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GROWTH PATTERN AND AGE DETERMINATION FOR *CECROPIA SCIADOPHYLLA* (URTICACEAE)[1]

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Cecropia species, ranging from Mexico to northern Argentina and the West Indies, are pioneer trees that colonize cleared areas with high light. To determine their ages to help pinpoint the date of the area's disturbance, we need to understand their developmental and architectural changes over time. The simple architecture of *Cecropia* conforms to the model of Rauh; that is, it has orthotropic axes with lateral flowering and rhythmic branching. The axes are made of a succession of nodes and internodes whose length and associated lateral productions remain measurable for years. Thus, by describing the tree trunk node by node, we can depict the sequence of events involved in tree development. For 25 trees of *C. sciadophylla*, from two stations in French Guiana and Colombia, we recorded internode length and any presence of branches, and flowers for each node. Using autocorrelation coefficients, we found a high periodicity in flowering and branching, with inflorescences at every 25 nodes, stages of branches spaced by a multiple of 25 nodes, and alternation of long and short nodes every 25 nodes. Considering that flowering is annual for many *Cecropia* species, the main conclusion of this work is that *C. sciadophylla* has strong annual growth, branching, and flowering rhythms. In addition, the age of the tree can be estimated retrospectively by observing its adult morphology.

Key words: Colombia; French Guiana; gap age; periodicity; phenological processes; plant morphology; synchronicity; Urticaceae.

Plant phenology can be defined as the study of the timing of recurring biological events, its causes with regards to biotic and abiotic forces, and the relation among phases of the same or different species (Leith, 1974). Classic studies on phenology are centered on the observation of processes such as flowering/fructification or foliation/defoliation in deciduous species (Wallace and Painter, 2002; Bawa et al., 2003; Hamann, 2004). Other events with a temporal pattern, such as growth expression (in terms of timing of elongation and variability in length or number of nodes elongated), ramification, nectar secretions, and germination are also part of this field of investigation (Sabatier and Puig, 1986; Loubry, 1994).

Methods employed in phenological studies usually consist of (1) compilation of herbarium data (Croat, 1975; Borchert, 1996; Primack et al., 2004), usually including rather imprecise information (e.g., ripe and unripe stages are rarely differentiated) and (2) observations over local plant populations, which occasionally include monitoring growth over long periods (Croat, 1975; Van Schaik et al., 1993; Newstrom et al., 1994; Sakai, 2001). However, an alternative approach not much documented for tropical species is a posteriori reconstruction of individual development by observation of morphological or macroanatomical markers that can be interpolated as the functional history of meristems (Hallé et al., 1978; Barthélémy and Caraglio, 2007). For instance, in the case of rhythmical growth (i.e., alternation between elongation and rest phases), growth suppression is often observed on axes as small internodes, modified leaves, cataphyll scars in rings (i.e., modified leaves that protect apical bud during rest phases), or changes in pith color on a longitudinal section of the stem. Using these markers, we can delimit growth units and measure their characteristics (e.g., length and number of nodes). Additionally, processes of ramification or flowering also leave characteristic scars, which vary in appearance with time and species.

In temperate zones, growth is usually rhythmical, synchronous, and periodic due to seasonal constraints (Hallé et al., 1978; Richards, 1996; Sakai, 2001). Scars left by buds during winter, can be used to delimit years and to reconstruct retrospectively plant development during long periods (Heuret et al., 2000, 2006; Nicolini et al., 2001; Sakai, 2001; Passo et al., 2002). In this way, plant topology can be better understood within a temporary frame. The implications of this approach are numerous because it may allow estimates of tree age and provide advance knowledge about growth, ramification, and flowering processes during plant ontogeny. In spite of the fact that topological approaches can complement, and even replace, monitoring growth studies, such approaches have not been widely used. In tropical zones, the diversities in plant development are expressed more continuously in time than in temperate latitudes. Thus, we can observe great variability in the expression of growth, ramification, and flowering processes (Comte, 1993; Edelin, 1993; Van Schaik et al., 1993; Loubry, 1994; Sakai, 2001). When growth is rhythmic, alternation between elongation and resting phases can be either periodic or irregular. At the individual level, axes can

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grow either synchronously or each one at its own rate. Thus, in tropical rain forests, plant topology at a fine level can be described according to available morphological markers, but it is difficult to ensure a temporary connotation from retrospective observations (Hallé et al., 1978). However, a precise analysis of plant structure using statistical models may allow one to reveal information that is hidden in empirical data (because of noise and combinatorial complexity related to multivariate observation). These hidden regularities enable researchers to make strong assumptions on the rules of plant construction in time (Guédon et al., 2001; Heuret et al., 2002).

