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# **Annual tree rings in *Goupia glabra* from a hyper-humid tropical forest; Colombia**

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Medellín, Colombia  
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*A mis padres Francisco León David Úsuga, y María Fabiola Flórez Gómez por darme la vida y brindarme las condiciones para maravillarme con los bosques y los árboles.*

"¡Naturaleza! Por ella estamos rodeados y envueltos, incapaces de salir de ella e incapaces de penetrar más profundamente en ella. Sin ser requerida y sin avisar nos arrastra en el torbellino de su danza y se mueve con nosotros hasta que, cansados, caemos rendidos en sus brazos. Crea eternamente nuevas formas; lo que aquí es, antes aún no había sido jamás; lo que fue no vuelve a ser de nuevo. Todo es nuevo, sin embargo, siempre antiguo. Vivimos en su seno y le somos extraños. Habla continuamente con nosotros y no nos revela su secreto. Actuamos constantemente sobre ella, sin embargo, no tenemos sobre ella ningún poder. Parece haberlo orientado todo sobre la individualidad y nada le importan los individuos.

Su vida está en sus hijos; pero ¿dónde está su madre? Ella es la única artista; cincelandos el material más uniforme en completos opuestos; arribando, sin rastro alguno de esfuerzo, a la perfección, a la más exacta precisión, aunque siempre bajo el velo de una cierta suavidad.

Cada una de sus obras tiene una esencia propia; cada uno de sus fenómenos una caracterización especial: y, sin embargo, su diversidad está en unidad. Ella representa una obra; no sabemos si ella misma la ve, y sin embargo ella actúa para nosotros, la audiencia. Vida incesante, desarrollo y movimiento existen en ella, pero ella no avanza. Cambia siempre y no descansa un solo momento. La quietud es inconcebible para ella, y ha depositado su reprimenda sobre el descanso. Es firme. Sus pasos son medidos, sus excepciones raras, sus leyes inmutables. Siempre tiene pensamiento y siempre piensa; pero no como hombre, sino como Naturaleza. Medita sobre una idea todo-comprensiva, que ninguna búsqueda puede hallar.

La humanidad reside en ella y ella en la humanidad. Con todos los seres humanos juegan el juego del amor, y se alegra entre más ganan ellos. Con muchos sus movimientos son tan secretos, que el juego acaba antes de que lo descubran." **Goethe**



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## Resumen

### Anillos de crecimiento anuales de *Goupia glabra* en el bosque tropical hiperhúmedo de Colombia

*Goupia glabra* es un árbol neotropical de gran importancia. Se distribuye por toda la Amazonía, los bosques de las Guayanas y América Central, desde Panamá hasta Guatemala. En Colombia, además de la Amazonía, también se encuentra en el valle medio del río Magdalena y sus afluentes, así como en el litoral Pacífico de América del Sur, desde el norte de Ecuador hasta el Tapón del Darién colombo-panameño, conocido como la Región Biogeográfica del Chocó (RBCH). *G. glabra* es una especie de árbol pionera de madera densa y de gran tamaño. Crece en áreas con precipitaciones medias anuales de 900 a 7400 mm, tanto en climas estacionalmente secos como siempre húmedos. En los bosques amazónicos, *G. glabra* es una especie arbórea hiperdominante y un árbol monodominante en algunos bosques de las Guayanas. Es la especie de gran tamaño más abundante (diámetro a la altura del pecho > 70 cm) en la Amazonía brasileña. A pesar de esto, hasta ahora no se ha publicado ningún estudio que relacione los anillos anuales con el clima en *G. glabra*. Quizás las dificultades para cosechar esta especie expliquen esta carencia. La existencia de pequeñas cicatrices el cambium dificulta la datación por anillos cruzados, ya que producen anillos falsos o dobles, también esta especie presenta discontinuidad tangencial y es común encontrar anillos en cuña. Cambios sutiles en la dirección de los radios medulares permiten detectar los verdaderos anillos anuales en esta especie. Nuestra cronología del ancho de los anillos de los árboles consta de 23 discos, 61 series, correlación entre series 0.434,  $p < 0.05$ . Se encuentra en la RBCH, la región más lluviosa de América, con una temperatura media anual de 25.9 °C y una precipitación media anual de 7219 mm. Febrero, el mes menos lluvioso, recibe una media de 350 mm y supera 2.8 veces la evapotranspiración potencial (127 mm). Nuestra cronología se correlacionó con la precipitación anual ( $r = 0.51$ ,  $p < 0.01$ ), y durante varios meses del año actual ( $p < 0.05$ ). Este estudio contradice tanto la ley de Liebig, que supondría que la cronología no respondería a la precipitación, como la ley de Shelford, que prevería respuestas negativas. También contradice a los dendrocronólogos tropicales que afirman que, en los bosques no inundados, las sequías anuales son responsables de la formación de anillos anuales. Nuestro estudio, bajo las precipitaciones más extremas jamás intentadas, amplía la frontera de la dendrocronología a los bosques tropicales siempre húmedos que comprenden aproximadamente el 30% de los bosques tropicales lluviosos.

**Palabras clave:** Dendroecología, Bosques siempre húmedos tropicales, Chocó Biogeográfico, ENSO.

## Abstract

### **Annual tree rings in *Goupia glabra* from a hyper humid tropical forest; Colombia**

*Goupia glabra* is a very important Neotropical tree. *G. glabra* is distributed throughout the Amazon, Guianas forests, and Central America from Panama to Guatemala. In Colombia, besides the Amazon, it is also found in the middle Magdalena River valley and its tributaries, and in the Pacific littoral of South America, North Ecuador to the Colombian-Panamanian Darien Gap called the Biogeographic Chocó Region (BCHR). *G. glabra* is a large, dense-wood pioneer tree species. It grows under mean annual rainfalls of 900 to 7400 mm in both seasonally dry and ever-wet climates. In the Amazon forests, *G. glabra* is a hyper-dominant tree species and a monodominant tree in some Guianas forests. It is the most abundant large species (diameter at breast height > 70 cm) in the Brazilian Amazon. Despite this, no study has been up now published linking annual rings and the climate in *G. glabra*. Perhaps the difficulties in crossdating this species explain this gap. The existence of small scars from damages to the cambium, apparently caused by insects, makes it difficult crossdating because false, or double rings, are produced. Subtle changes in the direction of the medullary rays allow the detection of true annual rings in this species. Our chronology of tree-rings width consists of 23 disks, 61 series, inter-series correlation 0.434,  $p < 0.05$ . It occurs in the BCHR, the rainiest in America, under a mean annual temperature of 25.9 °C and a mean annual rainfall of 7219 mm. February, the least rainy month, receives a mean of 350 mm and exceeds 2.8 times the potential evapotranspiration (127 mm). Our chronology correlated with annual precipitation ( $r = 0.51$ ,  $p < 0.01$ ), and during several months of the current year ( $p < 0.05$ ). This study contradicts both Liebig's law, which would assume chronology would not respond to precipitation, and Shelford's law, which would predict negative responses. It also contradicts tropical dendrochronologists who claim that in non-flooded forests, annual droughts are responsible for annual-rings formation. Our study, under the most extreme precipitations ever attempted, expands the frontier of dendrochronology to ever-wet tropical forests that comprise about 30% of tropical rainforests.

**Keywords:** Dendroecology, ever-wet tropical forest, Biogeographic Chocó Region, ENSO.





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# 1. Introduction

The Biogeographic Chocó Region (BCHR) extends along the northwest coast of South America, from San Lorenzo, North of Ecuador, to the Colombia-Panamanian Darién Gap. Among the 25 most biodiversity hotspots on Earth, the BCHR is the fourth (Myers et al., 2000) or the ninth (Pérez et al., 2019) most biodiverse. This region is the rainiest in the Americas and probably on Earth (Mesa and Rojo, 2020). There are twelve localities with over 8000 mm, and two exceeding 12,000 mm mean annual precipitation. López de Micay town (2.85°N, 77.25°W) has more than 13,000 mm of mean annual rainfall (Mesa and Rojo, 2020). Three factors contribute to the high rainfalls in this region: *i)* The low-level jet stream centred around 5°N, known as the Choco jet. This jet transports humidity from the Pacific Ocean to the nearby Pacific coast region, *ii)* Given the proximity of both the Western Cordillera of the Andes and the Baudó Range to the Pacific littoral, the Föhn effect produces copious orographic rains, mainly towards the western flank (Mesa and Rojo 2020). Finally, *iii)* the annual migration of the Inter-Tropical Convergence Zone (ITCZ) is responsible for the wet and dry seasons in the tropics around the Earth. The Chocó region is covered almost year-round by the mean amplitude of the ITCZ (Yan, 2005), implying copious rainfall each month, lacking a dry season.

Both the high biodiversity and the exceptional rainfalls in the BCHR deserve more attention from scientists in the context of global environmental change. Understanding the climatic variability of this region helps to understand Northern South America's climate variability. However, the low spatial resolution and short duration of the hydroclimatic instrumental records limit the interpretation and detection of climate change effects over the region. Since trees are the longest-living organisms in nature, dendroclimatology allows using of annual growth rings as proxies to expand the climate records greatly in time and space. Up now, in non-flooded tropical forests, the existence of annual tree rings (rhythmic growth), has been explained by the annual water deficits (Brienen et al., 2016; Schöngart et al., 2017; Zuidema et al., 2022). However, Giraldo et al. (2020) found annual tree rings in six species (*Goupia glabra*, *Cariniana pyriformis*, *Pourouma bicolor*, *Inga acreana*, *Inga sp.*, and *Mabea sp.*) from an ever-wet forest (over 7200 mm y<sup>-1</sup>) of the BCHR that match our study area. However, the environmental drivers triggering annual tree rings and the potential of some tree species for climate reconstruction in the ever-wet tropical forests remain little explored.

Some drivers of the annual tree rings in the ever-wet tropical forests have been proposed, such as slight variation in rainfall, soil moisture, solar irradiance, cloudiness, sunrise, and sunset time (Borchert and Rivera, 2001; Breitsprecher and Bethel, 1990;

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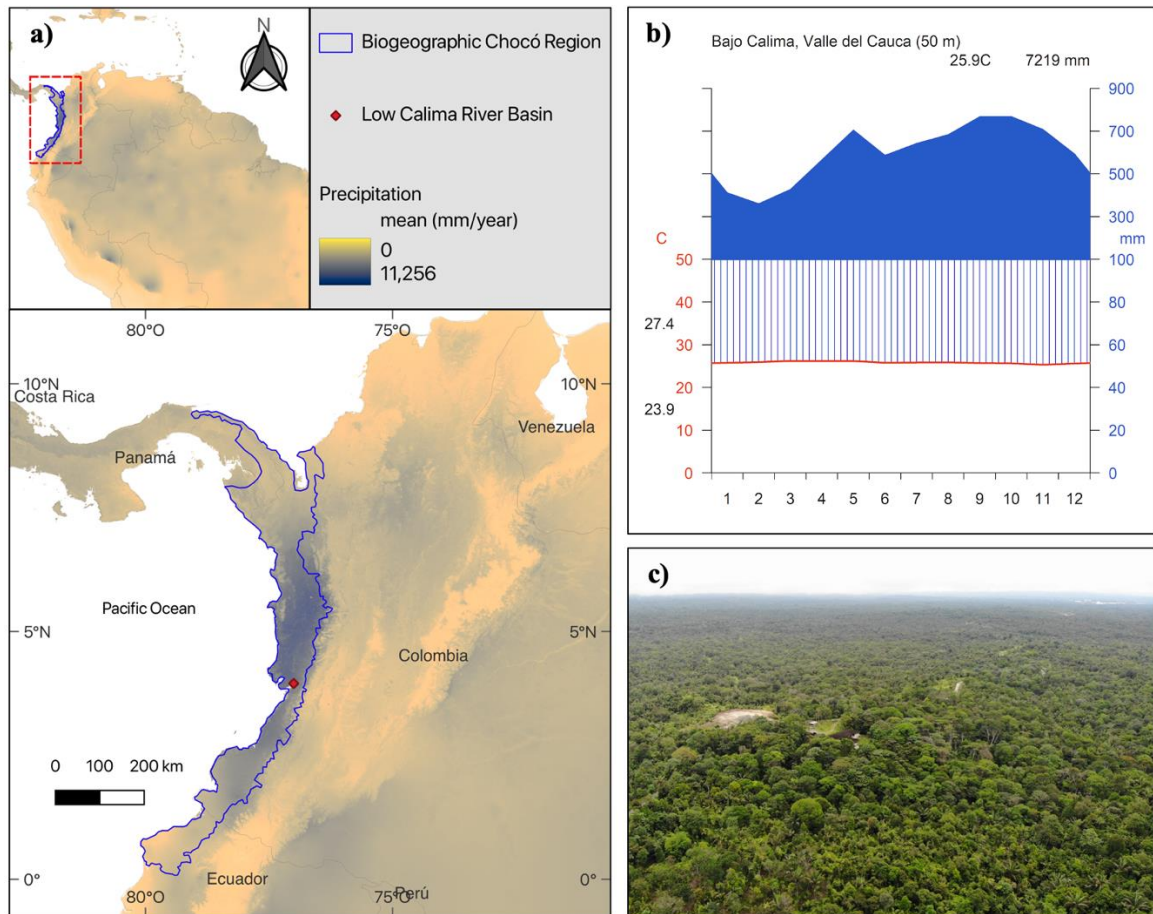
Clark and Clark, 1994; Giraldo et al., 2022; Moreno and del Valle, 2015; O'Brien et al., 2008) Satellite observations have found an increase in photosynthesis during the less rainy season in the non-water-limited Amazonian forests (Green et al., 2020; Restrepo-Coupe et al., 2013). Giraldo et al. (2020) hypothesize that in tropical ever-wet forests during the rainiest months, tree growth is null or very slow due to water excess and low light availability. In contrast, a fast tree growth during the less rainy months with appropriate water and light availability. To test such a hypothesis, we propose to use a tree-rings width series of *Goupia glabra* (Goupiaceae) growing in an ever-wet tropical forest of the BCHR, near the upper limit of its range of mean annual precipitation: from 966 to 7415 mm y<sup>-1</sup> (Fig. S 1) (Fick and Hijmans, 2017; GBIF, 2022). In this study, we aim: *i*) to establish tree-ring frequency in several independent trees of *G. glabra* from an ever-wet tropical forest, *ii*) to assess the role of climatic variables (precipitation, temperature, and solar radiation) as possible environmental drivers for tree growth, and *iii*) to determine the potential of tree rings for climatic reconstruction and to explore the relationships with regional ocean-atmospheric phenomena.

