

Growth and leaf demography of two *Cecropia* species

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(received: September 11, 1998; accepted: December 30, 1999)

ABSTRACT - (Growth and leaf demography of two *Cecropia* species). Allometry, growth and leaf demography of two *Cecropia* species, one with ant mutualist (*C. glazioui*) and another without it (*C. hololeuca*), were studied in an Atlantic Rain Forest area in the State of Rio de Janeiro, SE Brazil. Stem diameter was allometrically related to height in both species. *Cecropia glazioui* showed higher annual growth rates and longer internodes than *C. hololeuca*. Leaf phenology showed a seasonal pattern in both species, but the number of leaves on each plant was more variable along the year in *C. hololeuca* than in *C. glazioui*. Survivorship curves for leaves were intermediate between Deevey's Type I and Type II curves, with young leaves of *C. glazioui* showing a greater survival rate and life expectancy than those of *C. hololeuca*. Low variability in leaf production throughout the year and high survival rate for young leaves of *C. glazioui* may be characteristics related to its association with ants.

RESUMO - (Crescimento e dinâmica foliar de duas espécies de *Cecropia*). Alometria, crescimento e demografia de folhas de uma espécie de *Cecropia* associada com formigas (*C. glazioui*) e outra não (*C. hololeuca*) foram estudadas em área de Floresta Pluvial Atlântica, no SE Brasil. As relações entre os diâmetros dos caules e as alturas das plantas foram semelhantes nas duas espécies. *Cecropia glazioui* apresentou maior crescimento anual e entrenós maiores que *C. hololeuca*. A emergência e a mortalidade de folhas foram sazonais nas duas espécies, sendo o número de folhas mais variável ao longo do ano em *C. hololeuca* que em *C. glazioui*. As curvas de sobrevivência de folhas foram intermediárias entre os Tipo I e Tipo II de Deevey, sendo que folhas jovens de *C. glazioui* apresentam probabilidades de sobrevivência e expectativas de vida maiores que as de *C. hololeuca*. A produção de folhas menos variável durante o ano, e a maior sobrevivência de folhas novas em *C. glazioui* podem estar relacionadas à associação com formigas.

Key words - Allometry, Atlantic Rain Forest, *Cecropia*, growth, leaf demography

Introduction

The growth of a plant is determined in part by the dynamics and longevity of its leaves. Trees of the humid tropics show several seasonal patterns of leaf activity (Givnish 1984). Some hypotheses have been advanced to explain the adaptive significance of leaf life span. These hypotheses have usually been developed in specific environmental contexts to explain the deciduous-evergreen dichotomy (Chabot & Hicks 1982). The pattern of leaf production by evergreen plants ranges from almost continuous production in some pioneer species, to discontinuous leaf flushes in many mature-phase species (Coley 1983). Leaf ageing and senescence are currently interpreted as part of a programmed allocation of resources within the plant, and physiological ageing and leaf life span seem to be part of a more general adaptive strategy of plants (Thomas & Stoddart 1980, Chabot & Hicks 1982).

Leaf dynamics has been correlated with primary productivity (Franco 1985), litterfall patterns, sea-

sonality, successional status and herbivore pressure (Chabot & Hicks 1982, Coley 1983). It has been suggested that young leaves of early successional species are difficult for herbivores to find because they are unpredictable in time and space (Coley et al. 1985). Moreover, they may exhibit less costly defenses that are effective against unspecialized herbivores (qualitative defenses). On the other hand, mature leaves of late successional species are predictable and these species may invest in costly broad-span defenses (quantitative defenses) (Feeny 1976, Coley 1983, 1986, 1988). Thus, the phenological patterns of leaf production and leaf longevity may indicate the type of defense a given species should possess (Coley et al. 1985).

Cecropia species are common in the Neotropical flora. They are fast-growing trees characteristic of disturbed sites and early stages of forest succession (Davis 1970). Most species within this genus are inhabited by ants. The significance of the *Cecropia*-ants association has been discussed elsewhere (see Janzen 1969, 1973, Berg 1978, Luizão & Carvalho 1981, Andrade & Carauta 1982). There is ample evidence that ants are effective defenders of *Cecropia* plants (Janzen 1969, Schupp 1987).

The growth and survival of the ant colonies that inhabit *Cecropia* plants depend on the growth and

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leaf production rates of the plants. This mutualistic relationship suggests that plants with ant mutualists should show higher growth rates, higher leaf survival rates and leaf longevity than those without ant association. Thus, considering species of *Cecropia* with and without ant association, differences in allometry, growth and leaf demography between these species could be expected.

