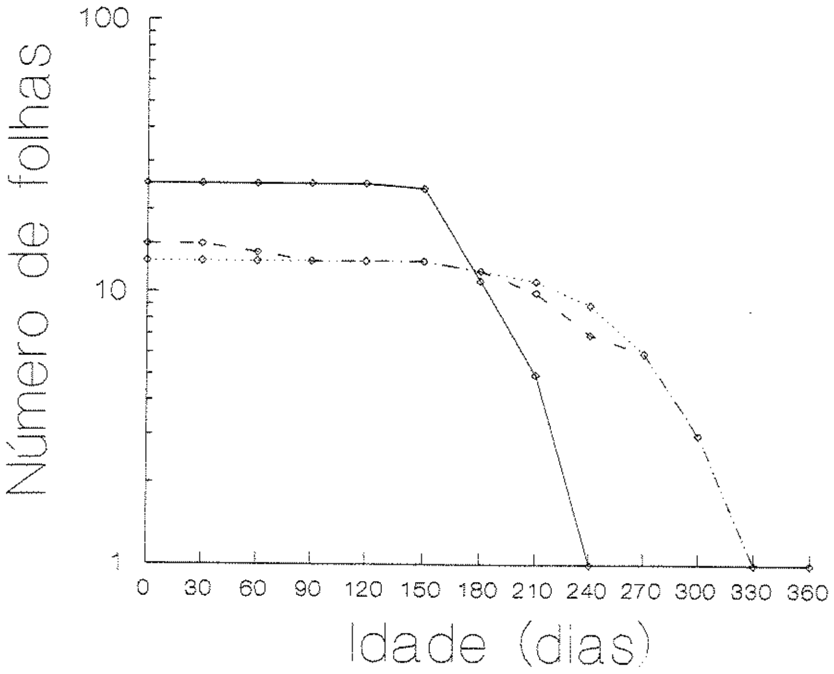


Fig. 6 - Curvas de sobrevivência de folhas de três espécies de *Cecropia* da Região Sudeste do Brasil, nascidas no mês de Maio de 1996. *C. glaziovii* = linha inteira; *C. hololeuca* = linha pontilhada; *C. pachystachya* = linha tracejada.

CONCLUSÃO GERAL

As oito espécies de *Cecropia* estudadas apresentaram variações morfológicas relacionadas a um gradiente de ocupação de áreas abertas para florestas, em ambos os locais, Amazônia e Sudeste do Brasil. *Cecropia hololeuca* e *C. sciadophylla* foram as espécies mais altas, com as maiores folhas, copa mais bifurcada, ocupando florestas e suas bordas. *Cecropia concolor* e *C. pachystachya* foram as menores espécies, com folhas menores e ocupam ambientes muito abertos. As outras espécies foram intermediárias entre estes dois extremos.

As relações alométricas do caule mostraram que as oito espécies de *Cecropia* estudadas oscilam ao longo da linha de crescimento isométrico entre diâmetro e altura. O fator de segurança diminuiu com o aumento da altura, mas não ultrapassou o limite de quebra do modelo de similaridade elástica. Na maioria das espécies, não foram encontradas mudanças nos expoentes das relações entre o diâmetro e altura em plantas ramificadas e não ramificadas. Apesar das espécies de floresta apresentarem uma grande área foliar, as relações alométricas não apresentaram diferenças nas inclinações das regressões; somente as médias ajustadas foram diferentes, o que indica que as diferenças entre as espécies estão mais relacionadas ao tamanho.

A ocorrência de possíveis diferenças no crescimento entre as espécies, sugeridas por algumas relações alométricas entre o número de folhas e altura, foi confirmada no estudo com as três espécies do Sudeste. *Cecropia glaziovii* e *C. pachystachya* produziram mais entrenós e folhas, durante um ano, do que *C. hololeuca*. A longevidade foliar das espécies foi menor para *C. glaziovii* do que para *C. hololeuca* e *C. pachystachya*. A mortalidade de folhas foi maior em *C. glaziovii* e também a rotatividade de folhas. Todas estas características podem ter alguma influência na ocorrência das formigas nas espécies.