Globally, we did not find any dendroclimatic study published in peer-reviewed journals or books in a climate with more than 7000 mm mean annual precipitation and in which all months are wet. Filling this research gap is our purpose.

## 2. Materials and methods

### 2.1 Study area.

The study area includes the Low Calima River Basin (LCRB) in the municipality of Buenaventura, department of Valle del Cauca, towards the center of the Colombian Pacific coast a). The study area is part of the BCHR (Fig. 1a). The most representative weather station in our research area is Bajo Calima. It is seated at 50 m asl. In this station, the mean annual rainfall is 7219 mm; the mean annual temperature is 25.9 °C, with very few variations throughout the year (Fig. 1b). Since the precipitation during the least rainy month exceeds about 2.8 times the potential evapotranspiration (Thornthwaite, 1948), these forests are ever wet.



**Fig. 1.** Regional context and local conditions of the sampling area: *a)* Low Calima River Basin (red dot), located at the center of the Biogeographical Chocó Region. Data are from WorldClim, 1970-2000 average (Fick and Hijmans, 2017). *b)* Walter-Lieth climate diagram for the study site. Solid dark areas represent the wet months with monthly precipitation  $\geq 100$  mm (lacking dry months). Data from Bajo Calima Meteorological Station are from the Institute of Hydrology, Meteorology, and Environmental Studies of Colombia (IDEAM). *c)* Picture of secondary forests of our study site seen from Pedro Antonio Pineda Tropical Forest Research Center, Universidad del Tolima.

The LCRB forests cover 60,200 ha of low hills from 50 to 150 m asl and slope up to about 45%. They are very low-fertility soils derived from tertiary sediments (Faber-Langendoen, 1992; Ladrach, 1985; Ladrach and Wright, 1995). Soils are a mixture of mottled grey-yellow clays with a soil pH of 4.3 to 5.0. The available P concentration is virtually undetectable, with low B concentration, and the levels of Al and Fe are toxic (Cannon, 1985; Faber-Langendoen, 1992; Faber-Langendoen and Gentry, 1991). From 1962 to 1993, these forests were handed over to two forestry companies. First, to

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Pulpaapel, then to Cartón de Colombia (CC) (Frisk, 1978; Ladrach, 1985; Lozano and González, 2011). These companies cut down all tree species by clear pulp and paper production, but the stems of less than 13 cm in diameter at breast height (DBH) and palms were not harvested (Pacheco, 2020). By 1993 when the company returned the concession to the State, it covered 96.7% of the LCRB area. Of which, about 35, 270 ha of forest around the main CC camp (3°55'N, 77°0'W), had been exploited (Forero, 2014; Ladrach and Wright, 1995; Pacheco, 2020). This date coincided with the application of the Colombian Law 70 of 1993. In this Law, the LCRB ownership was delivered, as collective property, to the Afro-Colombian community established there ancestrally (Lozano and González, 2011).c) Today, this camp belongs to the Pedro Antonio Pineda Tropical Forest Research Center of the University of Tolima (Forero, 2014). Around this camp, we did our research.

From 1962 until now, the local community has felled trees over 8 cm in DBH and other pieces of wood as one of their subsistence activities using the 90 km of forest roads left by forestry companies (Forero, 2014; Ladrach, 1985; Ladrach and Wright, 1995; Lozano and González, 2011). Therefore, practically, the entire study area is covered by secondary forests (Fig. 1 c).

## 2.2 Tree species ecology

*G. glabra* is an important Neotropical tree species. *G. glabra* grows in lowlands, both in ever-wet and in seasonally dry tropical terra firme forests from Guatemala to South America. Their annual rainfalls range from 900 to 7400 mm (Fig. S 1a). In the Amazonian forests, *G. glabra* is a hyper-dominant species. Its population has been estimated at 370 million trees with a DBH over 10 cm (ter Steege et al., 2013). It also lives in the Brazilian Cerrado (Duarte et al., 2021) and in the forests of northern South America in Venezuela, Guyana, Suriname, and French Guiana, where it comes to be a monodominant species (Lacoste and Alexandre, 1991) (Fig. S 1a). In Colombia, it is found, besides the Amazon region, in the Colombian Pacific, in the Middle Magdalena River Valley, and some valleys of its tributaries. *G. glabra* is highly plastic, which allows it to adapt to different environments (ITTO, 2017). It is a large-sized pioneer species. Its seeds are photoblastic and thermoblastic. This species regenerates both under the full sun and after forest fires (ITTO, 2017; Lacoste and Alexandre, 1991). Unlike most pioneer species, it is a very long-lived tree (Köhl et al., 2017; Lotfiomran and Köhl, 2017). It reaches heights of 50 m and diameters of 1.3 m over its buttresses of up to 2 m (Lacoste and Alexandre, 1991). The wood's basic density (0.72 g cm<sup>3</sup>) far exceeds other pioneers (Nogueira et al., 2007).



## 2.3 Sampling and laboratory work

In 2017 and 2019, we sampled 23 complete cross-sections (disks) of *G. glabra* in the study area. To do this, we were accompanied by local Afro-Colombian tree recognizers from the Las Brisas village, belonging to the Low Calima River Community Council. The tree recognizers took us to the sites where members of this community were felling trees. From each felled *G. glabra* tree that we found, we cut a disk at about 1.3 m from the base. From each tree, we collected botanical samples (when possible, with flowers and fruit for correct identification in the MEDEL herbarium of the Universidad Nacional de Colombia, Medellín. In the laboratory of Tropical Dendroecology, we dry the disks in forced-air ovens at 35°C for 10-15 days. We sanded one surface of each disk with progressively finer abrasive paper: 60, 80, 120, 500, 1200, and 2000 grans. In this way, the tree rings were visible enough with the naked eye or a 10X loupe.

We scan the samples at 2000 dpi in TIFF image format. To do this, we use Silverfast Professional Scan software (Tally, 2006) with the Epson Expression 10000XL high-resolution scanner calibrated for dendrochronology use by Regent Instruments Inc., Canada. We measured the tree-rings width on scanned images using ImageJ software (Abràmoff et al., 2004) and R Software (R Development Core Team, 2022). We plotted on the disks from pith to bark, about three transects per disk. As far as possible, the transects should be parallel to the medullary rays because they allow the identification of rings that are difficult to recognize. The growth rings were delimited by ROIs (regions of interest), containing their respective spatial information, which was processed in the R Software, generating the tree-rings width series and other calculations.

## 2.4 Crossdating and chronology

We obtained about three tree-rings width series per disk (DBH: 12-35 cm) growing under similar conditions (light exposure and slope). We use the dplR package (Bunn, 2010, 2008) for quality control, series synchronization, and generation of the chronology. We crossdated both at the individual disk and species levels. We use a 10-year spline function. First, we compare multiple radii within the same tree. Then, we gradually added the tree-ring series from other individuals of *G. glabra*, ensuring statistical and graphical synchronization and creating the ring width series. We use the autoregressive “Ar” method to remove all the low-frequency variation. Then, using a bi-weight robust mean, we developed a residual mean chronology of tree-ring width indices (RWI) to represent all trees sampled (Bunn, 2010).

We considered some statistics to assess the tree-rings chronology: The series intercorrelation accounts for the common signal recorded in all sampled trees. The expressed population signal (EPS) quantifies how well a chronology based on a finite number of trees represents the ideal chronology. When this value drops below 0.85, the chronology is dominated by an individual tree-level signal rather than by a stand-level. Subsample signal strength (SSS) measures the amount of signal captured by a subsample of series from the mean chronology. It is particularly important in climate reconstruction (Speer, 2010). Mean sensitivity (MS) measures the year-to-year variability in the tree rings. It ranges from 0 to 1. An MS of around 0.1 is so complacent. And a greater of 0.4, so sensitive being the crossdating process very difficult.

## **2.5 Tree-Ring periodicity**

We tested the formation frequency of tree rings using the radiocarbon bomb-peak method by sampling particular rings in each disk (Andreu-Hayles et al., 2015; del Valle et al., 2014; Giraldo et al., 2022). First, we assumed a priori annual tree-ring formation, assigning to each tree ring the corresponding calendar year from the last complete ring formed, the nearest to bark, and then counting backwards to the first around the pith (dendrochronological dates). Then, we collected about 20 mg of the wood for radiocarbon analyses in five specific tree rings in three disks: Tree code 01 (dendrochronological calendar years 1993 and 1997), tree code 64 (dendrochronological calendar years 1991 and 2003), and tree code 159 (dendrochronological calendar year 1993). The alpha-cellulose was extracted from each sample following a protocol by Steinhoff et al. (2017). Radiocarbon analyses were done at the Max Planck Institute for Biogeochemistry in Jena, Germany, by the accelerator mass spectrometry (AMS) technique. We used the software CaliBomb (Reimer et al., 2020) with the North Hemisphere Zone 3 curve (Hua et al., 2021) between 1941-2019 and one smoothing year function of CaliBomb to obtain the probable radiocarbon calendar dates (<http://calib.org/JS/JScaliBomb/NHZ3.f14c>) (Reimer et al., 2020). A comparison between dendrochronological dates and radiocarbon dates allows us establishment the tree-ring frequency.

## 2.6 Environmental data

We used mean monthly precipitation (1946 – 2017) and temperature (1960 – 2017) records from Bajo Calima Meteorological Station, located in the center of our study area. Also, we recover some missing data in the Bajo Calima station using three nearby stations from IDEAM. We used the mean monthly short-wave solar radiation (SWR  $W m^{-2}$ ) between 2000 and 2019 from Clouds and the Earth's Radiant Energy System—CERES datasets (<https://ceres.larc.nasa.gov/>) (Kato et al., 2013). To quantify the effects of remote environmental variables on trees growth we used monthly values of the Oceanic Niño Index (ONI: 1960-2016, [https://origin.cpc.ncep.noaa.gov/products/analysis\\_monitoring/ensostuff/ONI\\_change.shtml](https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_change.shtml)), the Southern Oscillation Index (SOI: 1960–2016, <https://www.ncdc.noaa.gov/teleconnections/enso/soi>) and the Multivariate ENSO Index (MEI: 1960–2016, <https://psl.noaa.gov/enso/mei.old/mei.html>).