The goals of this study were to examine allometry, growth, leaf life span and rates of emergence and death of leaves in two *Cecropia* species occurring in the same habitat, one associated with ants and the other not associated. I addressed the following questions: Are there differences in allometry and growth between species? Are there differences in leaf dynamics and leaf life span between species? Can the differences be related to ant association?

Material and methods

The study was carried out in an area of tropical moist Atlantic Forest, 370 m above sea level (located around the geographical coordinates of 22°27'S and 42°52'W), in the municipality of Piraí, State of Rio de Janeiro, Southeastern Brazil. The region has a wet season, extending from September to May, with a maximum of rainfall in January, and a dry season, extending from June to August, with a minimum of rainfall in July (Nimer 1977). This pattern was observed, with little variations, for 1983 and 1984 (figure 1), respectively the year before and the year of study.

Three species of *Cecropia* occur in this area: *C. pachystachya* Trécul, *C. glazioui* Sneth. and *C. hololeuca* Miq. The last two species were chosen for this study because they co-occur in the same habitat and are similar in size (Sposito 1999). Typically, the ventral petiole base of *Cecropia* leaves has a hairy mat (the trichilia) that produces glycogen-rich Müllerian bodies (Rickson 1971), while the leaf is being formed and for a short time after it has expanded (Folgarait & Davidson 1994). The quantity of Müllerian bodies produced by a plant is a function of the rate of leaf production, since trichilia of old leaves are inactive (Folgarait & Davidson 1994, Folgarait et al. 1994). Adult trees of *C. glazioui* are commonly inhabited by large colonies of *Azteca* ants (generally *A. muelleri* and, to a lesser extent, *A. alfari*), which occupy its hollow stems and branches, and consume the Müllerian bodies. *Cecropia hololeuca* has neither trichilia nor Müllerian bodies, and is not associated with specialized ants. This is the only extra-Amazonian species of the genus in Brazil that does not have an association with ants (Berg 1996).

Height (measured up to the base of apical stipule), stem diameter (measured at the base) and number of leaves were recorded for 63 unbranched individuals (0.2 to 4.0 m tall) of the two species (18 of *C. glazioui* and 45 of *C. hololeuca* - differences in number of individuals were due to both different abundance of individuals in the area and death of plants during the study period).

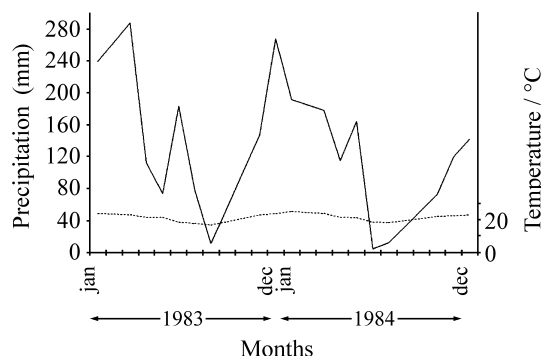


Figure 1. Monthly precipitation (mm) and mean temperature (°C) in Piraí, RJ, for 1983 and 1984. Data were obtained from 6° Distrito de Meteorologia do Rio de Janeiro (22°38'S and 43°54'W, 367 m a.s.l.). Precipitation (—), Temperature (.....).

Standard regressions were used to describe allometric patterns. Variables were \log_{10} -transformed before regressions were performed (King 1990, Kohyama & Hotta 1990, Niklas 1994). Comparisons between regression lines were made by an ANCOVA (Snedecor & Cochran 1980, Zar 1984).

To monitor growth, the individuals were marked and followed for seven recording periods in 1984 (February, March, May, June, August, September and October). Mean growth rates were estimated for each individual through the number and sizes of new internodes produced in each recording period, using the following formulae: $GRI = NI \cdot \Delta t^{-1}$; $GRH = (\Sigma SI) \cdot \Delta t^{-1}$; $MSI = (\Sigma SI) \cdot NI^{-1} \cdot \Delta t^{-1}$; where: GRI = growth in number of internodes, GRH = growth in height, MSI = mean size of internodes, NI = number of internodes produced during a sample period, SI = size of internodes produced during a sample period, Δt = days between samples.

All leaves on each plant were marked and the rates of emergence and death were obtained for each of the seven sampled periods. Emergence was considered to begin when the stipule tore and the leaf was exposed. A leaf was considered dead when no green tissue remained on it, or when it detached from the stem. Leaves that had been damaged by handling were excluded from further analysis.