CONSIDERAÇÕES FINAIS

Aspectos da morfologia e do crescimento em *Cecropia* foram aqui apresentados e discutidos. Alguns destes aspectos podem ser analisados do ponto de vista evolutivo, indicando possíveis mecanismos que possam ter influenciado a forma e tamanho em *Cecropia*, bem como a ocorrência de mirmecofilia no grupo. As observações finais que serão feitas são especulações sobre este estudo, oriundas destes resultados, de leituras e de um pouco de imaginação, pois a maioria carece ainda de comprovação.

O início da ramificação e da reprodução são eventos concomitantes na maioria das espécies estudadas, mas *C. concolor*, *C .ulei* e *C. pachystachya* normalmente iniciam a produção de inflorescências ainda no estágio monopodial. Supondo duas espécies simpátricas com crescimento semelhante, como no caso de *C. pachystachya* e *C. glaziovii*, a espécie que inicie sua reprodução precocemente, poderá recolonizar o ambiente aberto antes da outra. E ainda, a diferença entre a altura da primeira ramificação nas espécies também pode contribuir para aumentar a capacidade de colonização, pois quanto mais cedo a planta se ramifica, mais cedo ela aumenta o número de frutos produzidos. Estas diferenças no tempo do início da reprodução podem ter sido um mecanismo de diferenciação das espécies de *Cecropia*.

Diferenças no espaço interno do caule podem ter contribuído para a colonização de formigas e, ao mesmo tempo, modificado a capacidade de sustentação do caule das espécies. Algumas medidas ocasionais em plantas jovens de *Cecropia hololeuca* e *C. glaziovii,* mostraram que, na primeira, as paredes tendem a ser mais grossas. Como consequência, o espaço interno no caule poderia ser menor do que na espécie mirmecófila. Se existirem diferenças numa comparação de indivíduos de mesmo diâmetro, as espécies mirmecófilas deveriam apresentar paredes mais finas, aumentando o espaço interno do caule e favorecendo a ocupação por formigas. O espaço interno da planta é um fator limitante no estabelecimento de colônias de formigas em *Tachigali*

(Fonseca, 1993). Além disso, um caule mais oco pode ser mais flexível permitindo a ocupação de locais mais abertos, sujeitos à maior ação do vento. Portanto, uma alteração na forma do caule, com o aumento do espaço interno, pode ter diminuído a capacidade de sustentar uma biomassa maior de folhas, mas permitido um aumento de flexibilidade e facilitado a ocupação de habitats abertos, onde as plantas estão mais sujeitas à ação do vento.

A comparação do crescimento entre as três espécies mostrou que as espécies de *Cecropia* mirmecófilas produzem mais folhas e entrenós do que a não mirmecófila. Entretanto, é importante ressaltar que a tendência a um crescimento maior não significa, necessariamente, que este seja um benefício direto da mirmecofilia, principalmente devido à diminuição dos níveis de herbivoria. Fonseca (1994) questiona a associação entre ocupação por formigas e nível de herbivoria. Para ele, a ausência de formigas pode ser um efeito, e não a causa do alto nível de herbivoria nas plantas mirmecófilas naturalmente não ocupadas por formigas. Em outras palavras, ele questiona se a "performance" de plantas naturalmente não ocupadas é menor por causa da ausência de formigas, ou as formigas seriam incapazes de colonizar ou sobreviver em plantas de baixa produtividade. Este questionamento refere-se a uma comparação intraespecífica. Mas esta questão pode ser formulada para espécies não mirmecófilas de *Cecropia*. Será que as espécies não mirmecófilas de *Cecropia* perderam suas formigas por serem um recurso pobre? A ocorrência de formigas em caules de *C. hololeuca* já foi observada (F. A. M dos Santos e T. C. Sposito, obs. pes.), o que mostra que as rainhas podem não saber distinguir a espécie que pode fornecer alimento. É importante lembrar que tanto *C. hololeuca*, quanto *C. sciadophylla* apresentam pêlos na base do pecíolo, mas não formam triquílios. Um estudo anatômico comparativo das espécies poderia fornecer alguma indicação sobre estes pêlos das espécies não mirmecófilas, e os triquílios, que também são pêlos bastante aglomerados.