## 2.7 Data analysis

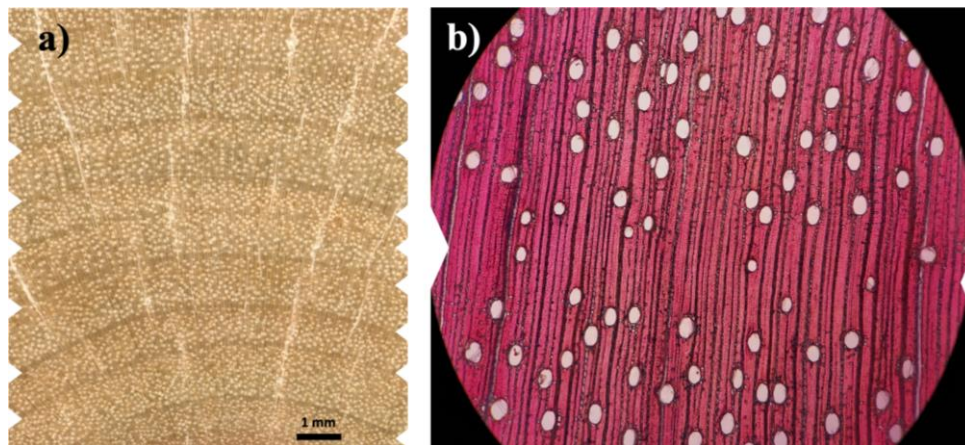
We determined the 12 months in which the highest Pearson correlation exists between precipitation and the RWI residual chronology occurs first, with a lag of one month each time, second with an advance of one month each time. Then, we assess the Pearson correlations between the residual chronology of RWI during the phenological year previously found versus the following both annual and monthly local and remote environmental variables: precipitation, temperature, SWR, MEI, ONI, and SOI. To calculate these correlations, we use the R-package Treeclim (Zang and Biondi, 2015) and the R-package ggpubr (Kassambara, 2022), which includes bootstrapped correlation analyses.



## 3. Results

### 3.1 Tree-ring anatomy characteristics

The tree rings of *G. glabra* from this ever-wet forest were present in all samples analyzed in our study. A diffuse-porous wood and two clearly defined bands characterize the growth rings. One is wide and lighter colored, and the other is a narrow darker band. The last band marks the end of the ring (Fig. 2b and Fig. S 2). The dark color of the band that establishes the boundary of the rings is usually interpreted in the anatomy of wood as containing smaller cells, with thicker cell walls and less lumen (Fig. S 2); therefore, with greater wood density (Speer, 2010). A particular effort was devoted to tree-rings delineating because most disks had eccentricities and several wedging rings in different directions into the same disks. We also found several scars produced apparently by insects that injured the cambium. These irregularities produced numerous missing and false rings. To delimit growth rings was necessary to consider other anatomical characteristics, making it easier the crossdating. We discovered a subtle change in the direction of rays in each ring. This characteristic was useful for delimiting less conspicuous ring boundaries (for details, see Fig. S 2).



**Fig. 2.** Anatomical tree-rings wood features of *Goupia glabra*. a) Macroscopic anatomical characteristics of tree rings (arrows) defined by thickened walls, resulting in density variations (darker boundaries) and diffuse-porous wood. b) microscopic features: The arrow represents a ring boundary delimited by thick-walled fibres.

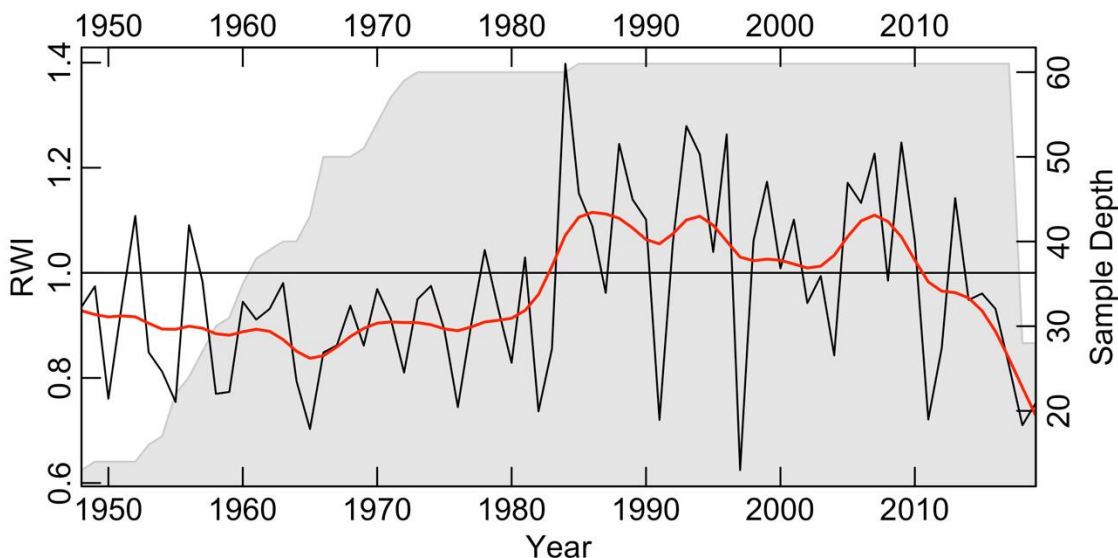
## 3.2 Chronology development

The 23 trees sampled in this study growing under similar conditions were successfully crossdated. The sampled trees on average have 68 years, the older is 153 years (1866 - 2019) and the younger is 47 years old (1972 - 2019). The total cross-dated series (4161 growth rings measured). The mean ring width was  $1.97 \text{ mm} \pm 0.53$ . The mean inter-series correlation ( $r = 0.43$ ;  $p < 0.05$ ) suggests the existence of a significant common environmental signal to all trees (Table 1 ).

Although the developed residual chronology covered from 1866 to 2019, 153 years of tree-rings records (Table 1), only one tree sampled is older than 71 years. Then, the reliable chronology (sample depth > 10 series of three trees) only covers from 1948 to 2019 (68 years) (Table 1). The MS of the chronology was around 0.40, and the first-order autocorrelation was  $-0.0463$  ( $p > 0.05$ ). The expressed population signal (EPS) was over 0.85 throughout the chronology covering from 1948 to 2019.

**Table 1** Descriptive statistics of the *Goupia glabra* chronology.

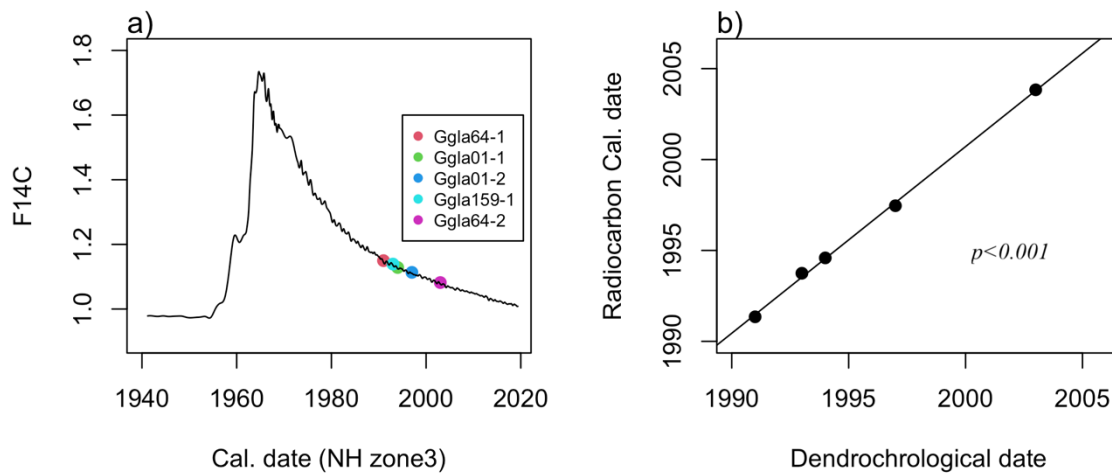
Characteristics	Value
Sampled trees	23
Number of series	61
Diameter range(cm)	12-35 cm
Number of rings	4161
Time- span	1948–2016 years
Average ring width	1.97 mm
Mean sensitivity	0.402
EPS	0.85
Interseries correlation	0.434 ( $p < 0.05$ )
SNR	5.483
AR1	$-0.0463$ ( $p > 0.05$ )



**Fig. 3.** Tree-ring width index (RWI) chronology of *G. glabra* (black line), whose variations are highlighted by a 10-year spline (red curve). The sample depth: number of series representing each portion of the chronology (the grey area).

### 3.3 Annual tree-rings formation

Fig. 4. a) shows the calibration curve modern fraction of  $^{14}\text{C}$  in Northern Hemisphere Zone 3 (1941-2019) (Hua et al., 2021) and the match of five tree rings analyzed over the calibration curve. b) The correlation between radiocarbon dates and Crossdating dates was  $r = 0.99$  ( $p < 0.001$ ) for the five tree rings analyzed (Table 1). This result validates both the crossdating of trees whose rings were analyzed and the annual tree rings formation of *G. glabra* in the study area.

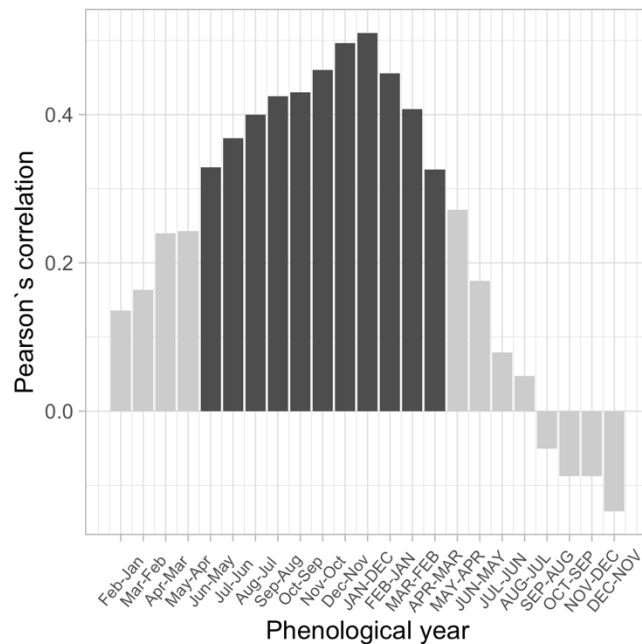


**Fig. 4** Radiocarbon dating and validation of annual tree-rings formation of *G. glabra*. a) dating superimposed of five samples (see **Table S 1**) on the calibration (cal.) curve of the bomb peak test atmospheric  $^{14}\text{C}$  in the Northern hemisphere zone 3 calibration curve (Hua et al., 2021), b) It shows the comparison between radiocarbon cal. date and dendrochronological date. The linear regression among five tree rings dated represents a one-to-one relationship ( $p < 0.001$ ).

### 3.4 Growth-climate relationships

In Fig. 5, we present what some authors have called the phenological year (López et al., 2014; Moreno and del Valle, 2015) Very high correlations ( $p < 0.01$ ) are observed for the 12 months beginning in June before the current year, and up to the twelve months beginning in April of the current year. The maximum correlation, the phenological year, coincides from January to December of the current year, also called the solar year ( $r = 0.51$ ,  $p < 0.01$ ).