The rates of emergence (bl) and death (dl) were estimated by dividing the number of new or dead leaves by the number of days between two sample periods. Recruitment rates (rl) were estimated by the difference between emergence and death rates. Leaf turnover rate was estimated by dividing the emergence rate by the death rate (Costa et al. 1991). Mean leaf turnover rate values were compared by a t-test between species (Zar 1984).

Growth rates and rates of leaf emergence and death were compared by observations of overlap in confidence intervals of median in box-plots (McGill et al. 1978). Variations in size of internodes of each individual was represented by a \log_{10} transformation of the variance of internode size measured in each individual. A log-transformation was used to obtain homoscedascity (Zar 1984).

The ages of leaves already present on plants at the first observation were estimated with the aid of the mean emergence rate calculated for each individual and by taking into account the

position of the leaves on the plant. The age of leaves produced during the study period was estimated by using the emergence rate. The age to death was considered as the age at which a leaf was last seen on a plant. The parameters of leaf life tables were calculated for age intervals of 30 days. Survivorship curves for leaves of the two species were compared by a Peto and Peto log-rank test (Pyke & Thompson 1986). Half-life (in days) was estimated by the formulae (Watkinson 1986): $t_{0.5} = (t \cdot \ln 2) \cdot (\ln N_0 - \ln N_t)^{-1}$, where: t = maximum longevity in days, N = number of leaves, and compared by a t-test for differences between species (Zar 1984).

Results

Stem diameter was allometrically related to height in both *Cecropia* species (figure 2) and there were no differences in allometric relations between species (between slopes: $F_{1:34} = 0.859$, $p = 0.364$; between intercepts: $F_{1:35} = 2.777$, $p = 0.101$).

Individual growth rates in height varied between 0.12 and 1.44 $\text{m} \cdot \text{yr}^{-1}$ in *C. glazioui* and between 0.04 and 2.76 $\text{m} \cdot \text{yr}^{-1}$ in *C. hololeuca*. In spite of the higher growth of some individuals of *C. hololeuca*, the growth rate of the two species was similar (figure 3a). Growth in *Cecropia* species can be affected by the number and size of internodes produced. The species studied did not differ in number of internodes produced per year (figure 3b) and in mean size of internode produced by individual (figure 3c), but the internode size was more variable in individuals of *C. glazioui* than in *C. hololeuca* (figure 3d).

Both species showed similar variation throughout the year in growth rates, in number of internodes produced and in internode length (figure 4), with low values in June and August. However, the internode length seems to be more variable throughout the year in *C. hololeuca* than in *C. glazioui* (figure 4e-f).

Individual rates of leaf emergence (bl), death (dl) and net change in the number of leaves (rl) did not differ between species (figure 5). Emergence rates (bl) were similarly variable along the year for the two species, and so were the death rates (dl) (figure 5a-d). *C. hololeuca* showed higher variation in rl than *C. glazioui* (figure 5e-f). *C. hololeuca* showed periods (May and November) with higher net increase (higher median values) and periods (June) with higher net decrease (lower median value) in the number of leaves. The absence of a relation between emergence (B) and death (D) rates in *C.*

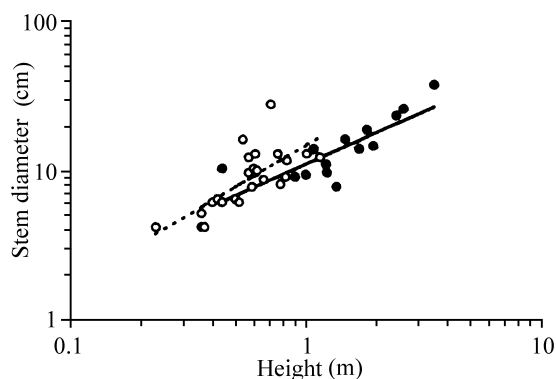


Figure 2. Allometry of stem diameter (D) and height (H): $\log D = 1.035 + 0.698 \log H$; $r^2 = 0.633$, $p = 0.001$ (*Cecropia glazioui*) and $\log D = 1.161 + 0.925 \log H$; $r^2 = 0.530$, $p < 0.001$ (*Cecropia hololeuca*). *Cecropia glazioui* (●), *Cecropia hololeuca* (○).

hololeuca ($D = 16.287 + 0.278 B$, $r^2 = 0.050$, $p = 0.158$) seems to account for the greater variation in number of leaves in this species, in contrast with *C. glazioui* where emergence and death rates were related ($D = 12.961 + 0.437 B$, $r^2 = 0.206$, $p = 0.049$) and the number of leaves was less variable. Mean leaf turnover rate (bl/dl) differed between species ($t = 2.598$, $p = 0.048$), being higher for *C. glazioui* (1.47 ± 0.25) than for *C. hololeuca* (1.01 ± 0.57).

