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DENDROCHRONOLOGY OF THE BRAZIL NUT TREE (*Bertholletia excelsa bonpl.*) IN THE AMAZON: WATER MEMORY AND VULNERABILITY OF RADIAL GROWTH TO PRECIPITATION DEFICIT

DENDROCRONOLOGIA DA CASTANHEIRA-DO-BRASIL (*Bertholletia excelsa bonpl.*) NA AMAZÔNIA: MEMÓRIA DA ÁGUA E VULNERABILIDADE DO CRESCIMENTO RADIAL AO DÉFICIT DE PRECIPITAÇÃO

DENDROCRONOLOGÍA DEL CASTAÑO DE BRASIL (*Bertholletia excelsa bonpl.*) EN LA AMAZONÍA: MEMORIA DEL AGUA Y VULNERABILIDAD DEL CRECIMIENTO RADIAL AL DÉFICIT DE PRECIPITACIÓN.

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ABSTRACT

Understanding the growth dynamics and climatic sensitivity of Bertholletia excelsa (Brazil nut tree) is essential for assessing tropical forest resilience and recent hydroclimatic variability in Amazonia. Despite its ecological and socioeconomic importance, dendrochronological information for this species remains limited, particularly regarding the mechanisms linking large-scale climate forcing to local growth responses. In this study, we developed and evaluated growth-ring chronologies from adult B. excelsa trees in native Amazonian forests to assess growth coherence and the strength of climatic signals. Ring widths were cross-dated using COFECHA, and chronology quality statistics—effective interseries correlation (rbar.eff), expressed population signal (EPS), signal-to-noise ratio (SNR), and first-order autocorrelation (AC)—were calculated using the dplR package in R. The master chronology exhibited strong internal coherence (rbar.eff = 0.38–0.46) and a robust common signal (EPS > 0.85; SNR > 5.0), confirming reliable cross-dating and representativeness at the population

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level. Moderate autocorrelation values indicated physiological persistence associated with hydrological memory. Radial growth was strongly controlled by hydroclimatic variability, with precipitation emerging as the primary limiting factor and temperature acting mainly as a stressor. Growth responses were particularly sensitive during the transition from the dry to the rainy season, when cambial reactivation and earlywood formation occur. Large-scale oceanic forcing associated with ENSO and Tropical Atlantic variability influenced growth indirectly by modulating local precipitation regimes and dry-season severity, resulting in lagged growth responses following drought events. These findings demonstrate that B. excelsa integrates climatic information across the full hydrological cycle and functions as a sensitive bioindicator of recent climate variability, providing valuable insights into forest vulnerability and resilience under ongoing climate change.

Keywords: Dendrochronology. Amazon Rainforest. Growth Rings. EPS. Climate Variability. Drought Response.

RESUMO

Compreender a dinâmica de crescimento e a sensibilidade climática de Bertholletia excelsa (castanheira-do-brasil) é essencial para avaliar a resiliência das florestas tropicais e a variabilidade hidroclimática recente na Amazônia. Apesar de sua importância ecológica e socioeconômica, a dendrocronologia da espécie ainda é limitada, especialmente quanto aos mecanismos que ligam forçantes climáticas de grande escala às respostas locais de crescimento. Neste estudo, foram desenvolvidas e avaliadas cronologias de anéis de crescimento de árvores adultas de B. excelsa em florestas nativas amazônicas para analisar coerência de crescimento e sinais climáticos. As larguras dos anéis foram sincronizadas com COFECHA e foram calculadas estatísticas como rbar.eff, EPS, SNR e AC com o pacote dplR no R. A cronologia apresentou forte coerência interna (rbar.eff = 0,38–0,46) e sinal comum robusto (EPS > 0,85; SNR > 5,0), confirmando confiabilidade e representatividade populacional. A autocorrelação moderada indicou persistência fisiológica associada à memória hidrológica. O crescimento radial foi fortemente controlado pela precipitação, com temperatura atuando como fator de estresse. As respostas foram mais sensíveis na transição entre estação seca e chuvosa, durante a reativação cambial e formação do lenho inicial. Forçantes climáticas como ENSO e variabilidade do Atlântico Tropical influenciaram o crescimento indiretamente ao modular a precipitação e a severidade da seca, gerando respostas com defasagem após eventos de estiagem. Esses resultados mostram que B. excelsa integra informações climáticas ao longo do ciclo hidrológico e funciona como bioindicador da variabilidade climática recente, contribuindo para compreender a vulnerabilidade e resiliência das florestas sob mudanças climáticas.

Palavras-chave: Dendrocronologia. Floresta Amazônica. Anéis de Crescimento. EPS. Variabilidade Climática. Resposta à Seca.

RESUMEN

Comprender la dinámica de crecimiento y la sensibilidad climática de Bertholletia excelsa (castaño de Brasil) es esencial para evaluar la resiliencia de los bosques tropicales y la variabilidad hidroclimática reciente en la Amazonía. A pesar de su importancia ecológica y socioeconómica, la dendrocronología de la especie aún es limitada, especialmente en relación con los mecanismos que conectan forzamientos climáticos a gran escala con respuestas locales de crecimiento. En este estudio se desarrollaron y evaluaron cronologías de anillos de crecimiento de árboles adultos de B. excelsa en bosques nativos amazónicos para analizar la coherencia del crecimiento y las señales climáticas. Las anchuras de los anillos fueron sincronizadas con COFECHA y se calcularon estadísticas como rbar.eff, EPS, SNR y AC con el paquete dplR en R. La cronología mostró una fuerte coherencia interna (rbar.eff = 0,38–0,46) y una señal común robusta (EPS > 0,85; SNR > 5,0), confirmando su

fiabilidad y representatividad poblacional. La autocorrelación moderada indicó persistencia fisiológica asociada a la memoria hidrológica. El crecimiento radial estuvo fuertemente controlado por la precipitación, mientras que la temperatura actuó principalmente como factor de estrés. Las respuestas de crecimiento fueron más sensibles durante la transición de la estación seca a la lluviosa, durante la reactivación cambial y la formación de la madera temprana. Forzamientos climáticos como ENSO y la variabilidad del Atlántico Tropical influyeron indirectamente al modular la precipitación y la severidad de la sequía, generando respuestas retardadas tras eventos de sequía. Estos resultados muestran que B. excelsa integra información climática a lo largo del ciclo hidrológico y funciona como bioindicador de la variabilidad climática reciente, ayudando a comprender la vulnerabilidad y resiliencia de los bosques frente al cambio climático.

Palabras clave: Dendrocronología. Selva Amazónica. Anillos de Crecimiento. EPS. Variabilidad Climática. Respuesta a la Sequía.

1 INTRODUCTION

Dendrochronology, the science that studies tree growth rings, has become a powerful approach for investigating growth dynamics and ecological processes in tropical forests (Da Costa et al., 2023; Portal-Cahuana et al., 2023). The high structural complexity and floristic diversity of these ecosystems, combined with the long timeframes required for monitoring permanent plots, limit the availability of long-term growth data. In this context, tree-ring analysis enables the retrospective reconstruction of radial growth trajectories, providing insights into functional strategies, longevity, and resilience of tree species under varying environmental conditions (Schöngart et al., 2002; Albiero et al., 2021). Understanding temporal growth variability and its relationship with ecological and climatic drivers is therefore essential for elucidating the mechanisms regulating the structure and functioning of Amazonian forests (Amaral et al., 2019; Andrade et al., 2019; Cintra et al., 2022; Miranda et al., 2024).

Recent advances in tropical dendrochronology have reinforced the importance of tree-ring chronologies for understanding forest responses to climate variability and global change, particularly in regions with limited long-term instrumental records (Groenendijk et al., 2025). These approaches provide high-resolution insights into hydroclimatic variability, ecosystem resilience, and the vulnerability of long-lived species to increasing drought frequency and warming. In the Amazon Basin, dendrochronological studies have increasingly focused on canopy and emergent species, revealing strong linkages between radial growth dynamics, precipitation regimes, and large-scale climate forcing.

In tropical regions, dendroclimatological approaches have been widely applied to investigate how climatic variables such as precipitation, temperature, and soil moisture influence annual tree growth, enabling the reconstruction of historical climate variability with annual resolution (Brienen et al., 2015; Granato-Souza et al., 2019; Baker et al., 2022). In the Amazon, tree growth is strongly associated with precipitation seasonality and highly sensitive to extreme drought events. Major droughts, such as those recorded in 2005 and 2010, have been linked to reduced radial growth, increased tree mortality, and declines in carbon sequestration capacity (Baker et al., 2022; Granato-Souza et al., 2019). Under ongoing climate change, projections of increasing temperatures and altered precipitation regimes indicate a potential shift toward critical thresholds of ecosystem stress, with implications for forest resilience and feedbacks to the global climate system (Flores et al., 2024; Boulton et al., 2022; Peters et al., 2015).

The advancement of dendrochronology in tropical forests has been supported by overcoming the traditional paradigm that annual growth rings are restricted to temperate

species. Although cambial dormancy in temperate regions is primarily driven by low temperatures, in tropical environments such as the Amazon, seasonal precipitation regimes are sufficient to induce periodic cambial activity and the formation of distinct annual rings (Schöngart et al., 2017; Locosselli et al., 2020). The validation of annual ring formation through complementary methods—including dendrometer monitoring, anatomical analyses, and radiocarbon dating—has strengthened the reliability of dendrochronological records in tropical species (Pacheco-Solana et al., 2023). This methodological framework has enabled the development of robust chronologies for long-lived Amazonian taxa, supporting their application in climate–growth studies.

Among Amazonian species suitable for dendrochronological studies, the Brazil nut tree (*Bertholletia excelsa* Bonpl.) stands out due to its ecological and socioeconomic importance. Widely distributed across the Amazon Basin, the species produces seeds of high nutritional and commercial value and represents one of the main non-timber forest products in the region. Its wood, characterized by high density and durability, has also historically been targeted for selective logging (Ferreira et al., 2023). Combined pressures from extractivism and past logging have contributed to its classification as a vulnerable species in regional, national, and international conservation frameworks (COEMA-PA, 2007; MMA, 2014; Americas Regional Workshop, 1998), with legal protection established by Brazilian legislation (Brasil, 2006). In this context, understanding growth dynamics and environmental sensitivity is essential to support conservation and sustainable management strategies.