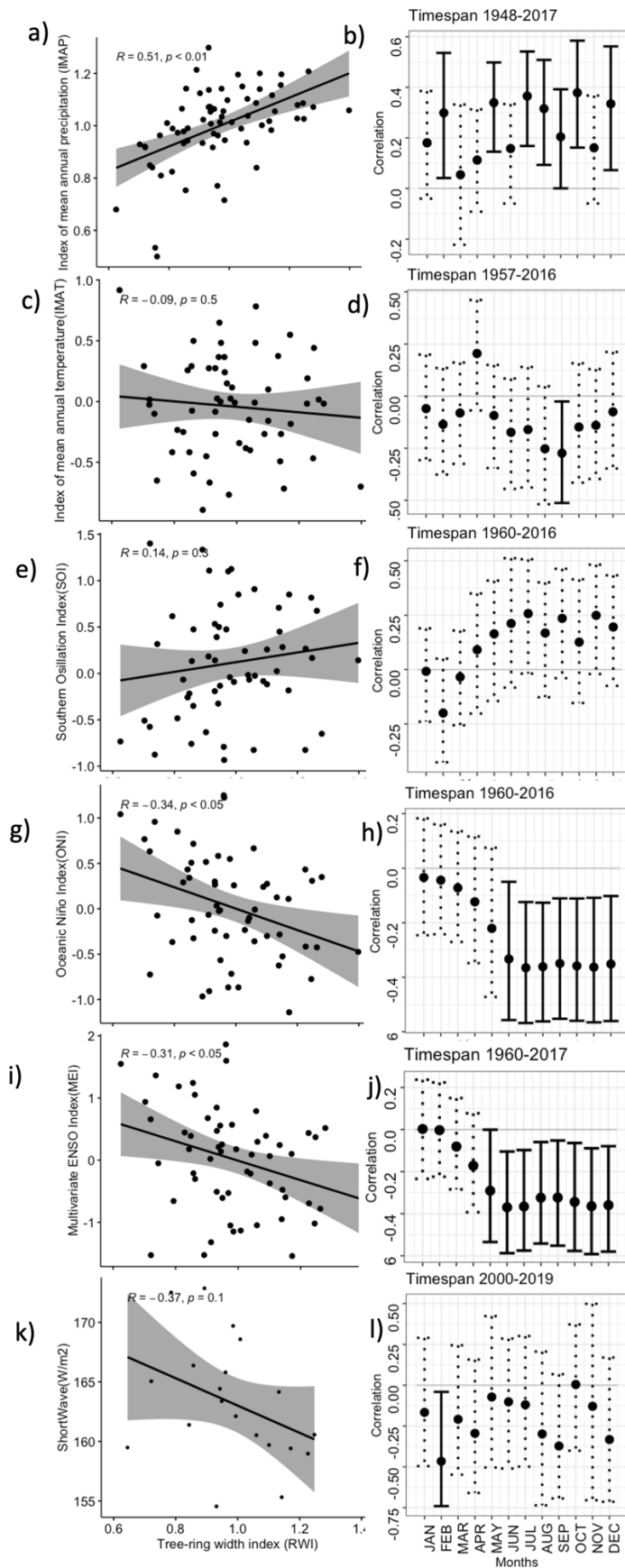




**Fig. 5.** Phenological year, the highest level of Person's correlation between annual precipitation and the residual chronology of *Goupia glabra* in the 23 correlations, corresponds to the current year, from January to December. Dark colour bars represent highly significant ( $p < 0.01$ ).

In the left panels (a, c, e, g, i, and k) of Fig. 6, we present the results of the correlations between the annual indices of the following variables: precipitation, temperature, the ENSO indices SOI, ONI, and MEI, and the SWR index with the *G. glabra* tree ring with index(RWI). In the right panels (b, d, f, h, and j) of Fig. 6, we present the monthly correlations of the same variables. Among all these variables, the highest annual correlation was a positive correlation with the rainfalls ( $r = 0.51$ ,  $p < 0.01$ ). Then, negative correlations with ONI ( $r = -0.34$ ,  $p = 0.01$ ), and with MEI ( $r = -0.31$ ,  $p < 0.05$ ). The other correlations were not significant at less for  $p < 0.05$ . The monthly correlations, right side panels of Fig. 6, were significant ( $p < 0.05$ ) for precipitation in February ( $r = 0.323$ ), May ( $r = 0.341$ ), July ( $r = 0.365$ ), August ( $r = 0.310$ ) October ( $r = 0.381$ ) and December( $r=0.324$ ). For ONI and MEI, the results are very similar: negative correlations from June to December ( $p < 0.05$ ). For temperature and SWR, the results were also similar. Each one has only a one-month negative significant correlation, September, ( $r = -0.273$ ,  $p < 0.05$ ) and February ( $r = -0.46$   $p < 0.05$ ), respectively (see Table S 2).

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**Fig. 6.** Annual Pearson's correlations, left panels (a, c, e, g, i, k), and monthly bootstrapped correlations, right panels (b, d, f, h, j, l) between the RWI residual chronology of *G. glabra* with precipitation (1948 -2017), temperature (1957-2017), the indices of El Niño Southern Oscillation (ENSO) SOI, ONI, and MEI (1960-2017), and the Short-Wave Radiation Index (2000-2016). The bars around the points in the right panels are the confidence intervals of the correlations. Continuous black bars indicate correlations with  $p < 0.05$ , black bars correlations with  $p < 0.05$ . Large black dots followed by small vertical dots are non-significant correlations ( $p > 0.05$ ) and their respective confidence intervals.

## 4. Discussion

### 4.1 The uniqueness of this study

In Amazon forests, the population of *G. glabra* has been estimated at 370 million trees over 10 cm in DBH (ter Steege et al., 2013). Among tree families, Goupiaceae ranks 11th among the most hyper-dominants. But, in terms of the number of individuals per family, *G. glabra* is the most hyper-dominant species. However, this is the first dendroclimatic study of this widely distributed Neotropical tree species.

Our chronology is also unique in that it is unsurpassed by any other in two respects: First, it is the chronology under the highest mean annual precipitation ever published, and second, February, the least rainy month with 350 mm on average, is the wettest so far recorded in dendrochronological studies (Fig. 1 and Fig. S 1). Among the 347 pantropical chronologies compiled by Zuidema et al. (2022), the maximum mean annual rainfall reached just 2600 mm.

### 4.2 Age of the trees

*G. glabra* is a very long-lived tree species (Köhl et al., 2017) found, by counting growth rings, trees up to 257 years old in the forests of Suriname. Other researchers (Laurance et al., 2004) inferred, for the same species, mean longevity of about 400 years and 675 years, maximum longevity in central Amazon forests. Why, then, was only one tree found 156 years old and only 68 years for the other 23 trees (Table 1). The low age of the trees found in the study area is due to being clear-felled between 1962 and 1993 by the pulp and paper companies (Pacheco, 2020). Perhaps trees that survived after 1962 were too small to be attractive to companies.

### 4.3 Tree-rings traits: Frequency, distinctiveness, and porosity

Some previous studies have determined the annual tree-ring frequency in *G. glabra*: both Détienne and Barbier (1988) and Détienne (1989) used cambial wounds and dendrometer bands, Ponds and Helle (2011) stable isotopes, and (Tanaka, 2005) cambial wounds. Other authors do not demonstrate the annual frequency of the tree rings in this species; they have assumed it across highly divergent climatically ecosystems (Cintra et al., 2013; Köhl et al., 2017; Lotfiomran and Köhl, 2017; Oliveira, 2010; Vetter and Botosso, 1989). (Oliveira, 2014) claim to have crossdated *G. glabra* tree rings, but no evidence is presented.

We agree with other researchers who have found difficulties in differentiating growth rings in *G. glabra*. For Miller and Détienne (2001) they are indistinct or absent. There are indistinct to several authors: (Duarte et al., 2021; Nahuz et al., 2013; Pons and Helle, 2011; Santini, 2013; Trevizor, 2011). In contrast, for Vetter and Botosso (1989), Vásquez and Ramírez (2005), Giraldo et al. (2020; 2022), and in this paper, the rings of *G. glabra* are distinct or well-defined by density changes due to increased fiber wall thickness ( Fig. 2a). Gómez (2019) managed to delimit the tree rings of *G. glabra* using artificial vision algorithms clearly and objectively around the complete disks of our study area.

### 4.4 Annual rings could thus be identified with certainty.

Our results on annual tree-rings formation in *G. glabra* depend on three independent facts: first, the successful tree-rings crossdating with an inter-series correlation of 0.434 ( $p < 0.05$ , **Table 1**), the second, in the 14C dating of five tree rings that reached a correlation of 0.99 ( $p < 0.01$ , Fig. 4) with dendrochronological dates, and third, significant correlations with both local environmental variables (Fig. 5), and (Fig. 6a, and Fig. 6b) and remote ones (Fig. 6g, and Fig. 6i)

We agree with other researchers who have found difficulties in differentiating growth rings, among other reasons, due to the frequency of false and missing rings (Détienne, 1989; Detienne and Barbier, 1988; Lotfiomran and Köhl, 2017). In the literature, we did not find any report on the abundant small scars on the surface of the disks produced, apparently, by insects. They are responsible for the presence of some irregularities, such as double and false rings. We solved these problems by observing that, in the interception of real annual growth rings with the medullary rays, it appears a faint change in the direction of rays lets us mark the rings.

*G. glabra* is a diffuse-porous species, regardless of the seasonality or amount of precipitation: with several dry months in French Guiana (Détienne, 1989) and Suriname (Lotfiomran and Köhl, 2017), in seasonal wooded savannas (Brazilian Cerrado) (Duarte et

al., 2021), in central Amazonia with few dry months (Duarte et al., 2021; Vetter and Botosso, 1989) under several dry months, in the State of São Paulo, southern Brazil (Santini, 2013), and in ever-wet forests with no apparent hydric seasonality Giraldo et al (2020; 2022) this study (Fig. 1, and Fig. S 1a). These facts suggest that the type of porosity in this species is not adaptive but probably, genetically determined. In some species, diffuse porosity is adaptive. For example, in the BCHR, *Cariniana pyriformis* generally is diffuse-porous. However, during the warmer and less rainy El Niño years, the tree rings change to be semi-rings-porous (Moreno and del Valle, 2015). Diffuse porosity is a broad classification where many other variables fit. Fonti et al. (2010) compiled eleven metrics used in time series of tree-rings porosity. There is a trade-off between maximizing hydraulic efficiency and avoiding embolism without modifying the diffuse porosity. This compensation effect was demonstrated with the diffuse-porous species *Azelia africana* in Burkina Faso (Balima et al., 2020) and *Chukrasia tabularis* in Bangladesh, growing in seasonally dry forests (Islam et al., 2019, 2018): High rainfall increases tree xylem vessel size while reducing vessel density maximizing hydraulic efficiency and faster growth. Low rainfall induces slow growth and reduces xylem vessel size while increasing vessel density minimizing the risk of drought-induced cavitation and embolism. Hypothetically, something similar must occur with *G. glabra* within their geographic range.

## 4.5 Growth-climate relationships

Our results reveal that each annual ring of *G. glabra* in our study area begins and ends its formation during the solar year from January to December (Fig. 5). But this does not imply that it grows during the twelve months of the year. This result was the same or alike found for other species from the BCHR: (i) Moreno and del Valle (2015) for *Cariniana pyriformis* found the same phenological year: January to December, (ii) Both Herrera and del Valle (2011) and López et al. (2014) reached the phenological year for *Prioria copaifera* one month in advance (February-January) for chronologies of TRW and number of vessels, respectively, correlated to the water levels of the Atrato River. The shift of one month is probably because the peak of the water levels in the river is out of phase by one month to precipitation. In contrast, in two chronologies in the hot semi-arid climate of the Guajira Peninsula, north of Colombia, the twelve months that showed the highest correlation with precipitation were October to September for *Parkinsonia praecox* (Ramírez and del Valle, 2012) and November to October for *Capparis odoratissima* (Ramírez and del Valle, 2011).

A principle in dendrochronology known as Liebig's Law of Minimum states that plant growth reflects the strongest limiting environmental factor. The mean annual rainfall in our study area is 7,219 mm a year (Fig. 1). It is very close to 7,415 mm a year, the maximum mean annual rainfall in which this species has been recorded (Fig. S 1 c) (Fick and Hijmans, 2017; GBIF, 2022). On the other hand, during February, the least rainy month, the mean rainfall of 350 mm exceeds 3.5 times the limit of dry month established in the Walter and Lieth climate diagram (Fig. 1b) and almost 2.8 times the monthly potential evapotranspiration (Thornthwaite, 1948). Therefore, we reasonably assume that both monthly and annual rainfalls far exceed the minimums rainfall for trees. Shelford's Law

of Tolerance states that for each organism's growth factors, a minimum, an optimum, and a maximum exist (Shelford, 1931). Considering Shelford's Law, we could argue that the

high annual and monthly rainfalls, being close to the maximum tolerated by *G. glabra*, should correlate negatively with the residual chronology of the WRI.

Contrary to our expectations, the correlation of the TRW chronology with annual rainfalls was significantly positive ( $r = 0.51$ ,  $p < 0.01$ , Fig. 5a). Even more, they overpassed the correlations reached by *C. pyriformis* ( $r = 0.33$ ,  $p < 0.05$ ) (Moreno and del Valle, 2015) and *P. copaifera* ( $r = 0.42$ ,  $p = 0.05$ ) from the same Chocó region, but with the mean rainfalls about a half of our study area. Using dendrometer bands in our same study area, Giraldo (2020) found that *G. glabra* grows from April to October, but growth rates began to decline in July to stop in October, the rainiest month (Fig. 1), which partially coincides with our results. Our data show significant positive correlations ( $p < 0.05$ ) of the TRW chronology with precipitation for February, the least rainy month (Fig. 1), and non-significant for October, the rainiest month, and November, months in which growth rates are close to zero (Giraldo et al., 2020) (Fig. 6b).

