Annual Tree Rings in the Rainiest Forests of the Americas

Jorge Andrés Giraldo Jiménez

Universidad Nacional de Colombia
Facultad Ciencias Agrarias, Área Curricular en Bosques y Conservación Ambiental
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Abstract

In this dissertation, I explore the dendrochronological potential of trees from a lowlands tropical wet forest (Precipitation over 7,200 mm y^{-1}), without seasonal water deficit or flooding. I study the causes and sensitivity of annual growth rings to climate variables in several tree species by different methods. I analyzed the anatomical features of 81 tree species (~ 45% showed well-defined tree rings) (Chapter 1). Then I present results of tree ring frequency and possible causes of tree ring formation. I observed both positive and negative growth answers to water and light availability, depending on the tree species, suggesting that either excess or deficit of growth factors may explain seasonal growth rhythms in some trees (Chapter 2). This fact is also observed by the intra-annual variability of stable isotopes in tree rings (Chapter 3). As a study case, I present a practical application of dendroecology as an effective tool for resolving disputes in forensic sciences, the first carried in the biogeographic Chocó region (Chapter 4). This research opens a new frontier for tree rings science, the ever-wet tropical forests without water deficit.

Keywords: dendrochronology, Chocó region, radiocarbon, stable isotopes, tropical trees.

Anillos de crecimiento anuales en la región más lluviosa de las Americas

Resumen

En esta disertación, exploro el potencial dendrocronológico de los árboles de los bosques siempre húmedos tropicales (Precipitación superior a 7,200 mm año^{-1}), que no presentan déficit hídrico o inundaciones periódicas. Se estudian las causas y la sensibilidad de los anillos de crecimiento anuales a variables climáticas en muchas especies de árboles, a través de diferentes métodos. Son analizadas las características anatómicas de la madera en 81 especies de árboles (~ 45% presentan anillos de crecimiento bien definidos) (Capítulo 1). En el Capítulo 2, se presentan los resultados de la frecuencia de anillos en muchas especies y se exploran los posibles detonantes ambientes de su formación. Se obtienen observaciones tanto positivas como negativas entre el crecimiento, el agua y la disponibilidad de luz, dependiendo de la especie; lo cual sugiere que tanto el déficit como el exceso del crecimiento pueden ser factores que determinan el crecimiento rítmico en algunas especies de árboles. Dicha evidencia También es observada a través de la variabilidad intra anual de las proporciones isotópicas del oxígeno en la celulosa ($\delta^{18}O_{celulosa}$) (Capítulo 3). Como un caso de estudio, se presenta una aplicación práctica de la dendrocronología como una herramienta efectiva para resolver disputas legales, siendo ese el primer ejemplo de dicha aplicación, llevado a cabo en la región biogeográfica del Chocó (Capítulo 4). Esta investigación abre una nueva frontera en la ciencia de los anillos de crecimiento, los bosques siempre húmedos tropicales carentes de déficit hídrico.

Palabras clave: dendrocronología, Región del Chocó Biogeográfico, radiocarbono, isótopos estables, árboles tropicales.

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Introduction

Tree growth rhythms are seasonal events observed on different plant tissues and organs such as vascular cambium, leaves, branches, and reproductive structures (Albert et al. 2019), genetically determined but modulated by environmental conditions (Lüttge and Hertel 2009; Fyllas et al. 2017). Vascular cambium rhythm is related to tree size increment (i.e., tree growth), commonly observed as wood anatomy changes due to variation in growth rate. Such wood anatomy changes appear as an accumulation of layers, also known as tree rings (Fritts 1976).

In the last century, the belief that tropical trees had no growth rings because of a lack of thermal or photoperiod seasonality, compared with temperate and boreal regions (Jacoby 1989; Whitmore 1990; McCarroll and Loader 2004; Turner 2004; Begon et al. 2006), led to the slow development of the tropical dendrochronology. However, when considering different triggering factors, tree-rings research in the tropics increased nearly exponentially. Over the last two decades, many studies have demonstrated the occurrence of annual tree rings in diverse tropical ecosystems such as semi-arid, dry, semi-deciduous, humid, and wet forests, savannahs, floodplains, estuaries, mangroves, and high mountains trees (Schöngart et al. 2002, 2017; Worbes 2002; Brienen and Zuidema 2005; Zuidema et al. 2012; Brienen et al. 2016). While temperature, water availability, and light availability may control tropical trees growth, varying across species and ecosystems (Rozendaal and Zuidema 2011); rainfall seasonality and flooding are considered the main dominant triggers to explain annual growth rings in lowland tropical trees (Brienen et al. 2016; Schöngart et al. 2017).

The booming of dendrochronology in tropics has allowed answering several questions about ecology, conservation, climatology, hydrology, growth modeling to sustained forest management, modeling the ontogenetic growth to obtain significant population traits as life span, mean life, and life expectancy, the phases of release and suppression of tree growth in forests, among others (Schöngart 2008; Rozendaal 2010; Ballantyne et al. 2011; Giraldo and del Valle 2011; Inga and del Valle 2017; Stahle et al. 2020). But most studies still focus on studying tree growth patterns, wood anatomy, and the causes and sensitivity of tree ring to climate variables (Schöngart et al. 2017; Marcelo-Peña et al. 2020; Pearl et al. 2020), probably due to the highly diverse ecosystems in which tree species develop different growth strategies.

Even though annual growth rings in many tropical tree species could be explained mainly by the seasonal water availability paradigm (Wagner et al. 2012; Brienen et al. 2016; Mendivelso et al. 2016; Schöngart et al. 2017); the environmental triggers of the growth ring in trees of the lowlands tropical rainforests (Precipitation over 7,200 mm y^{-1}), without seasonal water deficit or flooding, remain unexplored. This probably has been occurred by sampling difficulties or because scientists were unaware of the existence of such ecosystems.

Tropical tree diversity tends to increases with precipitations. Wetter tropical forests sustain the most diverse plant communities on Earth (Gentry 1988; Givnish 1999). Along the Pacific coast of South America, from Northern Ecuador to the Colombian–Panamanian Darien Gap, the Biogeographic Chocó Region is found, the rainiest on all American continents. This Region includes, according to recent research (Mesa and Rojo 2020), the rainiest place on Earth located at López de Micay village, which exceeds the 13,000 mm mean annual rainfall, is about 120 km South far from the study area. The Chocó Region is home to one of the greatest biological diversity on Earth, including many endemic species (Gentry 1988, 1989; Faber-Langendoen and Gentry 1991; Myers et al. 2000). The low-level jet stream (tropopause air current) centered around 5°N, known as the Chocó Jet, explains the high regional precipitation (Mesa and Rojo 2020). However, this region of the American Pacific is poor on instrumental records. Therefore, paleoclimatic records with an annual resolution are urgent to help determine with less uncertainty the trends of global change in the region.

Through this dissertation, I study the cambial growth rhythms (tree rings) and their frequency of the Chocó region. I explore possible causes and sensitivity of the growth rings to climate variables in several species from a lowland wet non-seasonal tropical forest with mean annual rainfall over 7,200 mm.

Hypothesis

According to Liebig's law, the growth of an organism is not controlled by all the available resources (light, temperature, water, nutrients, etc.); but by the scarcest resource in the environment, the limiting factor (Taylor 1934). This law is a simplification of the physiological response of plants to environmental pressure (Jones 1997). The limiting factor that controls annual tree growth each year represents the main variable recorded in the tree-rings thickness (Speer 2010; Stine 2019). Under this view, light availability, mainly photosynthetically active radiation, could be a limiting factor in high cloud cover regions such as non-seasonal hyper-humid forests. In particular, the light limitation could be extreme in the rainiest months in which cloud cover increases, inducing an annual pattern on tree growth (Restrepo-Coupe et al. 2013; Green et al. 2020). Then, the interaction between light and water availability may drive tree growth rhythms in tropical hyper-humid forests.

In ecology is well established that both deficit and excess of a growth factor produce stress limiting the plant growth (Schulze et al. 2019). Therefore, a law of the minimum and a law of the maximum should exist as limiting growth factors. These two laws are involved in Shelford's tolerance law (Niinemets and Valladares 2008): If other factors are not limiting, as the magnitude of a limiting factor increases, organisms respond by increasing their growth, up to a limit at which the response saturates. Subsequent increases in this factor produce less and less growth because the organism is growing under incremental stresses. So, in ever wet forests, the availability of water, measured as rainfall, should be close to the maximum tolerance threshold for some species. Hypothetically, too much precipitation maintains high water saturation in the soil, which reduces its aeration and favors hypoxic conditions in the roots limiting tree growth. I hypothesize that, in some species, light availability, soil moisture, and slight variation in rainfall exert control on cambial growth rhythms in hyper-humid tropical forests.

Throughout this dissertation, I try to contribute to the understanding of the causes of annual tree-rings formation, as a consequence of rhythmic growth, in several tree species from the biogeographic Chocó Region in Colombia. Classification of tree-ring structures in 82 species is contrasted with tropical literature. The dendrochronological potential of species, according to tree-ring visibility, is inferred from radiocarbon dating, dendrometers, cross-dating, or the stable isotopes ^{13}C and ^{18}O. I use these data to determine the sensitivity to climate variables as a surrogate of growth drivers. In a less rainy area of the same biogeographic region, I present a practical application of both annual tree rings and radiocarbon dating as an effective tool for resolving disputes in forensic sciences.

This dissertation probably contains the first dendroecological studies carried out in tropical hyper-humid forests, without an evident hydric seasonality, due to water deficit or flooding.

The objectives of this study are

- to determine the occurrence of tree rings structures in tropical tree species from the Biogeographic Chocó Region;
- to determine the promising species for dendrochronology according to an anatomical classification;
- to determine growth rings frequency in tree species by different methods (radiocarbon, cross-dating, and dendrometer observations);
- to assess possible environmental drivers of tree-rings formation;
- to establish the intra-annual variability of $\delta^{13}C$ and $\delta^{18}O$ in tree rings in two species and to explore their relationships with environmental variables;
- to evaluate the use of annual tree rings and radiocarbon dating as tools to resolves disputes in forensic sciences.

1. Chapter 1. Dendrochronological potential of trees from America's rainiest region

With Jorge I. del Valle, Carlos A. Sierra, Omar Melo

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Abstract: Hydric seasonality, dry or flooding periods, has been the explanation given by dendrochronologists for the formation of growth rings in tropical trees. However, under tropical hyper-humid conditions, there are species with growth periodicity and, therefore, with visible growth rings useful for dendrochronology. We classify, for the first time, the anatomical structures of the growth rings of the tropical trees from the Biogeographic Chocó Region. An annual rainfall >7,200 mm without hydric seasonality characterizes the studied forest. We classify the tree rings as present (well or poorly defined), or absent. We also considered the feasibility of tree-rings dating (dendrochronological potential). We characterized 81 species of trees belonging to 38 families. About 82% of species with growth rings, 46% well defined, and 36% poorly defined. Absent rings in only 18%. Dendrochronological potential was high (14%), medium (25%), low (43%), and null (18%). We contrast our results with vast literature around tropics. Our results suggest that still without any hydric seasonality, many tropical tree species develop growth rings. Our findings drive to new questions: What is the periodicity of tree rings in these non-seasonal hyper-humid environments? What other subtle seasonality could be involved in the growth periodicity of these species, or are they genetic?

Keywords**:** Tree rings, Non-seasonal rainfall, Biogeographic Chocó Region, Colombia

1.1 Introduction

In dendrochronology, the current paradigm states that exists a more likelihood of growth-rings formation in these cases: (1) in seasonally dry climates - water deficit- (Détienne and Barbier 1988; Vetter and Botosso 1989; Worbes 1995, 1999; Bullock 1997; Jalil et al. 1998; Borchert 1999; Enquist and Leffler 2001; Schöngart et al. 2002, 2017; Marcati et al. 2006; Brienen et al. 2009, 2016; Morel 2013; Groenendijk et al. 2014; Silva et al. 2019; Granato-Souza et al. 2019), (2) in periodically flooded environments which produce anoxic conditions for the root system (Worbes and Junk 1989; Schöngart et al. 2002, 2017; Worbes and Fichtler 2010; Brienen et al. 2016; Parolin et al. 2016), (3) in estuaries, due to variability in salt concentration (Menezes et al. 2003; Chowdhury et al. 2016; Phan et al. 2019), (4) in deciduous or semi-deciduous species (Borchert 1999; Lisi et al. 2008; Nath et al. 2016; Shimamoto et al. 2016), and (5) under seasonal variations in irradiance, time of sunrise or sunset, or sunlight intensity (Breitsprecher and Bethel 1990; Clark and Clark 1994; O´Brien et al. 2008; Marcati et al. 2016; Shimamoto et al. 2016; Lotfiomran and Köhl 2017). According to literature cited, hydric seasonality, dry periods, or periodic floods, are the dominant triggering variables for the formation of growth rings in tropical trees.

Because of high cloud cover limits the availability of photosynthetically active radiation (Clark and Clark 1994), even in non-seasonal tropical forests, light appears to be the most limiting factor during the rainy season. Cloudiness induces a reduction in photosynthetic photon flux density (PPFD): the higher the cloud cover, the greater is the reduction in PPFD (Graham et al. 2003). Besides, seasonal water highlighted the predominant role of water availability that determined seasonal variation in tree growth (Wagner et al. 2012). The availability of water in the soil could be more determinative than rainfall in the formation of annual rings (Détienne and Barbier 1988; Falcon-Lang 1999; Silva et al. 2019). On the other hand, the excess of water in the soil, cloudiness, and low solar radiation in wet tropical climates could result in reduced photosynthesis, lower rates of tree growth, and low aerial biomass in the forests (Álvarez et al. 2017).

Some researchers have found that trees of boreal origin (Laurasia) tend to form growth rings more frequently than those of tropical origin (Fahn 1967; Tomlinson and Craichead 1972; Aguilar-Rodríguez and Barajas-Morales 2005). This type of growth rings, like a fingerprint of its phytogeographic origin, implied that their formation is from the genetic background. The variables that trigger the formation of growth rings in tropical trees can affect species in the same forest differently. For instance, species with annual growth rings from the Atlantic rainforests in Brazil responded to four different triggering variables: the period of leaves abscission, flooding, photoperiod, and endogenous periodicity (Callado et al. 2001).

Although information on growth periodicity of trees species in tropical hyper-humid, non-seasonal climates is scarce, there are species where periodic growth observed through annual measurements of diameter (Clark and Clark 1994), phenological observations (Frankie et al. 1974), cambial activity (Breitsprecher and Bethel 1990; O´Brien et al. 2008; Bräuning et al. 2009), and annual rings (Fichtler et al. 2003; Moreno and del Valle 2014). All of these measurements suggested the existence of a possible triggering of growth rates associated with rainfall, the duration of the day, the angle of insolation, or a combined response between rain and light levels. The evaluation of species with growth rings is the first step in selecting those potentially useful in dendrochronological studies (Tarhule and Hughes 2002; Tanaka 2005; Groenendijk et al. 2014; Silva et al. 2016; Islam et al. 2018). The presence of growth rings suggests the existence of growth periodicity, which is probably regulated by some environmental factor. In this study, for the first time, we perform an anatomical classification of the tree-ring structure in the rainiest region of the Americas, the Colombian Pacific, in a lowland, wet, non-seasonal tropical forest with mean annual rainfall >7200 mm. The discovery of species with dendrochronological potential in a tropical hyper-humid and non-seasonal region would open a new frontier in dendrochronology.

1.2 Materials and methods

1.2.1 Study area

The *Chocó* Biogeographic Region extends across the Pacific of South America, from northern Ecuador to the Colombian-Panamanian Darien Gap. Most of this region, the rainiest in the New World (Poveda and Mesa 2000), is located along the Colombian Pacific coast, on the western flank of the Western Cordillera of the Andes. In some sites, mean annual precipitation exceeds 12,000 mm, with extremes of 18,449 mm in 1953 and 19,839 mm in 1936 (Mesa et al. 1997). The study was conducted in a wet tropical forest in the Holdridge system (Holdridge 1967) with 4,000 - 8,000 mm mean annual precipitation.

Specifically, the study area belongs to the Low *Calima* River Basin, where the Tropical Forest Centre Pedro Antonio Pineda of the University of Tolima (3°55´N, 77°07´W) is located there (Figure 1-1), which includes an area of influence of 66,700 ha of forest that belongs to the Community Council of the Low *Calima* River Basin.

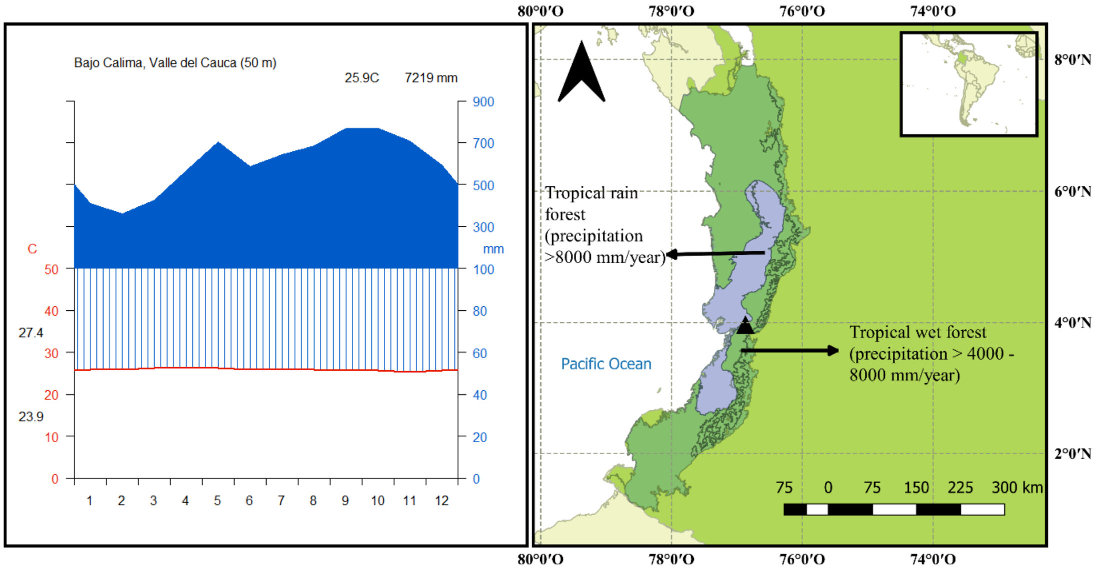

Figure 1-1: Study area in the Biogeographic Chocó Region, located both in the wet tropical forest and tropical rain forest life zones (Holdridge 1967). Walter and Lieth' ombrothermic climate diagram (Walter et al. 1975) of the Low *Calima* Climatic Station (triangle), which belongs to the Institute of Hydrology, Meteorology and Environmental Studies (IDEAM). The dark area indicates an excess of water year around (all months are hyper-humid)

1.2.2 Dry month analysis in study area

The climatic diagram (Figure 1-1) used widely by dendrochronologists incorporates the xerothermic index for intertropical climates of Gaussen (Bagnouls and Gaussen 1957). According to this criterion, a month is dry if rainfall is less than twice the mean monthly temperature expressed in millimeters of rain. For our case, that would be approximately 25.9 (2) = 51.8 mm. Even in February, the least rainy month, rainfall exceeded the dry month criterion by 7-fold: 350 mm compared with 51.8 mm. The North American climatologist (Thornthwaite 1948) incorporated the concept of Potential Evapotranspiration (PET) calculated from air temperature and day length. Under this concept, a month was dry if the precipitation was lower than the PET. (Holdridge 1967) developed an approximate formula based only on the mean monthly temperature to calculate the monthly PET. This formula, which is near the thermic tropic where our area of study is located, calculates Thornthwaite´s PET very well. As in the study area, the mean annual temperature and the mean temperature for each month were almost the same (Figure 1-1). If we assume that every month had 30.4 days, the Holdridge (1967) formula allowed us to estimate the monthly PET = (58.93) (25.9) / 12 = 127 mm. That is to say, the xerothermic index of Gaussen underestimated PET by about 2.4- times. However, even using the PET criterion, which is much more demanding than Gaussen's xerothermic index, rainfall in February still exceeded PET by about 2.7-times

1.2.3 Sampling

In the study area, a local Afro-Colombian ethnic group that inhabits these forests belonging to the Community Council of the Low *Calima* River Basin, among the subsistence, economic, and cultural activities they carry out, there is a sporadically felling of trees in small areas of the forest. As virtually all the species of trees existing there has some use in the wood market, from these trees, we collected complete cross-sectional discs. Then, this sampling was reasonably at random as recommend (Speer 2010) to represent a landscape. We also collected fifteen species existing in the region, but that did not appear in the sampling. They were found within the experimental area and arboretum of the Pedro Antonio Pineda Tropical Forest Center of the University of Tolima, most of them with increment borers because of restrictions of the University. For this purpose, we extracted 2-3 cores 5 mm in diameter from the trees at 1.3 m above the ground approximately. The holes produced by the increment borer were filled with wax, and antibacterial and healing products, to avoid penetration by insects and pathogens. From each tree, we also collected leaves, flowers, and fruits, whenever present, to aid in taxonomic identification.

1.2.4 Processing of wood samples

Wood samples were taken to the Tropical Dendroecology Laboratory of the National University of Colombia, Medellín, and dried to a constant weight at 28°C. Then, to highlight the growth rings, the samples were polished successively with abrasive sandpapers, from

60 to 600 grains. Samples were scanned at a resolution of 1,800 - 2,400 dpi in an Epson Expression 10,000XL Scanner. The high-resolution images allowed macroscopic characteristics to be observable up to 10-15µm. All images were processed with ImageJ 11.52i Software (Schindelin et al. 2012).

1.2.5 Observable anatomical characteristics

We identified the growth rings according to their type: (A) density changes due to an increase in the wall thickness of the fibers, (B) presence of marginal bands of axial parenchyma, or (C) differences in the diameter, distribution, and grouping of the pores: ring-porous, semi-ring-porous, and diffuse-porous. One or several types of these anatomical structures can be present in the same sample. We classified the presence of growth rings according to Silva et al. (2016) as well defined (+), poorly defined (±), or absent (-).

The analysis considers the difficulty or impossibility of dating the growth rings when are many anomalies such as false rings, wedging rings, tangential discontinuity, or lost rings. The analysis included the visual dating possibility of growth rings that is an essential procedure in dendrochronology. We made this classification by visual inspection using different degrees of magnification, granting these qualitative classifications: (1) null: there were no growth rings; (2) low: several poorly defined growth rings, difficult to mark, lost rings, too many together, or frequent tangential discontinuity; (3) medium: false or lost rings were evident and not frequent; or (4) high: growth rings were clearly defined with tangential continuity, and few false rings.

1.2.6 Growth ring periodicity

We determined the growth periodicity in some sampled species by using the bomb-peak dating method (Worbes and Junk 1989; Fichtler et al. 2003). Samples were prepared according to Steinhof et al. (2017) and were analyzed in an accelerator mass spectrometry (AMS) at the radiocarbon laboratory of Max Planck Institute for Biogeochemistry in Jena, Germany. To obtain chronological dates from the radiocarbon values, we used the calibration software Cali-Bomb (Reimer et al. 2004).

1.2.7 Pantropical growth ring potential

An exhaustive pantropical literature review was made on the dendrochronological potential of trees covering from Northern Subtropic to Southern subtropic and from sea level to high mountains. All types of known seasonality affecting the growth rings are included: temperature, droughts, and floods. We compare our results with the pantropical revision in terms of the number of studied species and percent of species with growth rings. We also determined which species in our study were reported with annual rings in studies carried out in seasonally climates from other neotropical regions.

1.3 Results and discussion

According to Gaussen xerothermic index (Bagnouls and Gaussen 1957) and the monthly potential evapotranspiration (Holdridge 1967), in the study area (Figure 1-1), on average, there are not ecologically dry months. However, because it is soil water-holding capacity and not precipitation that is the crucial factor for tree growth, water limitation in some species cannot be ruled out. Trees from wet environments are more water-demanding than those from dry climates which is a species-specific trait (Silva et al. 2019).

Eighty-one species were sampled from 38 plant families after a month of sampling. From the sampling, basically at random, it was found that 58% of the species were only represented by a single tree, which shows the high richness and diversity of trees existing in the study area. The families with the most number of species included Sapotaceae (7), Fabaceae (7), Malvaceae (5), Chrysobalanaceae (4), Moraceae (4), Myristicaceae (4), and Vochysiaceae (4). Of the total, 17 endemic species (21%) were recorded from Colombia: *Jacaranda hesperia*, *Dacryodes frangens*, *Marila macrophylla*, *Clusia leptanthera*, *Vismia rufa*, *Quararibea foenigraeca*, *Sterculia aerisperma*, *Qualea lineata*, and *Vochysia artantha*, which included eight species endemic to the Low Calima River Basin Region: *Licania caldasiana*, *Tapura costata*, *Tachigali colombiana*, *Magnolia calimaensis*, *Pterandra ultramontana*, *Henriettea maguirei*, *Coussapoa valaria*, and *Vochysia pacifica*. In addition to these, we sampled 14 endemic species of the Biogeographic Chocó Region (18%): *Campnosperma panamensis*, *Licania* sp, *Dipteryx oleifera*, *Humiriastrum procerum*, *Gustavia occidentalis*, *Huberodendron patinoi*, *Phragmotheca siderosa*, *Otoba latialata*, *Virola dixonii*, *Otoba lehmannii*, *Isertia pittieri*, *Pouteria buenaventurensis*, *Pouteria collina*, and *Cecropia virgusa*. The other species (not mentioned) have a much wider distribution (Table 1-1).

The macroscopic structures observed in the analyzed species (Table 1-1, Figure 1-2, Figure 1-3, Figure 1-4) can be seen with the naked eye or with only a few zooms as changes in the form of alternate bands of light and dark areas. This was interpreted as increases in wood density that were attributed to the thickening of the fiber cell walls (A), which may be gradual or abrupt (Figure 1-2). This ring pattern was dominant in the sampled species (52%) (Figure 1-4a). It sometimes occurred together with bands of marginal parenchyma (B) (Figure 1-3), which was present in 36% of the species (Figure 1-4a).

In 82% of the studied species, we found growth rings; 46% were well defined (distinct rings), and 36% were poorly defined with visible although faint rings. Only 18% of the species had no growth rings or discontinuous bands, where it is difficult to establish if growth rings were present (Figure 1-4b, Table 1-1).