The neotropical genus *Cecropia* Loefl., includes 61 species, distributed from southern Mexico to northern Argentina, with some species occurring in the Antilles (Wheeler, 1942; Berg, 1978; Berg, 2000; Berg and Franco, 2005; Stevens, 2007). It is the most important genus of pioneer trees in the neotropics; it grows rapidly and ably colonizes gaps (Álvarez-Buylla and Martínez-Ramos, 1992; Whitmore, 1998). *Cecropia* trees are dioecious plants, usually with a candelabrum-like branching system, following the architectural model of Rauh (Hallé and Oldeman, 1970; Hallé et al., 1978). Branching axes are orthotropic, with lateral flowering and rhythmic branching. Recent studies have shown that *C. obtusa* is highly regular in growth, ramification, and flowering (Heuret et al., 2002). From a retrospective reconstruction of its developmental pattern and the use of statistical tools borrowed from time series analyses (Guédon et al., 2001, 2003), Heuret et al. (2002) showed that the rate of node production, flowering, and ramification are respectively synchronous for sets of axes within an individual of *C. obtusa*. Additionally, they suggested that flowering and ramification processes are annual and synchronous at the population level. In this work, we focused on a second species of this genus, *C. sciadophylla*, characterized by a high life expectancy compared to other species of *Cecropia* and by a widespread distribution throughout the Amazonian basin, the Llanos region of Colombia and Venezuela, and the Guiana region (i.e., from French Guiana to eastern Venezuela). The objectives of this study were (1) to determine and compare the patterns of growth, ramification, and flowering for *C. sciadophylla* individuals in two populations, (2) to determine if the model of growth of *C. sciadophylla* is similar and comparable to the model of growth of *C. obtusa*, and (3) to propose a phenological hypothesis of development in *Cecropia* based on its architecture.

MATERIALS AND METHODS

Study site—Two populations of *Cecropia sciadophylla*, one in French Guiana and a second in Colombia, were studied. The French Guiana population was located at Saint-Elie road (5°30' N, 53° W), at ~16 km from Sinnamary. Climate in French Guiana is seasonal with a 3-mo dry season from mid-August to mid-November and a rainy season during the other 9 mo. Additionally, a short dry season may occur in February and March (Boyé et al., 1979). Mean annual rainfall is 3000 mm/yr. The Colombian population was located at Tinigua National Park on the east margin of the Guayabero River (La Macarena, department of Meta, 2°40' N, 74°10' W). Rainfall regime at Tinigua National Park is seasonal with a 2–3-mo dry period between December and March and a mean rainfall of 2782 mm/yr (Stevenson, 2006) (Fig. 1).

Morphological features of C. sciadophylla—*Cecropia sciadophylla* grows in well-drained areas, primary uplands, and gallery forest, and as a pioneer tree, it is commonly found in secondary forest, from sea level to ca. 1300 m a.s.l. (Berg and Franco, 2005). Individual trees can reach 30 m in height, phyllotaxy is alternate with a 5/12 spiral phylotactic fraction. The leaves are stipulate, large, and peltate. There are three lateral buds in the axil of each leaf (Fig. 2). The central bud is vegetative and may potentially give rise to a branch. Buds on each side correspond to two prophyllar axillary buds and may give rise to inflorescences, which are thus arranged in pairs, each comprising a set of spikes. Pistillate inflorescences have 3–6(10) spikes and staminate inflorescences have 8–15 spikes (Berg and Franco, 2005).

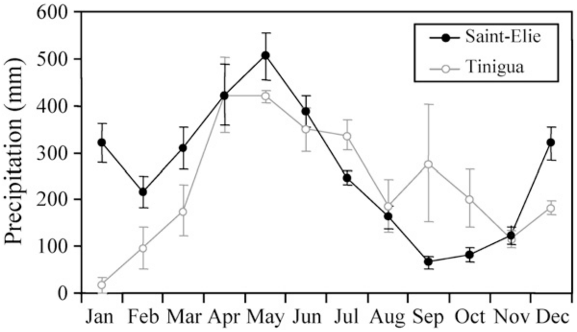

Fig. 1. Mean annual rainfall for Saint-Elie (14 yr) and Tinigua National Park (3 yr). Error bars are standard deviations.

The enveloping stipule or calyptra found on each node leaves a characteristic ring-shaped scar, that can be used to locate the limits of each internode down to the base of the tree. However, the frequent development of stilt roots makes it difficult to establish the location of the nearest internodes to the cotyledons. After abscission, the two inflorescence stalks leave characteristic scars that can be identified a posteriori on all parts of the tree (Fig. 2). Some inflorescences may be aborted and fall before anthesis, leaving smaller scars that can be distinguished from those left by fully developed inflorescences. Branches may also be aborted early in their development, when the bud is beginning to swell, leaving small, circular scars.

Plant material and measurements—Nineteen individuals (six pistillate and thirteen staminate) were felled and measured at Saint-Elie, while six individuals (four pistillate and two staminate) were measured at Tinigua Park. Only straight trees without any evident trauma were selected and felled. All data were collected during one week in September 2005 at Saint-Elie (eight observers), and during one week in January 2006 at Tinigua Park (two observers). All staminate and pistillate individuals measured had two or more tiers of branches on the main axis. For all trees, trunk girth at a height of 1.30 m (GBH) was measured, and diameter was estimated assuming a circular cross section (DBH). Tree height and the height and number of nodes until the first tier of branches (present or pruned) and appearance of the first inflorescence were recorded on the fallen tree.

Following Heuret et al. (2002) protocol, trunks formed by a succession of metamers were described node by node from base to top. Because of the frequent development of stilt roots, the number of nodes separating the cotyledons of the first node measured is uncertain. Three variables were recorded for each node: (1) length of the underlying internode, (2) state of the central bud as "0" for no branch and "1" for developed branch (pruned and dead branches were included in this category), and (3) state of the lateral buds as "0" for no inflorescence and "1" for developed inflorescence (detected as either presence of the inflorescence or its scar). Aborted inflorescences and branches were not recorded because criteria to determine these states are rather ambiguous.

