Floresta e Ambient., Rio de Janeiro, 2025; 32(2): e20230026
https://doi.org/10.1590/2179-8087-FLORAM-2023-0026
ISSN 2179-8087 (online)

ORIGINAL ARTICLE – Conservation of Nature

Ontogenetic Growth of *Cecropia pachystachya* Can Explain Recent History of Swidden Agriculture in a Riparian Forest

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Abstract

We evaluated the pontential architectural analysis of *Cecropia pachystachya* to estimate tree age and reconstruct growth history in the Brazilian Cerrado. By examining internode length, branch, and inflorescence scars, we employed a retrospective method developed for Amazonian species to date growth cycles in this seasonal environment. Variations in internode length facilitated annual delimitation, with individuals producing an average of 31.4 ± 4.8 nodes per year. Most trees were approximately six years old, aligning with farmer-reported land-use history. Growth analyses indicated a biannual pattern in internode production and flowering, likely influenced by solar insolation rather than rainfall. Branching exhibited weaker, supra-annual periodicity. Despite considerable inter-individual variability in *C. pachystachya*, internode length remained a reliable indicator of annual growth. These findings endorse architectural analysis as a cost-effective tool for ecological monitoring and estimating pioneer species age in landscapes impacted by swidden cultivation.

Keywords: Brazilian savanna, Cecropia, Fallow, Swidden cultivation, Plant morphology.

1. INTRODUCTION

Secondary forests are ecosystems that regenerate naturally following disturbances. Much of the tropical secondary forest cover results from former agricultural activities (Chazdon, 2003; De Marzo et al., 2023). However, concerns remain about the capacity of secondary vegetation to recover from anthropogenic disturbances (Laurance et al., 2006; Maurent et al., 2023), particularly in the context of swidden agriculture. This traditional practice involves slash-and-burn clearing of forest vegetation for crop cultivation, followed by fallow periods (Borges et al., 2023; Burgers et al., 2005; Marquardt et al., 2013; Pedroso Júnior et al., 2008). Due to its impacts on land use and forest cover, swidden agriculture is considered a primary driver of tropical deforestation (Angelsen, 1995; Padoch and Pinedo-Vasquez, 2010). This has led to socio-environmental conflicts between farmers and managers (Valle Junior et al., 2015; Zheng et al., 2016), and has negatively affected both food and nutritional security in rural communities and biodiversity conservation efforts (Oldekop et al., 2016; Shahabuddin, 2009). Therefore, identifying knowledge gaps and addressing misconceptions is essential for maintaining swidden-related practices and promoting forest ecosystem conservation (Fajrini, 2022).

Understanding disturbance effects on forest ecosystems offers valuable insights into the recovery potential of secondary forests (Chazdon, 2003; De Marzo et al., 2023). dentifying time since the last disturbance is crucial for monitoring recovery dynamics and supporting decision-making by researchers, environmental managers, and local communities. Testing methods that estimate recovery time after the most recent disturbance is therefore essential. Interviews with local stakeholders, remote sensing analyses, and dendrochronology of pioneer, light-demanding species are among the main tools for reconstructing disturbance histories and determining time since last use (Brienen et al., 2009; Martinez-Ramos et al., 1988; Neeff et al., 2006). However, each method has limitations: interviews may be incomplete or inaccurate; satellite images can be cloud-obscured or fail to capture timely changes; radiocarbon dating is costly; and not all species are suitable for dendrochronological analysis (Zalamea et al., 2008). Thus, employing multiple, complementary approaches is important to overcome individual limitations and improve accuracy.

Quantitative analyses of the architecture of tropical pioneer trees in the Cecropieae tribe have been applied to study secondary forest regeneration following anthropogenic disturbances, aiming to understand the temporal organization of growth, branching, and flowering throughout the tree's developmental trajectory (Baudoux et al., 2024; Heuret et al., 2002; Levionnois et al., 2023; Zalamea et al., 2013, 2012, 2008). By identifying morphological scars left by various organs (e.g., leaves, branches, inflorescences) and analyzing structural features such as variations in internode length and the position of reproductive and branching scars, these studies have shown it is possible to associate structural patterns with time, reconstruct the species' growth history, and estimate individual age (Zalamea et al., 2012). Although, several studies have examined the growth patterns of *Cecropia* species in the Amazon rainforest, no research has addressed species occurring in the Brazilian savanna, the Cerrado. This represents a critical knowledge gap, particularly because growth patterns in the Cerrado are shaped by its pronounced seasonality—marked by a long, severe dry season—and a rainfall regime that differs significantly from that of the Amazon (Nardoto et al., 1998; Oliveira-Filho and Ratter, 2002, 1995). Furthermore, Zalamea et al. (2013), through a meta-analysis of fertile herbarium specimens, noted that *C. pachystachya* Trécul exhibits annual flowering in the Cerrado. Since inflorescences leave prominent scars on the trunk throughout the plant's lifespan, it may be feasible to estimate the age of individuals of this species from the onset of sexual maturity.