The semi-ring-porous pattern (C), that is a characteristic generally reported in species that grow in dry environments, or at least, with a dry season (Worbes and Junk 1999), was exhibited by 13% of the species in combination with the other anatomical characteristics: The combination A-C occurred in 9% of the species, the combination A-B-C occurred in 2%, and the B-C pattern only occurred in 1% (Figure 1-4a, Figure 1-5). Although the growth rings were well defined, the possibility of dating them was not necessarily high, as occurred in *Symphonia globulifera*, *T. costata*, *Cedrela odorata*, and other species, where the possibility of dating them was only medium (Table 1-1). On the other hand, in species with poorly defined rings, the possibility of dating them was null as in *Hebepetalum humiriifolium*, low as in *Cespedezia spathulata*, or medium as in *Pourouma bicolor*; but never high.

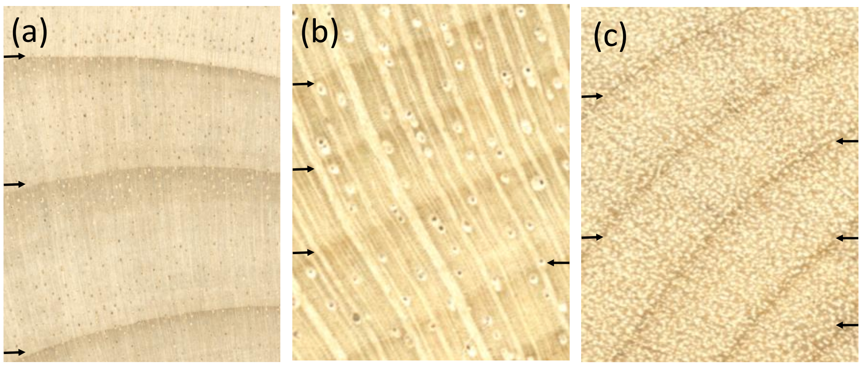

Figure 1-2: Species of trees sampled in the Low *Calima* River Basin, Biogeographic Chocó Region, with growth rings that were defined by increases in fiber wall thickness (A): (a) *Apeiba macropetala*, (b) *Phragmotheca siderosa*, (c) *Posoqueria latifolia*. The arrows indicate the growth rings

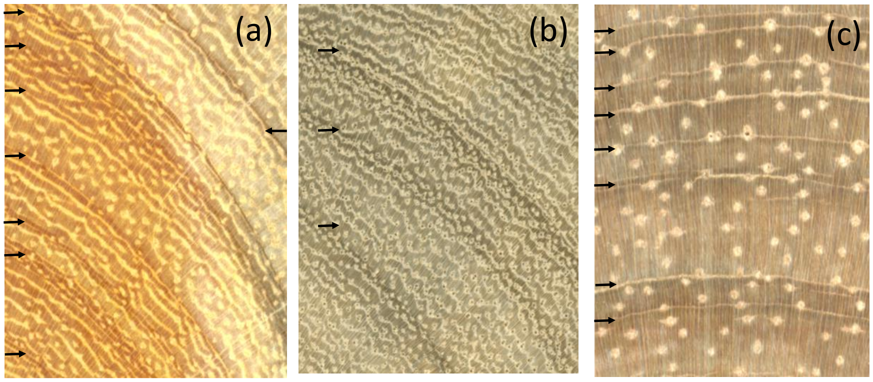

Figure 1-3: Species of trees sampled in the Low *Calima* River Basin, Biogeographic Chocó Region, with (A) growth rings defined by increases in fiber wall thickness and (B) parenchyma bands: (a) *Clarisia racemosa*, (b) *Zanthoxylum riedelianum*, (c) *Coussapoa valaria*. The arrows indicate growth rings

Table 1-1: Tree species sampled in the Low *Calima* River Basin, Biogeographic Chocó Region, characterized according to their growth rings. Visibility: well defined (+), poorly defined (±), absent (-). Anatomical structure: density changes due to increased fiber wall thickness (A), the presence of marginal bands of axial parenchyma (B), differences in diameter, distribution, and grouping of pores that delimited the ring (C). Porosity: diffuse-porous, semi-ring-porous or ring-porous. The possibility of dating: high, medium, low

Family	Species	Tree-ring visibility	Wood anatomy	Vessel antomy	Potential in Dendrochronology	Number of trees	Type of samples	Distribution
Anacardiaceae	*Campnosperma panamensis* Standl.	-	A	Diffuse-porous	None	2	Core	Biogeographic *Chocó*
Apocynaceae	*Aspidosperma excelsum* Benth.	+	A	Diffuse-porous	Low	1	Cross-section	Wide distribution
Apocynaceae	*Aspidosperma desmanthum* Benth. ex Müll. Arg.	+	A	Diffuse-porous	Low	2	Cross-section	Wide distribution
Bignoniaceae	*Jacaranda hesperia* Dugand.	+	A	Diffuse-porous	High	2	Core	Endemic
Boraginaceae	*Bourreria costaricensis* (Standl.) A.H Gentry	±	A,C	Semi-ring-porous	Low	1	Core	Wide distribution
Burseraceae	*Dacryodes frangens* Daly & M. C. Martínez	-	A	Diffuse-porous	None	1	Cross-section	Endemic
Burseraceae	*Protium* sp.	+	A	Diffuse-porous	Medium	1	Cross-section	Wide distribution
Calophyllaceae	*Calophyllum longifolium* Willd.	±	A,B	Diffuse-porous	Low	14	Cross-section (5) - Core (9)	Wide distribution
Calophyllaceae	*Marila macrophylla* Benth.	±	A	Diffuse-porous	Low	1	Cross-section	Endemic

Family	**Species**	**Tree-ring visibility**	**Wood anatomy**	**Vessel antomy**	**Potential in Dendrochronology**	**Number of trees**	**Type of samples**	**Distribution**
Chrysobalanaceae	*Hirtella americana* L.	±	A	Diffuse-porous	Low	1	Cross-section	Wide distribution
Chrysobalanaceae	*Hirtella* sp.	±	A,B	Diffuse-porous	Low	1	Cross-section	Wide distribution
Chrysobalanaceae	*Licania caldasiana* Cuatrec.	±	A,B	Diffuse-porous	Low	1	Cross-section	Endemic
Chrysobalanaceae	*Licania* sp.	-	A	Diffuse-porous	None	1	Cross-section	Biogeographic *Chocó*
Clusiaceae	*Clusia leptanthera* Cuatrec	±	A,C	Semi-ring-porous	Low	1	Cross-section	Endemic
Clusiaceae	*Symphonia globulifera* L. f.	+	A,B	Diffuse-porous	Medium	1	Cross-section	Wide distribution
Dichapetalaceae	*Tapura costata* Cuatrec.	+	B,C	Semi-ring-porous	Low	1	Cross-section	Endemic
Dichapetalaceae	*Sloanea* sp.	±	A	Diffuse-porous	Low	1	Cross-section	Wide distribution
Erythroxylaceae	NN	+	A	Diffuse-porous	Low	1	Cross-section	Wide distribution
Euphorbiaceae	*Mabea sp.* Aubl.	+	A	Diffuse-porous	High	2	Cross-section (1) - Core (1)	Wide distribution
Euphorbiaceae	*Hevea brasiliensis* (Willd. ex A. Juss.) Müll. Arg.	+	A,B	Diffuse-porous	Medium	1	Cross-section	Wide distribution
Fabaceae	*Dipteryx oleifera* Benth.	±	A,B	Diffuse-porous	Medium	1	Cross-section	Biogeographic *Chocó*

Family	Species	Tree-ring visibility	Wood anatomy	Vessel antomy	Potential in Dendrochronology	Number of trees	Type of samples	Distribution
Fabaceae	*Inga acreana* Harms	+	A,B	Diffuse-porous	Medium	1	Cross-section	Wide distribution
Fabaceae	*Inga rubiginosa* (Rich.) DC.	+	A,B	Diffuse-porous	Medium	1	Cross-section	Wide distribution
Fabaceae	*Schizolobium parahyba* (Vell.) S.F. Blake	+	A,B	Diffuse-porous	Medium	1	Core	Wide distribution
Fabaceae	*Pentaclethra macroloba* (Willd.) Kuntze	+	A,B	Diffuse-porous	Medium	2	Core	Wide distribution
Fabaceae	*Tachigali colombiana* Dwyer	+	A	Diffuse-porous	High	3	Cross-section	Endemic
Fabaceae	*Abarema* sp.	±	A,B	Diffuse-porous	Low	1	Core	Wide distribution
Goupiaceae	*Goupia glabra* Aubl.	+	A	Diffuse-porous	High	21	Cross-section	Wide distribution
Humiriaceae	*Humiriastrum procerum* (Little) Cuatrec.	+	A	Diffuse-porous	High	8	Cross-section	Biogeographic *Chocó*
Humiriaceae	*Sacoglottis* sp.	±	A	Diffuse-porous	Low	3	Cross-section	Wide distribution
Hypericaceae	*Vismia rufa* Cuatrec.	-	A	Diffuse-porous	None	1	Cross-section	Endemic
Lauraceae	*Nectandra* sp.	+	A	Diffuse-porous	Low	1	Cross-section	Wide distribution
Lauraceae	*Ocotea* sp.	+	A	Diffuse-porous	Low	1	Cross-section	Wide distribution

Family	Species	Tree-ring visibility	Wood anatomy	Vessel antomy	Potential in Dendrochronology	Number of trees	Type of samples	Distribution
Lecythidaceae	*Couratari guianensis* Aubl.	+	A	Diffuse-porous	Low	1	Cross-section	Wide distribution
Lecythidaceae	*Cariniana pyriformis* Miers.	+	A	Diffuse-porous	High	14	Cross-section	Wide distribution
Lecythidaceae	*Gustavia occidentalis* Cuatrec.	+	A,B	Diffuse-porous	Low	1	Cross-section	Biogeographic *Chocó*
Linaceae	*Hebepetalum humiriifolium* (Planch.) Benth.	±	A	Diffuse-porous	Low	7	Cross-section	Wide distribution
Magnoliaceae	*Magnolia calimaensis* (Lozano) Govaerts	+	A,B	Diffuse-porous	Medium	1	Core	Endemic
Malpighiaceae	*Pterandra ultramontana* H.P. Riley ex Cuatrec.	+	A,C	Semi-ring-porous	Low	2	Cross-section	Endemic
Malvaceae	*Huberodendron patinoi* Cuatrec.	+	A,B	Diffuse-porous	High	1	Core	Biogeographic *Chocó*
Malvaceae	*Apeiba macropetala* Ducke	+	A,C	Semi-ring-porous	High	6	Cross-section	Wide distribution
Malvaceae	*Quararibea foenigraeca* Cuatrec.	±	A,B	Diffuse-porous	Low	1	Cross-section	Endemic
Malvaceae	*Phragmotheca siderosa* Cuatrec.	+	A	Diffuse-porous	Medium	2	Cross-section	Biogeographic *Chocó*
Malvaceae	*Sterculia aerisperma* Cuatrec.	±	A,B,C	Semi-ring-porous	Low	3	Cross-section	Endemic
Melastomataceae	*Henriettea maguirei* (Wurdack) Penneys,	-	A,B	Diffuse-porous	None	1	Cross-section	Endemic

Family	Species	Tree-ring visibility	Wood anatomy	Vessel antomy	Potential in Dendrochronology	Number of trees	Type of samples	Distribution
	Michelang., Judd & Almeda							
Melastomataceae	*Miconia* sp.	-	A,B	Diffuse-porous	None	1	Cross-section	Wide distribution
Meliaceae	*Cedrela odorata* L.[1]	+	A,B,C	Semi-ring-porous	High	1	Cross-section	Wide distribution
Metteniusaceae	*Dendrobangia boliviana* Rusby	-	A	Diffuse-porous	Low	2	Cross-section	Wide distribution
Moraceae	*Castilla elastica* var. *costaricana* (Liebm.) C.C. Berg	+	A	Diffuse-porous	Medium	1	Cross-section	Wide distribution
Moraceae	*Clarisia racemosa* Ruiz & Pav	+	A,B	Diffuse-porous	Medium	1	Cross-section	Wide distribution
Moraceae	*Sorocea* sp.	±	A	Diffuse-porous	Low	1	Cross-section	Wide distribution
Moraceae	*Ficus* sp.	-	A,B	Diffuse-porous	None	1	Core	Wide distribution
Myristicaceae	*Osteophloeum platyspermum* (Spruce ex A. DC.) Warb.	±	A	Diffuse-porous	Medium	2	Cross-section	Wide distribution
Myristicaceae	*Otoba latialata* (Pittier) A.H. Gentry	+	A	Diffuse-porous	High	11	Cross-section	Biogeographic *Chocó*
Myristicaceae	*Virola dixonii* Little	+	A	Diffuse-porous	High	4	Cross-section	Biogeographic *Chocó*
Myristicaceae	*Otoba lehmannii* (A.C.Sm.) A.H.Gentry	±	A,B	Diffuse-porous	Medium	2	Core	Biogeographic *Chocó*

Family	Species	Tree-ring visibility	Wood anatomy	Vessel antomy	Potential in Dendrochronology	Number of trees	Type of samples	Distribution
Myrtaceae	*Myrcia* sp.	-	A	Diffuse-porous	None	1	Cross-section	Wide distribution
Myrtaceae	*Syzygium malaccense* (L.) Merr. & L.M. Perry	-	A	Diffuse-porous	None	1	Core	Wide distribution
Ochnaceae	*Cespedesia spathulata* (Ruiz & Pav.) Planch.	±	A,C	Semi-ring-porous	Low	1	Cross-section	Wide distribution
Olacaceae	*Minquartia guianensis* Aubl.	-	A	Diffuse-porous	Low	1	Cross-section	Wide distribution
Phyllantaceae	*Hieronyma alchorneoides* ALLEMAO	+	A,C	Semi-ring-porous	Medium	3	Core	Wide distribution
Rhizophoraceae	*Cassipourea* sp.	+	A,C	Semi-ring-porous	Low	1	Cross-section	Wide distribution
Rubiaceae	*Isertia pittieri* (Standl.) Standl.	-	A	Diffuse-porous	None	1	Cross-section	Biogeographic *Chocó*
Rubiaceae	*Posoqueria latifolia* (Rudge) Schult.	+	A	Diffuse-porous	Medium	1	Cross-section	Wide distribution
Rutaceae	*Zanthoxylum riedelianum* subsp. *hygrophilum* (Cuatrec.) Reynel	±	A,B	Diffuse-porous	Low	7	Cross-section (1) - Core (6)	Wide distribution
Salicaceae	*Casearia arborea* (Rich.) Urb.	±	A	Diffuse-porous	Low	1	Cross-section	Wide distribution
Sapotaceae	*Manilkara* sp.	±	A	Diffuse-porous	Low	1	Cross-section	Wide distribution

Family	Species	Tree-ring visibility	Wood anatomy	Vessel antomy	Potential in Dendrochronology	Number of trees	Type of samples	Distribution
Sapotaceae	*Pouteria buenaventurensis* (Aubrév.) Pilz	±	A	Diffuse-porous	Low	2	Cross-section	Biogeographic *Chocó*
Sapotaceae	*Pouteria engleri* Eyma	+	A	Diffuse-porous	Medium	1	Cross-section	Wide distribution
Sapotaceae	*Pouteria collina* (Little) T.D. Penn.	+	A,B	Diffuse-porous	Medium	1	Cross-section	Biogeographic *Chocó*
Sapotaceae	*Pouteria eugeniifolia* (Pierre) Baehni	-	A	Diffuse-porous	None	3	Cross-section	Wide distribution
Sapotaceae	*Pouteria* sp.	-	A,B	Diffuse-porous	None	1	Cross-section	Wide distribution
Sapotaceae	*Pouteria* sp.	±	A,B	Diffuse-porous	Low	2	Cross-section	Wide distribution
Simaroubaceae	*Simarouba amara* Aubl.	±	A,B	Diffuse-porous	Low	13	Cross-section	Wide distribution
Urticaceae	*Cecropia virgusa* Cuatrec.	±	A	Diffuse-porous	Medium	15	Cross-section	Biogeographic *Chocó*
Urticaceae	*Coussapoa valaria* C.C. Berg	±	A,B	Diffuse-porous	Low	1	Cross-section	Endemic
Urticaceae	*Pourouma bicolor* subsp. *bicolor* Mart.	±	A,B	Diffuse-porous	Low	5	Cross-section	Wide distribution
Vochysiaceae	*Qualea lineata* Stafleu	+	A	Diffuse-porous	Medium	7	Cross-section	Endemic
Vochysiaceae	*Vochysia artantha* Stafleu	-	A	Diffuse-porous	None	5	Cross-section	Endemic

Family	Species	Tree-ring visibility	Wood anatomy	Vessel antomy	Potential in Dendrochronology	Number of trees	Type of samples	Distribution
Vochysiaceae	*Vochysia pacifica* Cuatrec.	±	A,B	Diffuse-porous	None	2	Cross-section	Endemic
Vochysiaceae	*Vochysia* sp.	±	A,B	Diffuse-porous	None	4	Cross-section	Wide distribution

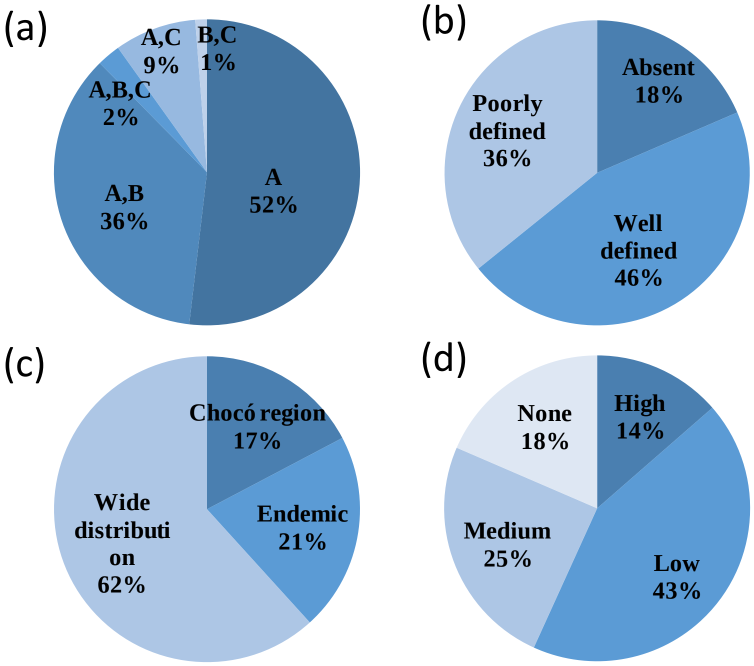

Figure 1-4: (a) Percentage of growth rings according to their type: changes in density due to an increase in fiber wall thickness (A), the presence of marginal bands of axial parenchyma (B), differences in diameter, distribution, and grouping of pores that delimited the ring (C), and combinations of the above, (b) Percentage of tree species sampled in the Low *Calima* River Basin, Biogeographic Chocó Region, with growth rings absent or present, (c) Percentage of species with growth rings classified according to their distribution range, (d) Classification of species with growth rings that could be dated

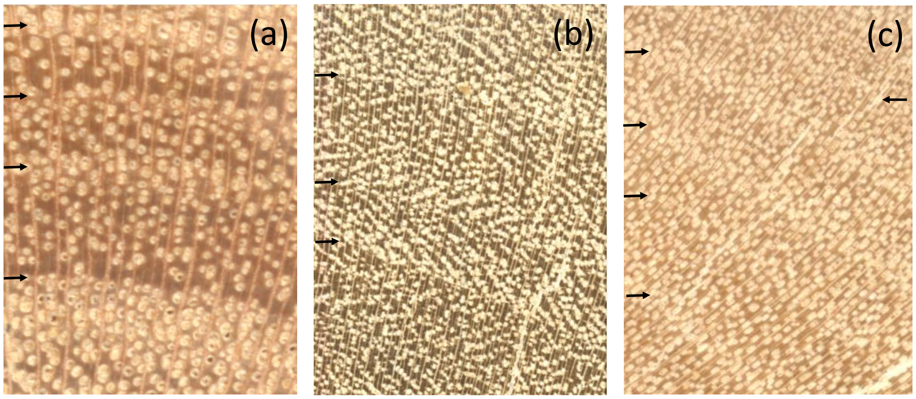

Figure 1-5: Semi-ring-porous trees species sampled in the Lower *Calima* River Basin, Biogeographic Chocó Region, (Type C) or combined with another anatomical trait. a *Clusia leptanthera*, b *Tapura costata*, c *Pterandra ultramonanta*. Arrows indicate growth rings

The possibility of dating the rings depends both on their presence and on their continuity, which is sometimes limited by competition (Figure 1-6a), traumatic rings produced by injuries in the cambium (Figure 1-6b), or other difficulties such as the anomalous architecture of the stems (Figure 1-6c, d). In these cases, the rings can be identified using complete cross-sectional discs, which are recommended in tropical dendrochronology (Détienne 1995; Worbes 2002; Brienen and Zuidema 2005). Undoubtedly, the minimal observation area when corers from increment borers are used makes dating difficult. In general, in 39% of the species, the dating of growth rings was feasible. These included both medium (25%) and high (14%) dating percentages (Figure 1-4d). Species such as *Goupia glabra* with visible growth rings (Table 1-1) may present areas with tangential discontinuity that can only be detected with complete cross-sectional discs (Figure 1-7a).

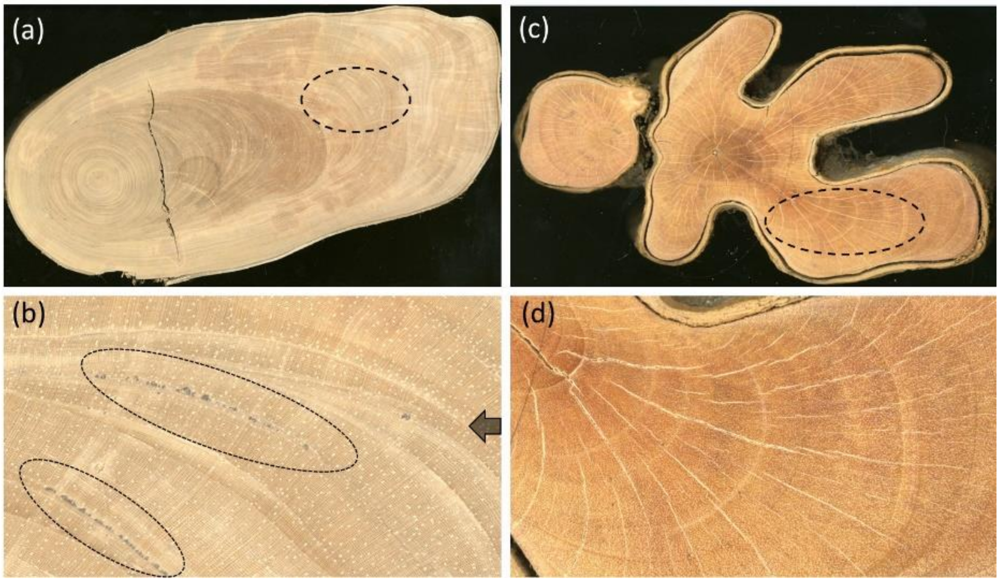

Figure 1-6: Irregularities in growth rings due to competition and architecture that was present in some tree species sampled in the Lower *Calima* River Basin, Biogeographic Chocó Region: (a) Irregular very eccentric discs with the pith very displaced in *Couratari guianenesis*, (b) Tangential discontinuity of the growth rings, and wedging rings (fused), followed by traumatic tissue in *Couratari guianenesis*; (c) Irregular wooden disc typical of *Aspidosperma excelsum*; (d) Faint growth rings in *Aspidosperma excelsum*.

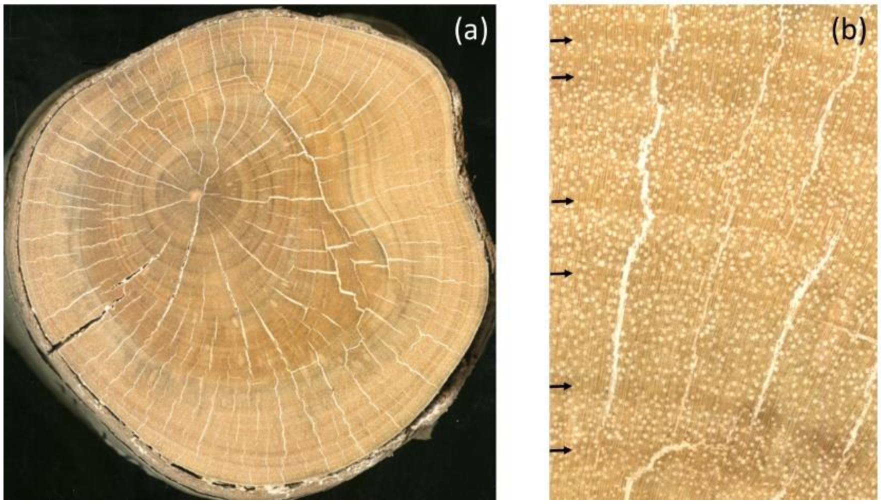

Figure 1-7: Growth rings of *Goupia glabra*. (a) Complete cross-sectional disc with growth rings as seen with the naked eye. (b) Growth rings in a rectangular cross-section of 1.5 cm x 2.3 cm

The results of this study show that, in contrast to the pessimistic opinion of many dendrochronologists and ecologists about the existence of growth rings in the tropics (Whitmore 1975; Schweingruber 1988; Evans and Schrag 2004; Poussart et al. 2004; Vaganov et al. 2006; Anchukaitis et al. 2008; Speer 2010; Hughes et al. 2011; Thomas 2014; Hu and Riveros 2016; Hirons and Thomas 2018; Nakai et al. 2018), in this non-seasonal hyper-humid tropical environment, many tree species have growth rings. Surprisingly, 66 species out of 81 sampled species (82%) showed growth rings that were visible with the naked eye (Table 1-1). Also, these species occurred in a rainier, non-seasonal environment than that in which any other researchers had previously attempted to study tropical growth rings (Table 1-2).

Among the 60 pantropical study areas cited in Table 1-2, which included trees that grew from the lowlands to high tropical mountains, and with all types of seasonality including droughts, floods, variation in temperature, and various combinations of those variables; these study areas included a broad latitudinal gradient going from the subtropics of the Northern Hemisphere to the subtropics of the Southern Hemisphere. In all of them, the percentage of trees with growth rings ranged from 3% to 100%. Our study ranked 17th in percentage of tree species with growth rings, surpassing most of the studies cited in Table 1-2. Nevertheless, the results of this chapter are one of only two without any seasonality. Although 16 studies reviewed in Table 1-2 exceeded the percentage of trees with growth rings report here (Table 1-2), the real potential of trees with growth rings in the Low *Calima* River Basin is even more considerable as discussed below.