According to our results, therefore, this species grows mainly during the rainiest months. Why, then, does *G. glabra* respond positively to such high annual and monthly rainfalls? Phytogeographically, *G. glabra* origin is from the Amazonian forests and the Shield Guianas forests regions (Gentry, 1982; Hammond, 2005). Relatively recently, it entered both central Colombian and Colombian Pacific. Then to Central America (Gentry, 1982). Studies indicate that some species retain the annual tree ring rhythms of their phytogeographic region of origin when they grow in different climatic conditions (Callado et al., 2001; Fahn, 1995; Silvia and Barajas, 2017). Other authors found that annual rings may lie from historical-evolutionary factors (dos Santos et al., 2017), or that the annual rings come from endogenous rhythms (Callado et al., 2001, 2013). We believe that all these findings are manifestations of memory in plants. Responses to multiple exposures to drought include not only changes in gene expression patterns and transcripts accumulation, but also epigenetic modifications. Such changes persist even after stress relief, representing a drought stress memory (Galviz et al., 2020). *G. glabra* is a supremely plastic species (Lacoste and Alexandre, 1991). In its phytogeographical environment of origin, it must face climates with one to two annual droughts and annual rainfalls from 900 to 3000 mm (Détienne, 1989; Hammond, 2005).

Under these conditions, the dry season drives interannual variability and annual tropical tree-rings width, as was found in 349 chronologies of 99 species, with annual rainfall up to 2600 mm (Zuidema et al., 2022). Hypothetically, *G. glabra* retains the memory of annual tree rings growing during the rainiest months, even in ever-wet environments as in our study area.

Another manifestation of this memory exists in its phenology. In the Amazon, the Guianas, and the Cerrado in Brazil, this species is evergreen but with a leaf fall peak during the dry season. There is no synchronism between different individuals in a population, and even, among different phenological stages, within the same crown (Lacoste and Alexandre, 1991). We have observed similar phenology in our ever-wet study area.

Regarding the annual and monthly temperatures, our hypothesis, considering both Liebig and Shelford laws, establishes that being close to the mean through the temperature range for this species (25.9°C in Fig. 1, range 20.5 to 28.5°C in Fig. S 1), they should not significantly correlate to the residual chronology of the WRI. According to our expectations, *G. glabra* shares with *P. copaifera* and *C. pyriformis* the non-significant negative correlations ( $p < 0.05$ ) of mean annual temperatures and the residual chronology, but with the lowest correlation ( $r = - 0.09$ ,  $p = 0.5$ ) (Fig. 6 c). Theoretically, according to Shelford's Law, within the distribution range of this species, the tree rings chronologies should correlate positively with the mean annual temperatures slightly above 20.5°C and negatively with the mean annual temperatures slightly under 28.5 °C like those in our study. But there are no other chronologies of this species to verify it.

The annual correlations for the remote variables SOI, MEI, and ONI of *G. glabra* had the same trend as those of *C. pyriformis* (Moreno and del Valle, 2015). But, in this last species, all were highly significant ( $p < 0.01$ ), while in *G. glabra*, ONI and MEI were barely significant ( $p < 0.05$ ) and for SOI it was non-significant ( $p = 0.29$ ) (Fig. 6e, Fig. 6g and Fig. 6i). Complementary sensitivity to the MEI and ONI monthly indices exists in the TRW chronologies of *C. pyriformis* and *G. glabra* in the Chocó region: Both correlate negatively with these ENSO indices but during different and complementary months of the current year: *C. pyriformis* from January to May ( $p < 0.01$ ) and *G. glabra* from June to December ( $p < 0.05$ ) ( Fig. 6h and j).





## 5. Conclusions

Here we present the first dendroclimatological research on the hyper-dominant tropical species *Goupia glabra* in the rainiest conditions never globally surpassed (mean annual rainfall of 7219 mm). The least rainy month of our study area overpasses 2.8 times the potential evapotranspiration. Here, we have demonstrated the incorrect of a widespread belief among tropical dendrochronologists: In non-flooded forests, annual droughts promote the formation of annual rings in tropical trees (Brienen et al., 2016; Schöngart et al., 2017; Zuidema et al., 2022) among many others. Furthermore, the correlation between the residual chronology and annual rainfall ( $r = 0.51$ ,  $p < 0.01$ ) exceeded those of the only previously existing chronologies for the Chocó region, the rainiest in the Americas: *Cariniana pyriformis* and *Prioria copaifera*, (Herrera and del Valle, 2011; Moreno and del Valle, 2015), with mean rainfalls close to half our study area. Our study exceeds 3.6 times the mean annual precipitation (2000 mm) and 5.8 times the minimum monthly precipitation (60 mm) of ever-wet tropical forests (Underwood et al., 2014) (**Fig. S 1 c**). So, our study area could better be called a hyper-ever-wet tropical forest. The most surprising thing is that being so close to the maximum rainfall recorded for this species (7400 mm per year) (**Fig. 1** and **Fig. S 1**), *G. glabra* still responds positively to rainfalls. Therefore, it does not comply with either Liebig's or Shelford's Law (Shelford, 1931; Speer, 2010). According to the first of these laws, it should not respond to such high rainfalls; according to the second law, the answer should be significantly negative.

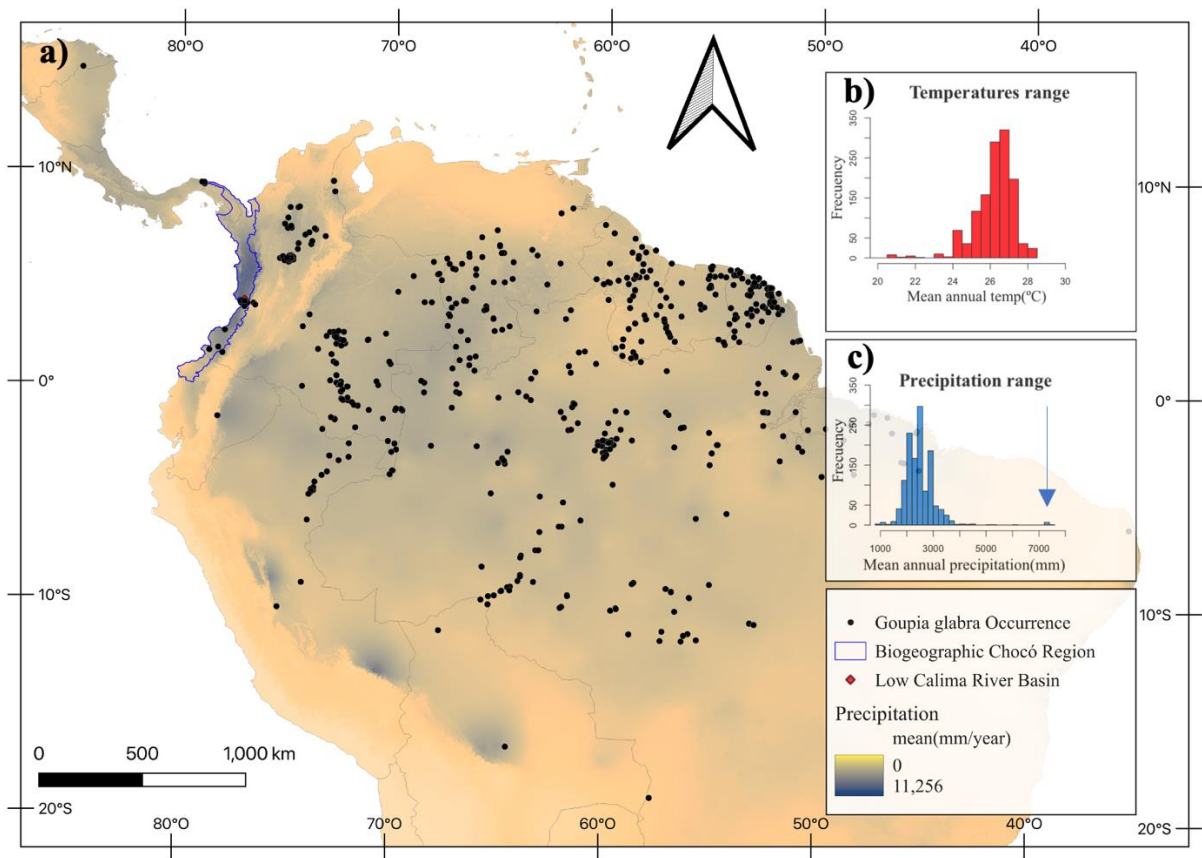
If we do not explore the tropical ever-wet and hyper-ever-wet tropical forests dendrochronologically, we will not be able to know how and why their trees respond to environmental variables and form annual growth rings. This study opens the enormous frontier of these forests to dendrochronological research, which represents about 30% of tropical rain forests (Underwood et al., 2014). These forests had been avoided by dendrochronologists due to unfunded prejudices.

In the extensive precipitation range of *G. glabra* (900 to 7400 mm mean annual rainfall, with and without dry seasons), there are these coincidences: annual ring formation, diffuse-porous rings, similar phenology, and that it grows during the rainiest season. We interpret this set of traits as a manifestation of memory in plants (Galviz et al., 2020). Hypothetically, *G. glabra* acquired these traits in its biogeographical region of origin. This region covers both seasonally dry and ever-wet Amazonian and Guianas forests. These genetically fixed traits are preserved by colonizing new areas of central Colombia, the Chocó region, and Central America.



# A. Supplementary Material

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**Fig. S 1.** Natural occurrence of the specie, precipitation, and temperature ranges. *a)* The black points indicate the natural occurrence of *G. glabra* where the specie has registered (GBIF 2022) and the layer shows the mean annual precipitation. *b)* the red histogram shows the temperature of each point of occurrence *c)* the blue histogram shows the precipitation range for each point registered and the blue arrow indicates the values of precipitation for the specie in the study area. Data are from WorldClim, 1970-2000 average (Fick and Hijmans, 2017).

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**Table S 1.** Age determination by post-bomb pike 14C of four trees *G. glabra*, the crossdating checking of annual formation of the tree rings for *G. glabra* are in Predated ring (year). F14C refers to the fraction 14C in per mil of radiocarbon analysis analyzed in an accelerator. Mass spectrometry (AMS) at the radiocarbon laboratory of Max Plant. Cal BC/AD refers to a midpoint year whit more probability using CALIBomb.

Sample code	Predated ring (Year)	F14C	Err (‰)	err	Calibrated date 1 AD	Calibrated date 2 AD	Cal BC/AD	Probability
<b>Ggla64-1</b>	1991	1.15	1.9	0.002	1990.4	1992.4	1991.35	0.796
<b>Ggla01-1</b>	1994	1.129	1.8	0.002	1994	1995.2	1994.59	0.775
<b>Ggla01-2</b>	1997	1.113	1.8	0.002	1996.9	1998.1	1997.46	1.0
<b>Ggla159-1</b>	1993	1.139	1.8	0.002	1993.6	1993.9	1993.75	0.542
<b>Ggla64-2</b>	2003	1.082	1.5	0.002	2003.6	2004.1	2003.84	0.77

**Table S 2.** Treeclim stationary bootstrapping between: Tree-ring width index (RWI) chronology of *G. glabra* and monthly climate data (temperature and precipitation) and the indices of El Niño Southern Oscillation (ENSO) SOI, ONI, and MEI (1960-2017), and the Short-Wave Radiation Index (1957-2016). The monthly climatic predictors, with the value of their corresponding coefficients, significance flags correspond to  $p < 0.05$ .