The objectives of this study are:

(i) To estimate the age of *C. pachystachya* individuals, a species that has not yet been studied in this context.
(ii) To compare the estimated age of the sampled *C. pachystachia* individuals with historical information regarding the timing of land clearing for swidden agriculture.

We predicted that the estimated age of the sampled individuals would correspond to the time since the last disturbance in the area. To test this, we applied the protocols proposed by Heuret et al. Heuret et al. (2002) and Zalamea et al. (2008) to analyze primary growth, branching, and flowering patterns of *Cecropia pachystachya*, a tropical pioneer species widely distributed in South America (Berg et al., 2005), and estimated the age of individuals sampled in areas traditionally used for swidden agriculture in the Cerrado. The fallow period duration was estimated through interviews with local farmers. We then evaluated the degree of convergence between these interview-based estimates and ages inferred from architectural analysis.

2. MATERIAL AND METHODS

2.1. Area of study

We studied *Cecropia pachystachya* Trécul in a Cerrado riparian forest fragment (Jalapão region, Mateiros, Tocantins; 10°32'51"S, 46°25'16"W; Fig. 1). The area has a tropical savanna climate (Aw; Köppen-Geiger), with 1,328 mm annual rainfall (Fig.2). Approximately 90% occurs October-April (peaking at 225 mm in January), while the dry season (May-September) receives minimal precipitation (0 mm in July) (ICMBio, 2014; INMET, 2022; Naturatins, 2003).

Sampling occurred in a seasonally flooded riparian forest fragment. This vegetation typically occupies valley bottoms or lower landscape portions, associated with small watercourses and functioning as a biogeographical corridor linking the Amazon and Atlantic Forests (Cabrera and Willink, 1973). In the study region, floodable swamp gallery forests have traditionally been used for swidden agriculture by quilombola farmers (Borges et al., 2016).

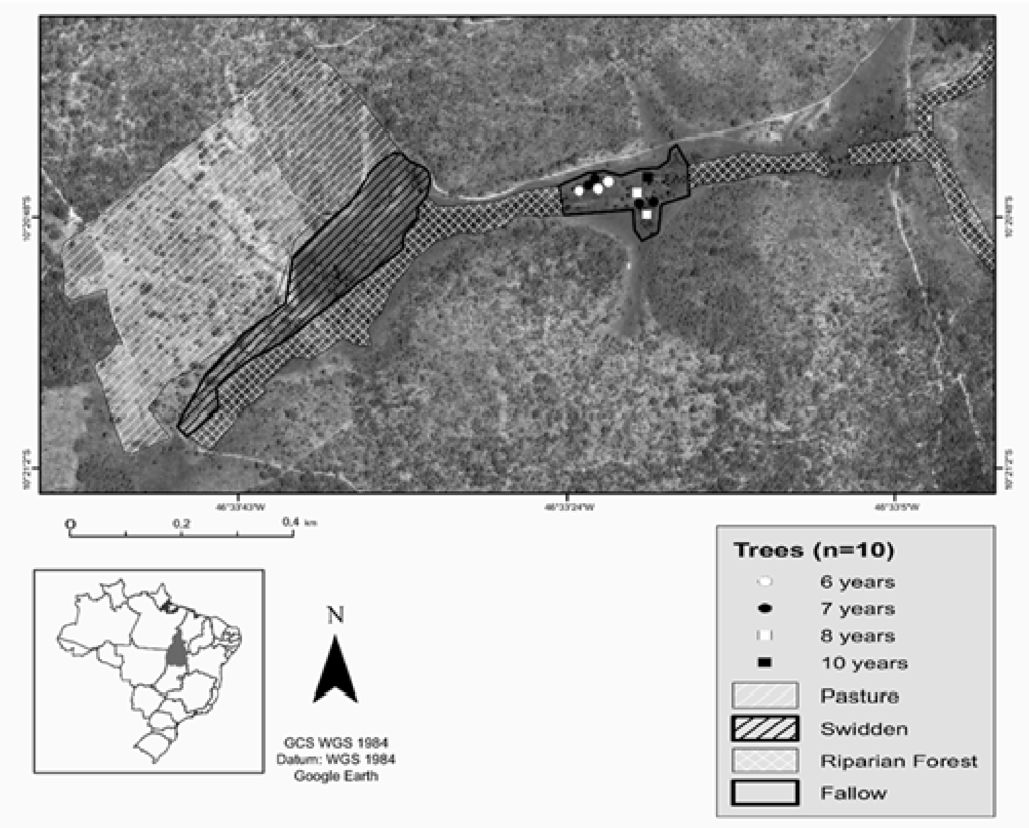

Figure 1. The study area is in Jalapão State Park (PEJ), where C. pachystachya individuals were sampled in a 6-year-old fallow (capoeira). Land-use types are differentiated by hatching: diagonal white (pasture), horizontal black (swidden fields), white crosshatching (riparian forests), and solid black (fallow). This illustrates vegetation distribution and land-use practices in the park.