1.3.1 Biodiversity of the Chocó Region

The study area of this dissertation is known for a very high richness and species diversity of tree species. Faber-Langendoen and Gentry (1991) found in this same area 241 dicot tree species with a diameter at breast height (dbh) ≥10 cm in only 1 ha of forest sampling, and only 2.4 individuals per each-one tree species sampled. In the sample from our study area, we found 2.9 individuals per species. If the the Faber-Langendoen and Gentry (1991) sampling was random and representative for our study area, we estimate that in just one hectare of forest in the Lower Calima River Basin, would be about 113 tree species with well-defined rings (0.47 x 241). If only a small fraction of these tree species have annual growth rings, or with any other constant periodicity, we would have discovered a gold mine of potential dendrochronological species in the non-seasonal tropical wet forests of the Biogeographical Chocó Region. Colombia, which contains 5,746 tree species, has more species of trees than any country in the world after Brazil. However, on a per square kilometer basis, Colombia has many more species than Brazil (Beech et al. 2017).

The *Chocó* Biogeographical Region is one of the most crucial tree diversity and endemism hot spots in the world (Prance 1982). Among the species with great dendrochronological potential, the following stand out due to the clarity of their rings: *Huberodendron patinoi*, *Cariniana pyriformis*, *Mabea sp*. *Inga acreana*, *Tachigali colombiana*, *Goupia glabra*, *Apeiba macropetala*, *Humiriastrum procerum*, *Nectrandra* sp*.,* *Ocotea* sp, *Clarisia racemosa*, *Otoba latialata*, *Virola dixonii*, *Posoqueria latifolia*, *Pouteria englerii*, *Pouteria collina*, and *Qualea lineata*. Nevertheless, the high diversity of tree species found in our study area has an Achilles heel: necessarily, the populations are very small, which difficult to obtain enough replicas for most species

1.3.2 About tree-rings formation in tropical hyper-humid regions

Based on the data in Table 1-2, and contrary to the prevailing hypothesis that periodic droughts or floods condition growth rings formation in tropical trees, the percentage of trees with growth rings does not seem to depend only on these environmental variables. For instance, Tarelkin et al. (2016) found no differences in the percentages of trees with distinct, indistinct, or absent growth rings between two forests with contrasting in both precipitation as seasonality in Central Africa (Democratic Republic of Congo). See more differ strikingly cases in Table 1-2.

In our study, the hypothesis of the existence of growth rings in deciduous or semi-deciduous tree species (Borchert 1999; Lisi et al. 2008; Nath et al. 2016; Shimamoto et al. 2016) applied only to *C. odorata*, *S. parahyba*, *D. panamensis*, *Goupia glabra*, *Couratari guianensis*, *Tachigali colombiana* and, *Humiriastrum procerum*, which are deciduous, and for *C. pyriformis*, which is a brevi-deciduous species. Together represent less than 12% of the studied species that exhibited growth rings in this study (Table 1-1). On the contrary, our results were more in agreement with other authors (Worbes 1999; Callado et al. 2001; Carlquist 2001; Fichtler et al. 2003; Aguilar-Rodríguez and Barajas-Morales 2005; Evert 2006; Tarelkin et al. 2016), who did not find an association between deciduousness and the formation of growth rings in tropical trees. In fact, according to these authors, neither do all deciduous trees have growth rings nor do all evergreens lack growth rings.

Based on the hypothesis related to phytogeographic origin, in which growth rings are more common in species from a boreal origin (Laurasia) (Fahn 1967; Aguilar-Rodríguez and Barajas-Morales 2005; Ramírez-Martínez et al. 2017), we found that all species of plant families with an assigned origin, except for two, were from Gondwana and centered on the Amazonian region. The two families from Laurasia were Lineaceae and Salicaceae (Gentry 1982).

1.3.3 Dendrochronological potential studies around tropics: Unclear pattern

We show a comparison from our study results with other studies from pantropical regions in Table 1-2 and Table 1-3. Some examples illustrate the inexplicable differences found by the authors cited in Table 1-2. The only other case in wet tropical forests without any seasonality was that of Araya (2012), who reported 22% with growth rings, almost four times less than in our study.

Some results emerge from Table 1-2: (1) There are growth rings in trees in all tropical forests around the world, (2) There were no clear trends for ring formation in terms of dry, moist, or wet climates, seasonality of rainfall, flooding, temperature, or any combination of these variables, (3) There was no trend with the latitudinal distance from the Equatorial line to the North and South subtropics. It is very striking that Miller and Détienne (2001) did not find growth rings in many tree species in French Guiana; by contrast, other researchers working in the same region, and other areas of the Neotropics, have reported annual growth rings in these same species. To cite a few examples, growth rings were found by several authors for *Himenaea courbaril*, *Carapa guianensis*, *Couratari guianensis*, *Dipteryx oleifera*, *Goupia glabra*, *Jacaranda copaia*, *Simarouba amara*, *Symphonia globulifera*, and many other species as cited by Brienen et al. (2016) and by Schöngart et al. (Schöngart et al. 2017). Curiously, when we analyzed the disciplinary background of investigators, a pattern emerged. Most studies in Table 1-2 that reported >70% of trees with growth rings were tropical dendrochronologists who did not follow the IAWA Committee (1989) classification of growth rings. In sharp contrast, all studies that reported <50% were performed by wood anatomists who followed this classification. Silva et al. (2019) compiled many proposals for the classification of the growth rings. But, the one most used by wood anatomists appeared to be that of the IAWA Committee, although they usually made modifications to it.

The IAWA Committee (1989) classifies the growth rings from dicot wood into two types: (1) distinct growth ring boundaries, (2) indistinct or absent growth ring boundaries. The limits of the rings are distinct if "there is an abrupt structural change in the limits between them, usually including a change in the thickness of the cell wall of the fibers and/or in the radial diameter of the fibers.” The separation between these two groups is highly subjective, but the creation of a single group for indistinct and absent and the emphasis on density changes can lead to classifying species with growth rings, even annual rings, within the second group. But, also, the emphasis given to increased fiber density tends to classify tropical species that have subtle, though perceptible rings, boundaries into the second group, as is the case in the very narrow parenchyma bands typical in the wood of tropical legumes (Worbes 1995). This family of plants has the highest number of species with annual rings (Brienen et al. 2016).

Most of the wood anatomists cited in Table 1-2 and Table 1-3 followed the IAWA Committee's standards, but in reality, few followed them literally, and they modified them to create three groups: (1) distinct, (2) indistinct, or (3) absent, although they may have used other terms that are roughly equivalent (Vásquez and Ramírez 2005; Marcati et al. 2006; Baguinon et al. 2008; Santini 2013; Silva et al. 2016; Tarelkin et al. 2016; Islam et al. 2018). Most tropical dendrochronologists follow the classification of Worbes (1995), which covers four basic types of rings: (1) reduction in diameter and increase in fiber density, (2) one or more marginal parenchyma bands, (3) parenchyma bands and fibers of different diameters, or (4) varying frequency and width of vessels within the rings. Combinations among these types often occur.

Dendrochronologists have found annual rings in virtually all dicot trees from temperate and cold regions (Schweingruber 1988, 2007; Speer 2010; D´Arrigo et al. 2014; Schweingruber and Börner 2018), except in the Mediterranean where many irregularities occur (Silva et al. 2019). However, Wheeler et al. (2007) who used the IAWA Committee´s standards, report for the regions of Europe (excluding the Mediterranean), Temperate Asia, and for North America, 85, 84, and 81 percent of trees, respectively, with distinct rings. The remaining species were in that sort of black box: indistinct or absent. Note that similar and even higher percentages there are in Table 1-2 in the tropics. It seems, therefore, that even in temperate and cold regions, the IAWA Committee’s criteria tend to underestimate the presence of growth rings in dicot species.

Table 1-2: Percentage of growth rings in tropical trees that grow in diverse environments with seasonality. In bold are the results of this chapter

Code	**Species with growth rings (%)**[1]	**Total species studied (n)**	**Site**	**Mean Rainfall (mm)**	**Mean temperature (°C)**	**Type of seasonality**	**Reference**
1	100	58	Pantanal, Brazilian Mato Grosso, South America	1,150	23–26[2]	Rainfall, temperature. flooding	Schöngart et al. (2011)
2	100	29	Amazonian *Terra Firme* forests, South America	2,000–3,000	26–27	Rainfall	Vetter and Botosso (1989)
3	100	28	Pantanal, Brazilian Mato Grosso, South America	1,182	20–31[2]	Rainfall, temperature, flooding	Póvoa de Mattos (1999)
4	100	17	*Terra Firme,* flooded and swampy Amazonian forests, Brazil, South America	2,100-2,810	27	Rainfall	Cintra et al. (2013)
5	94	48	Brazilian *Cerrado*, São Paulo, South America	1,450	20–26[2]	Rainfall, temperature, flooding	Marcati et al. (2006)
6	92	24	Seasonaly semi-deciduous forests Saoutheast Brazil, South America	1,370	15–23[2]	Rainfall, temperature	Lisi et al. (2008)

7	94	67	Pantanal, Brazilian Mato Grosso, South America	1,150	21–31[2]	Rainfall, temperature, flooding	de Arruda et al. (2017)
8	93	27	Rema-Kalenga Wildlife Sanctuary, Bangladesh, South Asia	2,370	25	Rainfall, temperature	Islam et al. (2018)
9	90	57	Diverse ecosystems, Colombia, South America	1,500–4,000	<24	Rainfall	Vásquez and Ramírez (2005)
10	90	27	Arid and dry savanna trees, Africa	500–1,000	28	Rainfall	Fahn et al. (1981)
11	89	19	Tana River, Kenya, Africa	370	28	Flooding	Maingi (2006)
12	88	78	Floodplain forests, Amazon, Brazil, South America	1,500–3,000	26	Flooding	Worbes and Fichtler (2010)
13	86	183	Seasonal deciduous forests of the north and center of Peru	730–2,680[3]	16–26[3]	Rainfall	Marcelo (2017)
14	87	52	Yucatan, Mexico, North America	1,036	25	Rainfall	Roig et al. (2005)
15	84	64	Amazonian *Terra firme* forests, Pará, South America	2,000–3,000	26	Rainfall	Trevizor (2011)
16	85	177	Central and South Brazil, South America	1,500–2,000	24–27	Rainfall, temperature	Alvim (1964)
17	**82**	**81**	**Biogeographic *Chocó* Region, Colombia, South América**	**7,219**	**25.9**	**None**	**This chapter**

18	82	22	South East Cameroon, Africa	4,082	27	Rainfall	Groenendijk et al. (2014)
19	82	38	Kodagu, Karnacata, India, South Asia	2,725	14–29[2]	temperature	Nath et al. (2016)
20	81	26	Eastern Amazon Forests, Brazil, South America	1,973	23	Rainfall	Campos et al. (2008)
21	79	226	Central Amazonian Forests, Brazil, South America	3,400	26	Rainfall	Tanaka (2005)
22	79	24	North Minas Gerais, Brazil, South America	814	22–26[2]	Rainfall, temperature	Barbosa et. al. (2018)
23	79	111	Moist forests (Atlantic Forest), Brazil, South America	1,278	15–25[2]	Rainfall, temperature	dos Santos et al. (2016)
24	79	179	Central Amazon, Brazil, South America	3439	26	Rainfall	Tanaka (2005)
25	78	239	All Philippines, Southeast Asia	1,500–3,500	26–28[2]	Rainfall, temperature	Baguinon et al. (2008)
26	78	37	Caparo Forest Reserve, Venezuela, South America	1,700	25	Rainfall	Worbes (1999)
27	77	90	Amazonian forests, Brazil, South America	1,500–3,000	26	Rainfall	Santini (2013)
28	77	65	All Sri Lanka, South Asia	900–5.000	26–28[2]	Rainfall	Baguinon et al. (2008)
29	77	13	Misiones, North Argentina, Subtropics, South America	1,700	15–25[2]	Temperature	Bognisegna et al. (1989)

30	76	21	Lowland dry forests, Oaxaca, South of Mexico, North America	930	26	Rainfall	Brienen et al. (2009)
31	75	79	Moist forests, Los Tuxtlas Biosphere Reserve, Mexico, North America	1,300–4,200	24–27[2]	Rainfall, temperature	Gutiérrez (2014)
32	70	56	All Ecuador, South America	1,000–3,000	> 12	Rainfall	MAE-FAO (2014)
33	70	27	Central Kalimantan, (Indonesia) South Borneo, Southeast Asia	2,572	27	Rainfall, flooding	Worbes et al. (2017)
34	71	24	Moist forests from Africa	2,000–3,000	27	Rainfall	Fahn et al. (1981)
35	66	61	South Brazil, South America	1,000–1,500	14–23[2]	Rainfall, temperature	Alves and Angyalossy-Alfonso (2000)
65	64	135	Bolivia, South America	1,000–4,000	<20	-	Gutiérrez et al. (2002)
37	61	26	Malaysia, Southwest Asia	1,800–3,000	26–27[2]	Rainfall	Abdul-Azim and Okada (2014)
38	59	97	Florida, USA, Sub tropical North America	1,500	10–26[2]	Temperature	Tomlinson and Craichead (1972)
39	58	38	Suriname, South America	2,209	26	Rainfall	Lotfiomran and Köhl (2017)

40	57	60	Amazon rain forests from Brazil, South America	2,000 – 3,000	27	Rainfall	Alvim (1964)
41	56	103	Democratic Republic of Congo, Africa	1,200 – 1,700	24 – 26[2]	Rainfall	Tarelkin et al. (2016)
42	54	91	All Thailand, Southeast Asia	1,000 – 2,200	26 – 31[2]	Rainfall, temperature	Baguinon et al. (2008)
43	53	176	Southeastern Brazil, South America	1,500 – 2,000	14 – 23[2]	Raifall, temperature	Alves and Angyalossy-Alfonso (2000)
44	53	108	Venezuela, South America	500 – 4,000	>12	Rainfall	León (2014)
45	52	217	North Brazil (Amazonia), South America	2,000 – 3,000	26	Flooding	Alves and Angyalossy-Alfonso (2000)
46	52	85	Lowland moist,fores, Java Island, Indonesia, tropical Asia	2,000 – 4,000	28	Rainfall	Fahn et al. (1981)
47	52	50	Moist forests of Chiapas, Mexico, North America	2,800	23	Rainfall	Brienen et al. (2009)
48	52	21	Lowland deciduous forest, Mexico, North America	700 – 1,000	22 – 26[2]	Rainfall, temperature	Ramirez et al. Ramírez-Martínez et al. (2017)
49	50	80	Peru, Moist Central Forest, South America	2,325 2,250	24 – 27[2] 15 – 19[2]	Rainfall, temperature	Beltrán and Valencia (2013)

						Rainfall, temperature	
50	47	38	Northeast Brazil, South America	500 – 1,500	26	Rainfall, flooding	Alves and Angyalossy-Alfonso (2000)
51	43	43	Premontane and lowland forests, Colombia, South America	1,500 – 4,000	>18	-	Arévalo and Londoño (2005)
52	40	25	Central-western Brazil, *Cerrado,* South America	1,000 – 2,000	20 – 26[2]	Raifall, temperature	Alves and Angyalossy-Alfonso (2000)
53	38	541	Pakistan, India, Sri Lanka, and Burma	-	-	-	Wheeler et al. (2007)
54	38	29	Dicot trees of a mountain moist forest, Mexico, North America	1,200 – 1,700	17	Rainfall	Aguilar-Rodríguez and Barajas-Morales (2005)
55	28	708	Dicot trees tropical Africa	-	-		Wheeler et al. (2007)
56	24	1273	Dicot trees Southeast Asia and the Pacific	-	-	-	Wheeler et al. (2007)
57	22	110	Wet non-seasonal forests, Costa Rica, Central America	6,000	25	No one	Araya (2012)
58	17	1695	Dicot trees Neotropics	-	-	-	Wheeler et al. (2007)

59	10	70	Sahel Savannah, Sudan, Africa	250 – 1,100	28	Rainfall,	Tarhule and Hughes (2002)
60	3	107	French Guiana (Guyana), South America	3,200	29	Rainfall	Miller and Détienne (2001)

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[1] When two or more studies have the same percentage, the one with the largest sample (n) is presented first

[2] The mean monthly temperatures of the coldest and warmest months, respectively

[3] Data taken in seven seasonal deciduous forests between 230 and 2200 m asl with average annual temperatures between 26°C and 16°C, respectively. The mean annual rainfalls vary from 730 to 2680 mm

Some researchers who have studied the growth rates of tropical trees and their climatic relationships using stable isotopes of ^{13}C and ^{18}O justified their use for the lack of growth rings in these species (Evans and Schrag 2004; Poussart et al. 2004; Hietz et al. 2005; Pons and Helle 2011; Hu and Riveros 2016; Nakai et al. 2018). However, most species studied by these authors were repeatedly reported by several tropical dendrochronologists to have annual growth rings. Such is the case for *Cordia alliodora*, *Carapa guianensis*, *S. amara*, *C. odorata*, and *Swietenia macrophylla* (Brienen et al. 2016; Schöngart et al. 2017), or at least they had growth rings as in *Samanea saman* (Skolmen 1974; de Arruda et al. 2017); and *Hieronyma alchorneoides* (León 2014), and this chapter in Table 1-1.

1.3.4 Species in this chapter with annual rings reported in other regions

Table 1-3 presents the species of this chapter with annual rings and their visibility reported by different authors. Thirty percent of the species from this chapter have been reported previously with annual growth rings in other regions. It suggests that they probably also form annual growth rings in the area of our study in Colombia. At the time of writing this chapter, we had only received radiocarbon analyses of the growth rings of six species, all with annual rings; these species were *Cariniana pyriformis* (171 y), *G. glabra* (70 y), *Pourouma bicolor* (36 y), *Inga sp* (62 y), *Mabea sp* (80 y) and, *Inga acreana* (100 y). Growth rings of the last three species had not reported before. Additionally, *C. odorata*, one of the trees sampled, had a known planting date where the number of rings coincided with the years since planting (9 y). That is, we found numerous species with dendrochronological potential in the rainiest region of the Americas where there is not hydric seasonality, which marks a milestone that contradicts the long-held prejudice of many dendrochronologists and wood anatomists that there are no growth rings in trees from these environments. This finding opens the frontiers of dendrochronology to these tropical environments that closed until now because of hypothetical and unjustified causalities, which had not been substantiated by empirical observations in situ, as prescribed by science.

Table 1-3: Species of this chapter reported with annual rings in other regions and in this chapter (in bold).

Species	Visibility		References	Annual rings and visibility	References
	This chapter	Other studies			
Apeiba macropetala[1]	+	±	Vásquez and Ramírez (2005)	+	Cintra et al. (2013)
		-	Araya (2012)		
Cariniana pyriformis	+	+	Arévalo and Londoño (2005)	+	Moreno and del Valle (2014)
		-	Sudworth and Mell (1911)	+	**This chapter**
		+	Vásquez and Ramírez (2005)		
Castilla elastica	+	-	Araya (2012)	+	Brienen et al. (2009)
Cedrela odorata	±	+	Alves and Angyalossy-Alfonso (2000)	+	Baker et al. (2017)
		+	Miller and Détienne (2001)	+	Köhl et al. (2017)
		+	Arévalo and Londoño (2005)	+	Lotfiomran and Köhl (2017)
		+	Vásquez and Ramírez (2005)	+	Rozendaal (2010)
				±	**This chapter**
				+	Worbes (2002)
Clarisia racemosa	+	-	Alves and Angyalossy-Alfonso (2000)	+	Rozendaal (2010)
		+	Beltrán and Valencia (2013)	+	Soliz-Gamboa et al. (2011)
		±	Gutiérrez (2014)	+	Tanaka (2005)

		+	Nahuz et al. (2013)		
		+	Santini (2013)		
Couratari guianensis	+	-	Alves and Angyalossy-Alfonso (2000)	+	Morel (2013)
		+	León (2008, 2014)		
		+	Miller and Détienne (2001)		
		-	Nahuz et al. (2013)		
		+	Santini (2013)		
		±	Trevizor (2011)		
		±	Vásquez and Ramírez (2005)		
Dipteryx panamensis	+	-	Miller and Détienne (2001)	+	Fichtler et al. (2003)
		±	Rojas (2000)		
		+	Vásquez and Ramírez (2005)		
		+	Wiedenhoeft (2011)		
Goupia glabra	+	+	Vetter and Botosso (1989)	±	Détienne and Baribier (1988)
		-	Miller and Détienne (2001)	+	Vetter and Botosso (1989) **This chapter**
		+	Vásquez and Ramírez (2005)	+	Köhl et al. (2017)
		±	Trevizor (2011)	+	Lotfiomran and Köhl (2017)
		-	Pons and Helle (2011)	+	Lopes de Oliveira (2010)

		±	Nahuz et al. (2013)	+	Cintra et al. (2013)
		-	Santini (2013)	+	Oliveira et al. (2014)
				+	**This chapter**
Hevea brasiliensis	+	+	Beltrán and Valencia (2013)	+	Jalil et al. (1998)
		±	Gutiérrez (2014)	+	Ohashi et al. (2001)
Inga acreana	+	+	Wiedenhoeft (2011)	+	**This chapter**
Inga rubiginosa	+	+	Alves and Angyalossy-Alfonso (2000)	+	Tanaka (2005)
Osteophloeum platyspermum	+	+	Marcelo (2017)	+	Lopes de Oliveira (2010)
		-	MAE-FAO (2014)		
Pentaclethra macroloba	+	+	León (2008)	+	Hazlett (1987)[2]
		+	Araya (2012)		Fichtler et al. (2010)
Pourouma bicolor	±	±	Tanaka (2005)	±	Tanaka (2005)
				±	**This chapter**
Schizolobium parahyba	+	+	Gutiérrez (2014)	+	Brienen et al. (2009)
		+	Vásquez and Ramírez (2005)	+	Lisi et al. (2008)
				+	Marcati et al. (2008)
Simarouba amara	±	-	Miller and Détienne (2001)	±	Détienne et al. (1988)
		+	Gutiérrez et al. (2002)	±	Fichtler et al. (2003)
		-	Araya (2012)		
		-	MAE-FAO (2014)	+	López-Ayala et al. (2006)
		±	Santini (2013)		

		±	Trevizor (2011)		
		+	Vásquez and Ramírez (2005))		
Symphonia globulifera	+	+	Arévalo and Londoño (2005)	±	Détienne et al. (1988)
		-	Miller and Détienne (2001)	±	Détienne (1995)
		-	Araya (2012)		
		+	Santini (2013)	+	Callado et al. (2001)
		±	Trevizor (2011)		

Using dendrometer bands in a non-seasonal wet forest at *La Selva*, Costa Rica, with an annual precipitation of about 4000 mm, O´Brien et al. (2008) found an annual diameter growth periodicity in both a deciduous (*D. panamensis*) and an evergreen species (*S. amara*), although not in the evergreen species *P. macroloba* (Table 1-1, Table 1-3). These three species had been reported to have annual rings in the same forest (Fichtler et al. 2003). Perhaps the growth periodicity of *P. macroloba* was so subtle that it is undetected by the instrument used by O´Brien et al. (2008).

The evergreen *H. alchorneoides* did not show annual periodicity in the diameter growth by O´Brien et al. (2008) but, in this chapter and also in León (2014), this species exhibited growth rings (Table 1-1). Something similar could have happened with *P. macroloba*, but it seems that, until now, the periodicity of its growth rings had never studied. O´Brien et al. (2008) could not identify a single triggering factor for the seasonal periodicity, phenology, and stem increments observed at *La Selva*. Hypothetically, they thought that deciduousness and periodic growth of species such as *D. panamensis* might have resulted from phylogenetic inertia in species that have their center of diversity in the Central and Northern Amazon, where the climate is more seasonal.

In sharp contrast to O´Brien et al. (2008), Hazlett (1987) and Breitsprecher and Bethel (1990) found evidence of periodic growth in *P. macroloba* in the same study area. Hazlett (1987) used dendrometer bands, and Breitsprecher and Bethel (1990) used radial dendrometers with data loggers that stored hourly measurements. Hazlett (1987) reported that *P. macroloba* grew at faster rates during the less rainy season of the year. But Breitsprecher and Bethel (1990) found that during these months, *P. macroloba* went into dormancy both in well-drained and in swamp forests. Perhaps because they used more precise instruments with a much higher temporal resolution, Breitsprecher and Bethel (1990) found a dormancy period in this species. *D. panamensis* was dormant during the less rainy season in two successive years, but only one tree was studied (Breitsprecher and Bethel 1990). This dormancy was undetected by O´Brien et al. (2008). Breitsprecher and Bethel (1990) suggested that variation in the daily amount of incoming solar radiation may be an environmental trigger of the annual growth periodicity at *La Selva*. Hazlett (1987), although not ruling out the annual endogenous growth control in *P. macroloba*, emphasized that during the less rainy period there was more illumination and higher temperatures, increasing growth rates that depended mainly on current photosynthesis.

In French Guiana, under a marked annual drought and 2,700 mm mean annual rainfall, Détienne et al. (1988) studied the diameter growth for five consecutive years using dendrometer bands and by marking the cambium with Mariaux windows to determine the periodicity of the growth rings in *S. amara*, G. glabra, and *S. globulifera*. They found a high correspondence between the monthly precipitation through the years and the monthly growth rates in *S. amara* and *G. glabra*. The relationship was less evident in *S. globulifera*. Growth rings were annual in all three species, but they were difficult to observe, especially in *G. glabra*. The authors attributed the formation of annual rings to annual droughts. By contrast, in flood-prone forests of the Mata Atlantica in Brazil, Callado et al. (2001) attributed the formation of annual rings in *S. globulifera* to endogenous periodicity.

Considering that the four species discussed in the last three paragraphs (*D. panamensis*, *S. amara*, *P. macroloba*, and *S. globulifera*) have been described previously as with annual growth rings and for which several environmental factors responsible for their formation are suggested in Table 1-3, how valid can these proposed variables for the study sites in Costa Rica at 10°26´N and in French Guiana at 5°04´N be for our study area? Our area of study is much closer to the Equatorial line (3°55´N) and, therefore, the length of the day, temperature, and sunshine irradiance are more constant throughout the year. Our study area receives almost twice the precipitation of the site in Costa Rica and nearly triples that of French Guiana. This last site also has a marked dry period, non-existent in our study area. However, all of those species have growth rings in our study area (Table 1-1, Table 1-3). Both these species, and the others in Table 1-1, respond to very subtle environmental cues, or the hypothesis for the origin of their growth rings must be modified totally. If it has accepted that the primary growth of some architectural models of tropical trees has genetically determined periodicity, endogenous secondary growth periodicity could be an alternative hypothesis for some species included in this chapter. Silva et al. (2019) proposed this classification for the growth rings: (1) obligatorily with growth rings, developing rings independently of environmental conditions; (2) facultative, growing rings depending on the variation of one or more environmental factors; and (3) obligatorily without growth rings, never forming growth rings, independently of environmental conditions. If the trees species with growth rings in Table 1-1 are not sensitive to subtle environmental cues, we must conclude that these species are obligatory with growth rings. Precise measurements with dendrometer bands suggest that there are ever growing species that form annual rings, and so, the cambium does not enter into dormancy. It is enough for tree-ring formation in these species that the cambium reduces its activity substantially, but without a complete halt (Silva et al. 2019). This seems to be the case in *C. insignis*, *C. obtusifolia*, *Minquartia guianensis*, and *S. amara* (O´Brien et al. 2008), *Schefflera morototoni*, *G. glabra*, *S. globulifera,* and *S. amara* (Détienne and Barbier 1988; Morel 2013), *Shorea patoiensis*, *S. pinanga* and *S. dasyphylla* (Fujii et al. 1999), *S. leprosula*, *S. acuminata*, *S. parvifolia*, and *Dryobalanops sumatrensis* (Sass et al. 1995; Wang and Hamzah 2018), and young trees of *Terminalia superba* (E de Faÿ 1992). Perhaps this is one of the reasons why some of these species have faint rings. For this reason, a third group of species with periodic growth, but without cambial dormancy, should exist.