Um outro aspecto que vale a pena ser estudado em *Cecropia* refere-se a uma possível capacidade de hibridização das espécies, visto que muitas delas apresentam o mesmo número de cromossomos (Berg 1978), são polinizadas pelo vento, ocorrrem em simpatria e coincidem seus períodos de floração.

Apesar de ser um grupo muito estudado, as embaúbas podem ainda gerar muitos estudos interessantes, visto que algumas questões relacionadas a mirmecofilia e ao habitat das espécies ainda permanecem inexploradas. Seria muito interessante que as variações dos caracteres vegetativos das espécies fossem mais consideradas nos estudos evolutivos, principalmente neste gênero onde a forma e arquitetura das árvores sugerem possíveis relações adaptivas.

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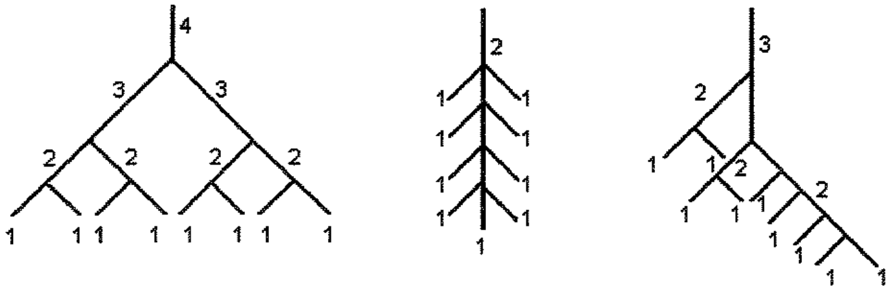
ANEXO I - Cálculo da taxa de ramificação do capítulo 1

O tipo de ramificação das árvores consiste de um único caule dando origem a uma série de divisões de pequenos ramos terminais. No método de ordenação de Strahler (1957), os ramos terminais são de ordem 1 e dois destes ramos se encontram formando um ramo de ordem 2. Dois ramos de ordem 2 se encontram formando um ramo de ordem 3 e assim vai até o tronco principal. Quando dois ramos de ordem diferente se encontram, o ramo formado leva o número de ordem do maior dos dois ramos. Finalmente dois ramos contíguos de mesma ordem constituem apenas um ramo.

A figura 1 exemplifica o modelo de ordenação de Strahler. Na figura 1**a** temos 8 ramos de 1ª ordem, 4 de 2ª ordem, 2 de 3ª ordem e 1 de 4ª ordem. O logaritmo do número de ramos em cada ordem, quando plotado contra a ordem do ramo produz uma relação linear. O antilog do valor absoluto da inclinação desta reta é a taxa de bifurcação ou taxa de ramificação (*Tr*). Um determinado valor de *Tr* implica que há, em média, *Tr* vezes o número de ramos de cada ordem na ordem inferior. A menor taxa de ramificação possível num sistema ordenado por este método é 2,0. Este valor é encontrado quando existe uma simetria dicotômica (Fig. 1**a**). Quando a ramificação ocorre por uma série de ramos laterais, qualquer valor de *Tr* acima de 2,0 é possível teoricamente. O sistema da Figura 1**b** tem uma *Tr* = (9,0). Graus intermediários de simetria produzem valores baixos de taxa de ramificação. O sistema da Figura 1**c** tem valor de 3,0. Não existe limite teórico para a Tr neste sistema (Barker *et al.* 1973).



Tr = 2 *Tr* = 9 *Tr* = 3

(a) (b) (c)

Figura 1 - Padrões de ramificação ordenados para calcular a taxa de ramificação (*Tr*) de acordo com Strahler's (1957) (extraído de Barker *et al.* 1973).