Leaf emergence rates were density independent (considering the population of leaves in one individual) for both species ($r^2 = 0.126$, $p = 0.133$ for *C. glazioui* and $r^2 = 0.083$, $p = 0.064$ for *C. hololeuca*), while leaf death rates in *C. hololeuca* was density-dependent (plants with more leaves showed higher death rates; Death rate = $5.348 + 2.292$ number of leaves, $r^2 = 0.197$, $p = 0.003$), but not in *C. glazioui* (Death rate = $17.890 + 0.782$ number of leaves, $r^2 = 0.050$, $p = 0.359$).

Leaf life tables (table 1) and survivorship curves (figure 6) showed a similar pattern for both species. Survivorship curves were intermediate between Deevey's Type I and Type II curves and did not differ significantly between species ($LR = 2.574$, $p > 0.05$). However, leaves of *C. glazioui* had a greater life expectancy and lower mortality rates than those of *C. hololeuca*, up to 120 days (table 1). Leaves of *C. glazioui* had a half-life 34 percent greater and mean longevity 18 percent greater than those of *C. hololeuca* (table 2).

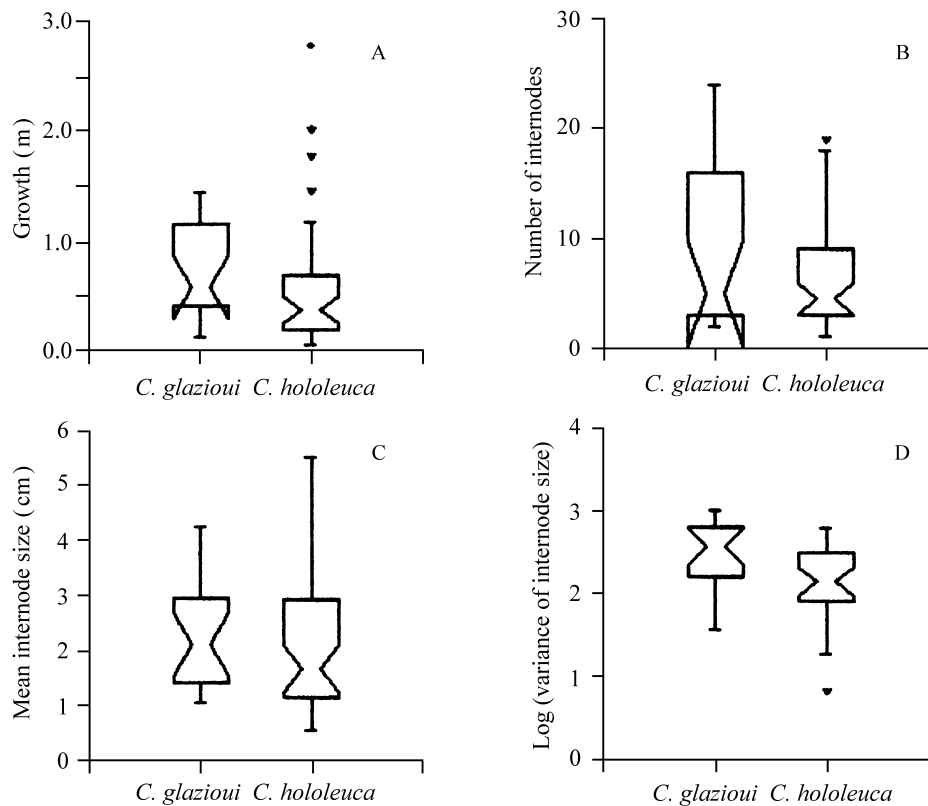


Figure 3. Box-plot of growth characteristics for individuals of *Cecropia glazioui* and *C. hololeuca* in Piraf, RJ. A. growth rates ($\text{m}\cdot\text{yr}^{-1}$); B. number of internodes produced per year; C. mean internode size (cm); D. \log_{10} variance of internode size. In a box-plot graph, the box comprises 50% of data. Boxes are notched (narrowed) at the median and return to full width at the lower and upper 95% confidence interval values. Inner and outer fences are defined by interquartile ranges. Asterisks are “outside values” and “far outside values” are circles. If the confidence intervals do not overlap, the median of the species are different (McGill et al. 1978).

Discussion

Similar allometric relations are expected in plants within the same life form and similar ecological traits (King 1990, Kohyama & Hotta 1990). The relations observed here are comparable to those obtained by Alvarez-Buylla & Martínez-Ramos (1992) for unbranched individuals of *Cecropia obtusifolia*. This suggests that the allometric relations between stem diameter and height in *Cecropia* species are a phylogenetic characteristic and are not affected by ant association, in spite of differences in internodes length.