Despite its ecological and economic importance, dendrochronological studies on *Bertholletia excelsa* remain limited. Existing research has demonstrated the species' potential for tree-ring analysis (Schöngart et al., 2015; Caetano-Andrade et al., 2020; Caetano-Andrade et al., 2024), yet important gaps persist regarding its growth responses to climatic variability, particularly in eastern Amazonia and in the state of Pará. In particular, the relative influence of precipitation, temperature, and large-scale climate forcing on radial growth remains insufficiently resolved for natural populations in this region.

Therefore, the objective of this study was to evaluate the relationship between climatic variables and radial growth of *Bertholletia excelsa* within the instrumental period in a native forest of the Tapajós National Forest, eastern Amazonia. Specifically, we analyzed the influence of precipitation and air temperature on growth dynamics, focusing on recent hydroclimatic variability rather than long-term paleoclimate reconstruction. We hypothesize that drought events and increased temperatures reduce radial growth due to hydraulic limitation and thermal stress.

The selection of precipitation and temperature as key variables is justified by their central role in regulating secondary growth in tropical forests (Brienen et al., 2015; Schöngart et al., 2017). In the Amazon, precipitation controls cambial dormancy and constitutes the dominant climatic signal recorded in tree rings, whereas elevated temperatures tend to intensify hydraulic stress and constrain growth (Baker et al., 2022). Establishing climate–growth relationships based on these variables provides a robust framework for quantifying the climatic sensitivity of *B. excelsa* and contributes to the development of adaptive forest management strategies under ongoing climate change.

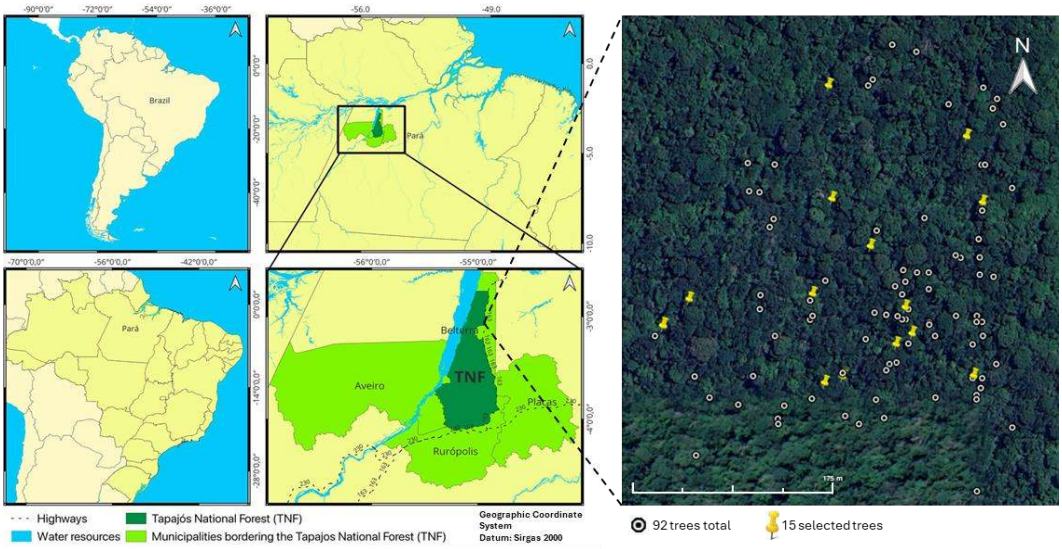
2 MATERIALS AND METHODS

2.1 STUDY SITE DESCRIPTION

The study was conducted in a native stand of *Bertholletia excelsa* located at kilometer 85 of the BR-163 highway, within the Tapajós National Forest (FLONA Tapajós), municipality of Belterra, Pará State, Brazil (Figure 1).

Figure 1

Location of the Bertholletia excelsa Bonpl. population sampled in the municipality of Belterra, State of Pará, Brazil



Source: Authors, 2026.

The soils in the study area are classified as Dystrophic Yellow Latosols (Oxisols) with a clayey texture, according to the Brazilian Soil Classification System (Moura et al., 2025; Oliveira Junior and Correa, 2001).

The regional climate is classified as tropical monsoon (Am), characterized by high annual precipitation and marked seasonality. Based on historical data (1973–2017) from the

Belterra meteorological station (code 82246), located approximately 50 km from the study site, annual precipitation ranges between 1500 and 2000 mm. A distinct dry season occurs from July to November, when monthly precipitation falls below 60 mm, while the rainy season extends from December to June, with peak rainfall in March (Martorano and Pereira, 1993).

For dendroclimatic analyses, a hydrological year from May of the previous year to April of the current year was adopted, based on the seasonal transition in precipitation patterns.

Regional precipitation variability is strongly influenced by large-scale climate drivers. El Niño events are associated with reduced rainfall and increased temperatures in eastern Amazonia, intensifying dry-season conditions (de Souza Freitas et al., 2024). In contrast, La Niña events tend to enhance precipitation due to the strengthening of the Intertropical Convergence Zone (ITCZ) (Nascimento, 2017). Additionally, variability in sea surface temperatures in the Tropical South Atlantic modulates the latitudinal position of the ITCZ through the Atlantic dipole mechanism, influencing moisture transport and rainfall patterns in the region (Figliuolo, 2017; Franca and Mendonça, 2016).

2.2 SAMPLING AND SAMPLE PREPARATION

A total of 92 individuals of *Bertholletia excelsa* were initially inventoried within a 300 × 300 m permanent plot. From this population, 15 individuals were selected for dendrochronological analysis based on strict criteria, including good phytosanitary condition, absence of stem damage, clear ring boundaries, and suitability for cross-dating.

In November 2018, three increment cores were collected per individual at breast height (1.30 m) using a motorized increment borer. Samples were prepared following standard dendrochronological procedures (Schweingruber, 1996; Speer, 2010).

The cores were air-dried, mounted on wooden supports, and progressively polished using sandpaper of increasing grit size (80 to 600) to enhance the visibility of anatomical features.

2.3 GROWTH-RING IDENTIFICATION AND ANATOMICAL CRITERIA

Growth-ring boundaries were identified through macroscopic anatomical analysis using a stereomicroscope (Nova XTX 5C) at 10× magnification. Samples were scanned at high resolution (1200 dpi; HP Scanjet G4050), and ring widths were measured with Image Pro Plus software at a precision of 0.01 mm (Schweingruber, 1996; Larson, 1969).

Ring delimitation was primarily based on the presence of banded reticulate axial parenchyma, which represents a reliable anatomical marker for annual ring boundaries in

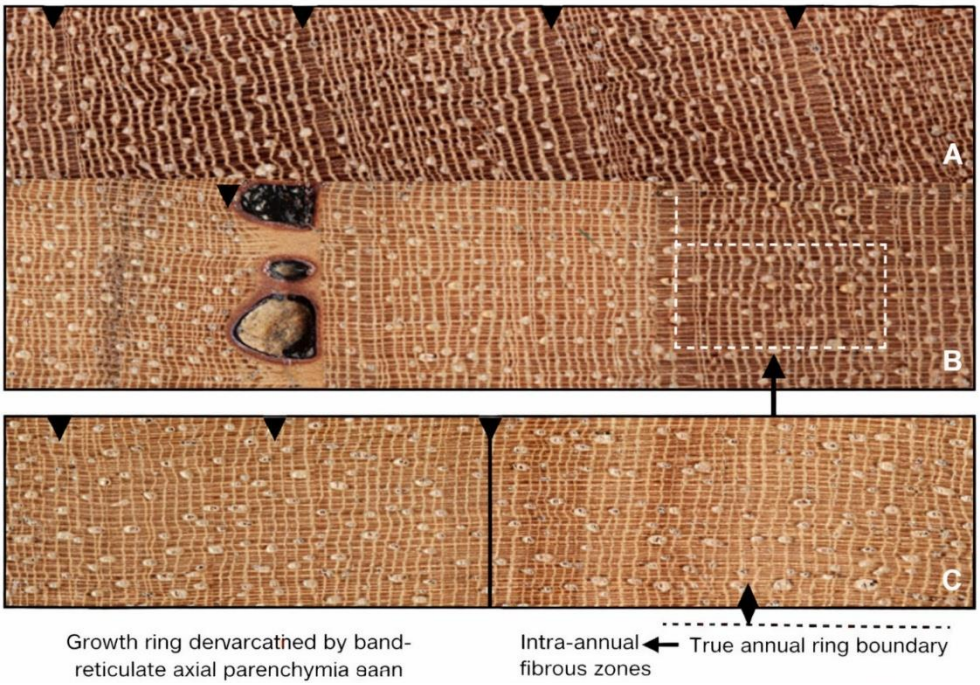
Bertholletia excelsa. Anatomical anomalies such as traumatic canals and intra-annual fibrous zones were identified but excluded as annual markers.

The identification of annual rings followed the recommendations of the IAWA Committee (Wheeler et al., 1989), and only boundaries validated by both anatomical criteria and statistical cross-dating were accepted.

Annual growth-ring boundaries were defined based on the recurrent presence of banded reticulate axial parenchyma, which constitutes the primary anatomical marker for ring delimitation in this species (Figure 2).

Figure 2

Transverse section of Bertholletia excelsa wood illustrating the anatomical criteria used for growth-ring identification. (A) True annual growth-ring boundary defined by changes in the organization of banded reticulate axial parenchyma. (B) Traumatic canal associated with localized cambial disturbance (arrow). (C) Intra-annual fibrous zones (asterisks) representing short-term growth interruptions within a single growing season; the true annual ring boundary is indicated by the arrowhead



Source: Authors, 2026.

2.4 STATISTICAL ANALYSES AND CORRELATION WITH CLIMATIC VARIABLES

Ring-width series were cross-dated using the COFECHA program to verify temporal accuracy and internal consistency among samples (Holmes, 1983; Fritts, 2001). Pearson correlation coefficients were calculated in 20-year moving windows, and series showing low

correlation with the master chronology were excluded based on a significance threshold (α > 0.3281; p = 0.01).

A master chronology was developed by detrending individual series using a negative exponential function to remove age-related growth trends while preserving interannual variability. Analyses were conducted in R (version 3.6.2) using the dplR package (Bunn, 2010).