Variable	Month	Coefficient	Significance	Confidence interval lower	Confidence interval upper
Precipitation (timespan 1947 – 2017)	January	0.186	False	-0.41	0.374
	<b>February</b>	<b>0.323</b>	<b>True</b>	<b>0.059</b>	<b>56.4</b>
	March	0.055	False	0.254	0.327
	April	0.111	False	-0.102	0.312
	<b>May</b>	<b>0.341</b>	<b>True</b>	<b>0.14</b>	<b>0.505</b>

Variable	Month	Coefficient	Significance	Confidence interval lower	Confidence interval upper
	Jun	0.16	False	53	0.338
	<b>July</b>	<b>0.365</b>	<b>True</b>	<b>0.18</b>	<b>0.554</b>
	<b>August</b>	<b>0.31</b>	<b>True</b>	<b>0.076</b>	<b>0.51</b>
	September	0.208	False	-0.011	0.371
	<b>October</b>	<b>0.381</b>	<b>True</b>	<b>0.141</b>	<b>0.588</b>
	November	0.159	False	-0.051	0.368
	<b>December</b>	<b>0.324</b>	<b>True</b>	<b>0.064</b>	<b>0.566</b>
	January	-0.055	False	-0.327	0.227
	February	-0.135	False	-0.394	0.152
	March	-0.081	False	-0.31	0.141
	April	0.21	False	0.061	0.452
	May	-0.088	False	-0.332	-0.16
Temperature (Observed years: 1957 - 2016)	Jun	-0.185	False	-0.456	0.1
	July	-0.165	False	-0.439	0.162
	August	-0.257	False	-0.527	0.069
	<b>September</b>	<b>-0.273</b>	<b>True</b>	<b>-0.501</b>	<b>-0.003</b>
	October	-0.144	False	-0.412	0.16
	November	-0.136	False	-0.406	0.119
	December	-0.078	False	-0.368	0.198
SOI (Observed years: 1960 - 2016)	January	-0.018	False	-0.224	0.185
	February	-0.197	False	-0.424	0.057
	March	-0.034	False	-0.237	0.167

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Variable	Month	Coefficient	Significance	Confidence interval lower	Confidence interval upper
	April	0.084	False	-0.186	0.34
	May	0.159	False	-0.13	0.403
	Jun	0.202	False	-0.059	0.473
	July	0.26	False	-0.037	0.493
	August	0.156	False	-0.134	0.391
	September	0.228	False	-0.019	0.455
	October	0.126	False	-0.145	0.411
	November	0.244	False	-0.011	0.47
	December	0.185	False	-0.05	0.428
	January	-0.035	False	-0.233	0.159
	February	-0.043	False	-0.225	0.137
	March	-0.075	False	-0.265	0.111
	April	-0.128	False	-0.351	0.089
	May	-0.22	False	-0.481	0.063
ONI (Observed years: 1960 - 2016)	<b>Jun</b>	<b>-0.335</b>	<b>True</b>	<b>-0.561</b>	<b>-0.07</b>
	<b>July</b>	<b>-0.369</b>	<b>True</b>	<b>-0.57</b>	<b>-0.139</b>
	<b>August</b>	<b>-0.362</b>	<b>True</b>	<b>-0.557</b>	<b>-0.137</b>
	<b>September</b>	<b>-0.351</b>	<b>True</b>	<b>-0.549</b>	<b>-0.123</b>
	<b>October</b>	<b>-0.361</b>	<b>True</b>	<b>-0.564</b>	<b>-0.124</b>
	<b>November</b>	<b>-0.368</b>	<b>True</b>	<b>-0.576</b>	<b>-0.126</b>
	<b>December</b>	<b>-0.361</b>	<b>True</b>	<b>-0.572</b>	<b>-0.115</b>

<b>Variable</b>	<b>Month</b>	<b>Coefficient</b>	<b>Significance</b>	<b>Confidence interval lower</b>	<b>Confidence interval upper</b>
MEI (Observed years: 1960-2016)	January	0.006	False	-0.218	0.245
	February	-0.001	False	-0.205	0.231
	March	-0.076	False	-0.28	0.172
	April	-0.173	False	-0.395	0.105
	May	-0.295	False	-0.528	0.007
	<b>Jun</b>	<b>-0.378</b>	<b>True</b>	<b>-0.592</b>	<b>-0.108</b>
	<b>July</b>	<b>-0.367</b>	<b>True</b>	<b>-0.59</b>	<b>-0.105</b>
	<b>August</b>	<b>-0.324</b>	<b>True</b>	<b>-0.553</b>	<b>-0.061</b>
	<b>September</b>	<b>-0.322</b>	<b>True</b>	<b>-0.559</b>	<b>-0.043</b>
	<b>October</b>	<b>-0.343</b>	<b>True</b>	<b>-0.578</b>	<b>-0.049</b>
	<b>November</b>	<b>-0.366</b>	<b>True</b>	<b>-0.581</b>	<b>-0.069</b>
	<b>December</b>	<b>-0.355</b>	<b>True</b>	<b>-0.581</b>	<b>-0.071</b>
ShortWave.W.m2 . (Observed Years 2000 - 2019)	January	-0.15	False	-0.458	0.271
	<b>February</b>	<b>-0.46</b>	<b>True</b>	<b>-0.766</b>	<b>-0.039</b>
	March	-0.211	False	-0.588	0.263
	April	-0.285	False	-0.636	0.167
	May	-0.09	False	-0.506	0.367
	Jun	-0.107	False	-0.5	0.313
	July	-0.13	False	-0.503	0.295
	August	-0.329	False	0.77	0.177
	September	-0.36	False	-0.697	0.048
	October	0.022	False	-0.389	0.399

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Colombia

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Variable	Month	Coefficient	Significance	Confidence interval lower	Confidence interval upper
	November	-0.101	False	-0.681	0.515
	December	-0.284	False	-0.687	0.207

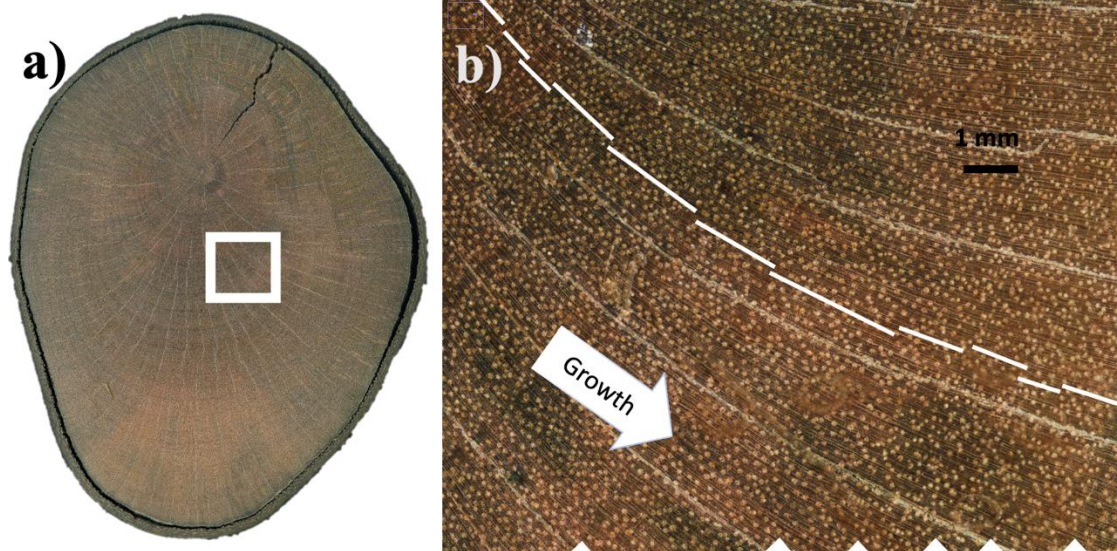
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### 1.1. Some *Goupia glabra* anatomy traits important to detect annual rings.

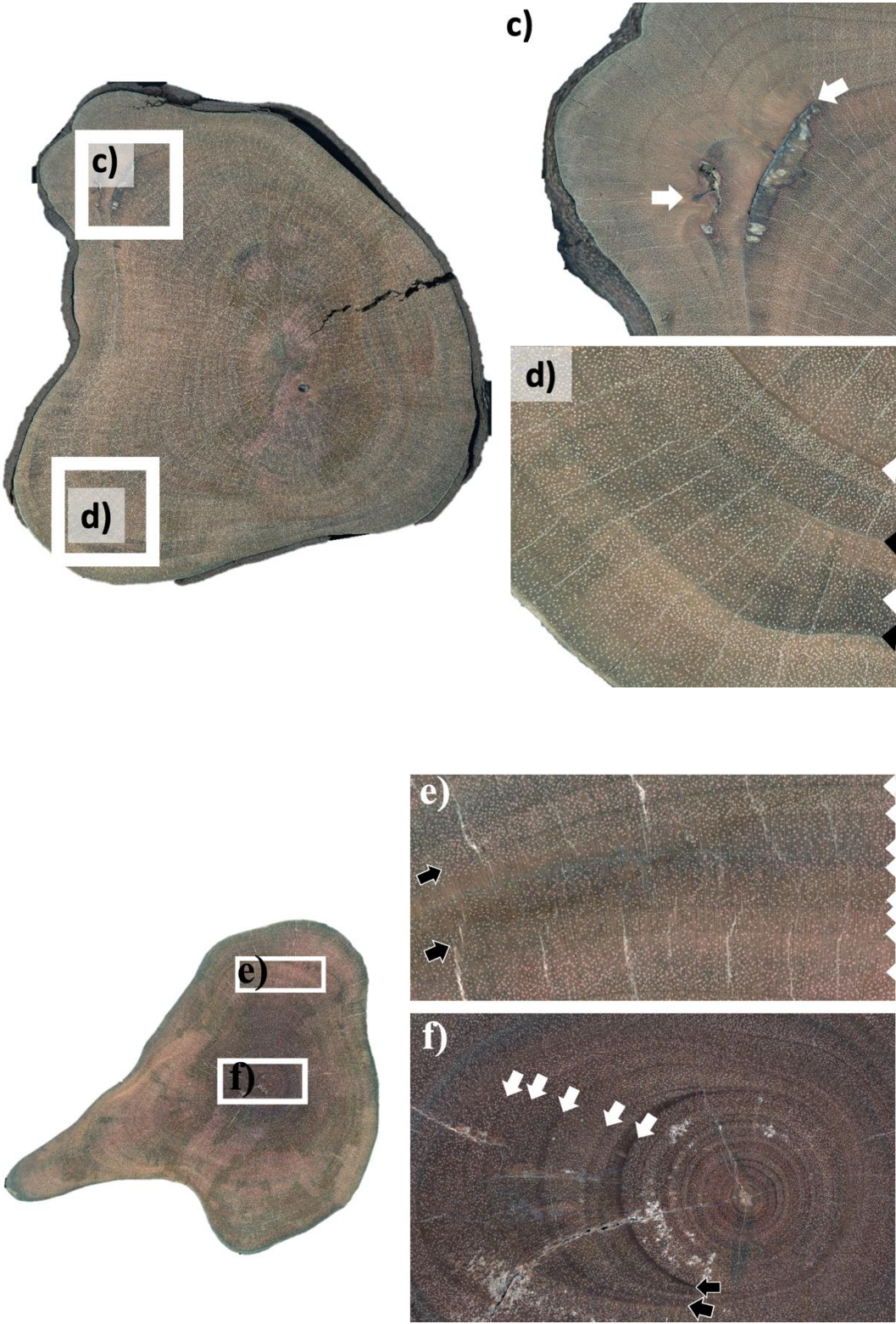
In this species, we observed that the presence of parenchyma axial cells was less common in tree-ring limits and with fewer vessels. We also observed that fewer vessels, accompanied by abrupt or tiny changes in vessel size, indicate tree-rings limits. We found that small directional changes in the medullary rays are useful to define an annual ring.

The specie has three anatomical features that make it difficult for the crossdating process. They are, first, small scars, apparently produced by injuries of insects in some sectors of the complete circumference around the disks (Fig. S 2 **c-d**). Second, tangential discontinuity is common to this specie, when it occurs, the only criteria for discarding or validating a true tree ring is through the Crossdating process. The third anatomical features are wedge growth rings (Fig. S 2 **c-d**), when wedge rings occur it's not possible realize a correct delimitation of the tree rings.



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**Fig. S 2.** Anatomical characteristics of tree rings of *G. glabra*. *a)* Complete cross-section *b)* the white lines indicate the slight medullary ray deviations that suggest each annual ring. *c)* the white arrows indicate scars area over the xylem, two scars probably produced by insects induced false ring formation. *d)* The black arrows show two false rings associated with the scars, and the white arrows indicate true tree rings. *e)* white arrows over the right side indicate true tree rings and black arrows show the wedge ring area where is not possible to recognize the tree rings with anatomical characters of wood. *f)* white arrows indicate true tree rings, and the black arrows indicate the wedge growth ring area.