In 11 of the 17 species found with annual rings by dendrochronologists (Table 1-3), and with growth rings and annual growth rings in this chapter, some wood anatomists did not find growth rings at all, or they grouped them as indistinct or absent. Two U.S. Forest Service wood anatomists, who studied the anatomy of *C. pyriformis* and *Swietenia macrophylla*, did not observe growth rings in these species (Sudworth and Mell 1911). Both species have been described repeatedly by other anatomists as having growth rings (Table 1-3) and by dendrochronologists with annual growth rings marked by increased fiber density (Brienen et al. 2016; Schöngart et al. 2017). Détienne and Barbier (1988) described as annual the growth rings of *G. glabra*, *S. amara*, and *S. globolifera* in the French Guiana forests, and Détienne (1995) also confirmed the annual rings of *S. globulifera*. But Miller and (2001), with one author in common and in the same forest, did not find growth rings in any of the three species. How do we explain such contradictory results?

A way to avoid subjectivity in the identification of growth rings is to develop computer vision methods on high-resolution scanned images for the identification and measurement of several growth ring variables. In this way, the types of rings could be determined automatically, and their variables measured quickly and safely. Not without challenges, the development of this technique would be the entrance to the fourth revolution of knowledge for dendrochronology and wood anatomy.

Dendrochronology would learn a great deal thoroughly investigating the trees of these non-seasonal, hyper-humid tropical climates. In highly complex tropical ecosystems there may be emerging properties and nonlinearities that seem not contemplated in dendrochronological studies of the temperate region.

Dendrochronology in the temperate region operates linearly according to Liebig´s law. This law states that growth is dictated not by total resources available, but by the scarcest resource (limiting factor). However, ecology teaches us that both the deficit of a growth factor and its excess produce tension and limit growth. Therefore, a law of the minimum and a law of the maximum should exist as limiting factors for growth. These two laws are involved in Shelford's tolerance law (Niinemets and Valladares 2008): If other factors are not limiting, as the magnitude of a limiting factor increases, organisms respond by increasing their growth, up to a limit at which the response saturates. Subsequent increases in this factor produce less and less growth because the organism is growing under incremental stresses. Consequently, Shelford's law is non-linear and depicts a unimodal curve (Figure 1-8). Under a non-seasonal, hyper-humid tropical climate, we cannot exclude the possibility that soil moisture exerts tension on tree growth of some species. Then, the correlation between tree growth rates and annual precipitation would be negative and not positive as the law of the minimum stipulates. In fact, this has already been demonstrated for temperature in tropical lowland trees where the correlation between rings width and mean annual temperature is often negative (Herrera and del Valle 2011; Ramírez and del Valle 2011; del Valle et al. 2012; Moreno and del Valle 2014), in line with what we might call the law of the maximum.

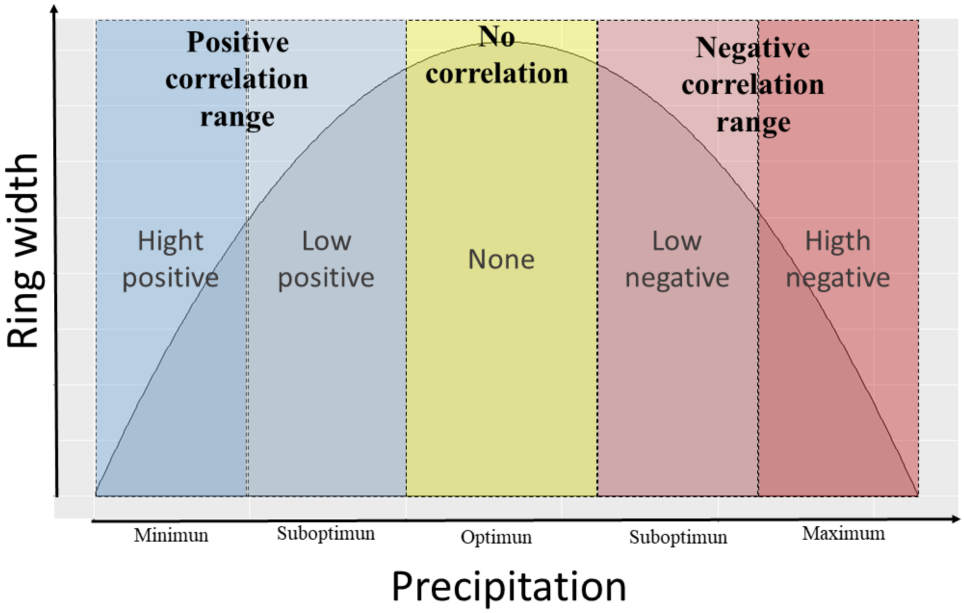

Figure 1-8: It shows a representation of Shelford's tolerance law for dendrochronological applications. There is a limiting factor: by water deficit in the soil (left), and by an excess of water in the soil that increasing the anoxic conditions for roots (right). Towards the center of the curve, the rings should be complacent. Consequently, the response of ring widths to soil moisture must be non-linear.

However, the range of tolerance to soil moisture is different for each species, and their populations respond to the resources available depending on the assemblage of species in which they are inserted (Niinemets and Valladares 2008). Thus, for a given soil moisture content, different species may respond in different ways, and even the same species: subsidy or stress. In temperate regions, the cambium of virtually all tree species synchronously enters into dormancy during autumn and is activated during spring. Therefore, there is minimal uncertainty about when trees grow or stop growing. Something similar is assumed to occur when there is hydric stress in the tropics. The cambium of trees in temperate regions responds to temperature and day length cues (Evert 2006). In seasonal tropical climates trees respond to droughts or floods (Evert 2006; Brienen et al. 2016; Schöngart et al. 2017), although day length or irradiance may also be involved

(Callado et al. 2001; Silva et al. 2019). But, if in non-seasonal tropical wet climates trees form growth rings, as proved in this chapter, will there be synchrony between the different species? And, to what cue or cues will these trees respond when they are only at 3°55´ from the Equatorial line?

We should not rule out that genetically controlled periodicities that regulate their frequencies may exist, at least in some species (Fahn 1967; Tomlinson and Craichead 1972; Tomlinson and Longman 1981; Jacoby 1989; Mushove et al. 1995; Callado et al. 2001; Silva et al. 2019). In perennials, the molecular and genetic factors that influence these clocks are gradually becoming disentangled with Populus as a prototype (Johansson 2010). Today it is known that these periodicities are controlled genetically (Lüttge and Hertel 2009; Johansson 2010). The input to the clock in Populus is mediated by the phytochrome-A photoreceptor to detect the circa-annual clock (Johansson 2010). A large number of genes have identified that expressed during the radial woody growth of plant stems (Liu et al. 2014). There are two types of periodicity: (1) synchronization of behavioral and physiological processes to cyclic environmental factors, or extrinsic adaptive value, and (2) coordination of internal metabolic processes, or intrinsic adaptive value (Sharma 2003). These periodicities are also called exogenously and endogenously controlled, respectively, by scientists who have developed the architectural models for trees (Hallé et al. 1978; Barthélémy et al. 1995; De Reffye et al. 2008; Nicolini et al. 2012; Palubicki 2013). In our opinion, tropical dendrochronology should devote to this task in the coming years.

Growth rings have both genetic and environmental origins, but little scientist knows about the contribution of each of these factors in the growth ring formation (Schweingruber 2007). In temperate regions, the sharp contrasts between temperatures and day lengths throughout the year make it challenging to discriminate environment influence from genetic factors. In non-seasonal, tropical hyper-humid climates that are very close to the Equatorial line, such as in our study area, mean monthly temperatures and day lengths are nearly constant the year round. Hypothetically, this circumstance suggests that, if any other subtle environmental factor as cloudiness is not involved in these growth rings periodicities; genetic factors are the principal causes of the growth rings formation in this environment.

1.4 Conclusions

We report here the existence of growth rings for trees growing under an extreme humid tropical environment without marked seasonality in precipitation, temperature or solar irradiance. From a total of 81 trees studied, ~ 45% showed well-defined growth rings. The percentage of trees with growth rings was even higher than in other tropical regions with more seasonal climates. A survey of the literature suggests no clear relationship between climate and ring formation, but curiously, an association with ring-detection criteria developed by different research communities. The large proportion of growth ring in the trees in this tropical non-seasonal region, suggests that other environmental factors, or even from the genetic origin, may determine growth-rings development in trees.

Some questions to be answered by dendrochronology for non-seasonal hyper-humid tropical environments would be (1), what are the periodicities of the growth rings? (2), what is the relationship between high rainfall and growth rings? (3), what other subtle seasonality or cues might be involved in these periodicities?

We believe that future researches in non-seasonal tropical regions such as those with extreme precipitation would help to understand better the factors controlling growth ring formation in tropical trees.

2. Chapter 2: Growth rhythms of trees from the rainiest neotropical region

With Jorge I. del Valle, Diego A. David, Sebastián González-Caro, Conrado Tobón, Carlos A. Sierra

Abstract: The occurrence of annual growth rings as a consequence of the seasonal activity of vascular cambium in tropical trees has been explained, either by the annual water deficit or annual floods. However, little is known about annual tree-ring drivers under tropical hyper-humid conditions without evident yearly dry periods. Shelford's law states that both the deficit and the excess of environmental resources limit plant growth. Accordingly, we hypothesize that reduced solar radiation, excess soil moisture, and slight reduction of precipitation control annual growth rings in tropical hyper-humid forests without annual dry periods. We first test the occurrence of rhythmic growth in several tree species from the Biogeographic Choco Region (annual rainfall 7,200 mm) using three different methods: Radiocarbon (^{14}C) dating, tree rings synchronization, and dendrometer bands. Then, we assess the effect of some environmental drivers, namely rainfall, short wave radiation, temperature, and soil moisture, on tree growth (tree rings and dendrometers). We observe both positive and negative growth answers to water and light availability, depending on the tree species. This fact suggests that both excess or deficit of growth factors may explain seasonal cyclicity of growth rhythms in some trees, strengthening our hypothesis. We show, for the first time, the occurrence of annual growth rhythms in several tropical tree species under extreme ever wet conditions. A new frontier is here open for tree rings science, transforming the long-held belief that there was no rhythmic tree growth in hyper humid environments.

2.1 Introduction

Plant growth rhythms are seasonal or cyclic events occurring on different tissues and organs such as meristems, roots, leaves, and reproductive structures (Lüttge and Hertel 2009; Albert et al. 2019). For tree species, growth rhythms are driven by environmental conditions such as climate, light availability, and soil conditions (Lüttge and Hertel 2009; Fyllas et al. 2017). In temperate and highly seasonal regions tree growth generally follows an annual cycle expressed as cyclic tree ring formation driven by temperature seasonality and water availability (Babst et al. 2019; Stine 2019; Pearl et al. 2020). In contrast, growth rhythms in tropical trees and their drivers are less studied (García-Cervigón et al. 2020).

The occurrence of annual growth rings as a consequence of the seasonal activity of vascular cambium in tropical trees has been an intriguing subject of study for ecologists, silviculturists, and biologists (Worbes 2002; Yáñez-Espinosa et al. 2010; Shimamoto et al. 2016; Albert et al. 2019). Hence, establishing the exact age of tropical trees is a challenging task, mainly when anatomical tree-ring structures are unclear, or even when they are well defined, arises the question, what is the frequency of their formation? (Stahle 1999; Ricker et al. 2020). Tropical tree-ring frequency is commonly determined using ^{14}C of specific tree rings (Bomb-peak-method) (Worbes and Junk 1989; Fichtler et al. 2003; del Valle et al. 2014; Andreu-Hayles et al. 2015), complemented by detailed observations of growth in vascular cambium using dendrometers, microsections, and xylem wounds (Worbes 2002; Lisi et al. 2008; Shimamoto et al. 2016; Hogan et al. 2019; Pumijumnong et al. 2019). Also, successful cross-dating (i.e., tree-ring synchronization between samples) has been helpful to analyze the environmental drivers of tropical tree-rings formation (Stahle 1999; Trouet et al. 2006; Remane and Therrell 2014).

The tropical dendrochronology paradigm has evolved fast during the last 30 years. A few decades ago, the common belief was that tropical trees had no rhythmic growth because of a lack of thermal seasonality, compared with temperate and boreal regions (Whitmore 1990). However, the accumulation of evidence on annual rings in the tropics suggests that dry periods or periodic floods are the dominant triggering variables leading to tropical tree-ring formation (Rozendaal and Zuidema 2011; Brienen et al. 2016; Schöngart et al. 2017). But, pieces of evidence of annual tree rings in wet tropical climates, without water deficit or flooding (Fichtler et al. 2003; Moreno and del Valle 2014; Giraldo et al. 2020), challenge current assumptions about the factors inducing growth-ring formation in tropical trees. In particular, Chapter 1 showed a high percent of tree-rings structures in several tree species (82%, n = 81) from the Choco region, the rainiest in the New World (precipitation over 7,200 mm y^{-1}). While it is not clear what factors rule periodic growth rhythms in tropical trees under such conditions, slight variation in rainfall, soil moisture, solar irradiance, cloudiness, sunrise and sunset time could be considered as possible drivers (Breitsprecher and Bethel 1990; Clark and Clark 1994; Borchert and Rivera 2001; O´Brien et al. 2008; Moreno and del Valle 2014).

According to Liebig's law, the growth of an organism is not controlled by all the available resources (light, temperature, water, nutrients, etc.) but by the scarcest environmental resource (i.e., limiting factor) (Taylor 1934). The limiting factor that controls annual tree growth is the main variable recorded in the tree-rings thickness (Speer 2010; Stine 2019). Under this view, light availability, mainly photosynthetically active radiation, would be a limiting factor in high cloud cover regions such as non-seasonal hyper-humid forests. In particular, the light limitation would be extreme during the rainiest months in which cloud cover increases, producing an annual pattern on tree growth. Indeed, tree growth in seasonal tropical forests is limited by light availability during the rainy season (Graham et al. 2003). Recent observations based on satellite information indicate an increase in canopy photosynthetic activity during the less rainy period in the tropical wet forests without water deficit (Green et al. 2020). It implies a reduction in growth and productivity during the rainiest months as a consequence of water excess (Muller-Landau et al. 2021), or photosynthetically limited for both high cloudiness and an excess of precipitation (Restrepo-Coupe et al. 2013). Then, the interaction between light and water availability may drive tree-growth rhythms in tropical hyper-humid forests.

In fact, according to Shelford´s law (Shelford 1913, 1931), all organisms have both minimum and maximum thresholds for the different environmental factors that control their population growth. Near these thresholds, organisms grow under stress and constrained by both deficit and excess. So, in hyper-humid forests without any dry season, the availability of water measured as rainfall should be close to the maximum tolerance threshold for some species. Hypothetically, too much precipitation maintains high water saturation in the soils, which reduces its aeration and favors hypoxic conditions in the roots, limiting tree growth. Considering both Liebig´s and Shelford´s laws, we hypothesize that at least in some species, light, soil moisture, and slight reductions in precipitation control tree growth rhythm in hyper-humid tropical forests without evident dry periods. In contrast, we expect to find negative correlations between rainiest months and tree growth. In this study we aim: i) to determine the growth ring frequency in some species with well-defined tree rings, growing in a hyper-humid tropical forest, ii) to describe intra-annual growth patterns in some of these species, iii) to assess possible environmental drivers of tree growth in a hyper-humid tropical forest. This information can provide new insights into the interaction between physiology and environmental drivers of growth rhythms in the neotropical rainiest region, little studied until now.

2.2 Materials and methods

2.2.1 Study area

This study was carried out at the low *Calima* River Basin (3°57´12.54´´ N, 76°59´27.96´´ W), which belongs to the Choco Biogeographic region, in northern South America, near the Pacific coast of Colombia (Figure 2-1). This region is the rainiest in the New World. In some places, mean annual precipitation is over 12,000 mm (Mesa et al. 1997; Poveda and Mesa 2000; Mesa and Rojo 2020). In the *Yurumanguí* village (120 km South from our study area), recorded rainfall in 2018 was 26,987 mm (Mesa and Rojo 2020). The low-level jet stream (tropopause air current) centered around 5°N, known as the Chocó Jet, explains the high regional precipitation (Mesa and Rojo 2020). Furthermore, the high floristic richness, endemism, and increasing deforestation place the Choco region as one of the most biodiverse hotspots in the World with high priority for conservation (Myers et al. 2000; Fagua and Ramsey 2019; Pérez-Escobar et al. 2019). Small hills with slopes up to 45° with elevations ranging from 40 - 100 m above sea level characterize the study area. Soils are mottled grey-yellow clay-loam, poor in soil nutrients and high iron and aluminum concentration (Faber-Langendoen and Gentry 1991).

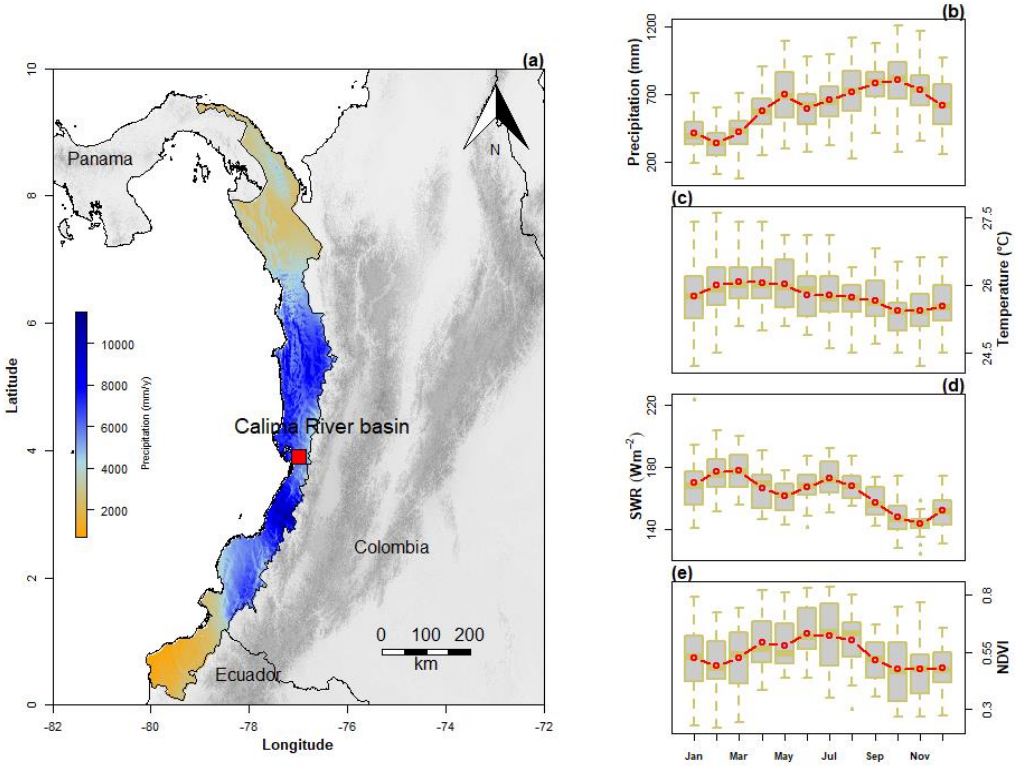

Figure 2-1: The study area. (a) *Calima* River Basin (square), located in the Chocó Region, with an area of explicit precipitation gradient (data from https://chelsa-climate.org/) (Karger et al. 2017). Mean monthly precipitation (b) and temperature (c) data from *Bajo Calima* meteorological station, which belongs to the Institute of Hydrology, Meteorology, and Environmental Studies of Colombia (IDEAM). Mean monthly values of short-wave solar radiation SWR (W m^{-2}) (d), available from Clouds and the Earth's Radiant Energy System - CERES (https://ceres.larc.nasa.gov/) and mean monthly NDVI (Normalized Difference Vegetation Index) (e), data from Modis/Terra vegetation indices (https://lpdaac.usgs.gov/products/mod13q1v006/).

2.2.2 Tree-ring samples and dating

We obtained entire cross-sections for multiple tree species, taking advantage that Afro-Colombian ethnic groups sporadically felling trees for their economic and cultural activities. We choose 14 species with well-defined to poorly defined tree rings, but that could be dated to establish their tree-ring frequency by the radiocarbon bomb-peak method (Worbes and Junk 1989; Fichtler et al. 2003). A priori, we assumed the annual formation of tree rings. Then, we assigned the calendar year to the last ring formed, either complete or incomplete: 2016 was the sampling year, and from there, we counted regressively to the pith. We collected about 20 mg of the wood sampled in each tree ring for radiocarbon analyses from specific rings dated by regressive counting between 1957-2010. Samples were prepared following Steinhof et al. (2017) to extract alpha-cellulose and were analyzed at the radiocarbon laboratory of Max Planck Institute for Biogeochemistry in Jena. We calibrated the radiocarbon results using Cali-Bomb (Reimer et al. 2004) with Northern Hemisphere Zone calibration data (NHZ2) to obtain calendar dates. Finally, such calibrated dates were compared with the assumed calendar years (dendrochronological dates) and counting the number of rings as the difference between dated rings, allowing us to establish the tree-ring frequencies (del Valle et al. 2014).

Our study area bears an exceptional richness and diversity of tree species with many endemic and rare species (Gentry 1989); but their populations tend to be small, and most tree species are scattered on the landscape. Therefore, it is not easy to sample several trees from most species. For these reasons, we used only four tree species with available tree samples ($n \geq 4$ trees) growing at similar sites and conditions (illumination and slope), to check tree-ring synchronization. Samples were prepared according to standard procedure as described by Speer (2010). In an Epson Expression 10000XL scanner, we obtained high-resolution images (1800-2400 dpi), allowed us to observe macroscopic wood features up to 10- 15 *μm*. Tree-ring measurements were obtained by combining ImageJ (Fiji) 11.52i software (Schindelin et al. 2012) and R software (R Core Team 2020). Cross-dating was carried out at the tree level first. Then, we gradually added other tree-ring series, ensuring statistical and graphical synchronization. The quality control, series synchronization, and generation of chronologies were carried out with the dplR package (Bunn 2008, 2010).

2.2.3 Environmental data

From the *Bajo Calima* Meteorological Station (IDEAM), mean monthly rainfall data (1947-2017) and mean monthly temperature data (1957-2016) were available. Some lacking records were estimated with the closest five meteorological stations also from the Bajo *Calima* basin. Due to the lack of ground instrumental measurements of solar radiation, we use the mean monthly short-wave solar radiation: SWR (W m^{-2}) satellite-derived product available from Clouds, and the Earth's Radiant Energy System - CERES (https://ceres.larc.nasa.gov/), as a surrogate of the incoming photosynthetically active radiation between 2000-2019. The Normalized Difference Vegetation Index (NDVI) was obtained from MODIS time series in the study region previously filtered to reduce cloudiness and missing data. These data were extracted from the *MODISTools* R package (Tuck et al. 2014). We used time series from ten points selected into the study area, in which forest cover has been maintained in the last 20 years. For each point, we averaged NDVI data for each month between 2000-2019.

2.2.4 Field measurements

We installed 20 automatic band dendrometers (Tree-Hugger®, Global Change Solutions) at tree diameters 15- 30 cm and at tree heights from 1.3 to 3 m to avoid buttress. Measurements were recorded hourly and data downloaded every five weeks. Before installing the dendrometers, we cleaned the stem surfaces to avoid the proliferation of epiphytes around them. The first ten dendrometers were installed in April 2018; after few months, most of them stopped recorded measurements. Then, we installed a second group in October 2019; most of them were still working until our last download in February 2021. The malfunctions issues of devices, non-measurement periods, or damage must be attributed to a permanently high relative humidity in the study area. For this study, we selected four species with well-defined tree rings, but the recordings of just two (*Goupia glabra*, *n* = 6 and *Apeiba macropetala, n* = 3) were used because they present the complete records in different replicates, which is much more suitable for a better understanding of growth rhythms along the year. These same two species were analyzed by the tree-rings series. We also installed two soil moisture and soil temperature stations (Campbell Sci®) at two depths, 10 and 30 cm. The frequency of measurements was 30 min. All these measurements were carried between 2018 – 2020. For an accurate determination of soil water content, we calibrated the measurements according to Frumau et al. (2006). We carefully debugged the data by removing aberrant measurements, mainly present in dendrometer data. Most of them related to irregular changes in the battery voltage of devices.

As a first step, we transformed circumference increment data to radial increment data assuming that stems were cylindrical. To standardize the measurements, we subtracted all the first measurements in dendrometers allowing each dendrometer data to illustrate similarities among the same species. This procedure allowed us to average the data monthly and to eliminate short-term fluctuations of stem girth due both daily changes in soil humidity and the effect of diurnal fluctuations of temperature and radiation. The mean monthly, cumulative and standard deviation growth was obtained for an entire year. All filter procedures and statistical analyses were performed using the R software (R Core Team 2020).

2.2.5 Data analyses

We considered some parameters to assess the suitability of tree-ring series: series intercorrelation which measure the strength signal common in all sampled trees (Speer 2010). The mean correlation coefficient among tree-ring series (rbar) as an indicator of common signal strength (Speer 2010; Cook and Pederson 2011). The expressed population signal (EPS) measure of the common variability in a chronology, values below 0.85 suggest few trees dominate de level signal (Speer 2010). The Signal to noise ratio (SNR) is a measure of the amount of desired signal is recorded in the chronology (Cook and Kairiukstis; Speer 2010). Mean sensitivity as a measurement of variability in tree ring width, values ranging between 0.2 and 0.4 are considered sensitive enough for climate reconstruction (Speer 2010).