Cecropia sciadophylla fructification pattern at Tinigua National Park—Phenological data were collected during three yearly cycles at Tinigua National Park (April 1990–March 1991, August 1996–July 1997, and February 2000–January 2001). The information was recorded in 12 transects (about 450 m each) in which we biweekly observed all *C. sciadophylla* individuals that had flowers and/or fruits (Stevenson et al., 1998). This information was complemented by feeding observations in *C. sciadophylla* fruiting trees during the same periods (Stevenson, 2006).

Statistical analysis—Tree topology, i.e., the relative positions of the different botanical units described (nodes and axes), was coded as sequences and analyzed using the AMAPmod software (Godin et al., 1997a, b; Godin et al., 1999).

An interesting statistical tool to separate and characterize growth components is based on the assumption of a decomposition model, in which the ontogenetic growth component and environmental component are combined in an additive manner (Guédon et al., 2007). To analyze fluctuation of internode's length, we used classical methods of time series analysis relying on a decomposition

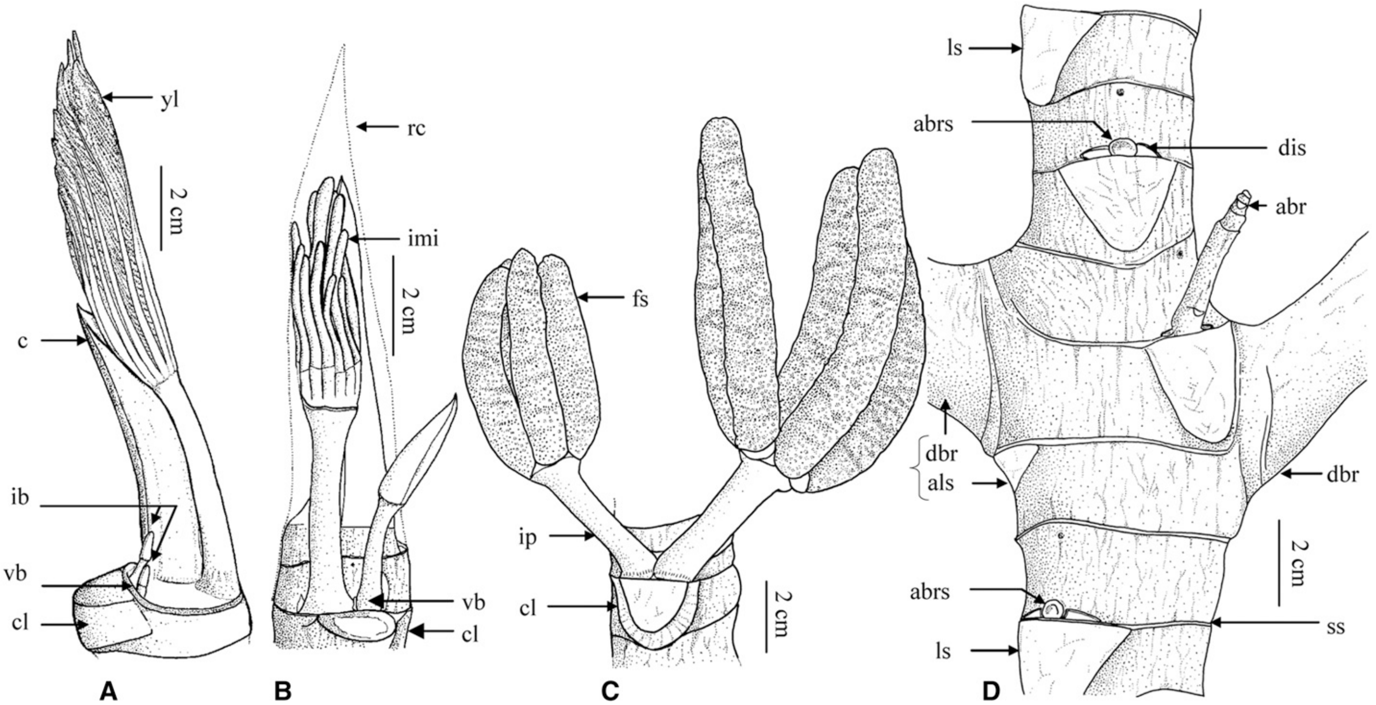

Fig. 2. Types of axillary products in *Cecropia sciadophylla*. Three buds can be seen in the axil of young leaves. (A) The buds on either side of the central bud may develop into inflorescences with several spikes. (B) Immature inflorescences are protected by a bract that acts as a sheath. The species is dioecious. Female inflorescences have 3–6 spikes (C), while male inflorecsences have 8–15 smaller spikes (B). (D) Example of scars resulting from axillary bud functioning. *Figure abbreviations*: abr = aborted branch, abrs = aborted branch scar, als = aborted leaf scar, c = calyptra (stipule), cl = pruned leaf, dbr = developed branch, dis = developed inflorescence scar, fs = female spike, ib = inflorescence bud, imi = immature male inflorescence (the protective bract has been removed), ip = inflorescence peduncle, ls = leaf scar, rc = removed calyptra, ss = stipule scar, vb = vegetative branching bud, yl = young leaf.