2.5 STATISTICAL EVALUATION AND CHRONOLOGY QUALITY

Chronology quality was assessed using standard dendrochronological metrics, including effective mean interseries correlation (rbar.eff), first-order autocorrelation (AC), Expressed Population Signal (EPS), and Signal-to-Noise Ratio (SNR) (Wigley et al., 1984; Cook and Kairiukstis, 1990).

The EPS was used to evaluate the representativeness of the chronology, with values above 0.85 indicating a robust population signal. The SNR quantified the strength of the common signal relative to individual variability.

To account for non-independence among multiple radii sampled from the same tree, rbar.eff was calculated as a corrected measure of interseries correlation using the dplR package.

2.6 CLIMATE–GROWTH RELATIONSHIPS

Climate–growth relationships were analyzed using the treeclim package in R (Zang and Biondi, 2015). Monthly precipitation (mm) and mean air temperature (°C) from the Belterra meteorological station were used for the period 1973–2017.

The influence of large-scale climate variability was assessed using the Niño 3.4 index (ENSO) and the Tropical South Atlantic (TSA) sea surface temperature index (ERSSTv5, NOAA). Correlation analyses were performed using the Dynamic Correlation and Response (DCC) method with a 17-month window, spanning from June of the previous year to October of the current growth year.

Hydrological memory effects were evaluated through lagged correlations (Lag 1 and Lag 2) between climate variables and radial growth.

3 RESULTS

3.1 CHRONOLOGY DEVELOPMENT AND QUALITY ASSESSMENT

The standardized individual ring-width series of *Bertholletia excelsa* were combined to construct a single master chronology representing the population-level growth signal. Only

well cross-dated series, verified through COFECHA, were included in the final chronology, ensuring temporal accuracy and internal coherence among samples (Table 1).

Table 1

Quality statistics of the Bertholletia excelsa master chronology

Parameter	Value	Interpretation
Number of trees	7	Individuals effectively incorporated into the master chronology
Number of series	17	Ring-width series successfully validated through cross-dating
Common period	1943–2017	Time interval shared by all contributing series
Chronology length (years)	74	Temporal extent of the master chronology
rbar.eff	0.33	Effective mean interseries correlation, corrected for non-independence
EPS	0.86	Adequate representation of the population signal (≥ 0.85)
SNR	6.1	Dominance of the common signal over individual noise
First-order autocorrelation (AC)	0.34	Moderate physiological persistence between consecutive years

Caption: *rbar.eff* = effective mean interseries correlation corrected for multiple radii sampled per tree; *EPS* = Expressed Population Signal; *SNR* = Signal-to-Noise Ratio; *AC* = first-order autocorrelation. Source: Authors, 2026.

All parameters were calculated for the **master chronology**, following standard dendrochronological procedures (Wigley, Briffa & Jones, 1984; Cook & Kairiukstis, 1990).

Chronology quality was assessed using standard dendrochronological statistics calculated over the common overlap period of all contributing series. The effective mean interseries correlation (rbar.eff) indicated moderate to strong coherence among individual series, demonstrating the presence of a robust common signal. The Expressed Population Signal (EPS) consistently exceeded the commonly accepted threshold of 0.85, confirming that the master chronology reliably represents the theoretical population signal despite the limited number of sampled trees.

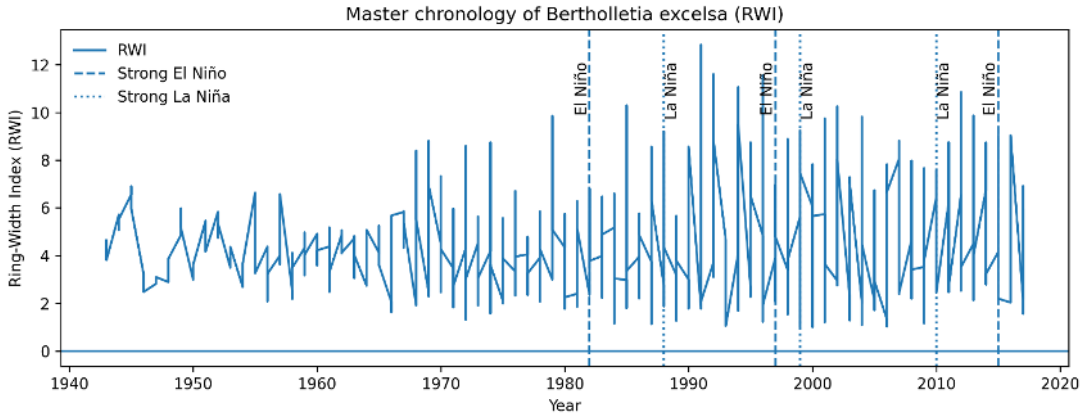
The Signal-to-Noise Ratio (SNR) further supported the strength of the common growth signal relative to individual variability, while first-order autocorrelation (AC) values reflected physiological persistence between consecutive growth years, consistent with carry-over effects commonly observed in tropical tree species. Together, these metrics indicate that the developed master chronology is statistically robust and suitable for subsequent dendroclimatic analyses.

The temporal evolution of the **master chronology** is shown in Figure 3, which illustrates the standardized ring-width index (RWI) and highlights the coherence of growth variability across the study period. This visual representation confirms the internal

consistency of the chronology and provides the basis for interpreting growth responses to local and large-scale climatic drivers presented in the following sections.

Figure 3

Master chronology of Bertholletia excelsa expressed as standardized ring-width index (RWI). Dashed vertical lines indicate the initial year of strong El Niño events (1982, 1997, and 2015), whereas dotted vertical lines represent the initial year of strong La Niña events (1988, 1999, and 2010). The figure illustrates the temporal evolution of growth variability and highlights the influence of major ENSO phases on radial growth dynamics



Source: Authors, 2026.

3.2 CROSS-DATING PERFORMANCE AND SELECTION OF INDIVIDUAL SERIES

Interseries correlations and sensitivity values used for series selection are summarized in Table 2.

After confirming the robustness of the master chronology (Section 3.1) and the anatomical validity of annual growth-ring boundaries (Section 3.2), cross-dating performance was evaluated to determine which individual series could be reliably retained for chronology construction and subsequent climatic analyses.

Table 2

Set of chronological series selected using intercorrelations evaluated in the COFECHA software

Identification	Chronological extent	Intercorrelation	Sensitivity	Individual diameter(cm)
A2305R1	1973-2017	0.621	0.429	77.0
A2305R2	1973-2017	0.372	0.312	77.0
A2305R3	1973-2017	0.430	0.376	77.0
A1701R3	1983-2017	0.065	0.544	87.3
A1706R2	1955-2017	0.211	0.406	78.7

A1706R3	1955-2017	0.161	0.425	78.7
A2221R1	1968-2017	0.256	0.678	72.6
A2221R2	1968-2017	0.435	0.647	72.6
A2221R3	1968-2017	0.226	0.587	72.6
A2304R1	1965-2017	0.216	0.445	32.4
A2304R2	1965-2017	0.332	0.485	32.4
A2309R1	1943-2017	0.225	0.309	49.2
A2309R2	1943-2017	0.360	0.320	49.2
A2309R3	1943-2017	0.380	0.324	49.2
A1704R1	1970-2017	0.406	0.497	170.0
A1704R2	1970-2017	0.451	0.492	170.0
A1704R3	1970-2017	0.529	0.452	170.0
Total / Mean	74 years	0.330	0.442	81.03
COFECHA critical correlation		0.3281		

Source: Authors, 2026.

From the initial set of sampled individuals, only series that met strict cross-dating criteria were retained. Series selection was based on visual cross-dating, statistical verification using COFECHA, and consistency with the anatomical markers of annual ring formation. Series exhibiting low interseries correlation, ambiguous ring boundaries, or evidence of disturbance that compromised temporal alignment were excluded from further analyses.

As a result, seven individuals contributing a total of 17 well-dated ring-width series were selected for the final master chronology. These series showed strong temporal alignment and coherence with the common growth signal, reinforcing the reliability of the chronology despite the limited sample size. The retained series span a common overlap period sufficient to capture interannual variability and major hydroclimatic anomalies affecting the study area.

This quality-controlled subset of individual series constitutes the empirical basis for the master chronology and ensures that subsequent analyses of growth–climate relationships are grounded in accurately dated and biologically meaningful data. The validated selection of series thus provides a robust foundation for examining the influence of local and large-scale climatic drivers on radial growth, as presented in the following sections.

3.3 GROWTH RESPONSES TO LOCAL CLIMATIC VARIABILITY

To avoid ambiguity in the interpretation of climate–growth relationships, it is important to define the growing season of Bertholletia excelsa in eastern Amazonia. In the study region, cambial dormancy typically occurs during the dry season (July–November), when partial leaf exchange takes place, whereas active xylem formation (xylogenesis) occurs predominantly during the subsequent rainy season, from December to June. Therefore, climatic conditions in December represent the onset of the current growing season rather than the previous one.

Based on the robust master chronology established in Section 3.1 and the quality-controlled selection of individual series described in Section 3.3, the relationship between radial growth of *Bertholletia excelsa* and local climatic variability was examined. Analyses focused on monthly precipitation and air temperature, which represent the primary climatic controls on cambial activity in tropical forests. Correlation coefficients between the standardized ring-width index and local climatic variables are shown in Figure 4.

Radial growth exhibited a strong dependence on precipitation seasonality, with positive correlations observed during months of increased rainfall within the current growth year. Periods of reduced precipitation were consistently associated with growth suppression, indicating that water availability constitutes the dominant limiting factor for secondary growth at the study site. Accordingly, the significant positive correlation with precipitation in December reflects the role of rainfall in triggering cambial reactivation and earlywood formation at the beginning of the current growth year, rather than carry-over effects from the previous growing season..