To assess the relationship between tree-ring frequency and environmental parameters, we use the R-package *treeclim* (Zang and Biondi 2015) to perform bootstrapped correlation analysis between tree-ring chronologies and mean monthly precipitation, mean monthly temperature, and SWR (W m^{-2}) from September of the previous year to August of the current year. We choose such a period according to our field observations: in some species, leaf shedding and new leaves occur from September to February and flowering from February-May. The selected period includes the probable growing season for the studied species. We also, used the NDVI as complementary information to give us an idea of the possible phenological changes of the vegetation in the study area.

To assess the effect of environmental drivers in the intra-annual tree growth, we used a cross-correlation test between monthly dendrometer series from two species (*G. glabra* and *A. macropetala*) and monthly data of precipitation, soil water content, short-wave radiation, and NDVI. This analysis was run using the *ccf* function in the *base* R package.

2.3 Results

Tree-ring frequency was checked by calibrated dates of ^{14}C in calendar years and dendrochronological dates (Appendix A). According to this result in the 14 species tested, tree-ring formation occurs annually. In 10 tree species, the accuracy of the results is much more evident because the annual resolution is clear in different tree samples or adjacent tree rings from the same tree sample. Four species with a single dated ring also allow establishing annual periodicity in ring formation. The comparison between all radiocarbon vs. dendrochronological dates matched extremely well and within one-year margin error (*mean* = 0.05, *Sd* = 0.54) (Figure 2-2). The species phenology or growth season, which in some cases start the previous year, are the attributable reasons for some small differences (Figure 2-2). In just one radiocarbon sample of *Tachigalii colombiana*, we found a significant difference between calibrated dates and dendrochronology dates (1.5 years), caused by sampling error, probably including wood from an adjacent tree ring; however, the annual tree ring annuity was confirmed by other samples from the same tree, and by other different trees (discs).

Four species: (*Humirastrum procerum*, *Qualea lineata*, *Apeiba macropetala*, *Goupia glabra*) with a sample size between 4 and 12 trees, growing under similar conditions, were successfully cross-dated. Despite the small sample available, we confirmed tree-rings synchronization (Table 2-1). Two species with the largest replicates *Q. lineata* and *G. glabra* presented suitable values of serial correlation (0.42 – 0.46, $p < 0.05$, respectively), running r-bar (0.36 – 0.31 respectively), and expressed population signal EPS (0.87 – 0.89

respectively) (Table 2-1). The other two species had the highest and the lowest mean series correlation: *A. macropetala* (0.49, $p < 0.05$) and *H. procerum* (0.41, $p < 0.05$), respectively. And both species reveal low EPS values (Table 2-1). *H. procerum* and *G. glabra* are prone to form wedging rings close to wounds, where tree rings usually vanished. We carefully avoid those sectors in the cross-sections when delineating and measuring growth rings.

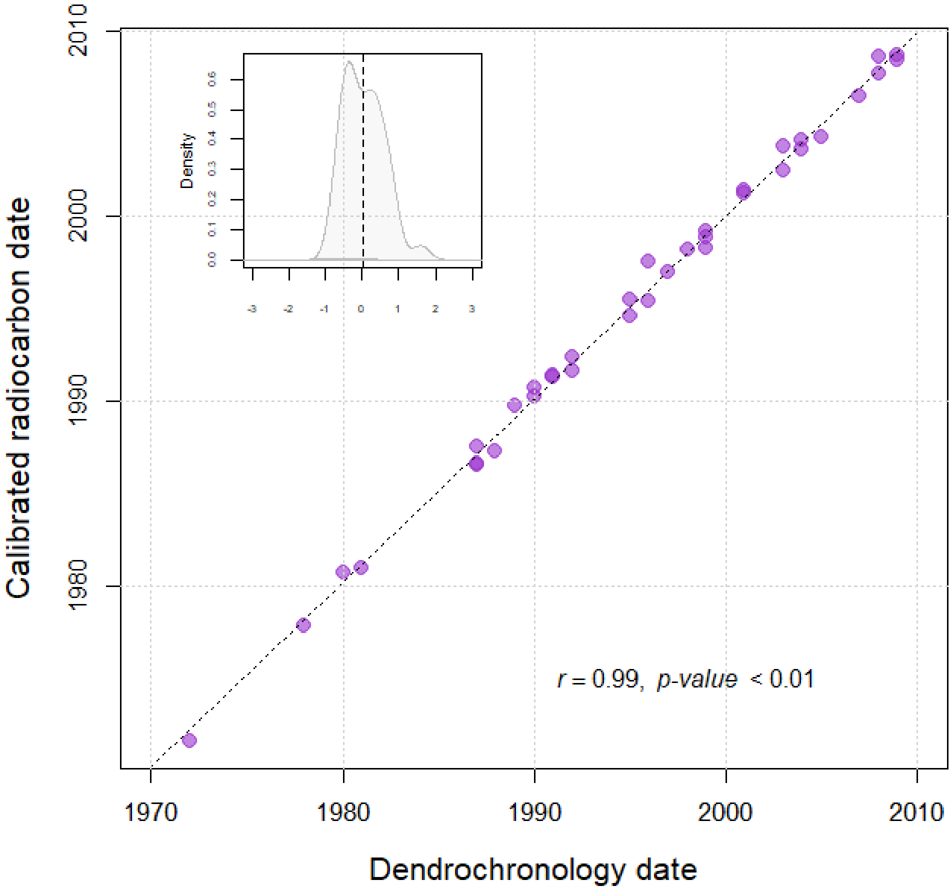

Figure 2-2: Relationship between dendrochronology dates and calibrated radiocarbon dates (n= 36) from 14 species, see Appendix A. The histogram represents the difference between corresponding dates.

Table 2-1: Descriptive statistics of four cross-dated tree species from low *Calima* River Basin. ***rmean***: mean series intercorrelation. ***rbar***: running bar; ***EPS***: Expressed population signal; ***SNR***: Signal noise to ratio. **MS**: mean sensitivity. *($p < 0.05$).

	Humirastrum procerum	*Qualea linneata*	*Apeiba macropetala*	*Goupia glabra*
Time-span (years)	1943-2016	1960-2016	1984-2016	1869-2019
Sampled tres (series)	6	7	5	12
Diameter range (cm)	15 - 50	10 - 60	45 - 50	10 - 30
Ring width and deviation (mm)	2.4 ±1.3	3.7 ± 2.1	8.3 ± 6.1	1.8 ± 1.1
Interseries correlation	0.49*	0.46*	0.41*	0.42*
rbar	0.28	0.36	0.31	0.32
EPS	0.82	0.87	0.833	0.89
SNR	4.58	6.76	4.98	8.58
MS	0.35	0.36	0.45	0.31

The results of the bootstrapped chronologies-climate correlations are contrasting between species (Figure 2-3). With *H. procerum* we observed negatively association with September precipitation of the previous year (r = - 0.33, $p < 0.05$) and with mean precipitation from September-October (r = - 0.35, $p < 0.05$) (Figure 2-3b), and that it was also significant correlated with the shortwave radiation from October previous and current January (October: r = -0.54, $p < 0.05$; January: r = 0.66, $p < 0.05$), also correlated with mean short wave radiation from December previous to current April (r = 0.56, $p < 0.05$) (Figure 2-3c).

The growth of *Q. lineata* was significantly positively associated with January precipitation of current year ($r = 0.38$, $p < 0.05$) and with mean precipitation from September previous to current January ($r = 0.28$, $p < 0.05$) (Figure 2-3f), but negatively correlated with shortwave radiation of previous December ($r = -0.45$, $p < 0.05$) (Figure 2-3g).

The *A. macropetala* growth is negative correlated with current year June and July precipitation (June: $r = -0.58$, $p < 0.05$; July: $r = -0.34$, $p < 0.05$) (Figure 2-3j) and with mean precipitation from current May to current September ($r = -0.44$, $p < 0.05$) as well as significantly correlated with shortwave radiation of the previous October, previous November, current March and current April (October: $r = -0.65$, $p < 0.05$; November: $r = -0.61$, $p < 0.05$; March: $r = 0. 68$, $p < 0.05$; April: $r = 0.59$, $p < 0.05$) and with mean current year shortwave radiation from January to May ($r = 0.77$, $p < 0.05$) (Figure 2-3k).

The tree-ring chronology of *G. glabra* was positively associated with May, July and August precipitation of the current year (May: $r = 0.23$, $p < 0.05$; July $r = 0.40$, $p < 0.05$; August: $r = 0.31$, $p < 0.05$), also positively correlated with mean precipitation from May to October of current year ($r = 0.43$, $p < 0.05$) (Figure 2-3n), also a negative correlation is observed with shortwave radiation in March of current year ($r = -0.42$, $p < 0.05$) and with mean current year shortwave radiation from January-June ($r = -0.36$, $p < 0.05$) (Figure 2-3o). Temperature had not significant associations with the analyzed chronologies (Figure 2-3).

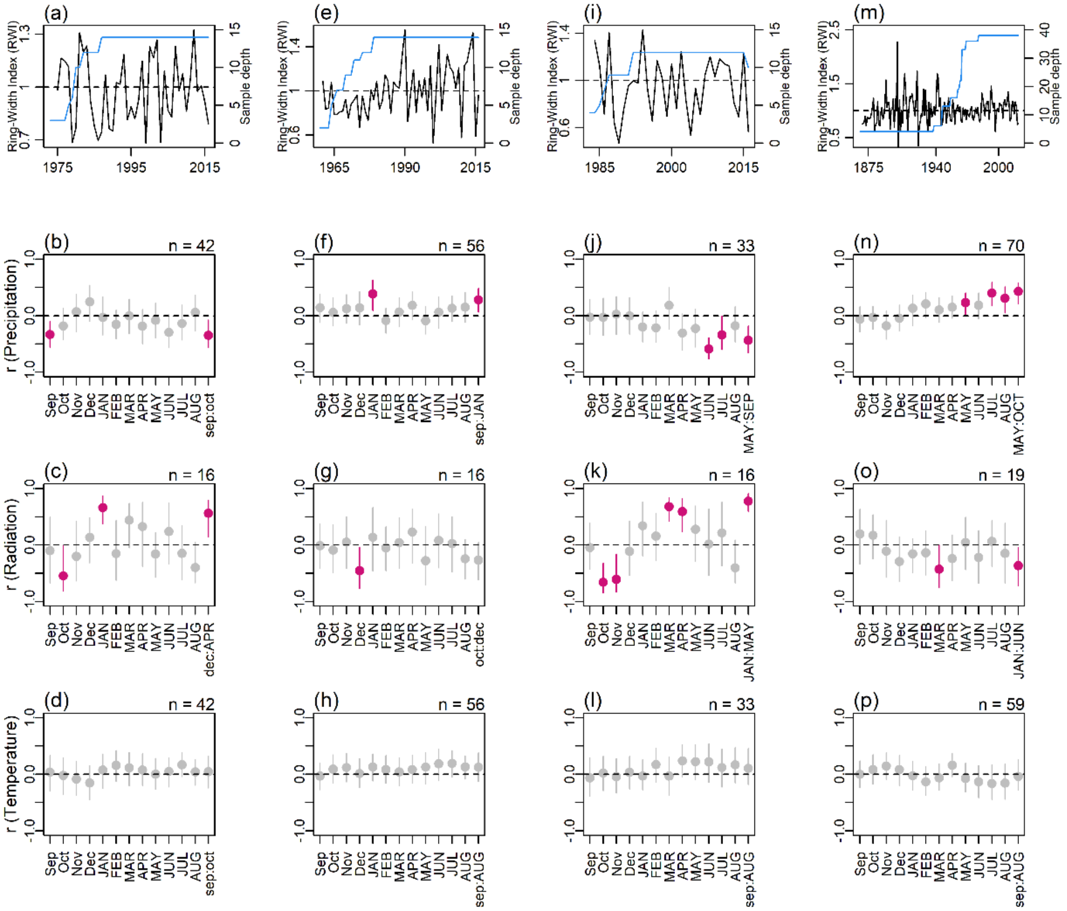

Figure 2-3: Tree chronologies and bootstrapped correlations with environmental variables. The first row of panels (a, e, i, m) represents the tree-ring chronologies, the second to the fourth row of panels represent, respectively, the chronologies association with precipitation, short-wave radiation (SWR) in W m^{-2}, and temperature. Numerals a, b, c, d, represent *Humiriastrum procerum* chronology and their correlation with precipitation, SWR and temperature, respectively. Numerals e, f, g, h, represent *Qualea lineata* chronology and their correlation with precipitation, SWR and temperature respectively. Numerals i, j, k, l, represent *Apeiba macropetala* chronology and their correlation with precipitation, SWR, and temperature respectively. Numerals m, n, o, p, represent *Goupia glabra* chronology and their correlation with precipitation, SWR, and temperature, respectively. Lower case months (previous year) and months in capitals (current year).

Dendrometer measurements provide evidence of intra-annual growth rhythms occurring differently in the two studied species (uncoupled growth) (Figure 2-4a – 2-4b). *A.*

macropetala growth is evident during January - August followed by abrupt reduction of growth (interpreted as dehydration of the stem) during August - October, before starting growing again during November-December. Its observation suggests growing start in November of the previous year and finishes in August of the current year. The *G. glabra* dendrometer growth reveals no growth and slight dehydration between January – March, followed by growth from April - October, then abrupt dehydration and no growth between October - December. Which means the complete growing season start in March of the current year and finish in February of the following year.

In Figure 2-4a – 2-4f, we present the graphical variation of tree growth and environmental factors variation along the year. Figure 2-4g – 2-4p allows us to obtain a better interpretation of the relationships based on cross-correlation comparisons. The comparison between both species (Figure 2-4g, 2-4h). *G. glabra* shows a significant positive relation with precipitation with zero lag (Figure 2-4i). Meanwhile, *A macropetala* presents a significant positive correlation with two months lagged (Figure 2-4m). The relationship between SMC and both species presents the highest significant correlation value with a lag of 2 months (Figure 2-4j and Figure 2-4n).

A significant and negative relation with 2 and 3 months lagged is observed between *G. glabra* and SWR (Figure 2-4k), but no relationship is observed between *A. macropetala* and SWR (Figure 2-4o). Finally, comparisons between *G. glabra* and NDVI show significant correlations with 1-2 months lag (Figure 2-4l). Moreover, *A. macropetala* comparisons with NDVI were positive and significant with a zero lag and one lagged month (Figure 2-4p).

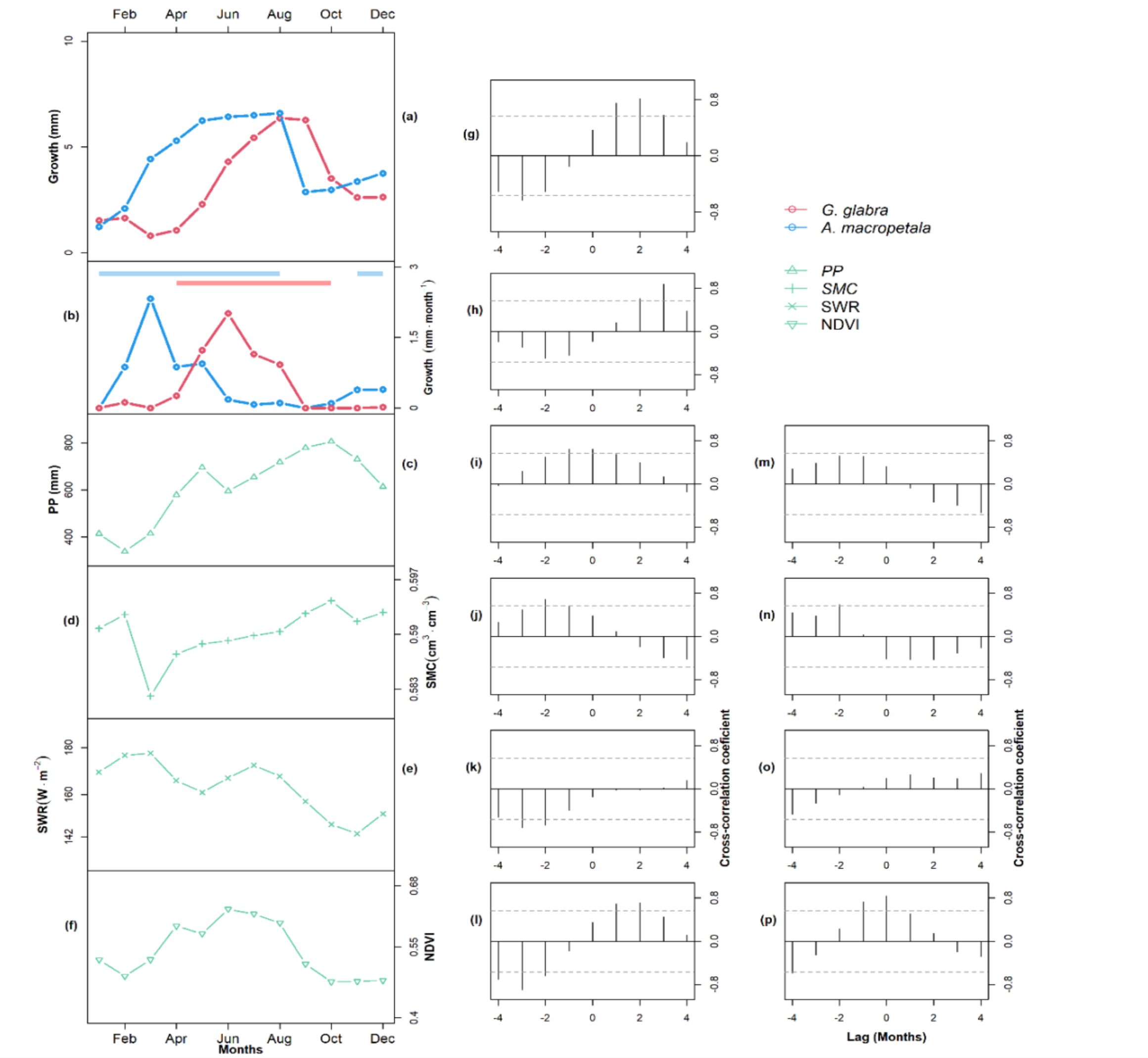

Figure 2-4: Comparison between mean monthly growth and environmental factors. (a) Mean monthly cumulative growth (mm). (b) Mean monthly growth rate (mm month^{-1}), the bars indicate the growth period. (c) Precipitation (PP) in millimeters (mm). (d) Mean monthly soil moisture content (SMC) expressed in volumetric units (cm^3 cm^{-3}). (e) Mean monthly short-wave radiation (SWR) in W m^{-2}. (f) Mean monthly normalized difference vegetation index (NDVI). (g-h) cross-correlation function between *G. glabra* and *A. macropetala*. (i-p) Cross-correlation function between mean monthly growth and environmental factors. (i) *G. glabra* vs. PP. (j) *G. glabra* vs. SMC. (k) *G. glabra* vs. SWR. (l) *G. glabra* vs. NDVI. (m) *A. macropetala* vs. PP. (n) *A. macropetala* vs. SMC. (o) *A. macropetala* vs. SWR. (p) *A. macropetala* vs. NDVI.

2.4 Discussion

We found evidence of annual growth rhythms on trees growing in a tropical hyper-humid forest without water deficit. These rhythms are inferred on three independent facts: annual growth rings synchronization (dendrochronological method) in several tree species, dendrometer observations, and the high correlation between radiocarbon and tree-ring estimated age in 14 tree species

This study is the first report of tree-ring annuity for 8 out of 14 tree species analyzed. The other tree species were reported with annual rings in other seasonal tropical forests: *C. racemosa* by bomb-peak method and cross-dating (Soliz-Gamboa et al. 2011); *G. glabra* by cross-dating (Oliveira et al. 2014; Lotfiomran and Köhl 2017); *S. globulifera* and *H. brasiliensis* by pinning method (cambium wounds), band dendrometers and phenology (Callado et al. 2001; Ohashi et al. 2001). Or inferred by a marked dry season each year in *A. macropetala* and *C. elastica*, (Brienen et al. 2009; Cintra et al. 2013). Curiously *C. elastica* and *C. racemosa* had been repeatedly reported with absent tree ring boundaries in descriptions performed by wood anatomists (Alves and Angyalossy-Alfonso 2000; Miller and Détienne 2001; Araya 2012; Beltran and Valencia 2013). Then, our finding challenges the generalized idea of a lack of tree growth rhythms and consequently tree rings in hyper-humid regions such as the rainiest forest of the Americas due to continuum water supply.

According to our hypothesis, in some species we expected to find negative correlations between the rainiest months and trees growth. Based on Shelford´s law, *H. procerum* and *A. macropetala* are close at their maximum thresholds for water excess and their minimum thresholds for light availability. Also, the high rainfall period is characterized by high cloud cover that may limit light availability for tree growth, which may explain the positive correlations between rainfall and photosynthetically active radiation. Then, rainfall can exert a direct negative effect by saturation the soil porosity with water, leading to hypoxia, and an indirect effect by reducing light due to increasing cloudiness. In these both species, tree-rings´ indices are negatively correlated with the rainiest season of the year, and positively correlated with the solar radiation during the less rainy months of the year (Figure 2-3). Based on dendrometer data for *A. macropetala*, the maximum growth rates occur during the less rainy months, and growth stops during September - October, the rainiest months, and is poorly related to solar radiation (Figure 2-4). These results suggest that the direct effect of rainfall on tree growth could be higher than the indirect. Few negative correlations between growth and rainfall have been reported in tropical rain forests (Clark and Clark 1994; Soliz-Gamboa et al. 2011). However, to separate the direct and indirect effect of rainfall on tree growth needs additional experiments to assess the effect of hypoxia, detailed field data of cloudiness, and of photosynthetically active radiation.

In contrast, both *Q. lineata* and *G. glabra* showed a positive relationship with water availability. In these species, the tree-rings´ indices are positively correlated to precipitation during the rainiest months (Figure 2-3). On the other hand, negative correlations between tree-rings´ indices and solar radiation during the less rainy months were found when light availability is high. These results suggest that water excess and low solar radiation could be limiting growth factors for some tree species but not for the entire tree community. Moreover, *G. glabra* is a widely distributed species across precipitation gradients from seasonal dry forests to hyper humid forests. This species could be considered as a long-lived pioneer tree species with broad physiological tolerances to water and light availability (Huc et al. 1994; Santos et al. 2012). Then, *G. glabra* can be strongly influenced by precipitation rather than solar radiation. *G. glabra* defoliates under dry periods (Lacoste and Alexandre 1991); it indeed defoliates during the less rainy month in our study area (personal observations), indicating a strong affiliation to precipitation regimes. *Q. lineata* is a shade-tolerant species distributed through most of the Choco region. The genus *Qualea* is broadly distributed in South American forests, from dry to wet forests. Then, some tree species that recently colonize hyper-humid forest retain their positive affiliation to precipitation regimes, while tree species that evolved during long evolutionary periods under hyper-humid conditions are better adapted to high rainfall to maximize their growth in less rainy months (Esquivel-Muelbert et al. 2017).

Given the abundance of one resource, it is probable that another one operates as limiting to growth. For this reason, it is plausible to find positive associations between the tree growths and the increasing of a limiting resource to (growth factor) when it begins to be gradually available, and null or negative associations when the same resource exceeds its abundance and another begins to be scarce. The growth answer with this new resource would begin to be positive as it increases.

Some environmental predictors used in this study can be unreliable indicators for our hypotheses. Soil moisture content follow the rainfall pattern; however, it presents little variation throughout the year (0.59 ± 0.003 cm^3 cm^{-3}) compared to other tropical regions (Solander et al. 2020). This is due to the round-the-year soil wet condition that induces almost permanent soil saturation. Probably most rainfall is evacuated by surface runoff rather than infiltration. Then, an experimental assessment will be required to test roots hypoxia as a limiting factor. NDVI is a good proxy for photosynthetically active radiation absorbed by the canopy, plant growth, and forest productivity (Glenn et al. 2008; Soudani et al. 2012). We observed two periods characterized by a decline in NDVI values during February (less rainy) and October (the rainiest), the months with the highest and the lowest light availability, respectively. Although dendrometer data from *G. glabra* tend to match NDVI variation, much more species and ground data should be included, validating phenological interpretations and forest productivity due to the exceptional richness of tree species and the different growth strategies.

2.5 Conclusions

In this study we show for the first time the occurrence of annual growth rhythms in several trees from a tropical forest with extremely wet conditions. It suggests that bot excess or deficit of growth factors may explain seasonal cyclicity of growth rhythms in tropical trees, strengthening our hypothesis. Although there are some limitations and problems in working with tree rings in hyper-humid forests, is not impossible. A new frontier its open for tree rings science, it means to extend the application of dendrochronology to hyper humid environments where it was believed that there was no rhythmic growth.

3. Chapter 3: Isotope signatures in tree rings reveal growth rhythms occurring in the least rainy season in a hyper-humid neotropical forest

With Jorge I. del Valle, Sebastián González-Caro, Carlos A. Sierra

Trees: submitted

Abstract: It is well known that growth-limiting factors such as periodic droughts can induce periodicities in woody tissue formation in tropical trees. In regions without seasonal droughts and with sufficient water for photosynthesis, periodicities in secondary growth have been previously reported but, it is not well-known what factors may induce these periodic growth rhythms. We obtained woody samples of two tree species, two individuals per species, from the Biogeographic Chocó region in Colombia, which is one of the rainiest on the planet, located close to the Pacific Ocean at the equatorial latitude. We measured stable isotopes of oxygen and carbon (^{18}O and ^{13}C) in wood samples across the last five growth rings in each species to obtain intra-annual variation in isotopes. We assessed whether isotope variation correlated with climatic variables, in particular, the pattern of precipitation regime. We found that both isotopes are correlated between them and with the ring widths. We also found that the δ^{18}O significantly correlated with the pattern of precipitation regime. Our results suggest that isotope variation could be considered a surrogate of tree growth in these hyper-humid and non-seasonal forests. They challenge previous ideas about the dominant effect of the dry season on tropical tree-growth periodicities, suggesting water excess as an additional limiting factor controlling growth rhythms in some tropical trees.

3.1 Introduction

Despite the high variability of plant growth rates among different species and environmental conditions, the climate is frequently suggested as the main driver for tree growth (Dannenberg et al. 2019). In trees, some studies have shown the effect of seasonal water availability or rainfall amount as the main limiting factor for growth and productivity in neotropical forests (Wagner et al. 2012). These studies usually compare individual tree species growing across rainfall and seasonality gradients (e.g., space for time substitution approach). However, the effect of climatic fluctuations over time in the same tree individuals is not entirely understood, particularly for tropical trees (Rahman et al. 2019). Therefore, improving our understanding of how tropical trees grow and respond to environmental drivers, and produce growth rhythms, are essential issues to predict tropical forests dynamics, their management, conservation, and adaptation to climate change.