The estimates of individual growth rates obtained here are in the range obtained by Schupp (1987) for *Cecropia obtusifolia* (between 0.05 and 2.00 $\text{m}\cdot\text{yr}^{-1}$), but are low compared with the growth

rates obtained for *C. peltata* (1.0 to 10.6 $\text{m}\cdot\text{yr}^{-1}$) and *C. obtusifolia* (0.7 to 12.4 $\text{m}\cdot\text{yr}^{-1}$) in Costa Rica (Davis 1970), for *C. insignis* (4.9 $\text{m}\cdot\text{yr}^{-1}$) in Barro Colorado (Brokaw 1987) and for *C. obtusa* (0.14 to 6.52 $\text{m}\cdot\text{yr}^{-1}$) in Carajás, PA, Northern Brazil (F.A.M. Santos & J.D. Hay, unpublished data).

Differences in internode length within individuals were observed for *C. peltata* and *C. obtusifolia* in Costa Rica and correlated with dry and wet seasons (Davis 1970). The same seasonal patterns were observed for *C. obtusa* in Northern Brazil (F.A.M. Santos & J.D. Hay, unpublished data). These differences attributed to rainfall seasonality may be used to infer age and past growth in these plants (Davis 1970) and to estimate age of gaps. Seasonality of precipitation seems to have a greater effect on the size of internodes of *C. hololeuca* than of *C. glazioui*,

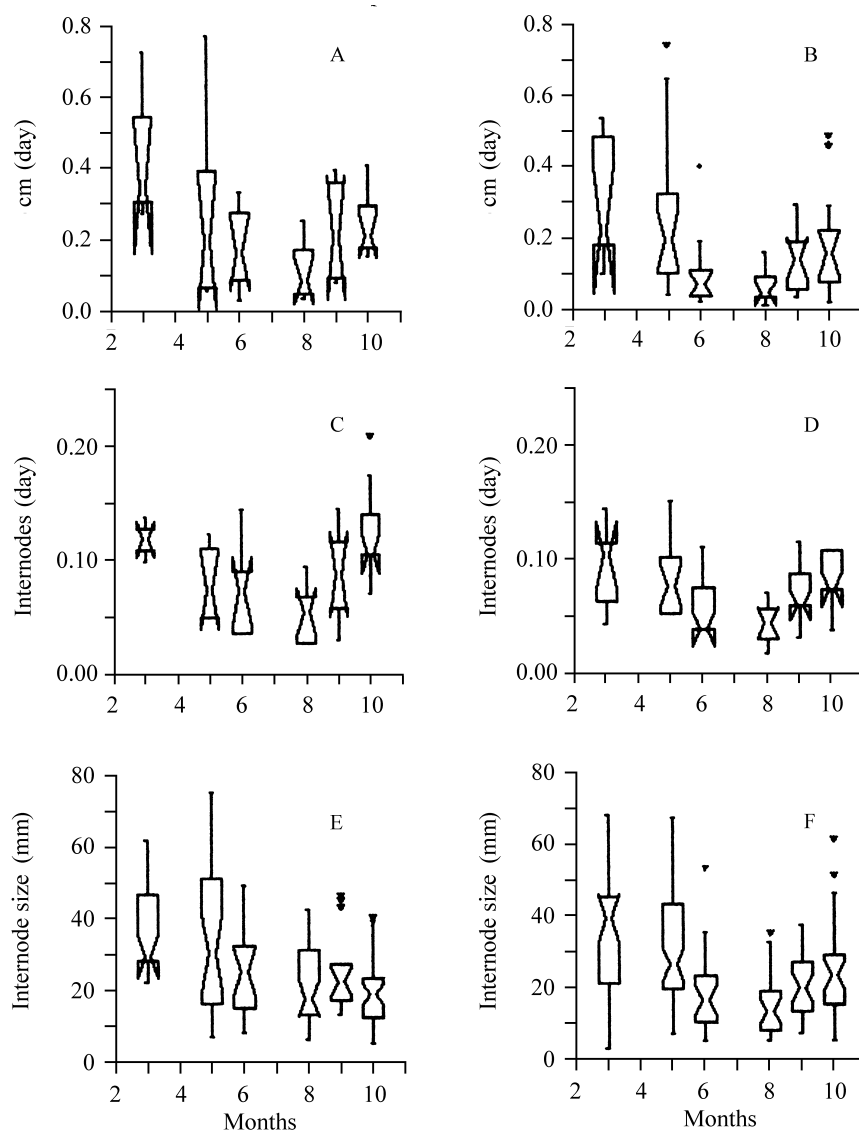


Figure 4. Box-plot of growth characteristics for individuals of *Cecropia glazioui* (A, C, E) and *Cecropia hololeuca* (B, D, F) in Pirai, RJ, for each sampled period. A-B. growth in $\text{cm}\cdot\text{day}^{-1}$; C-D. growth in $\text{internodes}\cdot\text{day}^{-1}$; E-F. internode length (mm). Box-plot legend as in figure 3.