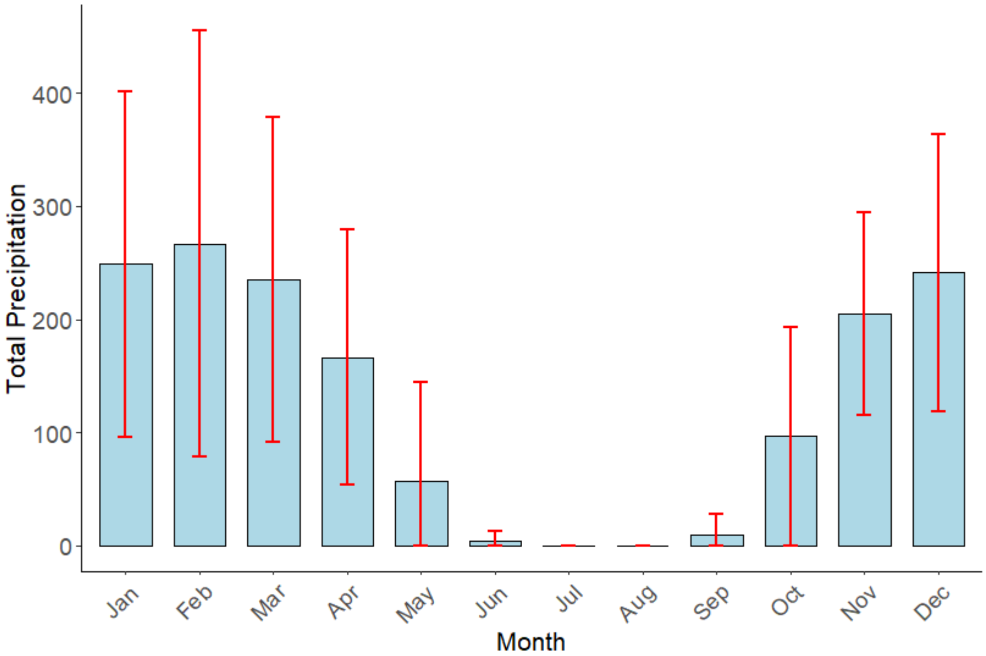

Figure 2. Average monthly precipitation in Mateiros, Tocantins (2007–2017). Blue bars show monthly mean precipitation; red error bars indicate ±1 SD. Rainfall peaks between November–March and is minimal June–August (INMET, 2019).” INMET, (2019).

2.2. Morphological features and architectural traits in the genus Cecropia

Cecropia species are widely distributed across the Neotropics and West Indies (Berg et al., 2005). These heliophilous pioneer trees rapidly colonize disturbed open areas (Whitmore, 1990). Their architecture follows Rauh's model, with orthotropic axes, lateral flowering, and rhythmic branching forming a candelabra-like structure. Internodes remain identifiable throughout the plant's lifespan, as stipules leave circular scars and petioles prominent scars on the bark.

C. pachystachya (locally "Embaúba") is a pioneer species in Cerrado forests and savannas. Trees can reach 12 m height, with stipulated, broad, peltate leaves. Each leaf axil contains three buds: a central vegetative bud (potential branch) and two lateral buds producing staminate or pistillate spikes in this dioecious species (Berg et al., 2005). The inflorescences leave characteristic circular scars on the axis. A smaller scar size indicates that the inflorescence was aborted, which in some cases allows the identification of transitional zones between successive internodes that bearing inflorescences and those where buds did not develop. Similarly, when pruned, branches leave distinct scars, enabling the identification of the former branch positions (Heuret et al., 2002; Levionnois et al., 2023).

2.3. Data collection

To analyze growth, branching, and flowering patterns, which enabled us to estimate the age of each individual, we felled and measured adult trees, defined as those displaying inflorescence scars or bearing inflorescences. Of the nine individuals sampled, some were not fertile at the time of felling, and we were therefore unable to determine their reproductive type. To analyze growth, branching, and flowering patterns—which enabled us to estimate the age of each individual—we felled and measured adult trees, defined as those displaying inflorescence scars or bearing inflorescences. Of the nine individuals sampled, some were not fertile at the time of felling, and we were therefore unable to determine their reproductive type. Only individuals established from seed, rather than from sprouting, were selected. We also ensured that the sampled trees had not suffered damage such as fire or mechanical breakage. The mean height of the sampled individuals was 8.5 ± 1.0 m, and the mean diameter at breast height (DBH) was 10.2 ± 1.9 cm.