The seasonality of environmental variables triggers tree growth rhythms and annual ring formation (Fritts 1976; Schweingruber 1988, 2007). Annual seasonal flooding, droughts, or salinity changes, as in estuarine ecosystems, can induce tropical trees to form annual rings (Callado et al. 2001; Schöngart et al. 2002; Menezes et al. 2003; del Valle et al. 2012; Parolin et al. 2016). Then, annual growth rings in many tropical tree species could be explained by the water as a limiting paradigm (Lisi et al. 2008; Groenendijk et al. 2014; Brienen et al. 2016; Silva et al. 2016; Schöngart et al. 2017). However, in Chapter 1, we showed that a high proportion of tree species (82% of sampled tree species, n=81) in a hyper-humid Neotropical forest in the Choco region of Colombia (precipitation >7000 mm y^{-1}) have tree rings structures. The presence of tree rings in such ecosystems without evident climatic seasonality suggests the existence of a regular growth periodicity (Fichtler et al. 2003; Moreno and del Valle 2014; Giraldo et al. 2020) challenge the current assumptions about the factors inducing growth ring formation in tropical trees. While little is known about growth rhythms in trees from ever wet tropical forests (without dry periods), slight variation in rainfall, soil moisture, solar irradiance, cloudiness, sunrise, and sunset time, have been considered as possible drivers of these rhythms (Breitsprecher and Bethel 1990; Clark and Clark 1994; Borchert and Rivera 2001; O´Brien et al. 2008; Moreno and del Valle 2014).

Stable isotopes of oxygen, hydrogen, and carbon in tree rings are a complement to conventional dendrochronological techniques. They can provide information on the physiological mechanisms that regulate wood growth (Evans and Schrag 2004; McCarroll and Loader 2004; Anchukaitis et al. 2008; van der Sleen et al. 2017). Plants take up carbon dioxide (CO_2) from the atmosphere and water (H_2O) from soils needed to form tissues and to maintain their metabolism (McCarroll and Loader 2004). Any change in environmental conditions as relative humidity, soil moisture, radiation, temperature, etc., is captured by plants and stored as chemical messages in their tissues in different proportions of stable isotopes ($^{13}C/^{12}C$, $^{18}O/^{16}O$, $^{2}H/^{1}H$) (Farquhar et al. 1982; Roden et al. 2000). Depending on environmental conditions, plants discriminate the relative proportions of isotopes taken up from the external environment and incorporate them accordingly in their tissues (Managave and Ramesh 2012). These isotope properties have been useful to study tree growth patterns. In particular, high-resolution isotope sampling (intra-annual or intra-ring sampling) has been useful to study the growth rhythms in tropical tree species (Evans and Schrag 2004; Hietz et al. 2005; Anchukaitis et al. 2008; Ballantyne et al. 2011; Managave and Ramesh 2012; Ohashi et al. 2016). Even in trees that lack growth rings, this method allows the detection of rhythms in woody tissue formation (Poussart et al. 2006; Pons and Helle 2011; Nakai et al. 2018). Thus, analyses of intra-annual variation of tree rings based on isotopes and high-resolution environmental data could improve our understanding of drivers of tree growth.

In the tropics, the higher the amount of annual precipitation, the greater the depletion of the heavy isotopes of oxygen and hydrogen in rainwater (Kurita et al. 2009). This phenomenon is known as the amount effect. It is caused by the early removal of heavy isotopes from clouds by rain so that further rain progressively becomes isotopically depleted (Dansgaard 1964; Rozanski et al. 1993; Risi et al. 2008; Wang et al. 2020). The amount effect leads to lower $\delta^{18}O$ values in plant cellulose that coincide with the growing season (Managave and Ramesh 2012; Brienen et al. 2016; van der Sleen et al. 2017). In trees growing in areas where rainfall is very high all months of the year, water deficit is not a limiting factor for growth. For these areas, we hypothesize that trees record the variability of the water source in cellulose $\delta^{18}O$ variability differently: Low values of $\delta^{18}O$ in the cellulose during slow or no growing periods (at ring boundaries). And higher values of $\delta^{18}O$ in the cellulose during the growing season (at the beginning or near the middle of the ring width), representing high and low precipitation, respectively. Furthermore, we expect to find higher values, or greater discrimination of $\delta^{13}C$, during growing periods with low rainfall, or higher incidence of solar radiation due to cloudiness dispersion (i.e., more negative values of $\delta^{13}C$). In contrast, during the period of lower radiation (higher cloudiness and higher precipitation), both lower CO_2 fixation and lower discrimination of the heavier carbon isotope (^{13}C) is expected.

In this study, we aim to establish the intra-annual variability of $\delta^{13}C$ and $\delta^{18}O$, in tree rings of *Humiriastrum procerum* and *Virola dixonii*, sampled in a non-seasonal tropical hyper-humid forest. Also, we aim to explore the relationships between isotope composition in tree rings with environmental variables. To our knowledge, this is the first study on isotope signatures in tree rings under such wet environments. So, we expect this analysis provides new insights about tree growth factors acting under extreme rainfall amounts in tropical forests.

3.2 Materials and methods

3.2.1 Study area

The Chocó Region extends along the Pacific coast of South America, from the north of Ecuador to the Colombia-Panama border (Darién Gap). This region is considered the rainiest in the New World (Poveda and Mesa 2000). In some places, the mean annual rainfall is over 12,000 mm y^{-1} (Mesa and Rojo 2020). In the study area, small hills with slopes up to 45° are frequent, with elevations ranging from 40 - 100 m above sea level. The soils are mottled grey-yellow clay loam, poor in soil nutrients, and with high iron and aluminum concentration (Faber-Langendoen and Gentry 1991). We sampled the studied tree species in the forests belonging to the Community Council of the Low *Calima* River Basin, around the Pedro Antonio Pineda Tropical Forest Center of the University of Tolima (3 ° 57´12.54´´ N, 76 °59´27.96´´ W). In the meteorological station, located within the study area, the mean annual precipitation exceeds 7200 mm y^{-1}. According to the Gaussen xerothermic index (Bagnouls and Gaussen 1957) and the monthly potential evapotranspiration (Holdridge 1967), on average, in the study area, there are no dry months (Walter et al. 1976). The least rainy month of the year is February, with an average of 370 mm, which almost triples the potential evapotranspiration (127 mm). The mean annual temperature of 25.9°C is almost constant during all months (Figure 3-1).

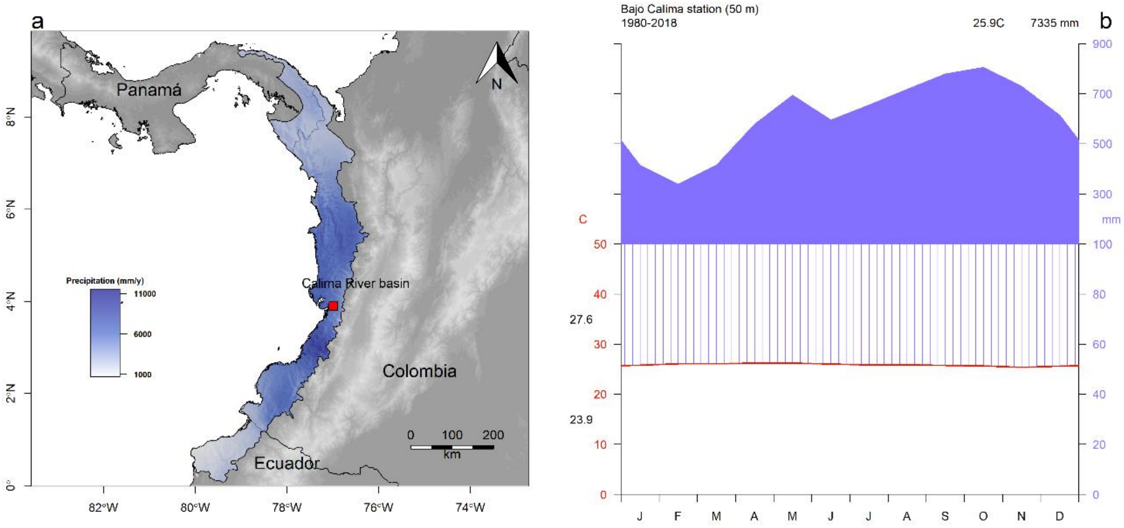

Figure 3-1: a. Study area within the Chocó Region with explicit precipitation gradient (Karger et al. 2017). b. Walter and Lieth's ombrothermic climate diagram (Walter et al. 1975) of the *Bajo Calima* Climatic Station (square), which belongs to the Institute of Hydrology, Meteorology, and Environmental Studies of Colombia (IDEAM). The dark area indicates an excess of water (all months are hyper-humid).

3.2.2 Sampled species

We sampled four cross-sectional disks of two tree species collected in the study area: two from *Humiastrum procerum* (Humiriaceae) and two from *Virola dixonii* (Myristicaceae). All trees sampled were growing under similar conditions as dominant trees (15-20 meters of height) of a closed canopy non-flooded secondary forest (about 70 years of secondary succession). A very high richness and species diversity characterize this forest, but their trees´ populations size is small (See Chapter 1 – 2). Individuals from the same species usually are 50 to 400 m spaced among them. Both sampled species shed their leaves between August to October (*V. dixonii* is a partially deciduous tree). Leaf flushing and new leaves are common between November to February. Little is known about flowering and fruit production of *V. dixonii*, but *H procerum* flowering occurs from February-March. Both species are wet-forest specialists, and their distribution range goes from Costa Rica to Ecuador.

3.2.3 Preparation of the Wood samples

Growth rings of these two species are well defined (Figure 3-2), easy to measure, and date, characterized by the increase in cell wall thickness of fibers, producing a darker area at the edge of the rings. In both species, vessels are diffuse-porous (Chapter 1). For each species, we measured their tree-rings width (three radii for each cross-section). We compared ring widths among individuals to ensure a good cross-dating. We test the tree-rings formation frequency by the radiocarbon bomb-peak method sampling one or two particular rings in the cross-sections (Figure 3-2a) (Fichtler et al. 2003; del Valle et al. 2014). We used the software Cali-Bomb (Reimer et al. 2004) to obtain calendar dates from the radiocarbon values.

For stable isotope analysis, we cut a radial block of wood approximately 5 mm thick and 10 mm deep from each cross-section, containing the last five tree rings closest to the bark (Figure 3-2b). After a clear identification of the boundaries of the rings, we cut each tree ring with a scalpel in several longitudinal slices with a thickness between 0.6-0.8 mm (Figure 3-2b). This method allowed us to divide each growth ring into a different number of slices. Each slice was packaged and labeled in Eppendorf tubes for the individual cellulose extraction process.

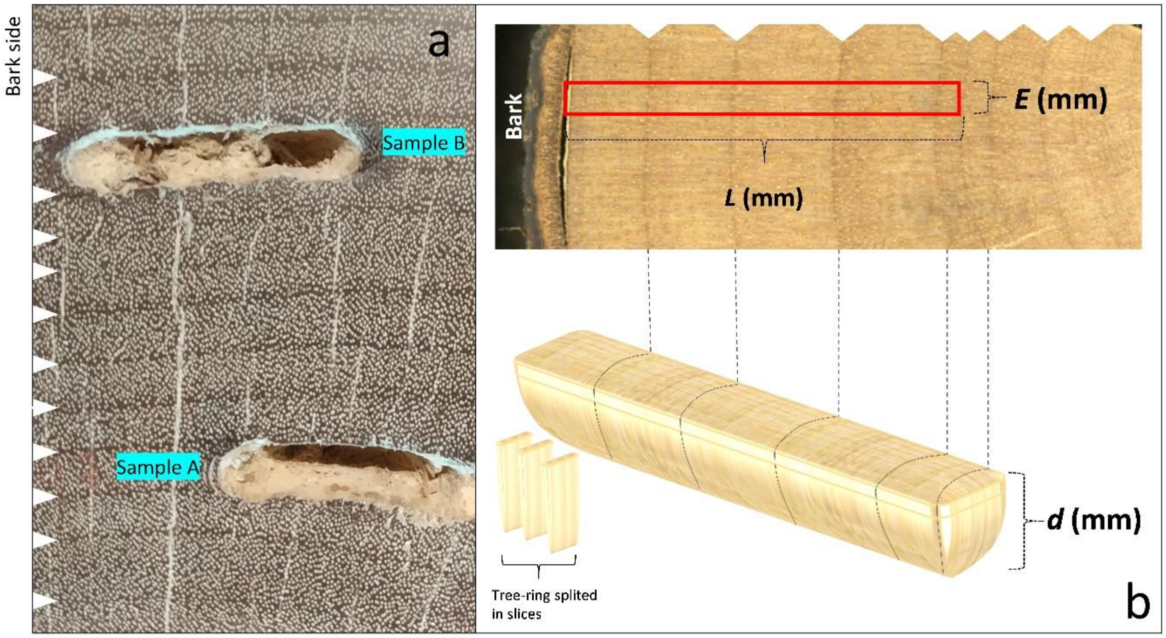

Figure 3-2: Wood samples for radiocarbon and stable isotopes analysis. a Sampled tree-rings for radiocarbon analysis in one cross-section of *Humiriastrum procerum.* b Rectangular section used for cellulose extraction and the analyses of stable isotopes in one cross-section of *Virola dixonii. L* is the length of the section in mm (the value of *L* is variable among trees, depending on the last five tree-rings widths). The width of the rectangular section was 5 mm. The depth (*d*) of rectangular sections was 10 mm. We obtained the slices with a scalpel and a stereomicroscope. The arrows on the edge of the images indicate the growth-rings boundaries.

We extracted cellulose in each wood sample (both from sampled rings for radiocarbon analysis as each split slice for stable isotope analysis), following the protocol described by Steinhof et al. (2017). The first and last step of the procedure involves washing the samples in a Soxhlet extractor for 12 hours with toluene-isopropanol (1:1) and H_2O, respectively. The intermediate steps include the application of different concentrations of acid ($NaClO_2$, CH_3COOH) and base ($NaOH$) in micro-filter funnels held in a multiport (temperature 65-70°C), which facilitated the bleaching of the samples and transforming them into pure α-cellulose.

3.2.4 Stable isotope analysis

We carried out the mass-spectrometric analysis of stable isotopes of carbon and oxygen at the BGC-IsoLab (Laboratory of Stable Isotopes of the Max Planck Institute for Biogeochemistry, Jena, Germany). Both isotope measurements were performed on wood from the same slice. Stable isotope ratios were measured using a Thermo Fisher TC/EA oven coupled to a Delta + XL mass spectrometer. The BGC-IsoLab uses three internal standards calibrated with Vienna Middle Standard Ocean Water (VSMOW) and the Standard Light Antarctic Precipitation (SLAP); so, all measurement results are presented on the VSMOW/SLAP references. Both samples and standards were placed in silver capsules and subsequently analyzed and standardized as described by Gehre et al. (2004). The proportion of isotopes is expressed in delta (δ) notation, using as international standards, VSMOW for oxygen and Vienna Pee Dee Belemnite (VPDB) for carbon. Isotopic ratios are reported as

$$\delta_{sample} = \left(\frac{R_{sample}}{R_{standard} - 1}\right) x1000,$$

where R_{sample} and $R_{standard}$ are the proportions of the heavy isotope versus the light isotope, for the sample and the standard, respectively. Given the low abundance of isotopes in the samples, they are expressed in values of per thousand (‰, per mil) (van der Sleen et al. 2017).

3.2.5 Oxygen isotopes in rain

Currently, there is no isotopic information on rainwater for the study site despite its ecological importance. This fact limits the possibility of directly comparing $\delta^{18}O$ values in wood and $\delta^{18}O$ in the rain. However, we use the database of the Global Network of Isotopes in Precipitation (GNIP) of the International Atomic Energy Agency (IAEA), whose database extends from 1961 to the present, providing the monthly composition of ^{18}O, ^{2}H, ^{3}H isotopes in the rain. Although in this network there are few data points for the Chocó region, to determine the relationship between the contents of $\delta^{18}O$ and monthly rainfall, we used data from lowland tropical areas around the world, characterized by high rainfall (over 2300 mm y^{-1}). We excluded isotopic data from islands because wind and precipitation regimes may not be analogous to continental patterns in our study area. Also, we ran the same correlation only for the site ‘Tulenapa’ (Urabá, Colombia), which is the nearest site with information in the GNIP dataset.

3.2.6 Statistical analysis

To assess the relationship between isotope measurements ($\delta^{18}O_{cellulose}$, $\delta^{13}C_{cellulose}$), tree-ring width, and climate, we ordered the isotope data from the most internal ring to the external one (close to bark) of the tree samples. We assigned monthly values of precipitation, temperature, relative humidity, cloudiness, solar brightness for each year, under the assumption that the most external ring corresponds to the year of sampling. We obtained the climatic variables from IDEAM, Colombia, and NASA Ges Disc-Earthdata (https://disc.gsfc.nasa.gov/). We ran correlation analyses among all variables and using the lme4 package in R (Bates et al. 2015). We employed generalized linear mixed-effects models (GLMMs) to assess the relationship between isotope data, tree-ring widths, and selected climatic variables. All variables were scaled (mean equals zero, and the standard deviation equals one), allowing comparison among model results. We ran the GLMMs with all the variables that showed significant cross-correlations. All models included an individual tree as a random factor controlling for repeated measurements in the same individual. Finally, we obtained the marginal and conditional R^2 for each model.

3.3 Results

Due to a lack of data on the isotopic composition of rain in our study area, we established a separate relationship with data from the GNIP database. This separate dataset showed a negative correlation between $\delta^{18}O$ in the rain and the monthly rainfall for the humid lowland tropics ($r = -0.39$, p–value < 0.05, $n = 96$). For a different area, less rainy, but in the same biogeographical region, we also observed a negative correlation between these variables ($r = -0.77$, *p-value* < 0.05, $n = 12$) (Figure 3-3). Precipitation at the area for which we have $\delta^{18}O$ data (Tulenapa) follows the same intra-annual pattern as our st1udy area. Therefore, we assume that $\delta^{18}O$ in rainfall for our site follows a similar pattern, which we use to explain the variation in our observations of $\delta^{18}O_{cellulose}$.

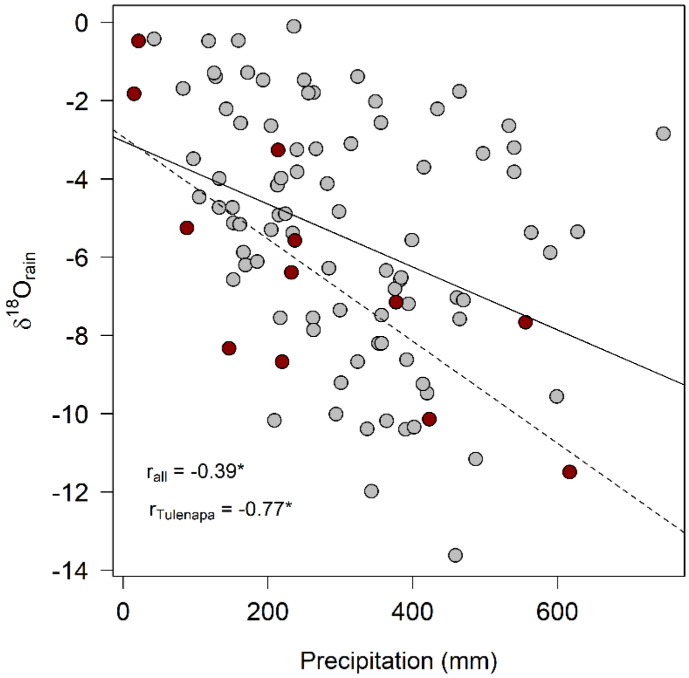

Figure 3-3: Relationship between $\delta^{18}O$ in the rainwater and the monthly rainfall for the humid lowland tropics. r_{all} uses 96 pairs of values (grey points and black line), and $r_{Tulenapa}$ use 12 values from January to December (red points and dashed line) from Tulenapa, Colombia, a place with isotopic data of rain within the Choco Region. * significance (95%). Data are available in Table S2.

The ^{14}C results in the $F^{14}C$ metric and their calibrations in the calendar years are presented in Table 3-1. We tested the isotopic signature of ^{14}C of different tree rings in all cross-sections. The number of years between calibrated dates was the same as the tree-ring number between radiocarbon sampled rings (Table 3-1), which confirms the annual nature of sampled species. According to this result, tree rings marked and counted allow us to know the real age of trees. Furthermore, the tree-ring width series match by crossdating between the two sampled trees of each species. We found mean significant serial intercorrelation values (*p-value* <0.05); in *H procerum* was 0.57, and 0.40 for *V. dixonii.* The series intercorrelation represents the common-level signal recorded in tree-ring for the available tree samples; few for developing a chronology, but enough to complement our stable isotope observations.

Table 3-1: Results of ^{14}C dating and calibration in calendar dates of the samples. Values in parentheses indicate the probability percent given by CALIBomb (Reimer et al. 2004) and mean calibrated date rounded to the first integer calendar year. DBH: diameter at breast height, (*) years difference estimated with the last ring.

Especies	**Sample ID**	**DBH (cm)**	**Height (m)**	**Radiocarbon Sample**	**F^{14}C**	**CALIBomb Calibrated age range (1 σ)**	**CALIBomb Calibrated age range (2 σ)**	**Mean calibrated date**	**Years difference between dated samples**	**Tree-ring number between dated samples**	**Tree age (years)**
				A	1.1482 ± 0.0019	[1990.7-1991.96] (1.0)	[1990.38+1992.63] (0.94)	1991			
	Hpro65	56.5	20	B	1.0881 ± 0.0016	[2000.75-2001.94] (1.0)	[2000.28-2002.61] (0.942)	2001	10	10	36
Humuriastrum procerum	Hpro82	29.9	18	A	1.0578 ± 0.0020	[2006.98-2008.87] (0.96)	[2005.88-2009.24] (0.89)	2008	8$^{(*)}$	8$^{(*)}$	43
				A	1.088 ± 0.00180	[2000.75-2001.98] (1.0)	[2000.26-2002.66] (0.941)	2001			
	Vdix43	13.4	15	B	1.0749 ± 0.0021	[2003.02-2004.65] (1.0)	[2002.34-2005.16] (0.926)	2004	2	2	36
				A	1.1717 ± 0.0021	[1988.46-1989.54] (1.0)	[1988.06-1990.00] (0.924)	1989			
Virola dixonii	Vdix199	22.98	18	B	1.1395 ± 0.0020	[1991.85-1993.16] (1.0)	[1991.08-1993.55] (0.950)	1992	3	3	36

We observed a cyclic pattern in $\delta^{18}O_{cellulose}$ values in the tree rings, which coincides with the beginning and the end of the tree-ring boundaries (Figure 3-4). Such seasonal variation is similar in the two radial sections of *H. procerum*; but not so clear in *V. dixonii* (Figure 3-4). Within rings of *H. procerum*, low values of $\delta^{13}C_{cellulose}$ appear (greater discrimination of $\delta^{13}C$), but there is no obvious pattern. The intra-annual variation of $\delta^{18}O_{cellulose}$ for *H. procerum* was from 20.7 to 29.5‰ and from 21.8 to 28.3‰ for *V. dixonii*. The $\delta^{13}C_{cellulose}$ values were less conspicuous and ranged from -29.5 to -28.1‰ in *H. procerum* and from -30.6 to -27.2‰ in *V. dixonii* (Figure 3-4). The local minimum values of $\delta^{18}O_{cellulose}$ coincided with the end and the beginning of the rings´ boundaries. These facts suggest non-random patterns that match the tree rings of *H. procerum* with their isotopic composition (Figure 3-4).

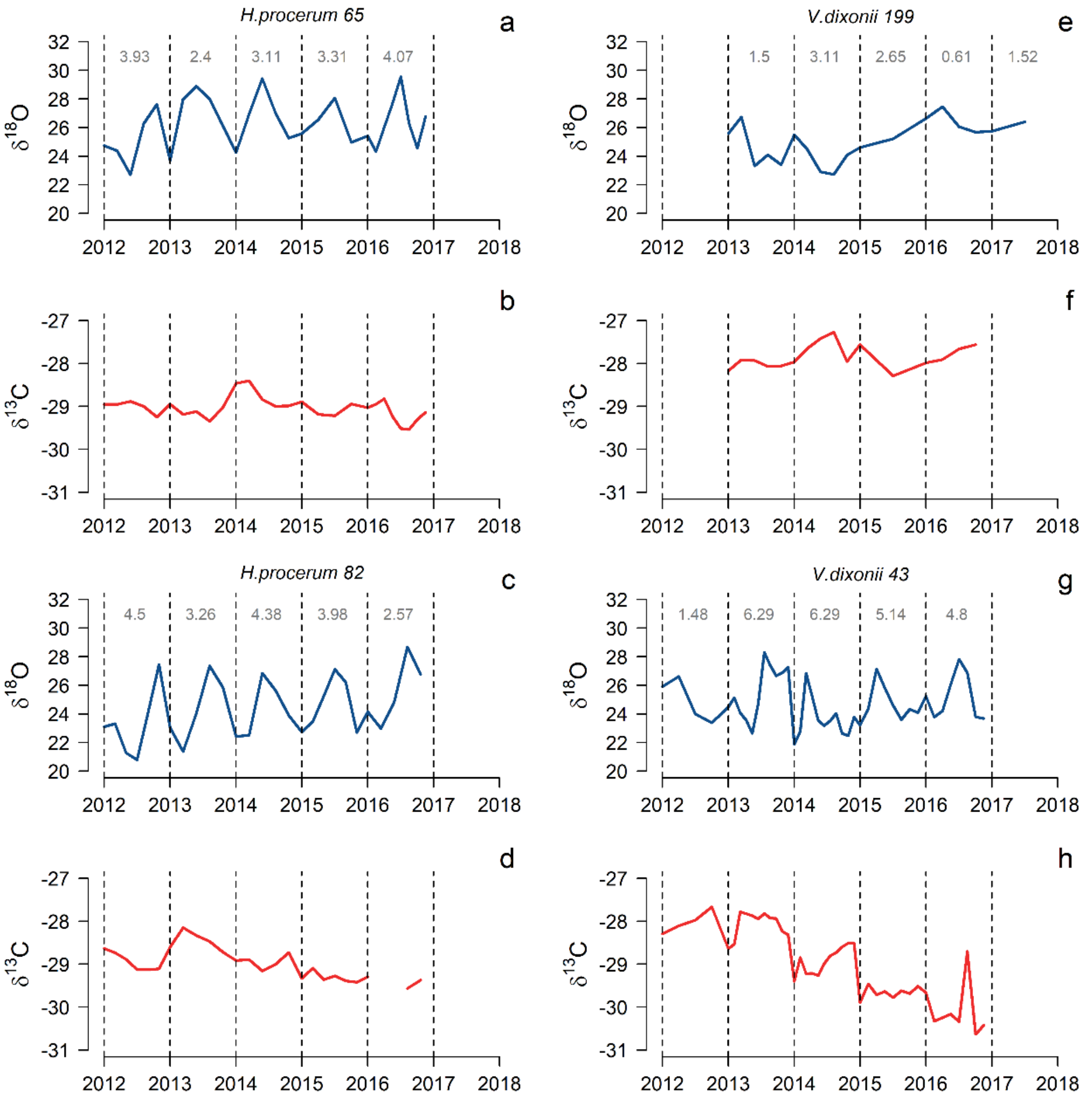

Figure 3-4: The radial variation of $\delta^{18}O_{cellulose}$ (blue) and $\delta^{13}C_{cellulose}$ (red) of two individuals of *Humiriastrum procerum*: sample code 65 (a, b) and 82 (c, d). The same for two individuals of *Virola dixonii:* sample code 199 (e, f) and 43 (g, h). Values at the top panels indicate tree-ring widths in mm. The vertical lines indicate the limits of the annual rings. The year corresponding to each ring appears at the bottom of each chart.