with a smaller variation in internode length in *C. glazioui* than in *C. hololeuca*. However, internode sizes seem to be more variable among individuals of *C. glazioui* than of *C. hololeuca*.

Leaf phenology showed a seasonal pattern in both species, the number of leaves being more variable in *C. hololeuca* during the year than in *C. glazioui*. Milton (1991) found that leaf production in *Cecropia insignis* for two years varied between 51.8

± 6.0 and 51.0 ± 7.0 leaves. yr^{-1} , with a peak of production of new leaves in the late rainy season. The two species studied here showed a similar pattern in time, in spite of having lower values for leaf production rate. A greater leaf turnover rate in *C. glazioui* may account for a minor seasonal variability in the number of leaves. In turn, this maintains the availability of the food resources for ants more constant,

Table 1. Life tables for leaves of *Cecropia glazioui* and *C. hololeuca*. x : age classes (in days); N_x : number of leaves in the age class x ; $l_x = N_x/N_0$; $d_x = l_x - l_{x+1}$; $q_x = d_x/l_x$; e_x (in days) = $T_x \cdot 30/N_x$ (where $T_x = \sum L_x$ and $L_x = (N_{x+1} + N_x)/2$).

x	N_x	l_x	d_x	q_x	e_x
<i>Cecropia glazioui</i>					
0	147	1.000	0.177	0.177	112.55
30	121	0.823	0.163	0.198	103.51
60	97	0.660	0.136	0.206	95.41
90	77	0.524	0.116	0.221	86.30
120	60	0.408	0.082	0.200	76.50
150	48	0.326	0.122	0.375	61.88
180	30	0.204	0.061	0.300	60.00
210	21	0.143	0.048	0.333	49.29
240	14	0.095	0.054	0.571	36.43
270	6	0.041	0.014	0.333	35.00
300	4	0.027	0.027	1.000	15.00
<i>Cecropia hololeuca</i>					
0	323	1.000	0.204	0.204	96.18
30	257	0.796	0.186	0.234	87.02
60	197	0.610	0.161	0.264	78.96
90	145	0.449	0.136	0.303	71.90
120	101	0.313	0.130	0.416	66.68
150	59	0.183	0.059	0.322	73.47
180	40	0.124	0.037	0.300	71.25
210	28	0.087	0.025	0.286	65.36
240	20	0.062	0.022	0.350	55.50
270	13	0.040	0.012	0.308	47.31
300	9	0.028	0.016	0.556	31.67
330	4	0.012	0.009	0.750	22.50
360	1	0.003	0.003	1.000	15.00

Table 2. Half-life (in days) and mean (arithmetic means \pm standard deviations) longevity (in days) of leaves of *Cecropia glazioui* and *C. hololeuca*.

	<i>C. glazioui</i>	<i>C. hololeuca</i>
Half-life	57.70	43.19
Mean longevity*	112.79 \pm 82.13	95.33 \pm 76.95

*Comparison between species: $t = 2.179$, $p = 0.030$.