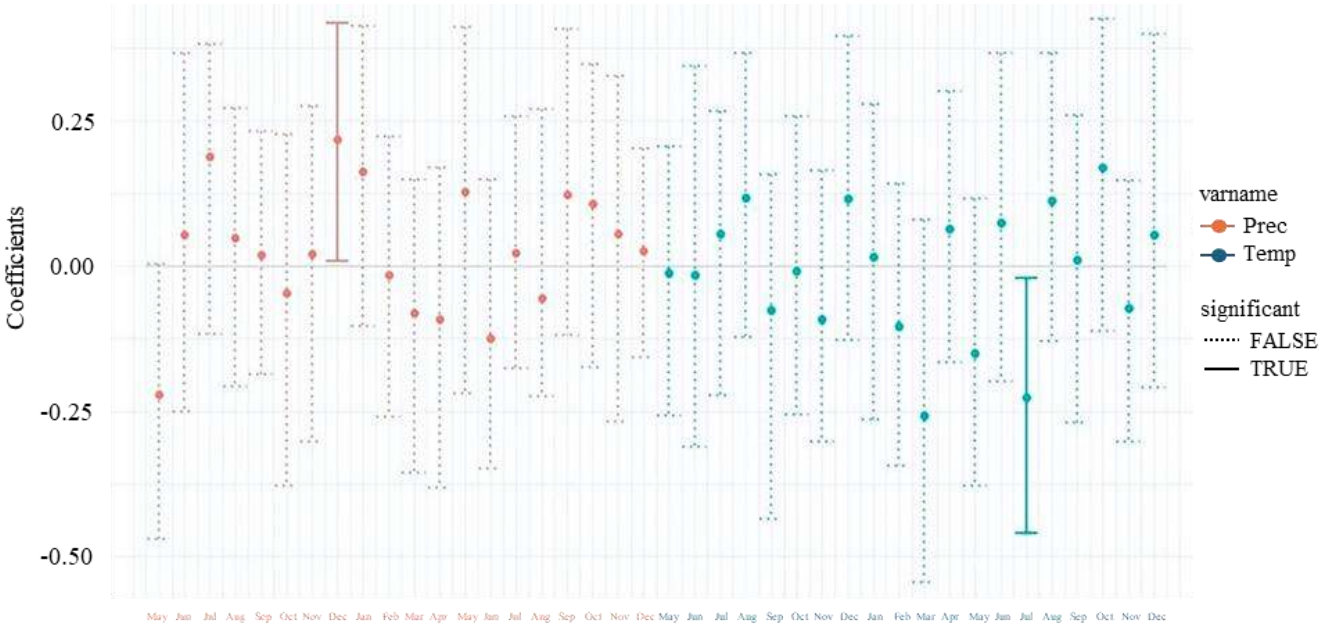
In contrast, air temperature showed predominantly negative correlations with radial growth, particularly during months characterized by elevated maximum temperatures. Higher temperatures likely intensified atmospheric demand and soil water deficits, thereby exacerbating hydraulic stress and constraining cambial activity. These responses suggest that temperature acts primarily as a stressor rather than a growth-enhancing factor under the climatic conditions of the eastern Amazon.

Notably, significant correlations extended beyond the immediate growing season, highlighting the importance of antecedent climatic conditions. Precipitation deficits and elevated temperatures during the late dry season and early wet season of the previous year influenced growth in the subsequent growth cycle, indicating a clear hydrological memory effect.

Together, these results demonstrate that radial growth of *B. excelsa* integrates climatic information across the full hydrological cycle rather than responding instantaneously to short-term conditions. This climate–growth relationship at the local scale provides the mechanistic basis for interpreting the influence of large-scale climate modes, such as ENSO and Tropical Atlantic variability, addressed in the following sections.

Figure 4

Correlation coefficients between the standardized ring-width index (RWI) of Bertholletia excelsa and local climatic variables (precipitation and air temperature) for the period 1973–2017.



Source: Authors, 2026.
Legend: Current months are written in uppercase and previous months are written with only the first letter capitalized. Coefficients: coeficientes; varname: variáveis; prec.: precipitação; temp.: temperatura; significant: significância; FALSE: not significant e TRUE: significant. Monthly correlations were calculated using the master chronology. Uppercase letters indicate months of the current growth year, whereas capitalized lowercase letters indicate months of the previous year. Positive correlation coefficients indicate enhanced radial growth associated with higher precipitation or lower temperature, whereas negative coefficients indicate growth reduction under drier or warmer conditions. Statistically significant correlations ($p < 0.05$) are highlighted.

3.4 INFLUENCE OF THE EL NIÑO–SOUTHERN OSCILLATION (ENSO) ON RADIAL GROWTH

Building on the local climate–growth relationships described in Section 3.4, the influence of large-scale climate variability associated with the El Niño–Southern Oscillation (ENSO) on radial growth of *Bertholletia excelsa* was evaluated. This analysis aimed to assess whether interannual anomalies in Pacific sea surface temperatures modulate growth beyond the effects of local precipitation and temperature.

The negative correlation with the Niño 3.4 index observed in September occurs during the late dry season, prior to the onset of cambial activity. This signal therefore represents a preconditioning effect, whereby ENSO-driven drought intensifies water stress, depletes soil moisture and carbon reserves, and compromises the physiological status of trees before growth resumes in the subsequent rainy season.

Correlation analyses between the master chronology and the Niño 3.4 index revealed a predominantly negative relationship between radial growth and warm ENSO phases. El

Niño events were associated with significant growth reductions, reflecting their role in intensifying dry-season length and severity in the eastern Amazon. These results indicate that ENSO acts as an important indirect driver of growth variability through its influence on regional hydroclimatic conditions.

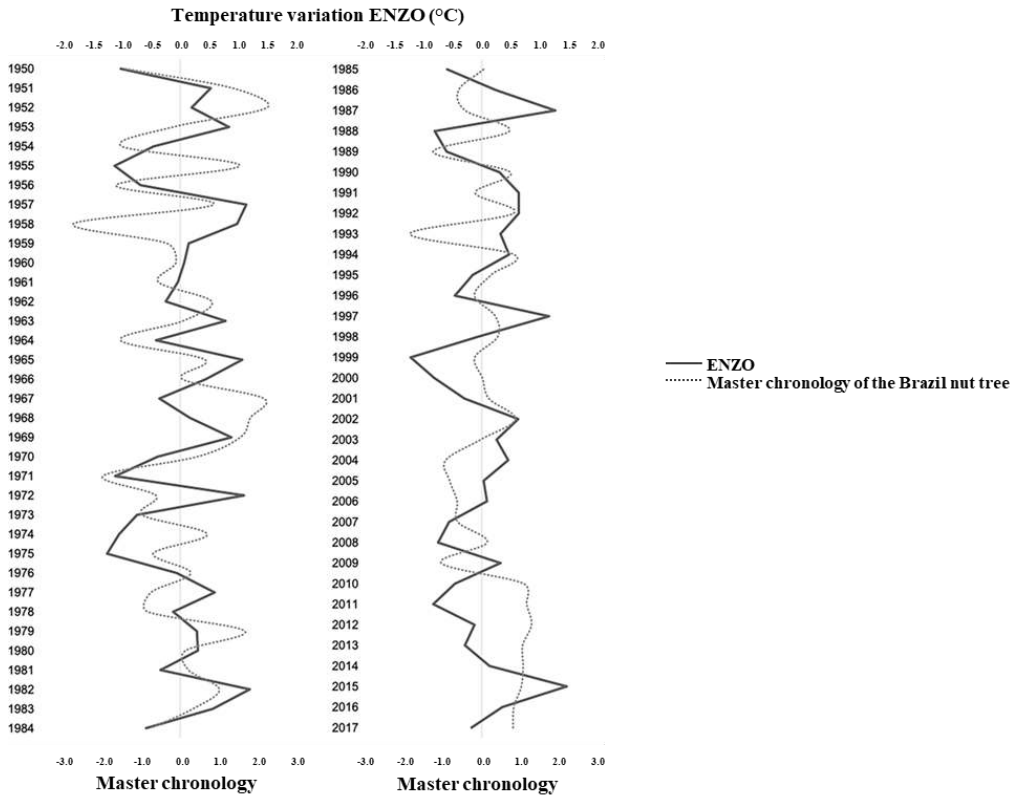
The ENSO signal exhibited temporal lags extending into the year following the event, consistent with delayed growth recovery observed after major droughts. Such lagged responses reinforce the presence of hydrological memory in *B. excelsa*, whereby reduced soil moisture availability and physiological stress during El Niño years affect cambial activity beyond the immediate event year.

Overall, the sensitivity of radial growth to ENSO highlights the vulnerability of *B. excelsa* to large-scale climatic anomalies that disrupt regional precipitation regimes. These findings complement the local climate analyses and demonstrate that growth variability in this species reflects the combined influence of local hydroclimatic conditions and remote climate forcing. The role of Atlantic climate variability is further examined in the following section.

The association between ENSO variability and radial growth is illustrated in Figure 5.

Figure 5

Variation of the Tropical Pacific Ocean surface temperature and the master chronology of Bertholletia excelsa Bonpl. individuals from 1950 to 2017



Source: Authors, 2026.

3.5 INFLUENCE OF TROPICAL SOUTH ATLANTIC VARIABILITY ON RADIAL GROWTH

Following the assessment of ENSO-related influences on radial growth (Section 3.5), the potential role of Tropical South Atlantic (TSA) sea surface temperature variability was examined to evaluate additional large-scale climatic controls on the growth of *Bertholletia excelsa*. Variability in the TSA is known to modulate atmospheric circulation and moisture transport toward eastern Amazonia, thereby influencing regional precipitation patterns.

Correlation analyses between the master chronology and the TSA sea surface temperature index revealed that warmer conditions in the Tropical South Atlantic were generally associated with reduced radial growth. Positive TSA anomalies are typically linked to weakened moisture transport from the Atlantic into the continent, resulting in suppressed rainfall over eastern Amazonia and enhanced dry-season intensity. These conditions likely exacerbate soil moisture deficits and increase hydraulic stress, leading to growth reductions in *B. excelsa*.

Similar to the ENSO signal, TSA-related growth responses were not restricted to the year of the climatic anomaly. Significant correlations extended into subsequent growth seasons, indicating delayed physiological recovery and reinforcing the presence of a hydrological memory effect. This lagged response suggests that Atlantic-driven drought conditions can have prolonged impacts on cambial activity beyond the immediate period of climatic forcing.

Taken together, the combined influence of Pacific (ENSO) and Atlantic (TSA) climate variability highlights the sensitivity of *B. excelsa* to large-scale ocean–atmosphere interactions that regulate hydroclimatic conditions in eastern Amazonia. These results demonstrate that radial growth in this species integrates both local climatic variability and remote climate forcing, providing a comprehensive framework for interpreting growth responses under current and future climate change scenarios.