principle. The different sources of variation, such as long-term changes in mean level and local fluctuations, are differentiated by the application of different types of filters that were initially analyzed for individual trees (Chatfield, 2003; for more information about the use of methods to analyze botanical sequences, see Guédon et al., 2007). The common procedure to deal with a trend is to apply a linear filter that converts the measured sequences $\{x_t\}$ into another $\{y_t\}$ by a linear operation

$$y_t = Smooth(x_t) = \sum_{r=-q}^{q} a_r x_{t+r} \ ,$$

where $\{a_r\}$ is a set of weights such as for each r, $a_r > 0$ and $a_r = a_{-r}$. To smooth out the local fluctuations and estimate the mean, weights should be chosen such that $\sum_r a_r = 1$. This linear operation is often referred to as a moving average, in which a smoothed curve is adjusted. To choose an appropriate filter is difficult and the choice remains partly arbitrary, so it is recommended to try a variety of filters to get a good idea of the underlying trend (Guédon et al., 2007). We chose to use the symmetric smoothing filter corresponding to the probability mass function of binomial distributions with parameters $n = 50$ and $p = 0.5$ or $n = 100$ and $p = 0.5$ to extract the trend of internode length sequences. Having extracted the trend, we looked at local fluctuation by examining the residuals. Residuals were extracted by division instead of substraction as is often done (Fritts, 1976):

$$Index(x_t) = \frac{x_t}{Smooth(x_t)}.$$

The underlying implicit hypothesis is that fluctuation amplitudes given by $|x_t - Smooth(x_t)|$ are roughly proportional to the corresponding trend level. This standardization allowed us to give the same status to fluctuations of both small and large amplitudes, which is important in old trees that have very short internodes compared to the first node at the trunk base.

An important tool for exploring sequences built from quantitative variables is provided by a series of quantities called sample autocorrelation coefficients, which measure the correlation between observations separated by different distances. The autocorrelation function measures the correlation between X_t and X_{t+k} as a function of the lag *k*. The sample autocorrelation function is an even function of the lag and hence needs to be plotted for *k* = 0, 1, 2, … We applied autocorrelation analysis to binary branching and flowering sequences as well as residual sequences obtained from filtered internode length sequences.

Mann–Whitney–Wilcoxon (MWW) nonparametric tests were used to compare tree height, diameter, first branch, and first inflorescence positions between the two populations because it allows comparisons of distributions derived from relatively small samples (Saporta, 1990).

RESULTS

Height, diameter, first branch, and inflorescence positions—Sampled trees had similar heights (mean 22.4 m) and total number of nodes (mean 467.3) in both populations, while stem diameter was significantly higher for trees at Tinigua than at Saint-Elie (Table 1). There were no significant differences in height until the first branch (mean 12.9 m) or the first inflorescence scars (mean 16.4 m) between populations. However, the number of nodes before the first branch or the first inflorescence was significantly higher for Saint-Elie trees than for Tinigua trees. For both populations, the first inflorescences were mainly positioned between the first and the third tier of branches.

Population level periodicity—Considering the whole trunk as a sequence described from tip to base, the frequency of observation of nodes with developed inflorescences according to node rank revealed that inflorescences were positioned at the same node rank for all measured trees at both populations (Fig. 3), whereas no evident pattern was found for branching position.

TABLE 1. Morphological characteristics of *Cecropia sciadophylla* trees from Saint-Elie and Tinigua Park populations (±SE). Letters identify significantly different means according to Mann–Whitney–Wilcoxon test.

Characteristic	Saint-Elie	Tinigua Park
Height (m)	22.1 ± 0.7^a	23.3 ± 1.1^a
Diameter (cm)	28.8 ± 1.2^a	42.2 ± 1.1^b
Total no. of nodes	477 ± 25^a	438 ± 17^a
First branch height (m)	13.1 ± 0.6^a	12.6 ± 0.7^a
First branch nodes	171 ± 9^a	102 ± 8^b
First inflorescence height (m)	16.2 ± 0.7^a	17.2 ± 0.8^a
First inflorescence nodes	243 ± 12^a	170 ± 15^b
No. of cycles before first branch	6.7 ± 0.3^a	5 ± 0.4^b
No. of cycles before first inflorescence	9.7 ± 0.5^a	7.7 ± 0.9^a
Total number of cycles	19.6 ± 1^a	18.8 ± 0.5^a

Considering the whole trunks, the Spearman autocorrelations rank function showed that flowering follows a sinusoidal pattern with periods of ~25 nodes for Saint-Elie and ~23 for Tinigua Park (Fig. 4A, B). Branching had no significant pattern. The autocorrelation function calculated for the residues sequences obtained by filtering the internodes length sequences with a moving average also had a strong periodicity. When the tendency was filtered with a symmetric smoothing filter corresponding to the probability mass function of binomial distributions with parameters 50 and 0.5, the autocorrelation coefficients calculated on the sequences of residues had a sinusoidal pattern with positive significant maxima at lags of 13 and 25 for Saint-Elie and lags of 24, 46, 76, 103, 126, and 149 for Tinigua Park. The same analysis with parameters 200 and 0.5 revealed positive significant maxima at lags of 26 and 52 for Saint-Elie population and at lags of 24, 46, 76, 103, 129, and 146 for Tinigua Park population (Fig. 4C, D).