## Bibliography

- Abràmoff, M.D., Magalhães, P.J., Ram, S.J., 2004. Image processing with ImageJ. *Biophotonics Int.* 11, 36–43.
- Andreu-Hayles, L., Santos, G., Herrera, D., Martín-Fernández, J., Ruiz-Carrascal, D., Boza-Espinoza, T., Fuentes, A., Jorgensen, P., 2015. Matching Dendrochronological dates with the Southern Hemisphere 14C bomb curve to confirm annual tree rings in *Pseudomedia rigida* from Bolivia. *Radiocarbon* 57, 1–13. doi:10.2458/azu
- Balima, L.H., Gebrekirstos, A., Kouamé, F.N.G., Nacoulma, B.M.I., Thiombiano, A., Bräuning, A., 2020. Life-span growth dynamics and xylem anatomical patterns of diffuse-porous *Afzelia africana* Sm. (Fabaceae) in different ecological zones in Burkina Faso. *Dendrochronologia* 64. doi:10.1016/j.dendro.2020.125752
- Borchert, R., Rivera, G., 2001. Photoperiodic control of seasonal development and dormancy in tropical stem-succulent trees. *Tree Physiol.* 21, 213–221. doi:10.1093/treephys/21.4.213
- Breitsprecher, A., Bethel, J., 1990. Stem-growth periodicity of trees in a tropical wet forest of Costa Rica. *Ecology* 71, 1156–1164.
- Brienen, R., Schöngart, J., Zuidema, P., 2016. Tree rings in the tropics: Insights into the ecology and climate sensitivity of tropical trees, in: Goldstein, G., Santiago, S.L. (Eds.), *Tropical Tree Physiology*. Springer, Switzerland, pp. 441–461. doi:10.1007/978-3-319-27422-5
- Bunn, A.G., 2010. Statistical and visual crossdating in R using the dplR library. *Dendrochronologia* 28, 251–258. doi:10.1016/j.dendro.2009.12.001
- Bunn, A.G., 2008. A dendrochronology program library in R (dplR). *Dendrochronologia* 26, 115–124. doi:10.1016/j.dendro.2008.01.002
- Callado, C., da Silva Neto, S., Scarano, F., Costa, C., 2001. Periodicity of growth rings in some flood-prone trees of the Atlantic Rain Forest in Rio de Janeiro, Brazil. *Trees* 15, 492–497. doi:10.1007/s00468-001-0128-4
- Callado, C.H., Roig, F.A., Tomazello-Filho, M., Barros, C.F., 2013. Cambial growth

- periodicity studies of south American woody species -a review. *IAWA J.* 34, 213–230. doi:10.1163/22941932-00000019
- Cannon, P., 1985. Comparative analysis of the soils in the Bajo Calima concession in the primary forest and after clearcutting. *Cart. Colomb. Cali, Colomb. Ninth Annu, Forestry research in the Bajo Calima concession*, pp.
- Cintra, B.B.L., Schietti, J., Emillio, T., Martins, D., Moulatlet, G., Souza, P., Levis, C., Quesada, C.A., Schöngart, J., 2013. Soil physical restrictions and hydrology regulate stand age and wood biomass turnover rates of Purus-Madeira interfluvial wetlands in Amazonia. *Biogeosciences* 10, 7759–7774. doi:10.5194/bg-10-7759-2013
- Clark, D.A., Clark, D.B., 1994. Climate-induced annual variation in canopy tree growth in a Costa Rican Tropical Rain Forest. *J. Ecol.* 82, 865–872.
- del Valle, J.I., Guarín, J.R., Sierra, C.A., 2014. Unambiguous and low-cost determination of growth rates and ages of tropical trees and palms. *Radiocarbon* 56, 39–52. doi:10.2458/56.16486
- Détienne, P., 1989. Appearance and Periodicity of Growth Rings in some Tropical Woods. *IAWA J.* 10, 123–132. doi:10.1163/22941932-90000480
- Detienne, P., Barbier, C., 1988. Rythmes De Croissance De Quelques Essences De Guyane Francaise. *Bois forêts des Trop.*
- dos Santos, M., de Assis Ribeiro dos Santos, F., Callado, C.H., Barros, C.F., da Silva, L.B., 2017. Growth rings in woody species of Ombrophilous Dense Forest: occurrence, anatomical features and ecological considerations. *Brazilian J. Bot.* 40, 281–290. doi:10.1007/s40415-016-0313-8
- Duarte, P.J., Borges, C.C., Ferreira, C.A., Cruz, T.M., de Souza, W.R.Q., Mori, F.A., 2021. Anatomical identification of tropical woods traded in Lavras, Brazil. *J. Trop. For. Sci.* 33, 95–103. doi:10.26525/jtfs2020.32.4.95
- Faber-Langendoen, D., 1992. Ecological constraints on rain forest management at Bajo Calima, western Colombia. *For. Ecol. Manage.* 53, 213–244. doi:10.1016/0378-1127(92)90044-A
- Faber-Langendoen, D., Gentry, A.H., 1991. The Structure and Diversity of Rain Forests at Bajo Calima, Choco Region, Western Colombia. *Biotropica* 23, 2. doi:10.2307/2388682
- Fahn, A., 1995. Seasonal cambial activity and phytogeographic origin of woody plants: a hypothesis. *Isr. J. Plant Sci.* 43, 69–75. doi:10.1080/07929978.1995.10676592
- Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces

- for global land areas. *Int. J. Climatol.* 37, 4302–4315. doi:10.1002/joc.5086
- Fonti, P., Von Arx, G., García-González, I., Eilmann, B., Sass-Klaassen, U., Gärtner, H., Eckstein, D., 2010. Studying global change through investigation of the plastic responses of xylem anatomy in tree rings. *New Phytol.* 185, 42–53. doi:10.1111/j.1469-8137.2009.03030.x
- Forero, L., 2014. Dinámica del bosque húmedo tropical en un periodo de 30 años de intervenciones y sus efectos en algunas variables edafológicas. Bajo Calima, Buenaventura, Colombia. Univ. Nac. Colomb. 110.
- Frisk, T., 1978. Utilización de las maderas tropicales mixtas para papel. *Organ. las Nac. Unidas para la Agric. y la Aliment.* Vol. 30, N, 63–64.
- Galviz, Y.C.F., Ribeiro, R. V., Souza, G.M., 2020. Yes, plants do have memory. *Theor. Exp. Plant Physiol.* 32, 195–202. doi:10.1007/s40626-020-00181-y
- GBIF, 2022. Infraestructura Mundial de Información en Biodiversidad. <https://www.gbif.org/es/occurrence/search> [WWW Document].
- Gentry, A.H., 1982. Patterns of Neotropical plant species diversity, in: *Evolutionary Biology*. Plenum Press, New York, pp. 1–84. doi:10.1007/978-1-4615-6968-8\_1
- Giraldo, J.A., 2022. Annual tree rings in the rainiest forests of the americas 131.
- Giraldo, J.A., del Valle, J.I., González-Caro, S., Sierra, C.A., 2022. Intra-annual isotope variations in tree rings reveal growth rhythms within the least rainy season of an ever-wet tropical forest. *Trees - Struct. Funct.* doi:10.1007/s00468-022-02271-7
- Giraldo, Valle, D., Sierra, Melo, O., 2020. Dendrochronological potential of trees from America's rainiest region. In: Pompa-García M, Camarero JJ (eds) *Latin American Dendroecology Combining tree-ring sciences and ecology in a megadiverse territory.*, Latin American Dendroecology. Springer International Publishing. doi:10.1007/978-3-030-36930-9\_6
- Gómez, A., 2019. Delimitación de anillos de crecimiento en la especie *Goupia glabra* mediante técnicas de visión por computador Alejandro. Universidad Nacional de Colombia Facultad.
- Green, J.K., Berry, J., Ciais, P., Zhang, Y., Gentine, P., 2020. Amazon rainforest photosynthesis increases in response to atmospheric dryness. *Sci. Adv.* 6, 1–10. doi:DOI: 10.1126/sciadv.abb7232
- Hammond, D.S., 2005. Tropical Forests of the Guiana Shield Ancient Forests in a Modern World, -Socio-economic Aspects of Guiana Shield Forest Use.

- Herrera, D.A., del Valle, J.I., 2011. Water level reconstruction of the Atrato river with tree rings of *Prioria copaifera*. *Sist. Inf. Científica Dyna*, , 121–130.
- Hua, Q., Turnbull, J.C., Santos, G.M., Rakowski, A.Z., Ancapichún, S., De Pol-Holz, R., Hammer, S., Lehman, S.J., Levin, I., Miller, J.B., Palmer, J.G., Turney, C.S.M., 2021. Atmospheric Radiocarbon for the Period 1950-2019. *Radiocarbon* 64, 723–745. doi:10.1017/RDC.2021.95
- Islam, M., Rahman, M., Bräuning, A., 2019. Impact of extreme drought on tree-ring width and vessel anatomical features of *Chukrasia tabularis*. *Dendrochronologia* 53, 63–72. doi:10.1016/j.dendro.2018.11.007
- Islam, M., Rahman, M., Bräuning, A., 2018. Long-term hydraulic adjustment of three tropical moist forest tree species to changing climate. *Front. Plant Sci.* 871, 1–16. doi:10.3389/fpls.2018.01761
- ITTO, 2017. Cupiúba, Kabukalli (*Goupia glabra*).
- Kassambara, A., 2022. Package : ggpubr. “ggplot2” Based Publication Ready Plots.”
- Kato, S., Loeb, N.G., Rose, F.G., Doelling, D.R., Rutan, D.A., Caldwell, T.E., Yu, L., Weller, R.A., 2013. Surface irradiances consistent with CERES-derived top-of-atmosphere shortwave and longwave irradiances. *J. Clim.* 26, 2719–2740. doi:10.1175/JCLI-D-12-00436.1
- Köhl, M., Neupane, P.R., Lotfiomran, N., 2017. The impact of tree age on biomass growth and carbon accumulation capacity: A retrospective analysis using tree ring data of three tropical tree species grown in natural forests of Suriname. *PLoS One* 12, 1–17. doi:10.1371/journal.pone.0181187
- Lacoste, J.F., Alexandre, D.Y., 1991. Le goupí (*Goupia glabra* Aubl), essence forestière d’avenir en Guyane: analyse bibliographique. *Ann. des Sci. For.* 48, 429–441.
- Ladrach, W., 1985. Forest research in the Bajo Calima concession. *Cart. Colomb. S.A., Cali Colomb. Ninth Annu.*
- Ladrach, W., Wright, J., 1995. Natural Regeneration in a Secondary Colombian Rain Forest. *J. Sustain. For.* 3, 15–38. doi:10.1300/j091v03n01\_02
- Laurance, W.F., Nascimento, H.E.M., Laurance, S.G., Condit, R., D’Angelo, S., Andrade, A., 2004. Inferred longevity of Amazonian rainforest trees based on a long-term demographic study. *For. Ecol. Manage.* 190, 131–143. doi:10.1016/j.foreco.2003.09.011
- López, J., Del Valle, J.I., Giraldo, J.A., 2014. Flood-promoted vessel formation in *Prioria copaifera* trees in the Darien Gap, Colombia. *Tree Physiol.* 34, 1079–1089.



- doi:10.1093/treephys/tpu077
- Lotfiomran, N., Köhl, M., 2017. Retrospective analysis of growth. A contribution to sustainable forest management in the tropics, IAWA Journal. doi:10.1163/22941932-20170173
- Lozano, L.A., González, J., 2011. Bajo Calima: riqueza biológica y cultural afectada por la extracción de maderas tropicales. Rev. LEBRET 0. doi:10.15332/rl.v0i3.52
- Mesa, O.J., Rojo, J.D., 2020. On the general circulation of the atmosphere around Colombia. Rev. la Acad. Colomb. Ciencias Exactas, Físicas y Nat. 44, 857–875. doi:10.18257/raccefyn.899
- Miller, R.B., Détienne, P., 2001. Major Timber Trees of Guyana. Wood Anatomy.
- Moreno, M.M., del Valle, J.I., 2015. Influence of local climate and ENSO on the growth of Abarco (*Cariniana pyriformis*) in Chocó, Colombia. Trees 29, 97–107. doi:10.1007/s00468-014-1094-y
- Myers, N., Mittermeyer, R.A., Mittermeyer, C.G., Da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858. doi:10.1038/35002501
- Nahuz et al., A., 2013. Catálogo de madeiras brasileiras para a construção civil, <https://medium.com/>. São Paulo.
- Nogueira, E.M., Fearnside, P.M., Nelson, B.W., França, M.B., 2007. Wood density in forests of Brazil's "arc of deforestation": Implications for biomass and flux of carbon from land-use change in Amazonia. For. Ecol. Manage. 248, 119–135. doi:10.1016/j.foreco.2007.04.047
- O'Brien, J.J., Oberbauer, S.F., Clark, D.B., Clark, D.A., 2008. Phenology and stem diameter increment seasonality in a Costa Rican wet tropical forest. Biotropica 40, 151–159. doi:10.1111/j.1744-7429.2007.00354.x
- Oliveira, C.L., 2010. Estimativas da dinâmica de carbono na biomassa lenhosa de terra firme na reserva de desenvolvimento sustentável amanhã por métodos dendrocronológicos. Instituto Nacional de Pesquisas da Amazônia - INPA.
- Oliveira, M.F., 2014. Critérios para o manejo sustentável de duas espécies madeireiras das florestas tropicais do Mato Grosso. Universidade Federal do Paraná.
- Pacheco, A., 2020. Assessing Forest Degradation in Bajo Calima – Colombia from Multi-Frequency and Multi-Temporal Synthetic Aperture Radar ( SAR ). University of Leicester.