Although the present analysis focuses on time-lagged correlations between the master chronology and SST indices, it is important to acknowledge that climate–growth relationships in Amazonian forests reflect the combined and seasonally structured influence of multiple ocean basins. The period analyzed (1950–2017) encompasses major ENSO and Atlantic variability events, allowing the assessment of their integrated influence on radial growth at the interannual scale.

4 DISCUSSION

The results of this study provide robust dendrochronological evidence supporting the sensitivity of the Brazil nut tree (*Bertholletia excelsa*) to hydroclimatic variability in the

Amazon. Rather than supporting long-term paleoclimate reconstructions, the developed chronology demonstrates strong potential for assessing recent climate variability and the impacts of ongoing climate change, particularly in relation to water availability and large-scale ocean–atmosphere interactions.

Despite the relatively small number of sampled trees (seven individuals), the validation of *B. excelsa* as a climate-sensitive species is supported by the statistical robustness of the master chronology. Chronology quality metrics derived at the population level, including effective mean interseries correlation (rbar.eff) and an Expressed Population Signal (EPS) exceeding the commonly accepted threshold of 0.85, indicate substantial coherence among individual series and confirm that the master chronology reliably captures the common climatic signal. In tropical dendrochronology, particularly for long-lived emergent species with high wood density, such sample sizes are common and considered adequate when chronology quality metrics demonstrate sufficient signal strength and representativeness. Nevertheless, this limitation should be considered when extrapolating the results beyond the studied population, highlighting the importance of future studies incorporating additional sites and individuals to strengthen regional-scale inferences.

4.1 ECOLOGICAL BACKGROUND OF *BERTHOLLETIA EXCELSA* AND IMPLICATIONS FOR CLIMATE SENSITIVITY

Bertholletia excelsa Bonpl. is a long-lived emergent tree species widely distributed across the Amazon Basin, occurring predominantly in terra firme forests on well-drained soils. Its biogeographic distribution spans eastern, central, and southwestern Amazonia, with population densities often shaped by historical and contemporary human influence, including indigenous management, selective protection, and long-term nut harvesting practices (Zuidema & Boot, 2002; Brienen & Zuidema, 2005). As a keystone socioecological species, *B. excelsa* plays a central role in the livelihoods of extractive communities and is legally protected from logging in several Amazonian countries, reinforcing its ecological and socioeconomic importance (Zuidema & Boot, 2002).

The species exhibits a marked seasonal phenology closely linked to the regional hydroclimatic regime. Partial or complete leaf exchange typically occurs during the dry season, followed by flowering toward the end of the dry period and fruit development during the subsequent rainy season (Brienen & Zuidema, 2005; Schöngart et al., 2015). Fruit maturation and seed dispersal may extend over more than one year, reflecting substantial carbon investment and reliance on stored reserves (Zuidema & Boot, 2002). This phenological pattern highlights the strong coupling between water availability, carbon

allocation, and reproductive effort, particularly during the transition from the dry to the rainy season.

Wood of *B. excelsa* is characterized by high basic density, commonly exceeding 0.70 g cm^{-3}, which confers mechanical stability but is generally associated with slow diameter growth rates (Latorraca et al., 2018; Perdigão et al., 2020). Reported mean radial growth rates are low compared to other Amazonian canopy species, typically ranging from 1 to 3 mm yr^{-1}, and show strong interannual variability driven by hydroclimatic conditions (Brienen & Zuidema, 2005; Schöngart et al., 2015). Tree-ring analyses combined with radiocarbon dating indicate that *B. excelsa* can attain ages well exceeding 300–500 years, underscoring its conservative life-history strategy and its capacity to integrate long-term environmental signals (Brienen & Zuidema, 2005; Caetano-Andrade et al., 2024).

These ecological traits—high wood density, slow growth, long lifespan, and strong phenological synchronization with seasonal rainfall—provide a mechanistic basis for the pronounced sensitivity and hydrological memory observed in the growth-ring chronologies. They also help explain the delayed recovery following drought events and the species' vulnerability to increasing dry-season intensity and warming (Schöngart et al., 2015; Caetano-Andrade et al., 2024). Incorporating this ecological context is therefore essential for interpreting the climate–growth relationships documented in this study and for assessing the resilience of *Bertholletia excelsa* under ongoing and future climate change scenarios.

4.2 DENDROCHRONOLOGICAL VALIDATION AND CHRONOLOGY QUALITY

The formation of annual and datable growth rings in *B. excelsa* was confirmed through the integration of macroscopic anatomical analysis and statistical cross-dating. Growth-ring boundaries were consistently defined by the presence of banded reticulate axial parenchyma (Figure 2A), a diagnostic feature that enabled reliable ring identification. Although high anatomical plasticity is often cited as a limitation for dendrochronological studies in tropical species (García-Cervigón et al., 2021; Rodríguez-Ramírez et al., 2020), the consistency of this parenchymal pattern in *B. excelsa* effectively overcame this challenge and aligns with previous anatomical descriptions for the species (Latorraca et al., 2018; Perdigão et al., 2020).

Chronology quality assessment, conducted for the master chronology over the common overlap period, demonstrated strong internal coherence. High EPS values (> 0.86) and Signal-to-Noise Ratio (SNR > 6.0) (Table 2) confirm that population-level growth variability is predominantly driven by a common environmental signal, consistent with established dendrochronological standards (Wigley, Briffa & Jones, 1984).

The effective mean interseries correlation (rbar.eff) further supports the reliability of the chronology by accounting for potential correlation inflation arising from multiple radii sampled from the same individual. This corrected measure of interannual synchrony indicates coherence levels comparable to or exceeding those reported for other climate-sensitive Amazonian species, such as *Hymenaea courbaril*, *Cedrela odorata* (Sousa, 2019), and *Cedrela nebulosa* (Layme-Huaman et al., 2018), reinforcing the climatic sensitivity of *B. excelsa*.

Moderate first-order autocorrelation (AC) values observed in the master chronology are consistent with physiological persistence commonly reported for emergent canopy species. This persistence likely reflects carry-over effects associated with the mobilization and storage of non-structural carbon reserves that sustain growth during periods of water limitation (Fritts, 2001).

4.3 GROWTH CONTROL BY LOCAL WATER SEASONALITY

Growth–climate relationships with local meteorological variables demonstrate that water availability constitutes the primary limiting factor for radial growth of *B. excelsa*, whereas temperature plays a secondary, predominantly stress-related role. Positive correlations with precipitation, particularly during the onset of the rainy season, indicate that water inputs in the late dry season and early wet season are critical for growth initiation and resource allocation.

The significant positive association with precipitation in December of the previous year suggests that the onset of the rainy season represents a key trigger for cambial reactivation. This timing coincides with canopy reconstitution and the initiation of the new growth cycle, highlighting the importance of antecedent water availability for subsequent radial increment.

In contrast, negative correlations with air temperature during the peak of the dry season, particularly in July, reflect growth suppression under conditions of elevated evaporative demand and reduced soil moisture availability. This response is consistent with the species' water conservation strategy, which includes partial leaf senescence during the dry season (Guerreiro et al., 2018), and reinforces the dominant role of precipitation and dry-season duration in controlling growth of emergent canopy species in the Amazon (Fichtler, Clark & Worbes, 2003; Schöngart et al., 2017).

The influence of climatic conditions extending into the year preceding ring formation provides clear evidence of a hydrological memory effect in *B. excelsa*, whereby growth integrates water availability over successive seasons. This memory effect becomes even

more pronounced when growth responses are examined in relation to large-scale climatic drivers, as discussed in the following sections.

4.4 SENSITIVITY AND HYDROLOGICAL MEMORY IN RESPONSE TO OCEANIC TELECONNECTIONS

Recent studies have demonstrated that drought severity in the Amazon is often modulated by the combined influence of Pacific and Atlantic SST anomalies, particularly when El Niño events co-occur with anomalous warming in the tropical North Atlantic. While the present study focuses on ENSO and the Tropical South Atlantic as primary drivers, the influence of the tropical North Atlantic likely contributes to the magnitude and persistence of drought-related growth suppression observed in Bertholletia excelsa. Future studies integrating spatiotemporal SST patterns across all major ocean basins using seasonal composites may further refine the mechanistic understanding of these teleconnections. In this context, the growth responses observed in the master chronology provide empirical evidence of how these combined oceanic forcings are recorded at the tree level.

The master chronology of Bertholletia excelsa revealed a clear sensitivity to large-scale ocean–atmosphere interactions, demonstrating that radial growth integrates not only local climatic variability but also remote forcing associated with Pacific and Atlantic climate modes. These teleconnections modulate regional hydroclimatic conditions in eastern Amazonia and exert a strong influence on tree growth through their control over precipitation patterns and dry-season intensity.

An integrative interpretation of the observed climate–growth relationships suggests that oceanic forcing influences the radial growth of Bertholletia excelsa primarily through its modulation of local hydroclimatic conditions, particularly during the critical transition from the dry to the rainy season. SST anomalies associated with ENSO and Atlantic variability regulate atmospheric circulation patterns, affecting rainfall onset, dry-season length, and soil moisture recharge. These processes directly control cambial reactivation and earlywood formation at the beginning of the growing season, which appears to represent the most sensitive phase of growth in this species.

Although the present study focuses on precipitation and temperature as primary climatic drivers, integrated indicators of water stress such as soil moisture deficits (e.g., Palmer Drought Severity Index) and atmospheric demand (e.g., Vapor Pressure Deficit) likely play a key mechanistic role in linking oceanic forcing to tree physiological responses. Future studies explicitly incorporating these indices may further disentangle direct and indirect pathways through which large-scale climate variability propagates from the oceans to tree

growth, as conceptually illustrated in path-based frameworks applied in previous dendroclimatic research (e.g., Brienen et al., 2010).

4.4.1 Influence of the El Niño–Southern Oscillation (ENSO)

The association between El Niño events and reductions in annual radial growth indicates that ENSO acts as a major driver of interannual growth variability in B. excelsa. Strong and moderate El Niño episodes were consistently linked to growth suppression (Figure 4), reflecting their role in intensifying dry-season severity and prolonging water deficits in the Amazon. This pattern is consistent with observations from the 2015–2016 El Niño, which caused widespread growth reductions and physiological stress in Amazonian tree species, including B. excelsa (Fortes et al., 2023).