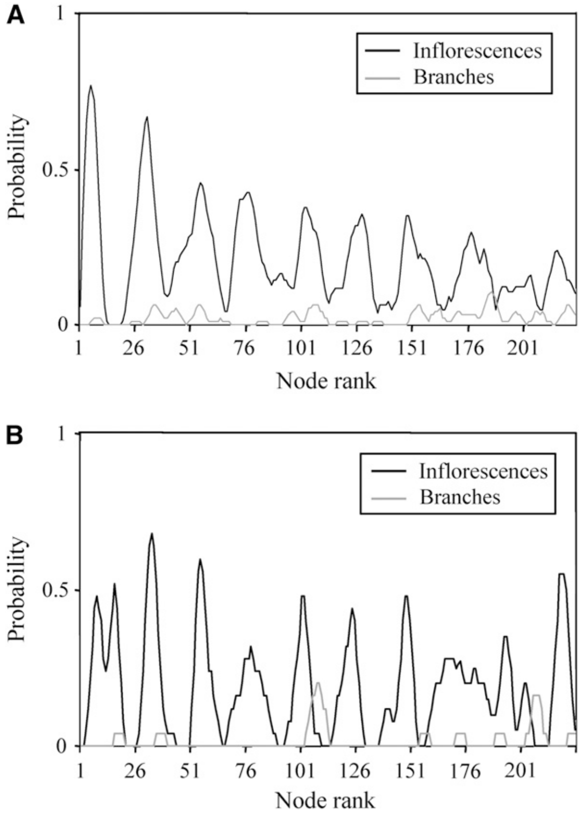

Fig. 3. Frequencies of nodes with developed inflorescences (black) or branches (gray) according to node rank from axis tip for (A) Saint-Elie ($N = 19$ trunks), and (B) Tinigua Park ($N = 6$ trunks).

An individual example—Figure 5 shows one characteristic tree from the Saint-Elie population. The Spearman autocorrelations rank for the flowering variable yielded positive significant maxima at lags of 14, 26, 49, 73, 99, and 122 (Fig. 5B). In Fig. 5A inflorescences are clearly regularly spaced by 25 nodes (ranks 236–237, 262, 286–289, 312–315). However, between the node ranks from 358 to 433, the inflorescences were more closely spaced, resulting in a positive autocorrelation coefficient every 14 lags. We also noted a fluctuation in the autocorrelation function with coefficients that increased on lags of 35, 61 and 85, without achieving statistically significant values.

Branch tiers were carried by nodes with ranks 203–207, 256, 308–310, and 429–432. For this particular individual, nonambiguous aborted branch scars were also identifiable near node ranks 129, 282, and 386. The autocorrelation function for the branching variable shows positive significant maxima at lags of 53, 105, 124, and 176 (Fig. 5B), which illustrate the fact that two tiers of branches were regularly spaced by multiples of ~25 nodes.

For the internodal lengths, the autocorrelation function calculated on the residues had positive significant maxima at lags of 26, 53, and 107 when the sequences were filtered with a binomial distribution with parameters 50 and 0.5 or 200 and 0.5. The use of a binomial distribution with parameters 50 and 0.5, however, highlighted positive significant maxima at lags of 68, 96, and 124. For a lag ranging from 0 to 75, this function had a strong periodicity of 25 nodes associated with a weaker periodicity of 14 nodes (Fig. 5C).

Fructification pattern of Cecropia sciadophylla at Tinigua National Park—The phenological data collected during three years for 10 individuals at Tinigua Park showed that the flowering pattern of *C. sciadophylla* is annual (Fig. 6). The peak of reproductive structure production is located in the months of January and February, the driest months for the study area (Stevenson et al., 1998).

Length of the successive cycles—The results presented allowed us to define periodical cycles for the growth, branching, and flowering processes of nearly 25 and 23 nodes in Saint-Elie and Tinigua Park populations, respectively. To switch the integration scale from node to cycle of development, we tried to segment the sequences into successive cycles from axis top to base. A first approach was to cut out the sequences in cycles of strictly 25 or 23 nodes according to the population considered. A second approach was to manually locate the limits of the cycles by delimiting homogeneous zones, using the variation in the internode length and the position of branches and inflorescences as a guide. For instance, in Fig. 5A, we positioned each limit right after the inflorescences zone where the internode lengths are increasing. The two methods produced similar results in terms of average length per cycle (calculated by summing the internode lengths within a cycle) and number of cycles per individual. Henceforth, the following results were calculated using the manual segmentation.

The number of cycles estimated for the studied individuals ranged from 16 to 20 yr for both populations (mean 19 ± 1) (Table 1). However, a remarkable individual of 33 cycles was