Data were collected in November 2017 and May 2018 by a single observer with local guides to access swidden agriculture areas. Fallow ages reported by guides during interviews served as references for architectural age estimates. For each tree, we measured girth at breast height (GBH) at 1.30 m and calculated diameter at breast height (DBH) assuming circular cross-sections. After felling, height was measured with a decameter. We recorded node counts to the first branch (present or pruned) and first inflorescence (present, pruned, or identifiable by scars).

From the top to the base of the trunk, we recorded internode length for each phytomer—the structural unit consisting of a node associated with its leaf (or leaves), axillary bud(s), and subtending internode—using a digital caliper. We also recorded the presence or absence of branches and inflorescences. To classify the development of the central bud, we applied the following coding system: (0) no development; (1) scar of an aborted branch; (2) pruned branch; and (3) presence of a developed branch. For lateral bud development, we used the following categories: (0) no development; (1) scar of an aborted inflorescence; (2) scar of a developed inflorescence; (3) developed inflorescence in anthesis (without spathes); and (4) immature inflorescence enclosed within the spathes.

In parallel with these morphological descriptions, we conducted a semi-structured interview (see Boyce and Neale, 2006) with a local farmer to gather information on the age and land-use history of a swampy gallery forest area used for swidden agriculture.

2.4. Statistical analysis

Data were encoded as a multi-tree graph object (Godin et al., 1997) and extracted using the VPlants package from the OpenAlea 2.0.0 software platform (Pradal et al., 2008). This Python-based package enables the representation and spatial localization of structures within multi-scale plant architectures. All subsequent statistical analyses were performed using R version 4.2.0 (R Core Team, 2022).

We applied time-series analysis to internode length, branching, and flowering sequences to identify periodic developmental patterns, following Guédon et al. (2007) architectural framework. Analysis involved: (1) preprocessing internode data to isolate environmental signals; (2) computing individual and mean correlograms for all variables; and (3) determining dominant population periodicities.

The observed growth sequences reflect a combination of long-term ontogenetic trends and short-term environmental fluctuations. To isolate the high-frequency signal primarily attributed to environmental factors (e.g., climate), we first decomposed the internode length sequences. A smoothed long-term trend was calculated for each tree using a symmetric low-pass filter, implemented as a moving average with binomial weights based on a B(n=190, p=0.5) distribution. This filter assigns greater weight to central nodes and progressively less to more distant ones, effectively capturing the underlying ontogenetic trajectory. To address boundary effects during the convolution process, the first and last values of the sequence were replicated.

Following the approach described by Fritts (2012), the smoothed trend was used to standardize the original sequence. Residuals were calculated as the ratio of observed internode length to the corresponding smoothed value at each node. These standardized residuals represent the detrended, high-frequency signal and were subsequently used in the autocorrelation analysis.

Autocorrelation analyses were conducted to detect significant periodicities in the internode length residuals, as well as in binary sequences of branching and flowering events (coded as 1 for presence and 0 for absence). For the binary branching and flowering sequences, the initial string of zeros preceding the first occurrence of each event was removed for each tree. This step ensured that the analysis focused exclusively on the periodicity of the process after its onset.

An individual correlogram was generated for each tree and each variable. We used Spearman's rank correlation—a non-parametric method that is robust to non-normal data distributions. The autocorrelation coefficient for each lag $k \in [1{:}100]$ was computed as follows (Eq. 1):

$$(1)\quad \rho\,(k) = cor\,(x_{1:(n-k)}, x_{(k+1):n})$$

where $\rho\,(k)$ is the correlation between the sequence and its lagged version, calculated using all effective (non-missing) values. The number of effective pairs n_k used for each lag was recorded and used to calculate (Eq. 2) the theoretical 95% confidence interval under the null hypothesis of no autocorrelation.

$$(2)\quad \mathrm{CI}_{95\%} = \pm\frac{1{,}96}{\sqrt{\mathrm{n_k}}}$$

Any autocorrelation coefficient exceeding this threshold was considered significant at the 5% level.