The significant negative correlation between the Niño 3.4 index and the ring-width index (RWI) during September of the previous year highlights the importance of antecedent climatic conditions. Warming of the central Pacific intensifies atmospheric subsidence over the Amazon, exacerbating dry-season water deficits and compromising the physiological status of trees prior to the onset of cambial activity in the subsequent growth year (Jiménez-Muñoz et al., 2016; Marengo & Espinoza, 2016).

More importantly, the persistence of negative growth responses at Lag 1 and Lag 2 provides strong evidence of a hydrological memory effect in B. excelsa. These lagged correlations indicate that growth recovery following severe droughts is not immediate, with impacts extending for up to two years or more. Such delayed responses are likely mediated by slow soil moisture recharge and depletion of non-structural carbon reserves, which constrain cambial reactivation even after climatic conditions improve (Phillips et al., 2010; Zanin & Satyamurty, 2020). This prolonged vulnerability suggests that recurrent ENSO-driven droughts may have cumulative effects on population growth under future climate change scenarios.

4.4.2 Influence of Tropical South Atlantic variability

In addition to Pacific forcing, variability in the Tropical South Atlantic (TSA) exerted a significant influence on radial growth of B. excelsa. Positive correlations between the TSA sea surface temperature index and growth during July to September of the previous year indicate that warmer Atlantic conditions can enhance regional moisture availability during critical pre-growth periods.

A warmer TSA is often associated with a strengthening and southward displacement of the South Atlantic Convergence Zone (SACZ), promoting increased moisture transport and

precipitation over eastern Amazonia (Jiménez-Muñoz et al., 2018; Marengo et al., 2018). Under such conditions, improved soil moisture availability during the late dry season likely facilitates physiological recovery and supports growth initiation in the subsequent year.

The contrasting responses to Pacific and Atlantic forcing—negative growth anomalies associated with ENSO and positive responses linked to TSA warming—demonstrate that B. excelsa functions as an effective integrator of multiple oceanic climate drivers. This dual sensitivity underscores the complexity of climate–growth relationships in Amazonian forests and highlights the importance of considering both Pacific and Atlantic influences when assessing forest resilience under scenarios of heterogeneous ocean warming (Caetano-Andrade et al., 2021).

4.5 ECOLOGICAL AND MANAGEMENT IMPLICATIONS UNDER CONTEMPORARY CLIMATE CHANGE

The consistency of the dendroclimatic signal and the pronounced sensitivity of B. excelsa to water availability confirm its role as a valuable bioindicator of hydroclimatic variability in the Amazon. Rather than supporting long-term paleoclimate reconstructions sensu stricto, the species provides important insights into recent climate variability and the ecological impacts of ongoing climate change.

The observed vulnerability and delayed growth recovery following El Niño events, evidenced by growth lags of up to two years, have direct implications for forest management. Adaptive management strategies should therefore consider adjustments to cutting cycles and the re-evaluation of the Minimum Cutting Diameter (MCD) following extreme drought events, allowing sufficient time for physiological recovery and reducing the risk of population-level decline. This recommendation is particularly relevant for species with conservative physiological strategies, such as B. excelsa, which tend to exhibit prolonged growth suppression under increasing temperatures and recurrent climatic extremes (Brienen et al., 2015; Sullivan et al., 2020).

Although the temporal extent of the chronology developed in this study is limited to a maximum of 74 years, it encompasses a period characterized by intensified warming, increased drought frequency, and major ENSO events. This temporal window enables the assessment of tree growth responses to contemporary climatic anomalies and extreme events. In this context, B. excelsa complements longer tree-ring records from other tropical species by providing species-specific insights into forest vulnerability and resilience during the current phase of anthropogenic climate change.

5 CONCLUSIONS

This study demonstrates that *Bertholletia excelsa* exhibits a clear and consistent response to hydroclimatic variability during the instrumental period, confirming its sensitivity to water availability, elevated temperatures, and large-scale climate anomalies such as El Niño events. Although the temporal extent of the chronology is limited, the species provides robust insights into recent climate–growth relationships and the impacts of ongoing climate change on Amazonian forests.

The main conclusions are as follows:

- Radial growth of *B. excelsa* is primarily regulated by precipitation seasonality, with growth suppression occurring during drought conditions and strong El Niño events.
- Growth responses show temporal lags of up to two years, indicating pronounced hydrological memory and delayed physiological recovery after climatic stress.
- Chronology quality metrics derived at the population level (rbar.eff and EPS) confirm that the master chronology reliably captures the common climatic signal despite the limited number of sampled individuals.
- The combined sensitivity to drought and warming highlights the vulnerability of *B. excelsa* under future climate change scenarios characterized by more frequent and intense extremes.
- These findings underscore the need for adaptive forest management strategies, including adjustments to cutting cycles and the Minimum Cutting Diameter (MCD), particularly following extreme climatic events.

These results indicate that oceanic climate modes influence the growth of Bertholletia excelsa primarily by modulating local hydroclimatic conditions, particularly during the critical transition from the dry to the rainy season, which emerges as the most sensitive phase for annual ring formation.

6 MANAGEMENT RECOMMENDATIONS AND ECOLOGICAL IMPLICATIONS

The dendrochronological evidence of water sensitivity, hydrological memory, and responsiveness to oceanic teleconnections in *Bertholletia excelsa* provides an applied framework for forest management and conservation under ongoing climate change. These implications are grounded in the species' documented responses to recent hydroclimatic variability and extreme events within the instrumental period.

6.1 IMPLICATIONS FOR FOREST MANAGEMENT AND CONSERVATION

The persistence of growth suppression for up to two years following strong El Niño events highlights the need for adaptive and climate-aware forest management. Management strategies that do not account for delayed physiological recovery may increase the risk of population-level decline in long-lived canopy species such as *B. excelsa*. In this context, temporary adjustments to cutting cycles and the re-evaluation of the Minimum Cutting Diameter (MCD) following extreme drought events may help reduce cumulative stress and allow sufficient recovery of growth and carbon reserves.

In addition, the sensitivity of *B. excelsa* growth to antecedent ENSO conditions suggests that dendrochronological information can complement climate-based early warning approaches. Growth responses linked to Niño 3.4 anomalies during the late dry season of the previous year provide a temporal window in which forest managers may anticipate periods of elevated stress and implement low-impact mitigation measures, such as reducing additional competitive pressures in managed stands.

Growth-ring records also offer opportunities for conservation-oriented selection of reproductive material. Individuals exhibiting rapid recovery or reduced sensitivity to historical drought events may represent valuable genetic resources for restoration and enrichment initiatives aimed at increasing forest resilience to water stress.

6.2 ECOLOGICAL IMPLICATIONS UNDER CONTEMPORARY CLIMATE CHANGE

The documented sensitivity of *B. excelsa* to drought conditions intensified by El Niño events, combined with projections of increased frequency and intensity of climatic extremes, places the species at heightened ecological risk. Recurrent growth suppression may alter competitive dynamics within the forest canopy, potentially favoring more drought-tolerant species and leading to gradual changes in forest structure and function (Sullivan et al., 2020).

As a keystone species with strong ecological and socioeconomic relevance, declines in *B. excelsa* growth and productivity may have cascading effects on associated fauna and on the livelihoods of extractive communities that depend on Brazil nut production (Brienen et al., 2015). These interactions underscore the broader implications of climate-driven growth limitations beyond individual tree performance.

Finally, the clarity of the climatic signal captured by the master chronology (high EPS and SNR values) and the sensitivity to both Pacific and Atlantic climate variability support the role of *B. excelsa* as a sentinel species for monitoring forest responses to contemporary climate change. Expanded dendrochronological networks across the species' distribution

range could provide cost-effective, high-resolution insights into forest vulnerability and resilience, complementing longer-term records from other tropical species.

Declaration of generative AI and AI-assisted technologies in the manuscript preparation process. During the preparation of this work the author(s) used [Gemini, ChapGPT and Deep Seek in order to find articles, check English (language and grammar and to write some technical concepts. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the published article.

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REFERENCES

Albiero-Júnior, A., Venegas-González, A., Camargo, J. L. C., Roig, F. A., & Tomazello-Filho, M. (2021). Amazon forest fragmentation and edge effects temporarily favored understory and midstory tree growth. Trees, 35(6), 2059–2068. https://doi.org/10.1007/s00468-021-02172-1

Amaral, M. R. M., Lima, A. J. N., Higuchi, F. G., Dos Santos, J., & Higuchi, N. (2019). Dynamics of tropical forest twenty-five years after experimental logging in central Amazon mature forest. Forests, 10(2), 89. https://doi.org/10.3390/f10020089

Amarilla, L. D., Tello, N. R., Cavalcante, M. C., Maués, M. M., & Galetto, L. (2024). Floral structure and nectary anatomy of Bertholletia excelsa (Lecythidaceae). Botany Letters, 1–9. https://doi.org/10.1080/23818107.2024.2391299

Americas Regional Workshop (Conservation & Sustainable Management of Trees, Costa Rica, November 1996). (1998). Bertholletia excelsa. The IUCN Red List of Threatened Species. https://doi.org/10.2305/IUCN.UK.1998.RLTS.T32986A9741363.en

Andrade, V. H. F., Machado, S. A., Figueiredo Filho, A., Botosso, P. C., Miranda, B. P., & Schöngart, J. (2019). Growth models for two commercial tree species in upland forests of the southern Brazilian Amazon. Forest Ecology and Management, 438, 215–223. https://doi.org/10.1016/j.foreco.2019.02.030

Baas, P., Wheeler, E., & Fahn, A. (1983). Some ecological trends in vessel characters. IAWA Journal, 4(2–3), 141–159. https://doi.org/10.1163/22941932-90000407

Babst, F., Bouriaud, O., Papale, D., Gielen, B., Janssens, I. A., Abernhofer, C., Nikinmaa, E., Ibrom, A., Wu, J., Köstner, B., Grünewald, T., Seufert, G., Ciais, P., Frank, D., & Mašek, J. (2014). Above-ground woody carbon sequestration measured from tree rings is coherent with net ecosystem productivity at five eddy-covariance sites. New Phytologist, 203(4), 1269–1283. https://doi.org/10.1111/nph.12589