We found significant negative correlations (*p-value* <0.05) between carbon and oxygen isotopic values in cellulose both at the borders and inside the rings with some environmental variables. We observed a negative correlation (r= -0.46) between the $\delta^{18}O$ at the border of the rings ($\delta^{18}O_{rb}$) and the mean precipitation during the quarter of January-February-March (P_{mean}JFM), and with precipitation of the driest month (P_{min}) (r= -0.49, n = 20). Other variables that correlate with δ $^{18}O_{rb}$ are ring width (Rw) (*r*= -0.58, *n* =20), mean cloudiness during the quarter of February-March-April (C_{mean}FMA) (*r*= -0.47, *n* =20). We obtained a negative correlation between $\delta^{13}C$, at the border of the rings ($\delta^{13}C_{rb}$), and Rw (*r*= -0.75, *n* =20). We also found significant correlations between isotopes: δ $^{13}C_{rb}$ versus the maximum value of $\delta^{13}C_{cellulose}$ within the ring (δ $^{13}C_{wr}$) (*r*= 0.66, *n* = 20, the only positive), and δ $^{13}C_{wr}$ versus the maximum value of $\delta^{18}O_{cellulose}$ within the ring (δ $^{18}O_{wr}$) (*r*= -0.54, *n* = 20) (Figure 3-5). We did not find significant correlations with other variables.

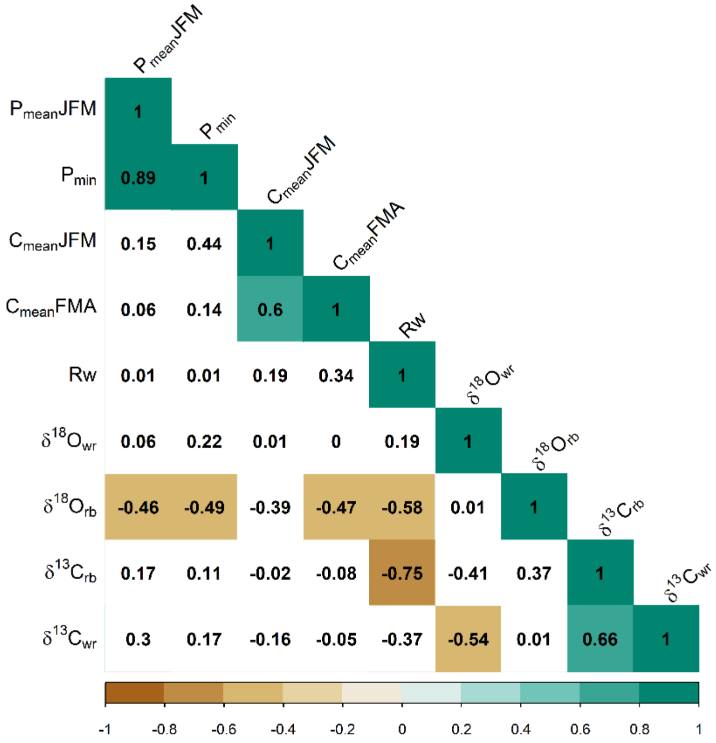

Figure 3-5: Pearson´s correlation matrix of the $\delta^{18}O$ and $\delta^{13}C$ values observed in the tree rings versus environmental variables (*p*-value <0.05). White cells lack statistical significance. $\delta^{18}O_{rb}$: $\delta^{18}O_{cellulose}$ value at the ring boundary, $\delta^{13}C_{rb}$: $\delta^{13}C_{cellulose}$ value at the ring boundary, $\delta^{13}C_{wr}$: the maximum value of $\delta^{13}C_{cellulose}$ within the ring, $\delta^{18}O_{wr}$: the maximum value of $\delta^{18}O_{cellulose}$ within the ring, P_{mean}JFM: mean rainfall during the January - February - March quarter, P_{min}: rainfall of driest month, C_{mean}JFM: mean cloudiness during the January - February - March quarter, C_{mean}FMA: mean cloudiness during the February - March – April quarter, RW: ring width.

We found similar results for the relationships among the variables depicted in Figure 3-5 using linear mixed-effect models and cross-correlation analysis. All models showed differences between marginal and conditional R^2 underlying the effect of the autocorrelation of woody tissue data within individuals rather than climatic effects. Our mixed effect models confirmed that these relationships are not an artifact of the sampling design (Table 3-2). We found that marginal R^2 duplicates the conditional R^2 (Table 3-2). This result means that the individual effects (random factors) exceed the effect of the precipitation surrogates (fixed factors) in the isotope variation. Also, $\delta^{13}C_{rb}$ had a higher individual variation than $\delta^{18}O_{rb}$ relative to ring width, based on the difference between marginal and conditional R^2. This result suggests that $\delta^{13}C_{rb}$ variation is affected differently among individuals, while $\delta^{18}O_{rb}$ depends on the wood accumulation rate. Finally, precipitation surrogates are related to $\delta^{18}O$ potentially as a product of tree growth.

Table 3-2: Generalized linear mixed-effects models to assess the relationship with some significant variables observed in cross-correlation analysis. $\delta^{18}O_{rb}$: $\delta^{18}O_{cellulose}$ value at the ring boundary, P_{mean}JFM: average rainfall during the January - February - March quarter, Pmin: precipitation during the driest month, C_{mean}JFM: average cloudiness during the January - February - March quarter, C_{mean}FMA: average cloudiness during the February - March – April quarter, RW: ring width. (p-value <0.05).

Model	Estimate	*t*-value	*p*-value	R^2 Marginal	R^2 Conditional
Intercept	1.3×10^{-15}	0.0	1.0		
$\delta^{18}O_{rb}$ ~ P_{mean}JFM	-4.8×10^{-1}	-2.94	0.01	0.20	0.54
Intercept	1.2×10^{-15}	0.0	1.0		
$\delta^{18}O_{rb}$ ~ Pmin	-4.8×10^{-1}	-2.65	0.018	0.20	0.47
Intercept	2.13×10^{-15}	0.0	1.0		
$\delta^{18}O_{rb}$ ~C_{mean}FMA	-4.04×10^{-1}	-2.06	0.05	0.16	0.34
Intercept	1.24×10^{-15}	0.0	1.0		
$\delta^{18}O_{rb}$ ~ Rw	-5.84×10^{-1}	-3.05	0.0067	0.32	0.32
Intercept	2.3×10^{-16}	0.0	1.0		
$\delta^{13}C_{rb}$ ~ Rw	-3.86×10^{-1}	-2.49	0.023	0.18	0.68

3.4 Discussion

This chapter reports annual tree-rings and intra-annual isotopic signals of two species growing in a hyper-wet and non-seasonal precipitation forest. Similar isotopic studies are scarce in the tropics and exceptional in such rainy environments (precipitation over 4000mm) (Van der Sleen et al. 2015).

We provide evidence of intra-annual variation related to precipitation regimen based on isotope variation of tree rings. In particular, isotope variation ($\delta^{18}O$) in cellulose follows patterns coinciding with the ring boundaries of *H. procerum* but not for *V. dixonii*. There is a correlation between the two isotopes, even if the surrogates of precipitation poorly correlate to $\delta^{13}C$. Furthermore, we found a negative relationship between stable isotopes in the cellulose and some precipitation variables; in particular, the mean precipitation during the driest quarter (386 ± 87 mm). Moreover, the ring widths are negatively related to the $\delta^{13}C_{cellulose}$ ($\delta^{13}C_{rb}$ and $\delta^{13}C_{wr}$). The environmental response of $\delta^{13}C$ is lower than that of $\delta^{18}O$, and therefore, more difficult to detect. Thus, we provide evidence of intra-annual variation related to precipitation regimen based on isotope variation in one of the most humid regions of the world.

The variation in isotope concentration in the tree wood samples correlates with the tree-ring boundaries. This pattern is clearer for $\delta^{18}O$ but not for $\delta^{13}C$, probably because $\delta^{18}O$ is less affected by physiological discrimination processes. The highest values of $\delta^{18}O_{cellulose}$ occur within the rings ($\delta^{18}O_{wr}$), i.e., during the growing period (Figure 3-4). Lower values of $\delta^{18}O_{cellulose}$ tend to occur close to ring boundaries ($\delta^{18}O_{rb}$). This because of high precipitation values or by leaf shedding. The studied trees develop their root systems in the first 40 cm of soil. In such a case, probably soil water $\delta^{18}O$ signature is the same as rainwater (McCarroll and Loader 2004). The first and second third of the rings are produced with water from the less rainy months, reflecting higher $\delta^{18}O$ value. In contrast, during the rainy months, at the end of growth rings (ring boundaries), rings reflect the low $\delta^{18}O$ value of the heavy rains (Figure 3-4). The $\delta^{18}O_{cellulose}$ contains reliable information about local rainfall. Their concentrations vary throughout the year, tightly coupled to rainfall. This result suggests an environmental $\delta^{18}O$ variation in the rainwater related to the water source: monthly precipitation explained by the “amount effect” hypothesis or the inverse relationship between monthly $\delta^{18}O$ and precipitation amounts (Risi et al. 2008; Managave and Ramesh 2012).

High concentrations of $\delta^{18}O$ during the less rainy season can be amplified in tree wood as because of water evapotranspiration from the soil surface and leaves (Managave and Ramesh 2012). Our results suggest that the growth of the two species occurs mainly during the lowest rainy period of the year. An excess of humidity during that period (January, February, March) drives a reduction in tree growth, evidenced by thinner growth rings (Figure 3-4, Figure 3-5). This situation coincides with low $\delta^{18}O$ values at the end of the ring, at the same time that precipitation increases significantly. Simultaneously, radiation decreases according to the relationship between $\delta^{18}O_{rb}$ and $C_{mean}FMA$. Therefore, an increase in precipitation during the JFM quarter may be synergistically combined with a reduction in solar radiation, contributing to reducing tree growth. Particularly, the *H. procerum* tree-rings index is positively correlated with the solar radiation during the less rainy months of the year and negatively correlated with the rainiest season of the year (Chapter 2).

The $\delta^{18}O$ signature in cellulose helps to identify the annual rings controlled by seasonal changes in precipitation. It reflects low values during the highest rainy season. Identifying annual growth increments is usually more effective with $\delta^{18}O$ than with $\delta^{13}C$ (Ohashi et al. 2016; van der Sleen et al. 2017). This fact is evident in our study (Figure 3-4). Some authors claim that the growth ring delimitation through isotopic signatures is possible only if the annual precipitation pattern is strongly marked (Managave and Ramesh 2012; Ohashi et al. 2016; van der Sleen et al. 2017). They suggest few or no isotope signature in areas where rainfall is even throughout the year. However, we found that small changes in monthly rainfall amounts are enough to be expressed in the $\delta^{18}O$ signature of tree-ring cellulose. Although the effect of leaf shedding during the rainiest month could exert an effect in such a season pattern.

The amplitude of the intra-annual variation of $\delta^{18}O$ and $\delta^{13}C$ in *H. procerum* are 8.7 ‰ and 1.41 ‰, respectively. The magnitude of this amplitude is similar to that reported, by other authors, for species that grow in climates with high seasonal rainfall changes (Pons and Helle 2011; Ohashi et al. 2016; Cintra et al. 2019). In *V. dixonii*, the amplitude of the isotopic variation throughout the growth rings was smaller in $\delta^{18}O$ (6.4 ‰) and larger in $\delta^{13}C$ (3.3

‰). Ohashi et al. (2016) found a mean amplitude of $\delta^{18}O$ in the cellulose of the growth rings of about 3 – 6 ‰ and a less distinct variation lower than 1‰ in $\delta^{13}C$. Pons and Helle (2011) showed that *Goupia glabra* (a common species in our study area) has a mean $\delta^{18}O$ amplitude of around 2‰.

The evidence provided by correlations between the seasonal patterns of $\delta^{18}O$ observed in the cellulose supports our hypothesis, at least for *H. procerum*, which tends to register lower $\delta^{18}O$ values in its growth rings as precipitation increases. In climates where trees grow during the rainy season, as water deficit is a limiting factor to growth, some researchers have observed maximum $\delta^{18}O$ values at ring boundaries when the precipitation is the lowest during the year (Evans and Schrag 2004; Ballantyne et al. 2011; Ohashi et al. 2016). In all these study areas, annual precipitation is substantially lower than in our study area; and they suffer from seasonal droughts where the water deficit is limiting for tree growth, which is not the case in our study area. Here, tree growth occurs during the less rainy season, as occurs in forest episodically flooded, and water excess is a growth-limiting factor. Consequently, low $\delta^{18}O$ values at the ring's boundaries and high values within the ring (Cintra et al. 2019). Therefore, we concluded that rainwater excess is the most likely limiting factor for tree growth in these two species. This conclusion is also supported by observations presented in Chapter 2 for *H. procerum* and independent observations of band dendrometers from two trees of the studied species (Figure 3-6).

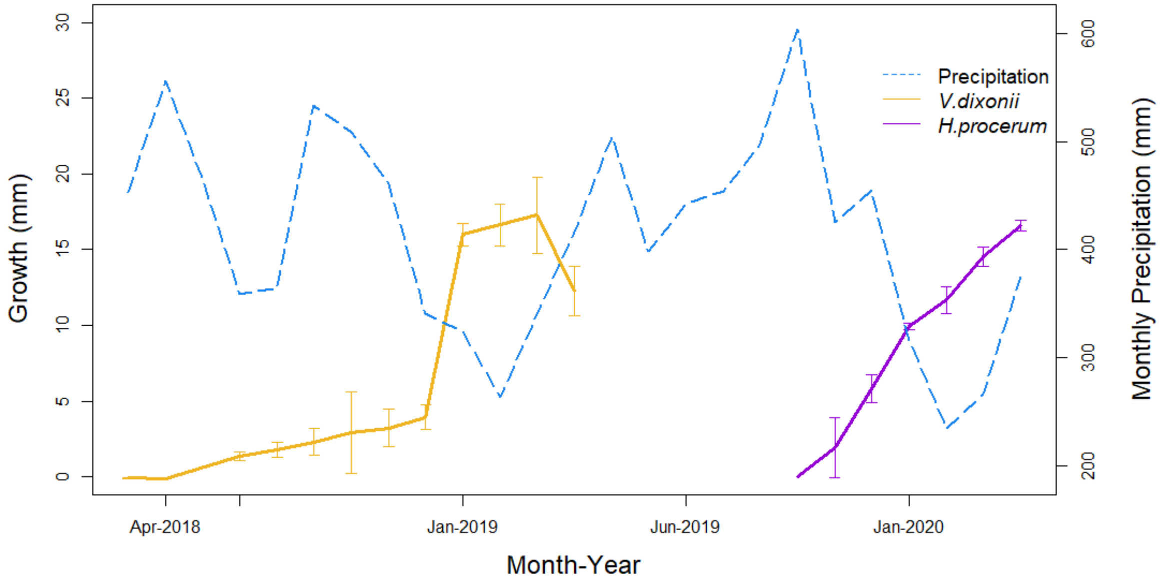

Figure 3-6: Automatic band dendrometer observations vs. precipitation. Curves with bars represent cumulative mean monthly growth of tree circumference (mm). The dashed line corresponds to mean monthly precipitation (mm month^{-1}).

In addition, studies on gross ecosystem productivity report high or increasing photosynthetic activity during the less rainy season in the tropical wet forests (absent water deficit), but photosynthetically limited due to high cloud coverage and rainfall (Restrepo-Coupe et al. 2013; Green et al. 2020). This fact means slow or no growth in rainiest months and high growth during less rainy months. In turn, the highest values of δ^{18}O occur during the first or second third of the rings corresponding to the earlywood, when the environmental conditions are favorable for growth because of low rainfall. Apparently, up to now, no previous research of this type has been carried out in such a highly humid environment and without marked seasonal contrasts of rain or flooding. More precise measurements (with large datasets) are critical for a broad understanding of tree growth and the productivity of these forests.

3.5 Conclusions

We found that $\delta^{18}O_{cellulose}$ is more robust than $\delta^{13}C_{cellulose}$ for identifying annual rings and to relate isotope composition to environmental variables. We believe that, the use of both $\delta^{18}O_{cellulose}$ as $\delta^{13}C_{cellulose}$ provides, complementary information to the analysis of tree rings in non-seasonal tropical environments. However, additional research is needed to expand this work to other species to obtain more information on isotope endmembers. In particular, it would be useful to perform isotopic measurements of the meteoric water source, which would allow us to pose new hypotheses about trees growing in nonseasonal hyper-humid tropical climates. Our results, in concert, suggest that the intra-annual growth rhythms of the studied trees are driven by water excess. In fact, according to Shelford´s law, all organisms have both minimum and maximum thresholds for the different environmental factors among which their population grows. Near these thresholds, organisms grow under stress, limited to both deficit and excess (Shelford 1931; Niinemets and Valladares 2008). So, in non-seasonal and hyper-humid forests (without dry periods), the availability of water, measured as rainfall, is close to the maximum tolerance threshold for some species.

4. Chapter 4. Radiocarbon and dendrochronology applied in a legal dispute: A case from Colombia

With Jorge I. del Valle

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Abstract: In 2015 a dispute arose between an electricity company (EC) and smallholder of a plantation teak when the company felled 80 trees (without consent of the owner) in a linear transect under a rural power-line-corridor (PLC) fragmenting the teak stand in two portions. EC stated that the area was no planted trees at the time of PLC establishing in 2008. The owner asserted he planted the stand in 2006 so in 2008 the company should have seen planted trees. We used the bomb ^{14}C signal of three felled trees and dendrochronological dating five trees: three felled by the EC, and two felled by us in 2016 to do this study to determine the age. We found that the first growth rings were dated in 2005 both in the trees felled by EC in 2015 and felled by us in 2016, one year before to that reported by the owner (2006). This year corresponds to the wood present in the cuttings at stand planting year. These facts are in agreement with the owner´s testimony. The plantation was 10 years old in 2015. Not seven or fewer years, as the EC alleges.

4.1 Introduction

The study of tree rings (dendrochronology) is a powerful tool to reconstruct the climatic variations throughout the last centuries (Cook and Kairiukstis; Fritts 1976; Schweingruber 1988; Speer 2010; Hughes et al. 2011). Tree rings allow us to date the occurrence of extreme climatic events such as maximum and minimum river flows, water levels in reservoirs, among others. Another application has been in geomorphological research, in which tree rings are useful to date and to study erosive processes such as landslides, rock, and debris fall, volcanic events, tsunamis, etc., and that extend from a few years to centuries (Haneca et al. 2006; Stoffel and Bollschweiler 2008; Speer 2010; Stoffel et al. 2011). In archaeology, tree rings have been employed to define the exact year in which the trees were felled, altered or used for the construction of artifacts or buildings (Speer 2010; Rubino and Baas 2019). In addition, dendrochronological methods have been useful to prove the authenticity of some art pieces and musical instruments (Grissino-Mayer et al. 2004; Bernabei et al. 2017). In summary, dendrochronology is a useful and scientifically accepted method to reconstruct the temporality of particular events.

In another context, the investigation and resolution of legal questions require the dating of specific events to make decisions based on accepted scientific methods. For example, the application of the dendrochronological methods focused on examining material related to an alleged criminal act or legal dispute rests in forensic sciences. The application of dendrochronology in criminalistics is called forensic dendrochronology (UNODC 2016). Its use ranges from ecological studies up to dating wood pieces from illegal logging, the origin of wood, dating of standing buildings, to dating wooden objects or objects that coincide with crime scenes, through the characterization of wood anatomy or tree rings (Jozsa 1985; Schweingruber 1988; Wolodarsky-Franke and Lara 2005; Ng et al. 2017; Köse et al. 2018; Lehmann and Arruda 2019). This method is highly accepted in temperate regions in which dendrochronology has been developed and widely used in many applications. In contrast, in the tropics, dendrochronological applications are more recent.

Although there have been dendrochronological researches in the tropics for more than a hundred years, only recently, the studies are growing exponential (Brienen et al. 2016). These studies have confirmed the presence of annual growth rings in at least 220 tree species in the Neotropics (Brienen et al. 2016; Schöngart et al. 2017). The integration of dendrochronological methods with radiocarbon dating has increased the accuracy and certainty in determining the exact year of a growth ring in tropical trees. For this purpose, tropical dendrochronologists frequently use the bomb-pulse radiocarbon, a term referring to the sudden increase of ^{14}C in the Earth's atmosphere due to hundreds of aboveground nuclear bombs tests intensified between 1950 until 1963, when the Limited Test Ban Treaty was signed (Worbes and Junk 1989). Here, we combined dendrochronology and the bomb-pulse dating method to improve the resolution of temporal events in a legal dispute related to land appropriation. In this case, we reconstruct the date of felling of some trees in a teak (*Tectona grandis*) plantation. It is worth noting that teak has showed annual growth rings in all places where this species has been studied (Pumijumnong et al. 1995; Deepak et al. 2010; D’Arrigo et al. 2011; Nocetti et al. 2011). Our hypothesis is that teak has annual rings in our study area.

Dispute context

During September 2006, a smallholder planted three hectares of teak (*Tectona grandis*) in Apartadó (Antioquia, Colombia). Teak is one of the most appreciated and valuable tropical timbers of the world's timber trade (Kollert and Kleine 2017)). For the plantation with a density of 1,233 trees/ha, the property owner (PO) used cuttings of about 50 cm in length and about 1cm in diameter from new branches of another teak plantation. This method allows an initial fast-growing and reduces tree mortality. In August 2015, nine years after the teak plantation, the staff of an electricity company (EC) entered the property to check a power-line-corridor (PLC) established in 2008 that crosses through the teak plantation. Allegedly without the owner´s permission, the EC staff felled 80 trees growing under the PLC, degrading and fragmenting the commercial area of the teak plantation in two stands. After the owner´s complaints, the EC asserted that the area was not planted at the moment of PLC establishment in 2008. According to the PO, he established the teak plantation in 2006, two years before that the PLC was constructed, and claimed that the EC officials must have seen the planted trees in this place. We were asked to establish how the age of both the stumps under the PLC and the living trees in the teak plantation surrounding the PLC.

4.2 Materials and methods

4.2.1 Study area

The teak plantation is located in Northern of *Chocó* Biogeographic Region, Colombia (7°53′05″N - 76°38′06″W), close to Colombia-Panamanian border. The area is hilly, with slopes ranging from slightly up to moderately inclined and an elevation ranging between 80 and 220 m altitudes. We obtained climate data from Tropical Rainfall Measuring Mission (TRMM) (TRMM 2011) from 2000 - 2015. Mean annual precipitation and mean annual temperature are 2,823 mm, and 26.7 °C, respectively. February, with about 65 mm, is the month with the lowest rainfall. During the other months´ rainfall is over 100 mm. The mean temperature is nearly the same all year round.

4.2.2 Field sampling

In 2016, we visited the study area to gather evidence that would support the facts (Figure 4-1). We measured the affected transect and counted the stumps of the felled trees under PLC. To determine the age of trees felled, we cut three cross-sections at random from the stumps felled in 2015 by the EC. To date the living trees from the plantation, we felled two trees and obtained a cross-section of each one close to the ground. The use of complete cross-sections is mandatory in this case because it is difficult to handle an increment borer near ground level and reach the pith.

4.2.3 Sample preparation

The cross-sections were processed in the Tropical Dendroecology Laboratory of the National University of Colombia at Medellin. The cross-sections were oven-dried at 28 °C, up to reach a constant weight. To highlight the tree rings, we polished the cross-sections with abrasive sandpaper, from 60 to 600 grains. The cross-sections were scanned at a resolution of 1,800 dpi in an Epson Expression 10,000XL Scanner calibrated for dendrochronological studies for Regent Instruments, Canada. The high-resolution images allowed us to characterize the tree-rings width with a precision of about 10-15µm. All images were processed with Image J11.52i software (Schindelin et al. 2012).

4.2.4 Tree ring analysis

We marked and counted the tree rings from the bark to the pith of each cross-section. We assigned calendar year 2016 to the last and still incomplete rings in the cross-sections of the trees felled by us, because the sampling of the cross-sections was done in mid-July 2016 and growth season of teak in this place occurs from March - December. The same procedure was performed for the cross-sections extracted from the stumps of the trees apparently cut down by the EC (according to PO testimony), but assigning 2015 to the last ring adjacent to the bark. In this way, all samples were dated, assuming an annual formation frequency of the tree rings. By comparing the number of rings in the cross-sections of both the trees felled by the EC in 2015 and by us in 2016, with the planting date provided by the PO, it allowed us to determine the frequency of ring formation.

Figure 4-1: Photos of the felled area in the teak plantation (1166 m2): A) image of the affected area taken in September 2015 by the property owner; B) the stump of one of the

felled trees; C) view of the felled area in July 2016, where some epicormic shoots of the felled trees are visible.

4.2.5 Radiocarbon analysis

To validate the planting date obtained under the hypothesis of annual ring formation, we used the modern radiocarbon fraction ($F^{14}C$) (Stenström et al. 2011). We extracted about 4 to 6g of wood from the oldest part of the trees, the closest to the pith of three cross-sections: One sample from a felled tree by the EC in 2015 (labeled TK2 in Table 4-1), and two pieces from two trees felled by us in 2016 (labeled TK4 and TK5 in Table 4-1). The first ring near the pith was the thinnest and came with the planted cuttings. The second ring was also very thin since teak dedicates most of the photosynthetic products during this first phase of the ontogenetic growth to roots, leaf production, and primary, not secondary growth (Rao and Rajput 1999; Husen and Pal 2006) Then, most of the wood for radiocarbon analysis by the conventional radiometric method had to be extracted from the third ring in samples TK2 and TK5, to complete the amount of wood needed for the analysis: a mixture of the 1st, 2nd and 3rd rings. In sample TK4, since all the initial growth rings were very thin, the fourth ring contributed most of the wood mixture sample used for radiocarbon analysis. The wood samples were sent to the Laboratory of Radiocarbon Analysis of the Institute of Health and Medical Ecology, in Ukraine (Code IHME), for the determination of $F^{14}C$ by the conventional radiometric method.