Individual correlograms were aggregated to synthesize the results and identify population-level patterns. A mean correlogram was calculated for each variable by taking the pointwise average of all individual autocorrelation coefficients at each lag k. Confidence intervals around the mean correlogram were computed using a parametric approach based on the Central Limit Theorem. For each lag k, the mean autocorrelation coefficient $\overline{\rho}_s(k)$ was calculated (Eq. 3) across all trees, and the 95% confidence interval was defined as:

$$(3)\quad \overline{\rho}_s(k) \pm 1{,}96 \times \frac{SD\left(\rho_s(k)\right)}{\sqrt{N_{trees}}}$$

where $SD(\rho_s(k))$ is the standard deviation of autocorrelations at lag k across individuals. In parallel, a global threshold was defined for each lag as (Eq. 4):

$$(4)\quad CI_{95\%} = \pm\frac{1{,}96}{\sqrt{\sum n_k}}$$

Finally, to visualize the most common periodicities within the population, we identified all lags with significant positive autocorrelation from each individual correlogram. The frequency distribution of these significant lags was then plotted as histograms to reveal the dominant periodic signals and their variability among trees.

3. RESULTS

The sampled individuals had a mean height of 8.5 ± 1.0 m and a mean diameter of 10.2 ± 1.9 cm, comprising approximately 228 ± 45 nodes. The first branching tier was located at 4.8 ± 1.5 m, corresponding to node 86 ± 21, while the first inflorescence appeared at 3.4 ± 1.6 m, at node 60 ± 22.

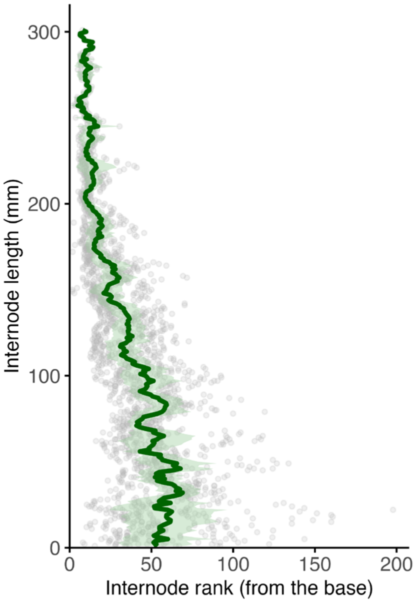

Figure 3. Variation in *Cecropia pachystachya* internode length along trunks (base to apex). Gray dots show raw values; colored lines indicate mean internode length per node rank across individuals. Shaded ribbons represent standard deviations.

From the stem base to approximately node 50 (Fig. 3), internode length averages around 5 cm, with occasional peaks reaching up to 15 cm. Beyond this point, internode length progressively decreases with increasing node rank, falling below 1 cm near the apex.

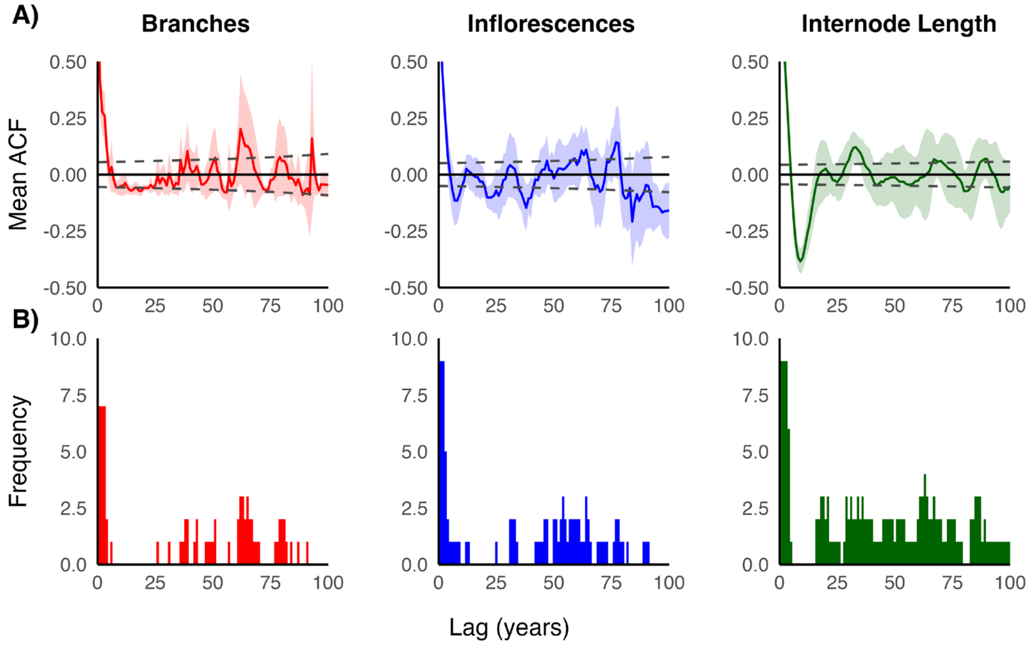

Figure 4. (A) Mean Spearman's rank autocorrelation functions for branching, flowering, and internode length residuals across all sampled individuals. (B) Frequency distribution of lags with significant positive autocorrelation detected at the individual level (aggregated across all trees).