Baker, J. C., Cintra, B. B. L., Gloor, M., Boom, A., Neill, D., Clerici, S., Leng, M. J., Helle, G., & Brienen, R. J. W. (2022). The changing Amazon hydrological cycle—inferences from over 200 years of tree-ring oxygen isotope data. Journal of Geophysical Research: Biogeosciences, 127(10). https://doi.org/10.1029/2022JG006955

Batista, A., Scolforo, P. G. V., Scolforo, H. F., De Mello, J. M., Guedes, M., & Soares Scolforo, J. R. S. (2020). Modeling tree diameter growth of Bertholletia excelsa Bonpl. in the Brazilian Amazon. Forests, 11(12), 1309. https://doi.org/10.3390/f11121309

Boulton, C. A., Lenton, T. M., & Boers, N. (2022). Pronounced loss of Amazon rainforest resilience since the early 2000s. Nature Climate Change, 12, 271–278. https://doi.org/10.1038/s41558-022-01287-8

Brando, P. M., Paolucci, L., Ummenhofer, C. C., Ordway, E. M., Hartmann, H., Cattau, M. E., Rattis, L., Medjibe, V., Coe, M. T., & Balch, J. (2019). Droughts, wildfires, and forest carbon cycling: A pantropical synthesis. Annual Review of Earth and Planetary Sciences, 47, 555–581. https://doi.org/10.1146/annurev-earth-082517-010235

Brazil. (2006). Decreto nº 5.975, de 30 de novembro de 2006. Diário Oficial da União. http://www.planalto.gov.br/ccivil_03/_ato2004-2006/2006/decreto/d5975.htm

Brasil. Ministério do Meio Ambiente. (2014). Portaria nº 443, de 17 de dezembro de 2014. Diário Oficial da União. http://www.mma.gov.br/portarias/443_2014.html

Brienen, R. J. W., & Zuidema, P. A. (2005). Relating tree growth to rainfall in Bolivian rain forests: A test for six species using tree ring analysis. Oecologia, 146(1), 1–12. https://doi.org/10.1007/s00442-005-0160-y

Brienen, R. J. W., & Zuidema, P. A. (2006). The use of tree rings in tropical forest management: Projecting timber yields of four Bolivian tree species. Forest Ecology and Management, 226(3), 256–267. https://doi.org/10.1016/j.foreco.2006.01.038

Brienen, R. J. W., Phillips, O., Feldpausch, T. R., et al. (2015). Long-term decline of the Amazon carbon sink. Nature, 519, 344–348. https://doi.org/10.1038/nature14283

Brienen, R. J. W., Caldwell, L., Duchesne, L., et al. (2020). Forest carbon sink neutralized by pervasive growth-lifespan trade-offs. Nature Communications, 11, 4241. https://doi.org/10.1038/s41467-020-17966-z

Bunn, A. G. (2008). A dendrochronology program library in R (dplR). Dendrochronologia, 26, 115–124. https://doi.org/10.1016/j.dendro.2008.01.002

Bunn, A. G. (2010). Statistical and visual crossdating in R using the dplR library. Dendrochronologia, 28(4), 251–258. https://doi.org/10.1016/j.dendro.2009.12.001

Caetano-Andrade, V. L., Flores, B. M., Levis, C., Clement, C. R., Roberts, P., & Schöngart, J. (2019). Growth rings of Brazil nut trees (Bertholletia excelsa) as a living record of historical human disturbance in Central Amazonia. PLOS ONE, 14(4), e0214128. https://doi.org/10.1371/journal.pone.0214128

Caetano-Andrade, V. L., Clement, C. R., Weigel, D., Trumbore, S., Boivin, N., Schöngart, J., & Roberts, P. (2020). Tropical trees as time capsules of anthropogenic activity. Trends in Plant Science, 25(4), 369–380. https://doi.org/10.1016/j.tplants.2019.12.010

Caetano-Andrade, V. L., Schöngart, J., Ayala, W. E., Melinski, R. D., Silva, F., Dobrindt, R., & Roberts, P. (2021). Advances in increment coring system for large tropical trees with high wood densities. Dendrochronologia, 68, 125860. https://doi.org/10.1016/j.dendro.2021.125860

Caetano-Andrade, V. L., Clement, C. R., Herrera-Ramírez, D., Larsen, T., Durgante, F., Boivin, N., Schöngart, J., Trumbore, S., & Roberts, P. (2024). Insights into growth, ring formation and maximum ages of Brazil nut trees (Bertholletia excelsa) using 14C dating and tree-ring analysis. Radiocarbon, 66(2), 306–325. https://doi.org/10.1017/RDC.2024.39

Cintra, B. B. L., Gloor, M., Boom, A., Schöngart, J., Baker, J. C. A., Cruz, F. W., Clerici, S., & Brienen, R. J. W. (2022). Tree-ring oxygen isotopes record a decrease in Amazon dry season rainfall over the past 40 years. Climate Dynamics, 59, 1401–1414. https://doi.org/10.1007/s00382-021-06046-7

Cintra, B. B. L., Gloor, E., Baker, J. C. A., Boom, A., Schöngart, J., Clerici, S., Pattnayak, K., & Brienen, R. J. W. (2025). Tree ring isotopes reveal an intensification of the hydrological cycle in the Amazon. Communications Earth & Environment, 6, 453. https://doi.org/10.1038/s43247-025-02408-9

Cook, E. R., & Kairiukstis, L. A. (Eds.). (1990). Methods of dendrochronology: Applications in the environmental sciences. Kluwer Academic Publishers. https://doi.org/10.1007/978-94-015-7879-0

Da Costa, W. P. L. B., Pinheiro, É. F. M., Latorraca, J. V. F., Moutinho, V. H. P., Carmo, F. H. D. J., Ataíde, G. C. V. S., Volpato, M., Aguiar, D. L., & Andrade, F. W. C. (2023). The climate change influence on Cedrela odorata L. radial growth in the Amazon. Sustainability, 15(24), 16755. https://doi.org/10.3390/su152416755

De Souza Freitas, B., Gomes, D. J. C., Lobato, R. R. C., Reis, M. A. G., Souza, A. M., Ferreira, M. S., & Bageston, J. V. (2024). Trend, anomaly and climatic behavior in Belterra, Western Pará. Brazilian Journal of Physical Geography, 17(5), 3137–3153. https://doi.org/10.26848/rbgf.v17.5.p3137-3153

Ferreira, A. T. B. (2009). Characterization of the anatomical structure of the wood, growth rings and resin canals of Pinus caribaea var. hondurensis (Master's dissertation). University of São Paulo. http://www.teses.usp.br/teses/disponiveis/11/11150/tde-18052009-151531/

Ferreira, M. L., Pereira, C. J. S., Souza, A. M., Galdino, T. G., Silva, B. S. S., & Reis, P. C. M. R. (2022). Microscopic characterization of the wood of the species Bertholletia excelsa Bonpl. In Proceedings of the V Brazilian Congress of Wood Science and Technology. https://v.cbctem.com.br/

Ferreira, P. D. S., Ramalho, F. M. G., Couto, A. M., Protásio, T. P., Monteiro, T. C., & Hein, P. R. G. (2023). Relationship among stiffness, wave propagation speed, density and moisture content of Pinus elliottii and Bertholletia excelsa wood specimens. Wood

Material Science & Engineering, 18(1), 151–160. https://doi.org/10.1080/17480272.2021.1996456

Fichtler, E., Clark, D. A., & Worbes, M. (2003). Age and long-term growth of trees in an old-growth tropical rain forest, based on analyses of tree rings and 14C. Biotropica, 35, 306–317. https://doi.org/10.1646/03027

Figliuolo, G. C. (2017). SST variability in the Tropical Atlantic in response to teleconnections of different ENSO and their impacts on precipitation in South America (Master's dissertation). INPA.

Figueiredo Filho, A., Retslaff, F. D. S., Longhi-Santos, T., & Stepka, T. F. (2017). Growth and age of regenerating native species under Araucaria angustifolia plantations in Paraná. Forest and Environment, 24, e00104814. https://doi.org/10.1590/2179-8087.104814

Flores, B. M., Montoya, E., Sakschewski, B., et al. (2024). Critical transitions in the Amazon forest system. Nature, 626, 555–564. https://doi.org/10.1038/s41586-023-06970-0

Fortes, S. L. K., Gonçalves, J. F. D. C., Costa, K. C. P. D., Lopes, J. D. S., Ferreira, M. J., Lima, R. M. B. D., & Nina Júnior, A. D. R. (2023). Growth and functional leaf traits of coppice regrowth of Bertholletia excelsa during an El Niño event in the central Amazon. Acta Amazonica, 53(1), 9–19. https://doi.org/10.1590/1809-4392202103653

Franca, R. R., & Mendonça, F. A. (2016). Rainfall in southern Amazonia: variability and extra-regional teleconnections. Confins, 29. https://doi.org/10.4000/confins.11580

Fritts, H. C. (2001). Tree rings and climate. Blackburn Press.

García-Cervigón, A. I., Mercado, L. N., Mendivelso, H. A., Toledo, M., & Camarero, J. J. (2021). Adjusting xylem anatomy and growth to inter-annual climate variability in two Fabaceae species. Dendrochronologia, 67, 125840. https://doi.org/10.1016/j.dendro.2021.125840

Gloor, M., Barichivich, J., Ziv, et al. (2015). Recent Amazon climate as background for possible ongoing and future changes of Amazon humid forests. Global Biogeochemical Cycles, 29(8), 1384–1399. https://doi.org/10.1002/2014GB004846

Granato-Souza, D., Stahle, D. W., Barbosa, A. C., Feng, S., Torbenson, M. C. A., Pereira, G. A., Schöngart, J., Barbosa, J. P., & Griffin, D. (2019). Tree rings and rainfall in the equatorial Amazon. Climate Dynamics, 52, 1857–1869. https://doi.org/10.1007/s00382-018-4227-y

Guerreiro, Q. L. M., Oliveira Júnior, R. C., Ruivo, M. L. P., Silva, K. E., Beldini, T. P., Guedes, M. C., Mota, A. F. L., Moraes, B. L. T., Santos, P. R. B., & Duin, I. M. (2018). Litter production in a natural stand of Brazil nut trees. African Journal of Agricultural Research, 13, 228–238. https://doi.org/10.5897/AJAR2017.12856

Holmes, R. L. (1983). Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bulletin, 43, 69–78

Jimenez, J. C., Barichivich, J., Mattar, C., Takahashi, K., Santamaría-Artigas, A., Sobrino, J. A., & Malhi, Y. (2018). Spatio temporal patterns of thermal anomalies and drought over

tropical forests. Philosophical Transactions of the Royal Society B, 373, 20170300. https://doi.org/10.1098/rstb.2017.0300

Jiménez-Muñoz, J. C., Mattar, C., Barichivich, J., Santamaría-Artigas, A., Takahashi, K., Malhi, Y., Sobrino, J. A., & Schrier, G. V. D. (2016). Record-breaking warming and extreme drought in the Amazon rainforest during El Niño 2015–2016. Scientific Reports, 6, 33130. https://doi.org/10.1038/srep33130

Larson, P. R. (1969). Wood formation and the concept of wood quality. Yale University.