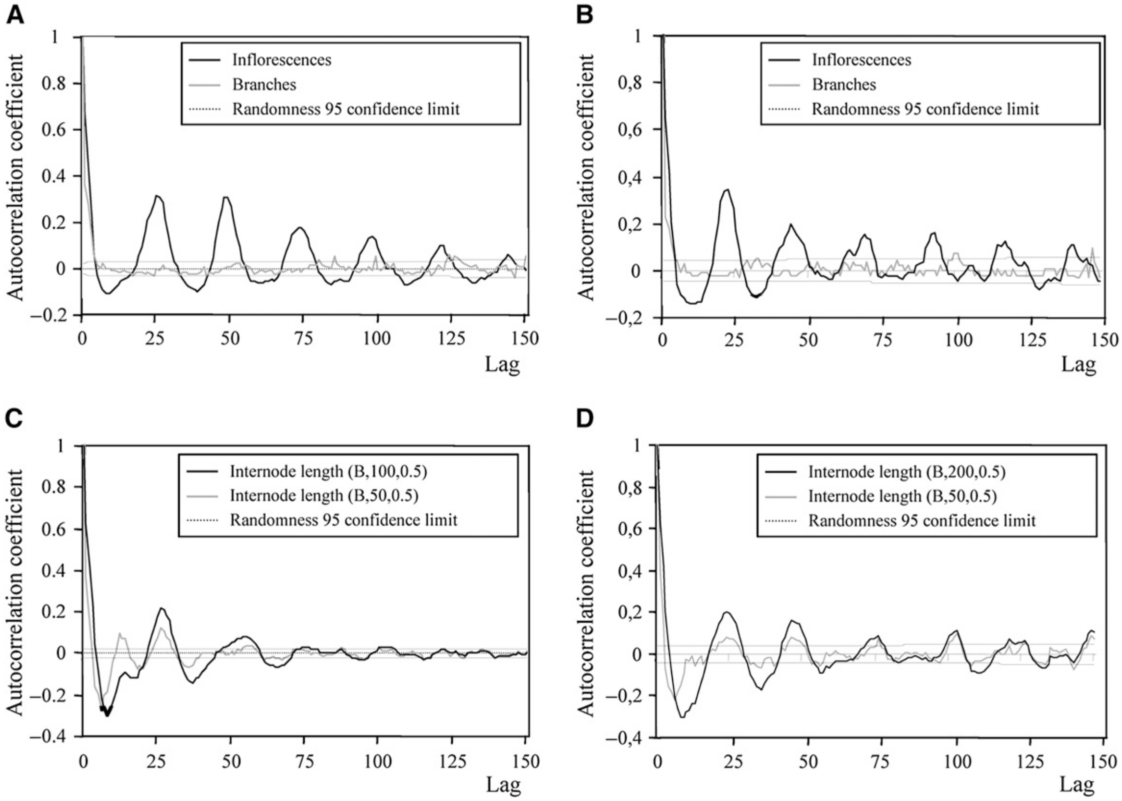

Fig. 4. Sample Spearman rank autocorrelation function (A) for Saint-Elie population (19 trees) and (B) Tinigua Park population (six trees) for axillary production (branching in black and flowering in gray). Sample Spearman rank autocorrelation function for (C) Saint-Elie population and (D) Tinigua Park population for the internode lengths residues filtered with two different parametric laws.

observed at Saint-Elie. The first tier of branches and the first inflorescence were developed on average after a slightly higher number of cycles in the Saint-Elie population than in the Tinigua population.

Considering the average length of successive cycles (Fig. 7A) and the average cumulative height per cycles (Fig. 7B), there was no significant difference between the two populations. Successive cycle lengths, initially with an average length of 2 m, progressively decreased to reach a stable cycle length of 0.25 m after nearly 20 cycles. At this stage, the height of the tree is around 21 m.

DISCUSSION

Our results show a strongly rhythmic and a clear topological periodicity in the spacing of branch tiers, flowers, and internodal elongation, with a period of 25 nodes for trees at Saint-Elie and 23 nodes for trees at Tinigua.

Many studies have suggested a high annual periodicity in flowering and fruit production processes in the genus *Cecropia*. In Barro Colorado Island (Panama), Milton (1991) described an annual flowering pattern for *C. insignis,* as did Frankie et al. (1974) and Fleming and Williams (1990), who showed the same pattern for *C. peltata* in Costa Rica and Cortés (2005) for *C. membranacea* at Tinigua National Park in Colombia. In all these cases, the flowering/fruit production period extends throughout the dry season. Although we do not know the rate of node production in *C. sciadophylla*, our results on flowering and fruiting period reinforce these precedent works and allow us to conclude that for the Tinigua population a cycle of 23 nodes in the flowering pattern corresponds to an annual rhythm. The frequency of nodes with developed inflorescence scars according to the node rank from the tip to the base (Fig. 3) also indicate that flowering is synchronous at the population level and that the phyllochron is stable among different trees as well as for individual trees during their ontogeny. By extension, branching pattern and fluctuation in internode lengths, which have the same periodicity of the flowering pattern, correspond to an annual rhythm. These conclusions are very close to the ones issued by Heuret et al. (2002), who found that the flowering and branching processes in *C. obtusa* are characterized by annual cycles of 35 nodes in French Guiana, based also on a retrospective analysis. In addition, their result was supported by previous work that showed that *C. obtusa* takes an average of 10 d to produce a new node (Lauri, 1988; Belin-Depoux et al., 1997).

Several elements distinguish the two populations of *C. sciadophylla* studied. (1) If the two populations seem to have an identical height, the first flowering and branching began earlier (in terms of number of nodes and age) for the Tinigua trees. It is possible that different growth situations, such as the density of individuals in the population, can be the origin of such a difference; many studies have shown that environmental conditions may advance or delay the flowering processes (Barthélémy, 1988; Barthélémy et al., 1995, 1997; Levy and Dean, 1998; Grosfeld et al., 1999; Simpson et al., 1999; Sakai, 2001; Nicolini et al., 2003). (2) Another difference between these populations is the greater diameter for trees of similar ages and sizes at the