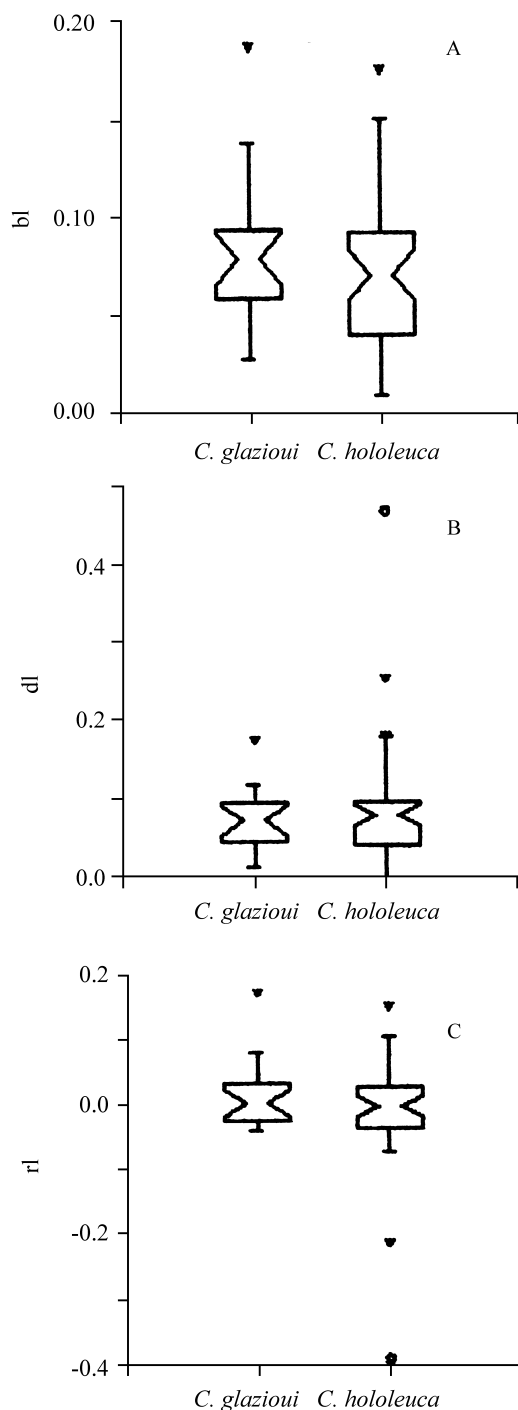


Figure 5. Box-plots of leaf dynamics characteristics for individuals of *Cecropia glazioui* and *C. hololeuca* in Pirai, RJ. A. rates of leaf emergence (bl); B. rates of leaf death (dl); C. net change in the number of leaves (rl). Box-plot legends as in figure 3.