Latorraca, J. V. F., Castro, J. P., & Santos, G. C. V. (2018). Guide to macroscopic identification of woods. Authors' Club.

Layme-Huaman, E. T., Ferrero, M. E., Palacios-Lazaro, K. S., & Requena-Rojas, E. J. (2018). Cedrela nebulosa: A novel species for dendroclimatological studies. Dendrochronologia, 50, 105–112. https://doi.org/10.1016/j.dendro.2018.06.004

Locosselli, G. M., Brienen, R. J. W., Leite, M. S., Gloor, M., Krottenthaler, S., Oliveira, A. A., Barichivich, J., Anhuf, D., Ceccantini, G., Schöngart, J., & Buckeridge, M. (2020). Global tree-ring analysis reveals rapid decrease in tropical tree longevity with temperature. PNAS, 117(52), 33358–33364. https://doi.org/10.1073/pnas.2003873117

Lorenzoni-Paschoa, L. D. S., Amaral, G. C., Pezzopane, J. E. M., Toledo, J. V., Abreu, K. M. P., Xavier, T. M. T., & Cuzzuol, G. R. F. (2022). Climate change and the ecophysiology of Bertholletia excelsa seedlings. Plant Growth Regulation, 98(1), 155–165. https://doi.org/10.1007/s10725-022-00841-w

Marcelo-Peña, J. L., Roig, F. A., Goodwin, Z. A., & Tomazello-Filho, M. (2020). Characterizing growth rings in Peru. Dendrochronologia, 62, 125728. https://doi.org/10.1016/j.dendro.2020.125728

Marengo, J. A., & Espinoza, J. C. (2016). Extreme seasonal droughts and floods in Amazonia. International Journal of Climatology, 36(3), 1033–1050. https://doi.org/10.1002/joc.4420

Marengo, J. A., et al. (2018). Changes in climate and land use over the Amazon region. Frontiers in Earth Science, 6, 228. https://doi.org/10.3389/feart.2018.00228

Martorano, L. G., Pereira, L. C., Cesar, E. G. M., & Pereira, I. C. B. (1993). Climatic studies of the State of Pará. EMBRAPA.

Miranda, D. L. C., Higuchi, N., Trumbore, S. E., Latorraca, J. V. F., Carmo, J. F., & Lima, A. J. N. (2018). Using radiocarbon-calibrated dendrochronology. Trees, 32(2), 587–602. https://doi.org/10.1007/s00468-018-1658-3

Miranda, D. L. C., Carmo, J. F., Santos, A. L., Nogueira, A. C. N., Silva, J. A. N., Silva, R. S., Stepka, T. F., & Lisboa, G. S. (2024). Dendrochronology applied to Amazon species. TreeDimensional Journal, 13, e2024039. https://doi.org/10.55746/treed.2024.07.039

Morris, H., Jansen, S., & Arber, A. (2016). Secondary xylem parenchyma. IAWA Journal, 37, 1–15. https://doi.org/10.1163/22941932-20160117

Moura, Q. L., Oliveira Júnior, R. C., Melem Júnior, N. J., Guedes, M. C., Costa, P., Santos, D. B., & Mota, A. F. L. (2025). Seasonal dynamics of litterfall nutrients in Brazil nut stand. Ambiente & Água, 20. https://doi.org/10.4136/ambi-agua.3113

Moutinho, V. H. P., Lima, J. T., Aguiar, O. S. R., & Nogueira, M. G. O. (2012). Wood anatomical features of matá-matá species. Revista de Ciências Agrárias, 55(2), 134–141.

Nascimento, J. A. P. (2017). Climatological classification relating CAPE, K index and precipitation. UFOPA.

Oliveira Júnior, R. C., & Correa, J. R. V. (2001). Characterization of soils of Belterra. Embrapa.

Oliveira, I. R. D., et al. (2018). Effect of tree spacing on growth and wood density. Southern Forests, 80(4), 311–318. https://doi.org/10.2989/20702620.2017.1393741

Pacheco-Solana, A., Oelkers, R., D'Arrigo, R., Santos, G. M., Rodriguez-Caton, M., & Tejedor, E. (2023). Radiocarbon and wood anatomy in Bolivia. Frontiers in Plant Science, 14, 1135480. https://doi.org/10.3389/fpls.2023.1135480

Padilha, N. D. S., Silva, C. J. D., Pereira, S. B., Silva, J. A. N., Heid, D. M., Bottega, S. P., & Scalon, S. P. Q. (2016). Growth of physic nut under water regimes. Ciência Florestal, 26(2), 513–521. https://doi.org/10.5902/1980509822752

Palheta, L. F., et al. (2017). Growth and ecophysiological responses of Brazil nut plants. Espacios Journal, 38(32).

Pará. (2007). Resolução COEMA nº 05.

Perdigão, C. R. V., et al. (2020). Wood anatomy of endangered species. IAWA Journal, 41(4), 490–509. https://doi.org/10.1163/22941932-bja10016

Peters, R. L., Groenendijk, P., & Vlam, M. (2015). Detecting long-term growth trends using tree rings. Global Change Biology, 21(5), 2040–2054. https://doi.org/10.1111/gcb.12826

Phillips, O. L., et al. (2010). Drought–mortality relationships for tropical forests. New Phytologist, 187(3), 631–646. https://doi.org/10.1111/j.1469-8137.2010.03359.x

Plavcová, L., et al. (2024). Variations in wood anatomy in Afrotropical trees. Annals of Botany, 134(1), 151–162. https://doi.org/10.1093/aob/mcae049

Portal-Cahuana, L. A., et al. (2023). Zanthoxylum rhoifolium for dendrochronology. Florestal Science, 33(1), e67592. https://doi.org/10.5902/1980509867592

Quintilhan, M. T., et al. (2021). Growth-ring boundaries of tropical tree species. Dendrochronologia, 69, 125878. https://doi.org/10.1016/j.dendro.2021.125878

Rodriguez, D. R. O., et al. (2023). Climate impacts on wood traits of Cedrela fissilis. Agricultural and Forest Meteorology, 333, 109392. https://doi.org/10.1016/j.agrformet.2023.109392

Rodríguez-Ramírez, E. C., et al. (2020). Plastic responses of Magnolia schiedeana. Forests, 11(7), 737. https://doi.org/10.3390/f11070737

Rowland, L., et al. (2015). Death from drought in tropical forests. Nature, 528(7580), 119–122. https://doi.org/10.1038/nature15539

Santos, G. M., Granato-Souza, D., Barbosa, A. C., Oelkers, R., & Andreu-Hayles, L. (2020). Radiocarbon analysis of Cedrela odorata. Quaternary Geochronology, 58, 101079. https://doi.org/10.1016/j.quageo.2020.101079

Schweingruber, F. H. (1996). Tree rings and environment. Paul Haupt Publishers.

Schöngart, J., et al. (2002). Phenology of Amazon floodplain forests. Journal of Tropical Ecology, 18(4), 581–597. https://doi.org/10.1017/S0266467402002389

Schöngart, J., Gribel, R., & Ferreira da Fonseca-Júnior, S. (2015). Age and growth patterns of Brazil nut trees. Biotropica, 47(5), 550–558. https://doi.org/10.1111/btp.12243

Schöngart, J., et al. (2017). Dendroecological studies in the Neotropics. In Dendrochronology: Tree-ring analyses and applications.

Scoles, R., et al. (2016). Survival and fruiting of Bertholletia excelsa. Forest and Environment, 23(4), 555–564. https://doi.org/10.1590/2179-8087.132015

Sousa, L. K. V. S. (2019). Dendrocronologia aplicada no manejo de árvores. ESALQ-USP.

Stokes, M. A., & Smiley, T. L. (1968). An introduction to tree-ring dating. University of Chicago Press.

Sullivan, M. J. P., et al. (2020). Long-term thermal sensitivity of tropical forests. Science, 368(6493), 869–874. https://doi.org/10.1126/science.aaw7578

Supran, G., Rahmstorf, S., & Oreskes, N. (2023). Assessing ExxonMobil's global warming projections. Science, 379(6628), eabk0063. https://doi.org/10.1126/science.abk0063

Veloso, H. P., Rangel-Filho, A. L. R., & Lima, J. C. A. (1991). Classification of Brazilian vegetation. IBGE.

Wheeler, E. A., Baas, P., & Gasson, P. E. (1989). IAWA list of microscopic features for hardwood identification. IAWA Bulletin, 10(3), 219–332. https://doi.org/10.1163/22941932-90000496

Wigley, T. M. L., Briffa, K. R., & Jones, P. D. (1984). On the average value of correlated time series. Journal of Climate and Applied Meteorology, 23, 201–213. https://doi.org/10.1175/1520-0450(1984)023
<0201:OTAVOC>2.0.CO;2

Worbes, M., et al. (2017). Tree growth rings in tropical peat swamp forests. Forests, 8(9), 336. https://doi.org/10.3390/f8090336

Zang, C., & Biondi, F. (2015). treeclim: An R package for proxy-climate relationships. Ecography, 38(4), 431–436. https://doi.org/10.1111/ecog.01335

Zanin, P. R., & Satyamurty, P. (2020). Hydrological processes in South America watersheds. International Journal of Climatology, 40(9), 4006–4038. https://doi.org/10.1002/joc.6442