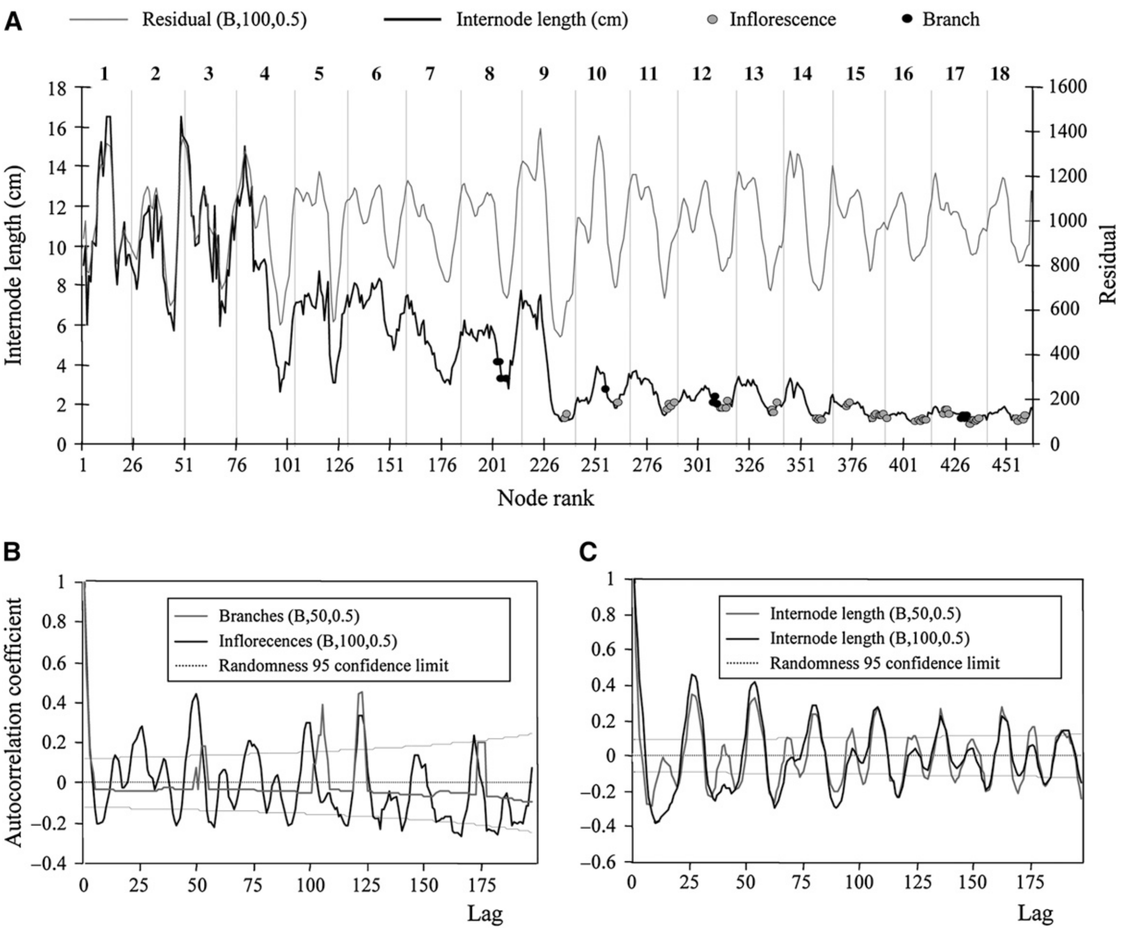

Fig. 5. Example of an individual case. (A) Internodal lengths (black line), residues after filtering (B, 100, 0.5) (gray line) and localization of branches and inflorescences (black and gray circles). (B) Sample Spearman rank autocorrelation function for inflorescences (in black) and branches (in gray) in the same individual. (C) Autocorrelation function on internodal lengths residues filtered with two different parametric laws.

Tinigua population. This disparity can be caused by different factors. For example, trees from Tinigua Park ramified earlier and bore slightly more branches than do the trees from Saint-Elie. We suspect that because this species is globally poorly branched, minor differences in the number of branches can have a strong repercussion in terms of leaf area over time and can induce strong differences in trunk diameter, which is an integrative variable (Shinozaki et al., 1964; Zimmermann, 1983). Another important factor that can be generating a greater diameter is the soil fertility. Fertile soils tend to become more common toward the Andes, and strong evidence for a positive relation between wood productivity and soil fertility has been found (Malhi et al., 2004). In addition to the period of 25 nodes, the trees of Saint-Elie seem to have another period of 12 nodes.

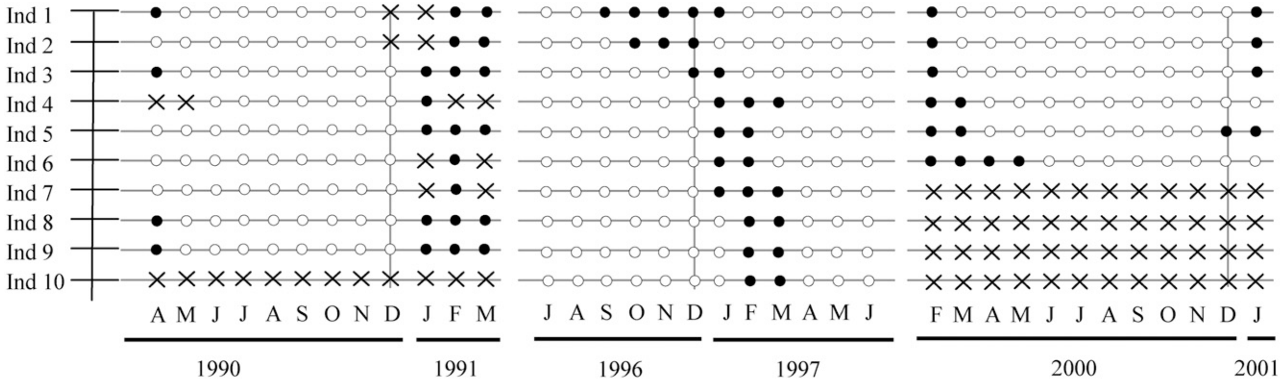

Fig. 6. Annual inflorescence production for 10 individuals (Ind 1–10) at Tinigua National Park in 3 yr of phenological monitoring. Absence of inflorescence is represented by open circles, a period of flowering or fruiting by filled circles, and a period without observation by an x.