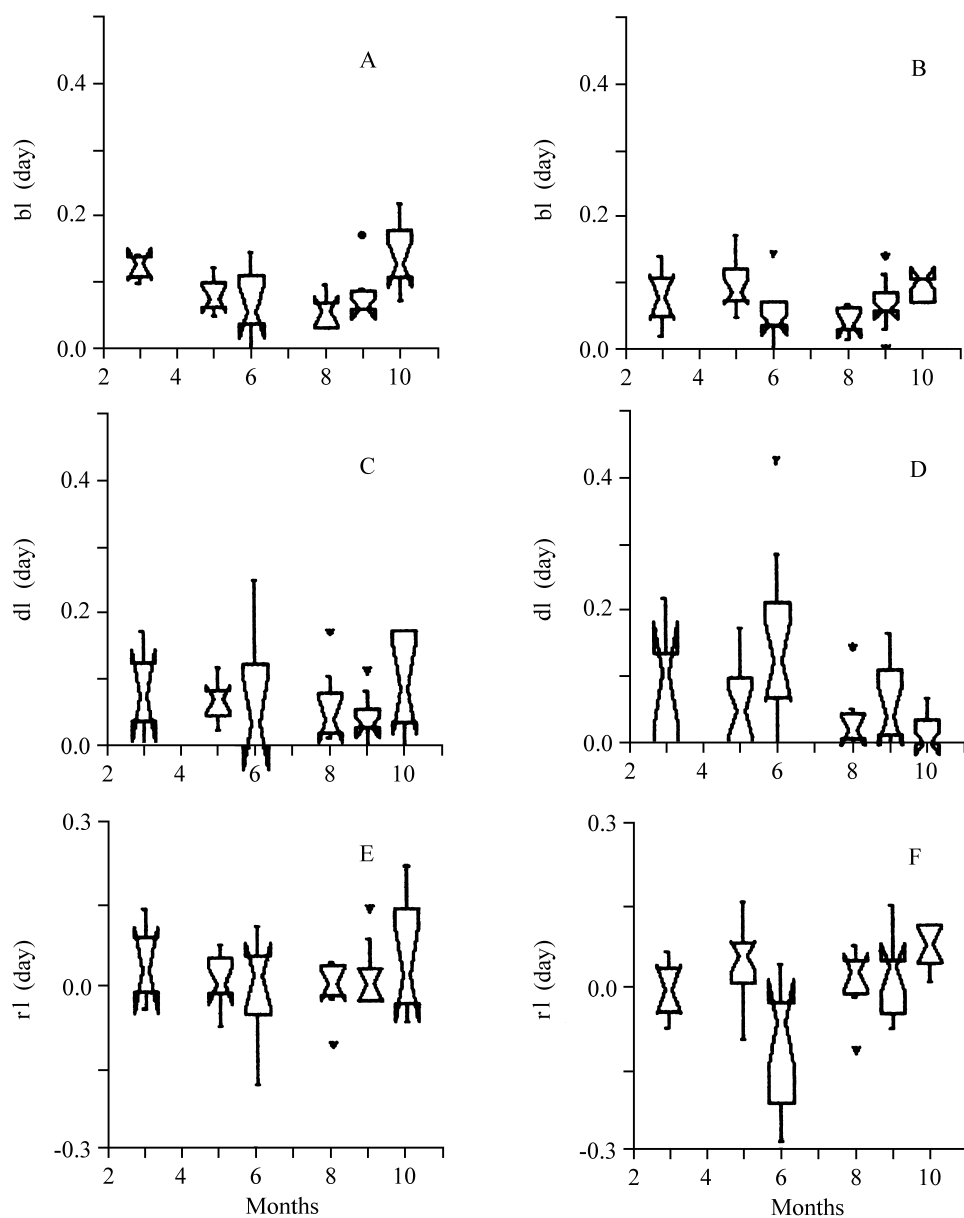


Figure 6. Box-plot of leaf dynamics characteristics for individuals of *Cecropia glazioui* (A, C, E) and *C. hololeuca* (B, D, F) in Pirai, RJ, for each sampled period. A-B. leaf emergence rate ($bl \cdot day^{-1}$); C-D. death rate ($dl \cdot day^{-1}$); E-F. leaf recruitment rate ($rl \cdot day^{-1}$). Box-plot legend as in figure 3.

since Müllerian bodies are produced only by new leaves.

Gap species grow in microhabitats with high availability of resources, and they can maintain fast growth and high leaf turnover rates and, because of this, leaves generally have short life spans of about

6.9 ± 3.9 months (Coley & Aide 1991). The figures obtained for the two *Cecropia* species fall in this range, but they are high if compared with leaf longevity obtained by Núñez-Farfán & Dirzo (1989) for *C. obtusifolia* (means = 67.89 to 74.82 days, with maximum longevity about 120 days).

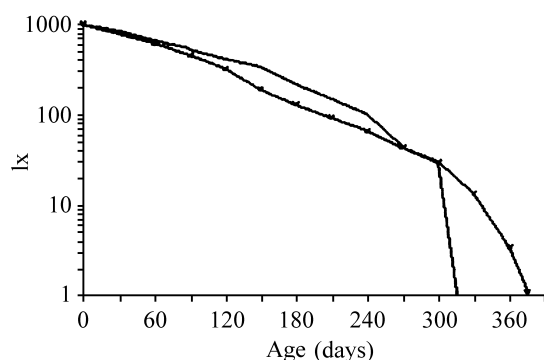


Figure 7. Survival curves for leaves of *Cecropia glazioui* (—○—) and *C. hololeuca* (—×—).

Leaves of *C. glazioui* showed higher survival and greater life expectancy than those of *C. hololeuca*. The higher chances of survival and greater life expectancy of *C. glazioui* leaves may be related to: (a) protection against herbivory conferred by their associated *Azteca* ants; (b) an increase in nutrient supply from ant rejects; (c) an increase in photosynthetic life of leaves due to cleaning of epiphylls and pathogens from leaf surface by the ants; or (d) differences in cost-benefits in the production and maintenance of leaves between the two species.

As time of damage is important in determining the impact of herbivory, the differences in survival of young leaves (up to 120 days) suggests that the ants are important for the defense of young *C. glazioui* leaves. On the other hand, this advantage in older leaves ceases and the survival rates are greater for *C. hololeuca*. This age (about 120 days) must be the time that the leaf trichilia activity stopped in *C. glazioui*. Consequently, the ant activity in these leaves is smaller and the importance of the ant defense is reduced. The greater maximum leaf life expectancy of *C. hololeuca* is in agreement with a slower turnover of its leaves and suggests that the costs for maintaining ants through the production of Müllerian bodies surpass the costs of chemical defenses against herbivores. An evaluation of ant colonization, production rate of Müllerian bodies, chemical compounds, and the herbivory rate in young and old leaves of these two species could elucidate some of these aspects.

Acknowledgements - This research was supported by the Brazilian National Council for the Development of Research and Technology (CNPq proc. 301746/83-4). I thank to the Department of Ecology, Biology Institute, UFRJ, where this research was developed, F.R. Martins, H.C. Morais, C.A. Joly, W.W. Benson, G.J. Shepherd and J.D. Hay for helpful criticism and suggestions. I thank the Brazilian Special Secretary for Environment (SEMA) for permission to work at the field site and logistical assistance.

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