Individual autocorrelation profiles (Fig. 4) showed oscillating patterns with significant positive coefficients, though at varying lags. Most frequent significant lags occurred at ~19 and 34 (internode length residuals), 63 (branching), and 32 or 65 (flowering). (Fig. 3b).

At the population level, the average correlogram retained an oscillatory structure. The mean autocorrelation coefficients exceeded the significance threshold at lags 33, 67, and 89 for internode length residuals (Fig. 4A). The peak observed at lag 20 was not statistically significant under the current smoothing filter (B[190, 0.5]) but became significant when the moving average window was adjusted by reducing the n parameter of the binomial distribution (tested for 30 < n < 150). For branching, the mean autocorrelation coefficients were significantly positive, with peaks at 39, 62, and 93. In the case of flowering, significant peaks were observed at lags 47, 58, and 64, while those at lags 12 and 31 did not exceed the significance threshold.

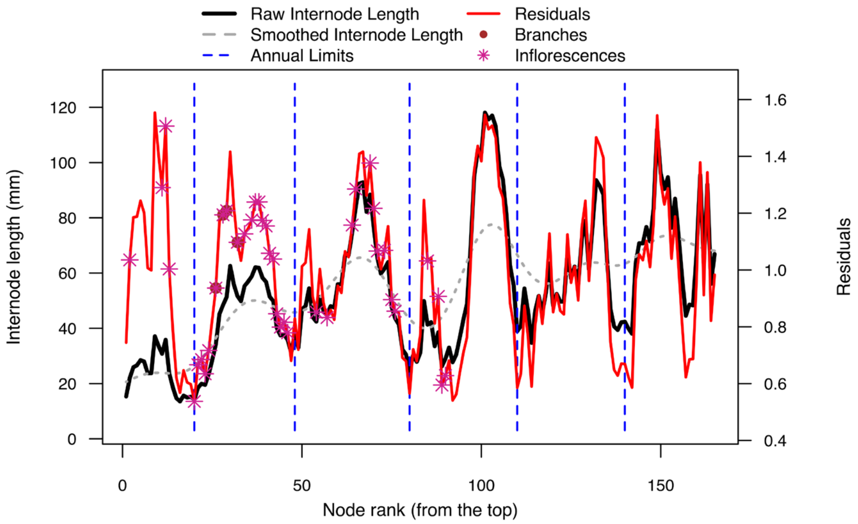

Figure 5. Individual case (Tree ID: P17) showing internode lengths (black line) and residuals (red line) after binomial filtering B(190,0.5) (gray dotted line). Branches (purple circles) and inflorescences (stars) are indicated. Blue dashed lines denote annual boundaries.

Figure 5 presents a representative individual exhibiting a significantly positive autocorrelation function, with peaks at node ranks 32 and 64. This tree showed limited branching activity, which prevented the detection of a clear periodic pattern in branch occurrence, and no evident periodic signal was observed for inflorescences. Based on an average annual node production of approximately 35 nodes, as indicated by the mean correlogram, we visually identified the most probable locations of annual boundaries by locating zones where internode lengths were shortest. These estimated annual limits are marked by vertical dashed blue lines. In this case, the tree was estimated to be six years old. Although the identification of annual boundaries can sometimes be complicated by bimodal patterns—characterized by additional internode shortening mid-season—pairwise comparisons among individuals enabled the proposal of a globally consistent and satisfactory delineation of year boundaries. Based on the segmentation of internode sequences into annual units, the mean number of nodes produced per year was 31.4 ± 4.80. (Fig. 6).

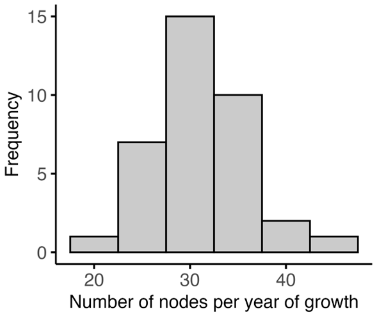

Figure 6. Distribution of annual node production across individuals after growth unit segmentation. Incomplete first and last years were excluded.