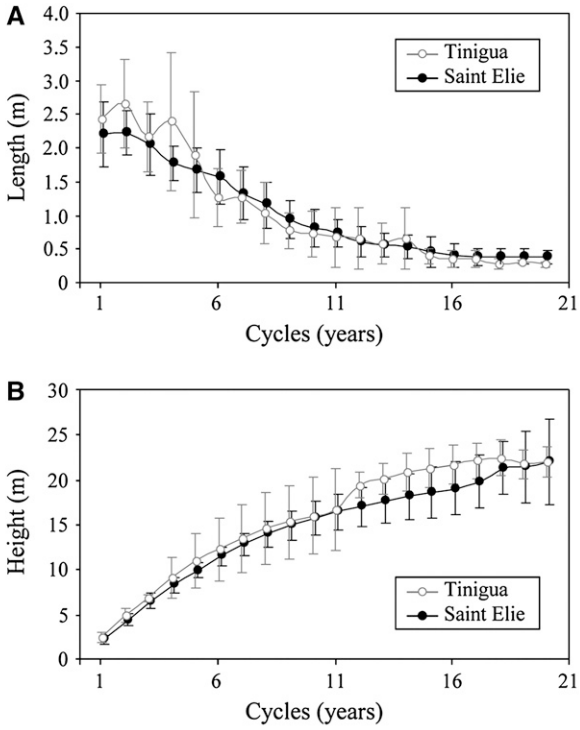

Fig. 7. (A) Average annual length of all trunks as a function of number of cycles. (B) Accumulated annual height average as a function of number of cycles (Saint-Elie Population: filled circles and Tinigua Park population: open circles, error bars are standard deviations).

This period was observed on the internode lengths and occasionally in the flowering sequences. For the trees of Tinigua, only one period of 23 nodes was observed.

Annual regularity in both populations has to be questioned based on the environmental factors that influence this periodicity (Borchert et al., 2005). For *C. peltata* and *C. obtusifolia* in Costa Rica, Davis (1970) described internode length variations that depended on the amount of annual rain, revealing that the internodes established in the dry season are shorter than those established in the rainy season. In the tropics, the movement of the intertropical convergence zone (ITCZ) produces a periodic change in rainfall that often plays a role as proximate and ultimate cause for tropical plant phenology (Van Schaik et al., 1993). In most tropical regions, a correlation between rainfall regime and plant phenology has been reported (Augspurger, 1981, 1983; Borchert, 1983; Reich and Borchert, 1984; Newstrom et al., 1994; Mduma et al., 2007), which demonstrates the existence of annual patterns of plant reproduction. The fact that two cycles per year (for the internode length variable) can occur at Saint-Elie population, while trees at Tinigua only have one annual rhythm is remarkable. The presence of two flowering periods per year is a recurrent phenomenon for the majority of the individuals in the Saint-Elie population. This second period does not present an evident synchrony between the studied individuals. Although it is possible to find years with two dry seasons at Tinigua National Park, the second dry season is weaker than the second dry season in French Guiana. Environmental factors, which could be the origin of this developmental periodicity in *Cecropia*, remain an open question; however, rainfall seems to be well correlated to the periodicity of plant development (Davis, 1970; Sakai, 2001).

From our study, based on a retrospective description of plant development, it is difficult to establish a link between the variations observed in an annual period of 25 nodes and annual fluctuations in climate such as rainfall regimes. Indeed, even though we found an annual cycle equivalent to 25 nodes, we cannot affirm that the phyllochron does not fluctuate during the year. The internode length fluctuation seems to indicate the opposite, however, because it is common to associate this character with elongation speed. Thus, if it is possible to establish a link between topology and developmental dynamics, the level of analysis should be annual and should necessarily involve adequate growth monitoring to determine possible intraannual fluctuations.

In this paper we used a protocol of measures similar to the one used by Heuret et al. (2002). The methodological contribution of Heuret et al. (2002) was the use of the autocorrelation coefficients to find periodicity in branching and flowering sequences. In this paper, we used time series analysis that relied on a decomposition principle to separate the ontogenetic and environmental components in sequences of internodal lengths. Combining that analysis with the autocorrelation analysis allowed us to find a high topological periodicity in growth and to propose a phenological developmental hypothesis in *C. sciadophylla* based on its architecture.

An important application of this study is the possibility of determining the age of *C. sciadophylla* individuals. Our data suggest that dividing the total number of nodes on the trunk by 25 or 23 is sufficient to determine the age of an individual. Additionally, given what was found for *C. obtusa* and *C. sciadophylla*, similar growth patterns may exist in other species of *Cecropia,* as observed in *C. ficifolia* (P.-C. Zalamea, unpublished data). The genus *Cecropia* is associated with the initial phases of neotropical forest regeneration (Berg, 1978; Vázquez-Yanes, 1980; Martínez-Ramos et al., 1988; Álvarez-Buylla and Martínez-Ramos, 1992; Richards, 1996; Brokaw, 1998; Whitmore, 1998; Berg and Franco, 2005), which makes the genus a good candidate for estimating the time since a forest disturbance. Nevertheless, flowering and ramification processes have been poorly studied in the genus. This study suggests the need for similar explorations in other *Cecropia* species with a wide distribution range and ecological and geographic variation, to evaluate the suitability of using *Cecropia* trees as a chronometer for dating the ages of neotropical forest gaps, forestry roads, and mining sites.

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