- Pérez, O.A., Lucas, E., Jaramillo, C., Monro, A., Morris, S.K., Bogarín, D., Greer, D., Dodsworth, S., Aguilar-Cano, J., Sanchez Meseguer, A., Antonelli, A., 2019. The Origin and Diversification of the Hyperdiverse Flora in the Chocó Biogeographic Region. *Front. Plant Sci.* 10, 1–9. doi:10.3389/fpls.2019.01328
- Pons, T.L., Helle, G., 2011. Identification of anatomically non-distinct annual rings in tropical trees using stable isotopes. *Trees* 25, 83–93. doi:10.1007/s00468-010-0527-5
- Poveda, G., Mesa, O., 2000. On the existence of Lloró (the rainiest locality on earth): enhanced ocean-land-atmosphere interaction by a low-level jet. *Geophys. Res. Lett.* 27, 1675–1678. doi:10.1029/1999GL006091
- R Development Core Team, 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ramírez, del Valle, 2011. Paleoclima de La Guajira, Colombia; según los anillos de crecimiento de *Capparis odoratissima* (Capparidaceae). *Rev. Biol. Trop.* 59, 1389–1405. doi:10.15517/rbt.v0i0.3406
- Ramírez, J.A., del Valle, J.I., 2012. Local and global climate signals from tree rings of *Parkinsonia praecox* in La Guajira, Colombia. *Int. J. Climatol.* 32, 1077–1088. doi:10.1002/joc.2335
- Reimer, P.J., Austin, W.E.N., Bard, E., Bayliss, A., Blackwell, P.G., Bronk Ramsey, C., Butzin, M., Cheng, H., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Hajdas, I., Heaton, T.J., Hogg, A.G., Hughen, K.A., Kromer, B., Manning, S.W., Muscheler, R., Palmer, J.G., Pearson, C., Van Der Plicht, J., Reimer, R.W., Richards, D.A., Scott, E.M., Southon, J.R., Turney, C.S.M., Wacker, L., Adolphi, F., Büntgen, U., Capano, M., Fahrni, S.M., Fogtmann-Schulz, A., Friedrich, R., Köhler, P., Kudsk, S., Miyake, F., Olsen, J., Reinig, F., Sakamoto, M., Sookdeo, A., Talamo, S., 2020. The IntCal20 Northern Hemisphere Radiocarbon Age Calibration Curve (0–55 cal kBP). *Radiocarbon* 62, 725–757. doi:10.1017/RDC.2020.41
- Restrepo-Coupe, N., da Rocha, H.R., Hutyra, L.R., da Araujo, A.C., Borma, L.S., Christoffersen, B., Cabral, O.M.R., de Camargo, P.B., Cardoso, F.L., da Costa, A.C.L., Fitzjarrald, D.R., Goulden, M.L., Kruijt, B., Maia, J.M.F., Malhi, Y.S., Manzi, A.O., Miller, S.D., Nobre, A.D., von Randow, C., Sá, L.D.A., Sakai, R.K., Tota, J., Wofsy, S.C., Zanchi, F.B., Saleska, S.R., 2013. What drives the seasonality of photosynthesis across the Amazon basin? A cross-site analysis of eddy flux tower measurements from the Brasil flux network. *Agric. For. Meteorol.* 182–183, 128–144.

- doi:10.1016/j.agrformet.2013.04.031
- Santini, L., 2013. Descrição macroscópica e microscópica da madeira aplicada na identificação das principais espécies comercializadas no Estado de São Paulo - Programas "São Paulo Amigo da Amazônia" e "Cadmadeira." Diss. 272.
- Schöngart, J., Bräuning, A., Barbosa, A.C.M.C., Lisi, C.S., de Oliveira, J.M., 2017. Dendroecological Studies in the Neotropics: History, Status and Future Challenges, in: Amoroso, M., Daniels, L., Baker, P., Camarero, J. (Eds.), *Dendroecology. Ecological Studies (Analysis and Synthesis)*, Vol 231. Springer, Cham, pp. 35–73. doi:10.1007/978-3-319-61669-8\_3
- Shelford, E., 1931. Some Concepts of Bioecology. *Ecol. Soc. Am. Stable* 12, 455–467.
- Silvia, A., Barajas, J., 2017. Anatomía de la madera de especies arbóreas de un bosque mesófilo de montaña: un enfoque ecológico-evolutivo. *Bot. Sci.* 51. doi:10.17129/botsci.1712
- Speer, J., 2010. *Fundamentals of Tree Ring Research*, The University of Arizona Press. Arizona.
- Steinhof, A., Altenburg, M., Machts, H., 2017. Sample Preparation at the Jena 14C Laboratory. *Radiocarbon* 59, 815–830. doi:10.1017/RDC.2017.50
- Tally, 2006. *SilverFast: The Official Guide*. John Wiley.
- Tanaka, A., 2005. Avaliação de anéis de crescimento de espécies florestais de terra-firme no município de Novo Aripuanã. Universidade Federal do Amazonas-UFAM.
- ter Steege, H., Pitman, N.C.A., Sabatier, D., Baraloto, C., Salomão, R.P., Guevara, J.E., Phillips, O.L., Castilho, C. V., Magnusson, W.E., Molino, J.-F., Monteagudo, A., Núñez Vargas, P., Montero, J.C., Feldpausch, T.R., Coronado, E.N.H., Killeen, T.J., Mostacedo, B., Vasquez, R., Assis, R.L., Terborgh, J., Wittmann, F., Andrade, A., Laurance, W.F., Laurance, S.G.W., Marimon, B.S., Marimon, B.-H., Guimarães Vieira, I.C., Amaral, I.L., Brienen, R., Castellanos, H., Cárdenas López, D., Duivenvoorden, J.F., Mogollón, H.F., Matos, F.D. de A., Dávila, N., García-Villacorta, R., Stevenson Diaz, P.R., Costa, F., Emilio, T., Levis, C., Schiatti, J., Souza, P., Alonso, A., Dallmeier, F., Montoya, A.J.D., Fernandez Piedade, M.T., Araujo-Murakami, A., Arroyo, L., Gribel, R., Fine, P.V.A., Peres, C.A., Toledo, M., Aymard C., G.A., Baker, T.R., Cerón, C., Engel, J., Henkel, T.W., Maas, P., Petronelli, P., Stropp, J., Zartman, C.E., Daly, D., Neill, D., Silveira, M., Paredes, M.R., Chave, J., Lima Filho, D. de A., Jørgensen, P.M., Fuentes, A., Schöngart, J., Cornejo Valverde,

- F., Di Fiore, A., Jimenez, E.M., Peñuela Mora, M.C., Phillips, J.F., Rivas, G., van Andel, T.R., von Hildebrand, P., Hoffman, B., Zent, E.L., Malhi, Y., Prieto, A., Rudas, A., Ruschell, A.R., Silva, N., Vos, V., Zent, S., Oliveira, A.A., Schutz, A.C., Gonzales, T., Trindade Nascimento, M., Ramirez-Angulo, H., Sierra, R., Tirado, M., Umaña Medina, M.N., van der Heijden, G., Vela, C.I.A., Vilanova Torre, E., Vriesendorp, C., Wang, O., Young, K.R., Baider, C., Balslev, H., Ferreira, C., Mesones, I., Torres-Lezama, A., Urrego Giraldo, L.E., Zagt, R., Alexiades, M.N., Hernandez, L., Huamantupa-Chuquimaco, I., Milliken, W., Palacios Cuenca, W., Pauletto, D., Valderrama Sandoval, E., Valenzuela Gamarra, L., Dexter, K.G., Feeley, K., Lopez-Gonzalez, G., Silman, M.R., 2013. Hyperdominance in the Amazonian Tree Flora. *Science* (80- ). 342, 1243092. doi:10.1126/science.1243092
- Thornthwaite, C.W., 1948. An approach toward a rational classification of climate. *Geogr. Rev.* 38, 55. doi:10.2307/210739
- Trevizor, T.T., 2011. Anatomia comparada do lenho de 64 espécies arbóreas de ocorrência natural na floresta tropical Amazônica no estado do Pará. Diss. Escola Superior de Agricultura “Luiz de Queiroz.”
- Underwood, E.C., Olson, D., Hollander, A.D., Quinn, J.F., 2014. Ever-wet tropical forests as biodiversity refuges. *Nat. Clim. Chang.* 4, 740–741. doi:10.1038/nclimate2351
- Vásquez, A., Ramírez, A., 2005. Maderas comerciales en el valle de Aburrá. Área Metropolitana del Valle de Aburrá, Medellín.
- Vetter, R., Botosso, P., 1989. Remarks on age and growth rate determination of Amazonian trees. *IAWA Bull. n.s.*, Vol. 10 (2), 1989 133-145 10, 133–145.
- Yan, Y., 2005. Inter tropical convergence zone (ITCZ), in: Oliver, J.E. (Ed.), *Encyclopedia of World Climatology*. Springer, Dordrecht, pp. 429–432.
- Zang, C., Biondi, F., 2015. Treeclim: An R package for the numerical calibration of proxy-climate relationships. *Ecography (Cop.)*. 38, 431–436. doi:10.1111/ecog.01335
- Zuidema, P.A., Babst, F., Groenendijk, P., Trouet, V., Abiyu, A., Acuña-Soto, R., Adenesky-Filho, E., Alfaro-Sánchez, R., Aragão, J.R.V., Assis-Pereira, G., Bai, X., Barbosa, A.C., Battipaglia, G., Beeckman, H., Botosso, P.C., Bradley, T., Bräuning, A., Brienen, R., Buckley, B.M., Camarero, J.J., Carvalho, A., Ceccantini, G., Centeno-Erguera, L.R., Cerano-Paredes, J., Chávez-Durán, Á.A., Cintra, B.B.L., Cleaveland, M.K., Couralet, C., D’Arrigo, R., del Valle, J.I., Dünisch, O., Enquist, B.J., Esemann-Quadros, K., Eshetu, Z., Fan, Z.X., Ferrero, M.E., Fichtler, E., Fontana, C., Francisco, K.S., Gebrekirstos, A., Gloor, E., Granato-Souza, D.,

Haneca, K., Harley, G.L., Heinrich, I., Helle, G., Inga, J.G., Islam, M., Jiang, Y. mei, Kaib, M., Khamisi, Z.H., Koprowski, M., Kruijt, B., Layme, E., Leemans, R., Leffler, A.J., Lisi, C.S., Loader, N.J., Locosselli, G.M., Lopez, L., López-Hernández, M.I., Lousada, J.L.P.C., Mendivelso, H.A., Mokria, M., Montóia, V.R., Moors, E., Nabais, C., Ngoma, J., Nogueira Júnior, F. de C., Oliveira, J.M., Olmedo, G.M., Pagotto, M.A., Panthi, S., Pérez-De-Lis, G., Pucha-Cofrep, D., Pumijumnong, N., Rahman, M., Ramirez, J.A., Requena-Rojas, E.J., Ribeiro, A. de S., Robertson, I., Roig, F.A., Rubio-Camacho, E.A., Sass-Klaassen, U., Schöngart, J., Sheppard, P.R., Slotta, F., Speer, J.H., Therrell, M.D., Toirambe, B., Tomazello-Filho, M., Torbenson, M.C.A., Touchan, R., Venegas-González, A., Villalba, R., Villanueva-Diaz, J., Vinya, R., Vlam, M., Wils, T., Zhou, Z.K., 2022. Tropical tree growth driven by dry-season climate variability. *Nat. Geosci.* 15, 269–276. doi:10.1038/s41561-022-00911-8