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ANEXO II - Demonstração da equação para calcular o diâmetro mínimo (d_{min}) (capítulo 2)

A altura crítica de tombamento (H) prevista pela fórmula de Greenhill (1881) *apud* McMahon (1973) é dada pela fórmula:

$$H = C\,(E/\rho)^{1/3}\,D^{2/3} \qquad \text{eq. (1)}$$

O texto de McMahon (1973) fornece os seguintes valores:

$C = 0{,}792$; $E = 1{,}05 \times 10^5$ kg/m^2; $\rho = 6{,}18 \times 10^2$ kg/m^3

Utilizando estes valores, foi calculado o diâmetro crítico de tombamento :

$$E/\rho = 169{,}9029 \quad \therefore \quad (E/\rho)^{1/3} = 5{,}538603$$

$$H = 0{,}792 \times 5{,}538603\,D^{2/3}$$

$$H = 4{,}386574\,D^{2/3} \quad \therefore \; H/4{,}386574 = D^{2/3} \;\therefore\; 1/4{,}386574 \times H = D^{2/3}$$

$$\therefore (0{,}227968)\,H = D^{2/3} \;\therefore\; (0{,}227968)^{3/2}\,H^{3/2} = D \;\therefore\; 0{,}108846\,H^{3/2} = \mathrm{D}$$

Se arredondarmos 0,108846 (0,109) para 0,1 temos:

$$\mathrm{D}_{min} = 0{,}1\ \mathrm{H}^{1,5} \;\therefore\; \mathrm{D}_{min} = 0{,}1\ \mathrm{H}^{1,5} \;\therefore\; \log D = 1.5 \log H - 1 \quad \text{eq.(2)}$$

Portanto, a eq. (2) foi utilizada para calcular o diâmetro crítico de tombamento. Embora não haja nenhuma citação no texto de McMahon (1973) sobre unidades, nesta equação o diâmetro deve estar em **cm** e a altura em **m**. Desta forma, coincide com as linhas apresentadas nas figuras dos trabalhos de McMahon (1973) (*D* e H em metros), Rich *et al.* (1986) (*D* e *H* em metros) e Alvarez-Buylla & Martinez-Ramos (1992) (*D* em centímetros e *H* em metros). A equação apresentada em Alvarez-Buylla & Martinez-Ramos (1992) não coincide com a eq.(2), porém a linha traçada na Figura 6.a do manuscrito é coincidente com a eq. (2), pois quando a altura =0, o diâmetro = 0,1.

Utilizando a Figura 2 de McMahon (1973), foi verificado que o intercepto em y = 0,001, para o diâmetro em **m**. Uma equação que considere *D* e *H* em **m**, deveria apresentar C = 17,06312, pois se considerarmos que ao medir *D* em **cm** temos que dividir o seu valor por 100 (10^2), para expressarmos em **m** podemos reescrever a equação como:

$$H = 17{,}06312\,(E/\rho)^{1/3}\,(D/100)^{2/3}$$

$$H = 17{,}06312\,(E/\rho)^{1/3}\,(1/100)^{2/3}\,(D)^{2/3}$$

$$H = 17{,}06312\,(E/\rho)^{1/3}\,(0{,}01)^{2/3}\,(D)^{2/3}$$

$$H = 17{,}06312\,(E/\rho)^{1/3}\,(0{,}046416)\,(D)^{2/3}$$

$$H = (17{,}06312 \times 0{,}046416)\,(E/\rho)^{1/3}\,(D)^{2/3}$$

$H = 0{,}792\ (E/\rho)^{1/3}\ (D)^{2/3}$

Houve portanto uma troca de escala, embora nenhum dos textos faça qualquer menção sobre isto. Portanto, as equações utilizadas no capítulo 2 foram baseadas nos valores e nas figuras das referências já mencionadas.

Anexo III - Glossário para o capítulo 2

Buckling limit - limite de tombamento ou limite de quebra

Tapering --> taper - afilar-se, adelgaçar-se

Second moment of area - Segundo momento de área - Simbolizado por *I*. Um parâmetro dimensional que quantifica a distribuição da massa numa seção transversal, em relação ao centro da massa desta seção transversal. Também conhecido como segundo momento de inércia.

Flexural stiffness = Resistência à flexão- Mede a habilidade de uma estrutura para resistir à flexão. Simbolizada por *EI*, o produto do módulo de elasticidade e do segundo momento de área.