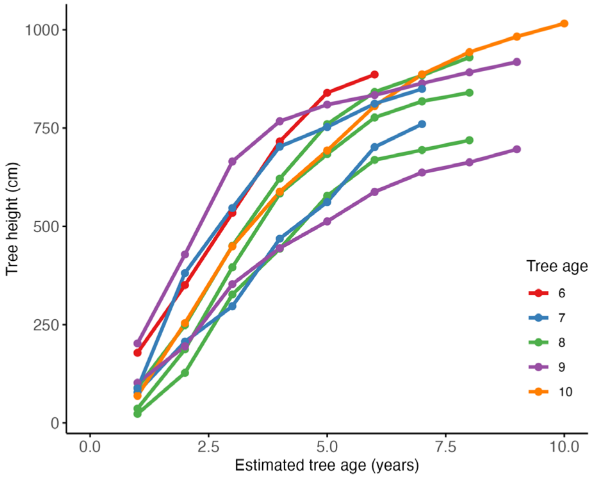

Figure 7. Retrospective height growth of individuals was reconstructed by summing internode lengths within each annual segment and cumulatively adding the yearly increments.

Based on our segmentation, the sampled trees ranged in age from four to eight years, with most individuals being six years old (Fig. 7). The reconstruction of height growth revealed a rapid initial growth phase, peaking at a mean annual increment of 182 ± 41.5 cm in the third year. Growth rates then gradually declined, reaching 32.2 ± 9.9 cm/year by the eighth year, resulting in a sigmoidal growth curve.

4. DISCUSSION

This study evaluated architectural analysis for reconstructing growth history and estimating age in *Cecropia pachystachya*. We adapted a dendrochronological approach developed for other Neotropical species to the seasonal Brazilian Cerrado. Results show promise but reveal challenges from high inter-individual variability and complex growth dynamics affecting annual unit delineation. Despite limited sampling, our findings provide preliminary insights into *C. pachystachya* life-history traits and support developing this low-cost method for tropical pioneer species studies.

Architectural dimensions and environmental constraints — Within our study site in the Cerrado, individuals of *C. pachystachya* exhibited reduced total height and an earlier onset of branching and flowering compared to conspecifics in the Atlantic Forest (Sposito and Santos, 2001; Sposito, 1999). This variation is likely attributable to the pronounced seasonality and low nutrient availability typical of Cerrado soils (Eiten, 1972). Both precipitation and edaphic constraints have been shown to significantly shape plant architecture in this ecosystem (Ferreira, 2002; Mistry, 2000).

Notably, *C. pachystachya* is often classified as a “weedy” species, characterized by rapid growth and a short lifespan (WFO, 2025)—a life-history strategy associated with reduced investment in height and mechanical safety factors (Sposito and Santos, 2001). These traits likely reflect an ecological opportunism syndrome, enabling the species to rapidly exploit resource-rich but short-lived windows following disturbance.

Growth, branching, and flowering patterns — Our age estimation method relies on linking vegetative growth patterns to climatic seasonality. Results show *C. pachystachya* internode length fluctuations strongly correlate with local rainfall, with short internodes typically corresponding to dry seasons. This aligns with Davis (1970) foundational work and has been validated for other *Cecropia* species across Neotropical environments (Heuret et al., 2002; Levionnois et al., 2023; Zalamea et al., 2008), including African invasions (Baudoux et al., 2024).

The consistent relationship in Cerrado’s seasonal climate confirms internode length as a reliable marker for annual growth cycle delineation in *C. pachystachya*. However, internode fluctuations often show bimodal annual patterns, inconsistent with the region's unimodal rainfall. This suggests more complex growth regulation, potentially involving endogenous rhythms or short-term climatic anomalies.

C. pachystachya shows high reproductive plasticity. While many individuals exhibited biannual flowering, substantial inter-individual variability prevented population-level statistical significance. This contrasts with the annual flowering reported for related *C. obtusa* and *C. sciadophylla* (Zalamea et al., 2012).

Two continuously flowering individuals and comparisons with Paraná's semi-deciduous forest populations (showing near-continuous flowering, briefly interrupted May-June(Mikich and Silva, 2001) further demonstrate this plasticity. Such reproductive variability may reflect the taxonomic complexity of the *C. pachystachya* species complex, including potential hybridization and unresolved species boundaries (Santos et al., 2020; Treiber et al., 2022).

Flowering pattern inconsistency reduced inflorescence scar reliability for annual delimitation compared to internode length. Branching events showed weaker but significant supra-annual periodicity, indicating developmental processes respond to environmental cues at different temporal scales.

A striking finding of this study was the apparent decoupling between the strong annual rainfall seasonality of the Cerrado, and the predominantly biannual rhythm observed in both vegetative growth and flowering. While variations in internode length have traditionally been attributed to water availability, this model alone does not account for the two distinct growth pulses observed per year. This suggests that C. *pachystachya* may be responding to a more subtle, bimodal environmental cue.

A compelling explanation is offered by the work of Borchert et al. (2015), who demonstrated that tropical daily insolation (day length × solar intensity) exhibits a biannual cycle from the sun's equatorial passage at equinoxes, creating two annual light availability phases independent of rainfall. The synchronous biannual rhythms in *C. pachystachya* growth and reproduction strongly suggest its phenology is tuned to these insolation dynamics.

Finally, the weak but significant supra-annual branching periodicity suggests distinct developmental processes respond to different temporal cues and resource-allocation strategies. These findings establish *C. pachystachya* as a valuable phenological model, though with a more complex 'biological clock' than congeners. Its sensitivity to multiple environmental signals (rainfall, insolation) and high intraspecific variability make it ideal for studying gene-environment interactions in plant life-history strategies.

Phyllochron and its Implications for the "Biological Clock" — Based on our annual delimitations, we estimated the mean annual node production for *C. pachystachya* to be 31.4 nodes, corresponding to a phyllochron of approximately 11.6 days per leaf. This average rate closely aligns with those reported for other well-studied *Cecropia* species, such as *C. obtusa* (~10 days; Heuret et al., 2002; Levionnois et al., 2023), *C. sciadophylla* (~14 days; Zalamea et al., 2012, 2008), and the invasive *C. peltata* in Cameroon (~10 days; Baudoux et al., 2024). While this consistency reinforces the broader idea of Cecropia as a potential 'biological clock,' our analysis also revealed marked inter-individual variability in the annual rhythm of *C. pachystachya*.

Autocorrelation analyses revealed greater individual divergence in *C. pachystachya*, producing flatter mean correlograms than the sharper patterns of Amazonian *C. obtusa* and *C. sciadophylla*. This variability complicates annual cycle delineation, showing the biological clock's precision varies by species and environment. A broader study with direct growth monitoring is needed to fully assess this variability and identify its ecological and physiological drivers.

Validation of Age Estimates and Colonization Lag — Our architectural analysis estimated the age of most sampled *C. pachystachya* individuals to be approximately six years, with one older individual estimated at ten years. This chronological framework aligns well with information provided by a local farmer, who reported that the area had been cleared for agriculture six to eight years prior to our sampling. The presence of younger individuals within this timeframe is ecologically coherent. The slight discrepancy observed in the ten-year-old tree may be explained by its position just outside the main area of disturbance, suggesting it may have already been established at the time of land clearing.

A temporal lag between disturbance and pioneer establishment is common, potentially due to dispersal limitation or seed bank depletion from fire/clearing (Zalamea et al., 2012). The convergence between our retrospective architectural analysis and the known land-use history provides strong validation for the use of this method to estimate the age of *C. pachystachya* individuals in this ecosystem.

Limitations and Future Directions — While validating this methodological tool, we note important limitations. The analysis used few individuals from one site. Expanding sampling across broader Cerrado ranges would better assess *C. pachystachya* phenotypic plasticity and confirm developmental pattern consistency along environmental gradients.

Second, retrospective architectural analysis would benefit from complementary long-term monitoring to better calibrate climate-morphology relationships (e.g., growth, flowering) and clarify phyllochron variability sources.

Finally, while rainfall is key, Cerrado's nutrient-limited soils also critically influence development. Future models should integrate both climatic and edaphic variables to better understand *C. pachystachya* growth strategies and life-history dynamics.

5. CONCLUSION

We validated architectural marker analysis for reconstructing Cecropia pachystachya life history. Results showed predominantly biannual vegetative growth (less pronounced in flowering) and confirmed internode length variation as a reliable seasonal indicator for age estimation. This reinforces Cecropia's role as a "biological clock" for dating Neotropical disturbances. Our findings demonstrate how field-based dendrochronological methods can be adapted for tropical species lacking growth rings, offering new approaches to study forest regeneration, species interactions, and invasion processes in seasonally dry ecosystems.

SUBMISSION STATUS

Received: 18 Jul. 2023
Accepted: 12 Feb. 2025
Associate editor: Fernando Gomes

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Sílvia Laine Borges Lúcio: conceptualization (equal), funding acquisition (lead), investigation (equal), visualization (supporting), writing–original draft (supporting), and writing–review and editing (supporting).
Patrick Heuret: conceptualization (equal), data curation (equal), formal analysis (lead), investigation (supporting), methodology (lead), writing - review & editing (equal).
Ludivine Eloy: conceptualization (equal), investigation (equal), writing–original draft (equal), writing–review, and editing (equal).
Isabel Belloni Schmidt: conceptualization (equal), funding acquisition (equal), project administration (equal), resources (equal), and software (equal).

DATA AVAILABILITY

The dataset supporting the results of this study is available at Zenodo: https://zenodo.org/records/15814202

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