The wood samples were grinded to a fine powder. Then were submitted to solid-liquid extraction in Soxhlet apparatus (6-7 hours). After extraction wood sample was dried at 105 °C about 3-5 hours to constant mass. Pre-treated wood samples were converted into benzene, using of benzene line (http://benzene-line.com/). Benzene sample was counted by liquid scintillation spectrometer (Quantulus 1220TM) using of Teflon vials (Skripkin and Kovaliukh 1997; Skripkin and Buzynnyi 2017).

To calibrate the radiocarbon analysis in $F^{14}C$, we used the bomb-pulse (post-bomb calibration) and the CALIBomb program (Reimer et al. 2004), and the Northern Hemisphere Zone 2 (NHZ2) calibration curve with one-year smoothing. The NHZ2 is the most appropriate calibration curve for the study site. This curve was extended from 1950 to 2010 with data from Hua et al. (2013).

4.3 Results

Our measurements made in the field indicated that the felled area was 1,166 m^2 (11.6 m x 100 m; 3.88% of the planted area). We counted 80 stumps of the original teak plantation as evidence of the felled trees (Figure 4-1). The results of the growth rings analysis are presented in Table 4-1.

The cross-sections allowed us to characterize the anatomy of the wood in the transverse plane (Figure 4-2). The teak growth rings can be observed by the naked eye; they are defined by bands of terminal parenchyma (white arrows in Figure 4-2). Vessel distribution is diffuse. The pores or vessels do not follow any clustering pattern. In all samples observed, the heartwood occupies three-quarters of cross-sections, which is notable from an economic point of view.

Table 4-1: Age determined in some trees cut down by the electric company and by us in the teak plantation, by counting the number of growth rings from the bark (felled date) to the pith.

Code	Disc diameter (cm)	Tree height (m)	First ring	Last ring	Number of rings (age[1])	Annotations
TK1	22.9	-	2005	2015	11	Tree felled in 2015 by the company
TK2	22.8	-	2005	2015	11	Tree felled in 2015 by the company
TK3	34.9	-	2005	2015	11	Tree felled in 2015 by the company
TK4	34.7	17.4	2005	2016	12	Tree felled in 2016 to this study
TK5	23.2	16.6	2005	2016	12	Tree felled in 2016 to this study

[1] Years old.

Tree-rings marked and counted allow us to know the real age of these trees (Table 4-1). Because the trees whose cross-sections were examined by us from the felled area (TK1, TK2, and TK3 in Table 1-4) were alive when cut down, we can assume all 80 felled trees were alive when they fell under the PTL. Therefore, the last growth rings formed, or under formation, present in these cross-sections were of the year 2015 (Figure 4-2A). Based on these last rings formed in 2015, by counting the rings, we established the date of formation of the previous rings up to the pith: The first tree rings correspond to 2005. Likewise, we determined that, in the trees cut down by us in 2016 (TK4, and TK5 in Table 1-4), the first rings dated from 2005, and by extension, the first rings of all planted trees were 2005.

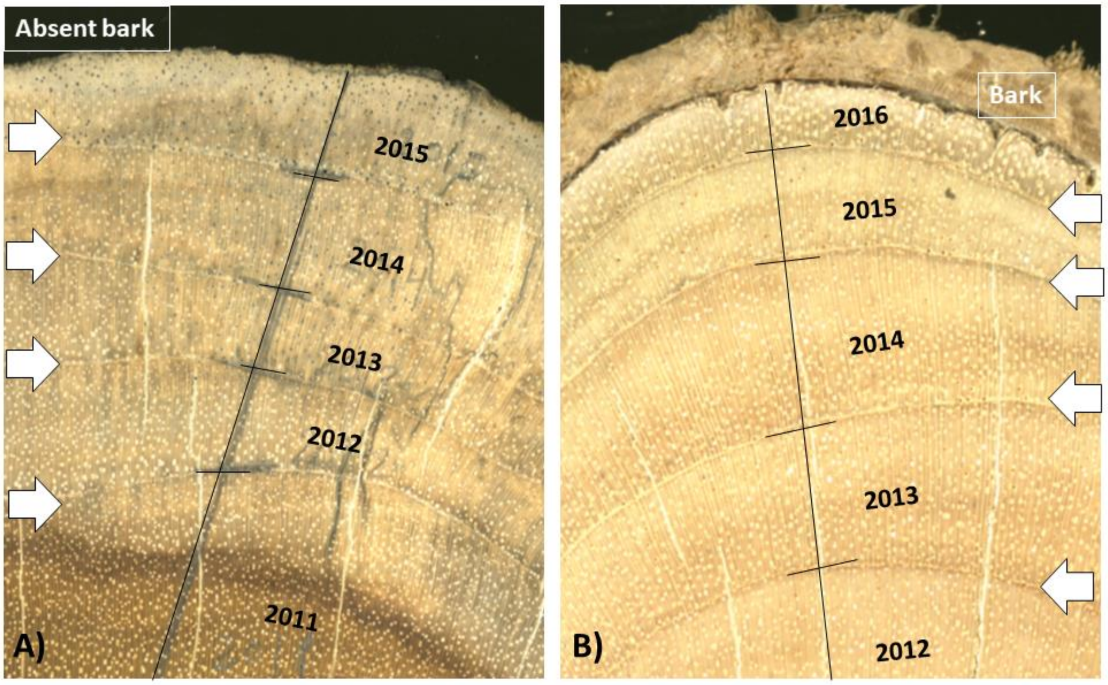

Figure 4-2: Photos showing the retrospective dating of the growth rings in teak cross-sections: A) cross-section from a tree felled in 2015 (TK2), absent bark probably due to fungi decay; B) cross-section from a tree felled in 2016 (TK4). White arrows indicate the growth ring boundaries.

There are two main findings. The first one is that in all cross-sections sampled, the first growth ring dated from 2005 (TK1 to TK5, in Table 4-1). This conflicts with the PO, who claims he planted the trees in 2006. However, as the PO indicates they did not plant seeds but cuttings, which already had one ring at time of planting. Therefore, the plantation in 2016 was 10 years old and trees were 11 years old. The other find is that the cross-sections of trees felled by us and felled by the EC differ in only one ring (Table 4-1 and Figure 4-2). These facts provide strong evidence of the annual nature of the growth rings in the study teak trees, proving the hypothesis.

Table 4-2: Results of ^{14}C dating and calibration in calendar dates of the samples TK2, TK4, and TK5.

Sample Code	Weigh (g)	$F^{14}C$	Calibrated age range (1 Sigma)	Calibrated age range (2 Sigma)	Mean calibrated date[3]
TK2[1]	4.7	1.058 ± 0.005	[2006.56 – 2009.12] (0.93)	[2005.21 - 2009.24] (0.88)	2007
TK4[2]	4.7	1.046 ± 0.005	[2008.52 - 2009.24] (0.42)	[2007.43 - 2009.24] (0.52)	2008
TK5[2]	5.7	1.062 ± 0.004	[2005.35 - 2007.84] (0.92)	[2004.84 - 2009.24] (0.90)	2007

[1] This is a dead tree felled in 2015 by the electric company.
[2] Trees felled by us in 2016.
[3] Date rounded to the first integer calendar year. Values in parenthesis values indicate of probability percent gives by CALIBomb.

The ^{14}C results in F^{14}C and their calibrations in calendar years are presented in Table 2-4 and Figure 3-4. As we explained in the methods, given the small amounts of wood supplied for the ^{14}C analysis by the first and second ring, closest to the piths of the cross-sections, the third and fourth growth rings supplied most wood for the three ^{14}C analysis. Then, the ^{14}C isotopic signature of the year 2007 dominates in the TK2 and TK5 samples, and that of

2008 in the sample TK4 in the *$F^{14}C$* analysis. Given that, in the cross-sections where the TK2 and TK5 samples were extracted, the third rings from the pith to the bark were dated by counting the rings as belonging to the year 2007, and the fourth ring of the TK4 sample to the year 2008, the ^{14}C dating also confirms the annual nature of the teak growth rings in the study area.

4.4 Discussion

Teak have showed annual rings many other places around tropical region (Pumijumnong et al. 1995; Deepak et al. 2010; D'Arrigo et al. 2011; Nocetti et al. 2011; Castaño 2016). Here we also find annual growth rings in teak by counting retrospectively from the last known date ring (Figure 4-2, and Table 4-2) to the pith and by bomb-pulse radiocarbon dating (Table 4-2).

Our results show that when the trees were cut down by the electricity company in 2015, the trees had 11 rings; that is, they were 11 years old (Table 4-2). The age of the trees does not coincide with the planting date because, because the PO used cuttings of almost 1 year old for planting. Therefore, the plantation was 10 years old in 2015.

It is evident that the cuttings were less than one year aged, and that their first rings were barely forming. However, since all the leaves are removed from the cuttings before planting, their growth stops. Only after the roots are formed with the energy supplied by the non-structural carbohydrates stored in the parenchymal tissue of the cuttings wood, appear primary growth´s shoots, and then the leaves, with which the first planting growth rings begin to form. These rings and the subsequent rings tend to be tiny. Given that it is well known that teak trees grow rapidly in height during the first years, but proportionally not so much in diameter (de Camino and Morales 2013). Consequently, the isotopic signature of the wood of the years 2007 and 2008 prevailed, given that most samples came from these growth rings. The first two rings, closer to the pith, produced very few amounts of wood useful for radiocarbon dating by the conventional radiometric method, which requires at least 4g of wood. To dating exactly the first ring of the cuttings planted and dated 2005 by rings count, we should have used the AMS (Accelerator Mass Spectrometer) radiocarbon dating method, which requires approximately 400 times less mass of wood samples, but it is much more expensive for a smallholder.

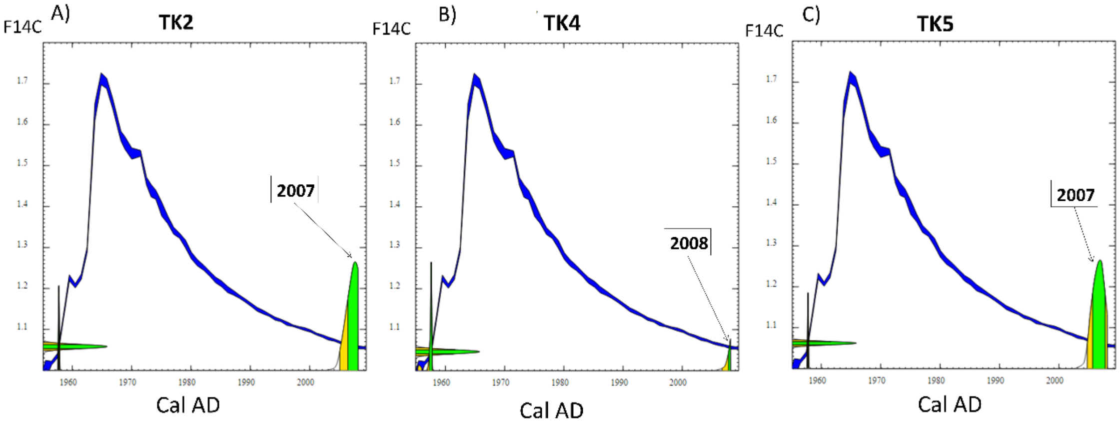

Figure 4-3: Graphs showing the post-bomb ^{14}C calibration dates with 2 σ of the samples TK2, TK4, and TK5 using CALIBomb: A) sample TK2 dated the year 2007 after the bomb-spike with an 88% probability, or the year 1957 with a 12% probability, before the spike; B) sample TK4 dated the year 2008 with a 52% probability, or the year 1957 with a 48% probability; C) sample TK5 dated the year 2007 with a 90% probability, or the year 1957 with 10% probability

The vessel distribution observed was diffuse (Figure 4-2A and 4-2B), in spite that wood anatomists often describe the teak growth rings defined by circular to semicircular porosity (pores grouped at the beginning of the ring), accompanied by a terminal parenchyma band (Vásquez and Ramírez 2005; Richter and Dallwitz 2009). This suggests a kind of plasticity of the hydraulic traits, under conditions with abundant irrigation or rain, this anatomy may change as evidenced by recent work (Nocetti et al. 2011; Cardoso et al. 2015). It is important to note that this study area over 2,823 mm a year in rainfall.

As shown in Table 4-2 and Figure 4-3, the probability of the dating with 2σ after the spike of the bomb-pulse was 88% (2007), 52% (2008), and 90% (2007) for samples TK2, TK4, and TK5, respectively. The reason why the radiocarbon dates were not 2005, as shows the dendrochronological analysis, but 2007- 2008 (Table 4-2), is because the wood samples used for dating are composed of a mixture of wood coming from 1th, 2th 3th tree rings in

TK2 and Tk5, and from 1tst to the 4th rings in TK4. However, radiocarbon results and the tree-rings analysis validate the annual tree-rings frequency of tree rings in the teak of our study area.

CALIBomb, as well as other programs to calibrate radiocarbon dating with the bomb-pulse, systematically assign a higher probability to the dates after the bomb spike (del Valle et al. 2014). Therefore, more important than these probabilities are the knowledge we have about the most likely dates. That is, are they before or after the bomb spike? In this study, there is no doubt that they are after the bomb spike; all dates obtained in Table 4-2 are 100% likely.

4.5 Conclusion

Dendrochronology and ^{14}C dating combined emerge as a tool for effectively resolving some disputes in forensic sciences related to tree cutting dating in tropical tree plantations. During post-bomb years, the precise dating of the first growth ring around the pith of trees using AMS ^{14}C dating would be a great advantage.

5. General conclusions

Tropical dendrochronology has faced successfully several obstacles: The belief that tropical trees had no annual growth rings, the complexity of wood anatomy, the lack of knowledge on physiological processes or mechanisms of woody plant species to induce annual tree rings formation, the variety of ecosystems with different climatic conditions, and the vast plant diversity in the tropics. However, the colossal effort made by several scientists in the past decades, teaches us that every obstacle is a research opportunity.

Most ecologists call tropical rain forests to several different ecosystems of the tropical lowlands with annual rainfall over 2,000 mm. Only the Holdridge system discriminates between moist forests (2,000 <4,000 mm), wet forests (4000 <8000 mm), and rainforest (over 8000 mm) and explicitly recognize the existence of the hyper-humid tropical forests.

The existence of hyper-humid forests in the Chocó Biogeographic Region, with no apparent water seasonality, as well as the observation of the wood of its trees that, at the naked eye, revealed the existence of growth rings, were the opportunities we took advantage of.

The exceptional species richness of these forests in which, on average, there are only about two trees of the same species in one hectare is also an Achilles heel for dendrochronologists: As most trees are rare species, for dendrochronological studies is very difficult to collect enough replicas. However, we found that, in these forests, there are some relatively common species ubiquitously dispersed in the landscape with high dendrochronological potential, such as *Qualea lineata*, *Goupia glabra*, *Apeiba macropetala*, and *Humiriastrum procerum*, all except *G. glabra*, new for dendrochronology.

We are aware that we have only opened a small window in the challenge of studying the dendrochronology of tropical hyper-humid forests. But this first investigation invites other researchers to explore this new mine of tree species for dendrochronological studies, to use their rings as climate proxies. Therefore, new research should be carried out looking for species with annual rings and dendrochronological potential. New researches should focus on the most long-lived tree species to go back into the most remote past possible.

In this research, we found that, in contrast to the belief of many scientists, of 81 species studied in Chapter 1, 82% had growth rings, 46% with well-defined rings, and 18% with high dendrochronological potential. In chapters 1, 2, and 4, we show that 17 tree species growing in the Biogeographic Chocó Region of Colombia have annual growth rings. Of these trees, eight are new for dendrochronology. All 17 radiocarbon-dated species resulted in annual growth rings (Chapter 2 and Chapter 4). Four species that had between four and twelve replicates in Chapter 2 resulted in annual growth rings, dated both by dendrochronological and radiocarbon methods. The tree rings widths were sensitive to different environmental signals.

This research allowed answering several questions, extending the application of dendrochronology to the little-explored hyper-humid environments. Our observations in concert with Shelford law suggests that bot excess or a deficit of growth factors may explain seasonal cyclicity of growth rhythms in tropical trees. In two species (*H. procerum*, *A macropetala*) tree-rings index were negatively correlated with the rainiest season, and positively correlated with the solar radiation during the less rainy season. However, other two species (*Q lineata*, *G. glabra*) reveal a behavior typical of the species growing in zones experience a dry season, or reduced precipitation for several months. In these two species, the more water, the better the growth response, as suggested by the positive association between tree-ring indices and precipitation. In such a case, it seems that some tree species that colonize hyper-humid forest retain their positive affiliation to the original precipitation regimes. Other tree species that evolved under hyper-humid conditions are better adapted to high rainfall maximizing their growth during less rainy months.

The growth period of *H. procerum* occurs during the less rainy season, based on the positive comparisons between the tree-rings index with the solar radiation during the less rainy months; and the negative correlation with the rainiest yearly season. The $\delta^{18}O$ concentrations we observed during the less rainy season can be amplified in the ring wood because of water evapotranspiration. An excess of humidity during that period (January, February, March) drives a reduction in tree growth, evidenced by thinner growth rings. This situation coincides with low $\delta^{18}O$ values at the end of the ring, at the same time that precipitation increases significantly.

Given the abundance of one resource, it is probable that another one operates as limiting to growth. For this reason, it is plausible to find positive associations between the tree growths and the increasing of a limiting resource when it begins to be gradually available. And null or negative associations when the same resource exceeds its abundance and another begins to be scarce. The growth answer with this new resource would begin to be positive as it increases.

Since the distant studies of Geiger in 1915, describing annual growth rings in *Tectona grandis* from Indonesia, and of Coster, who in 1927 found annual rings in tropical tree species also from Indonesia, of Alan Mariaux's studies in 1967 discovering annual tree rings in many tropical species from Africa. Since the revival of tropical dendrochronology with Martin Worbes' studies in the Amazon during the 1980s, tropical hyper-humid forests had been, with very few exceptions, practically avoided or unknown by dendrochronologists. Until today, tropical dendrochronology has worked, in several subdisciplines, with species from all environmental conditions in which trees can grow in the tropics, except for hyper-humid lowland forests without evident hydric seasonality.

This research begins to fill a gap in knowledge in tropical dendrochronology. The claims of many renowned scientists, based on prejudice rather than evidence, are beginning to fall. The species with dendrochronological potential discovered here, and the many more that must be in these forests, await some attention from the dendrochronological scientist's community. This is the main conclusion of my dissertation.

A. Appendix: Age determination by post-bomb ^{14}C and by tree rings

Appendix A. Age determination by post-bomb ^{14}C and by tree rings in samples from 14 tree species. Calibrated ages were obtained by CaliBomb software (Reimer et al. 2004), and with Northern Hemisphere Zone post-bomb calibration data (NHZ2). **Pre-dated ring (year):** dendrochronological age; **F^{14}C:** modern fraction of ^{14}C (Postbomb); **Calibrated date 1 σ and 2 σ (Prob)**: Mean calibrated age range with 1 sigma and two sigmas, values in parentheses indicate of probability percent given by CALIBomb. The lowest probabilities are not included. **Cal AD:** Mean calibrated age**. Diff.:** Difference between Cal AD and Pre-dated ring (year). **First ring: date of the** first distinct ring in the sample, the pith or close to it. **Last ring: date** of the last ring closets to the bark or sampling year.

Tree species	Family	Sample code	Pre-dated ring (year)	F^{14}C	Calibrated date 1 σ (Prob.)	Calibrated date 2 σ (Prob.)	Cal. AD	Diff.	First ring	Last ring	Age (years)
Apeiba macropetala	Malvaceae	Amac40_1	1999	1.0998 ± 1.9‰	1999.3 (1.0)	1999.2 (0.95)	1999.2	0.2			
		Amac40-2	2005	1.072 ± 2.4‰	2004.3 (0.983)	2004.4 (0.914)	2004.3	-0.7	1995	2016	21

Tree species	Family	Sample code	Pre-dated ring (year)	F^{14}C	Calibrated date 1 σ (Prob.)	Calibrated date 2 σ (Prob.)	Cal. AD	Diff.	First ring	Last ring	Age (years)
		Amac42_1	1999	1.104 ± 2.3‰	1998.3 (1.0)	1998.3 (0.962)	1998.3	-0.7			
		Amac42-2	2003	1.0748 ± 2.3‰	2003.9 (1.0)	2003.8 (0.925)	2003.8	0.8	1985	2016	31
		Amac104_1	1997	1.1105 ± 2‰	1996.9 (1.0)	1997.0 (0.947)	1997.0	0.0	1978	2016	38
Castilla elastica	Moraceae	Cela183-1	2009	1.0524 ± 2.3‰	2008.6 (0.882)	2008.3 (0.8)	2008.5	-0.5	1935	2016	81
Clarisia racemosa	Moraceae	Crac186-1	2009	1.0496 ± 2.2‰	2008.9 (0.61)	2008.5 (0.65)	2008.7	-0.3	1997	2016	19
Goupia glabra	Goupiaceae	Ggla64-1	1991	1.1497 ± 1.9‰	1991.2 (1.0)	1991.3 (0.93)	1991.3	0.3	1979	2016	37

Tree species	**Family**	**Sample code**	**Pre-dated ring (year)**	**F^{14}C**	**Calibrated date 1 σ (Prob.)**	**Calibrated date 2 σ (Prob.)**	**Cal. AD**	**Diff.**	**First ring**	**Last ring**	**Age (years)**
		Ggla64-2	2003	1.0819 ± 1.5‰	2002.4 (1.0)	2002.6 (0.931)	2002.5	-0.5			
Hevea brasiliensis	Euphorbiaceae	Hbra130-1	1996	1.1188 ± 1.8‰	1995.5 (1.0)	1995.3 (0.94)	1995.4	-0.6			
		Hbra130-2	1998	1.1046 ± 1.8‰	1998.2 (1.0)	1998.2 (0.964)	1998.2	0.2	1968	2016	48
Humiriastrum procerum	Humiriaceae	Hpro100-1	1972	1.4925 ± 2‰	1971.8 (1.0)	1971.7 (0.969)	1971.7	-0.3			
		Hpro100-2	1978	1.3302 ± 2.3‰	1978.0 (1.0)	1977.8 (0.927)	1977.9	-0.1	1922	2016	94
		Hpro65-1	1991	1.1482 ± 1.9‰	1991.3 (1.0)	1991.5 (0.94)	1991.4	0.4	1980	2016	36

Tree species	**Family**	**Sample code**	**Pre-dated ring (year)**	**$F^{14}C$**	**Calibrated date 1 σ (Prob.)**	**Calibrated date 2 σ (Prob.)**	**Cal. AD**	**Diff.**	**First ring**	**Last ring**	**Age (years)**
		Hpro65-2	2001	1.0881 ± 1.6‰	2001.3 (1.0)	2001.4 (0.942)	2001.4	0.4			
		Hpro82-1	2008	1.0578 ± 2‰	2007.9 (0.96)	2007.6 (0.889)	2007.7	-0.3	1947	2016	69
		Iacr20-1	1987	1.1832 ± 2.3‰	1987.7 (1.0)	1987.5 (0.927)	1987.6	0.6			
Inga acreana	Fabaceae	Iacr20-2	1989	1.1633 ± 2.2‰	1989.9 (1.0)	1989.8 (0.91)	1989.8	0.8	1916	2016	100
		Ing16-1	1987	1.1934 ± 1.9‰	1986.7 (1.0)	1986.6 (0.915)	1986.7	-0.3			
Inga sp.	Fabaceae	Ing16-2	1992	1.1455 ± 1.8‰	1991.7 (1.0)	1991.7 (0.948)	1991.7	-0.3	1954	2016	62

Tree species	**Family**	**Sample code**	**Pre-dated ring (year)**	**$F^{14}C$**	**Calibrated date 1 σ (Prob.)**	**Calibrated date 2 σ (Prob.)**	**Cal. AD**	**Diff.**	**First ring**	**Last ring**	**Age (years)**
		Mabe25-1	1992	1.14 ± 1.8‰	1992.5 (1.0)	1992.3 (0.951)	1992.4	0.3			
Mabea sp	Moraceae	Mabe25-2	1995	1.1181 ± 1.8‰	1995.6 (1.0)	1995.4 (0.931)	1995.5	0.5	1947	2016	69
		Olat12-1	2001	1.0889 ± 2.1‰	2001.2 (1.0)	2001.3 (0.93)	2001.3	0.3	1968	2016	48
		Olat14-1	1980	1.2677 ± 2.7‰	1980.8 (0.901)	1980.9 (0.89)	1980.8	0.8			
		Olat14-2	1990	1.1584 ± 2‰	1990.3 (1.0)	1990.4 (0.907)	1990.3	0.3	1970	2016	46
Otoba latialata	Myristicaceae	Otat80	2004	1.0759 ± 2.9‰	2003.6 (1.0)	2003.7 (0.923)	2003.6	-0.4	1963	2016	53

Tree species	**Family**	**Sample code**	**Pre-dated ring (year)**	**$F^{14}C$**	**Calibrated date 1 σ (Prob.)**	**Calibrated date 2 σ (Prob.)**	**Cal. AD**	**Diff.**	**First ring**	**Last ring**	**Age (years)**
Pterandra ultramontana	Malpighiaceae	Pult88-1	1988	1.1868 ± 2.6‰	1987.4 (1.0)	1987.2 (0.925)	1987.3	-0.7	1953	2016	63
		Qlin103-1	2004	1.0736 ± 2.6‰	2004.0 (0.997)	2004.2 (0.917)	2004.1	0.1			
Qualea lineata	Vochysiaceae	Qlin103-2	2007	1.0638 ± 3.1‰	2006.3 (0.97)	2006.7 (0.898)	2006.5	-0.5	1956	2016	60
Symphonia globulifera	Moraceae	Sglo86-2	1981	1.2655 ± 2.1‰	1981.0 (0.922)	1981.0 (0.904)	1981.0	0.0	1966	2016	50
Tachigalii colombiana	Fabaceae	Tcol128-1	1996	1.1074 ± 1.8‰	1997.5 (1.0)	1997.7 (0.972)	1997.6	1.6			
		Tcol128-2	2008	1.0516 ± 1.8‰	2008.7 (0.806)	2008.4 (0.769)	2008.6	0.6	1974	2016	42

Tree species	Family	Sample code	Pre-dated ring (year)	$F^{14}C$	Calibrated date 1 σ (Prob.)	Calibrated date 2 σ (Prob.)	Cal. AD	Diff.	First ring	Last ring	Age (years)
		Tcol51-1	1999	1.1012 ± 1.9‰	1999.0 (1.0)	1998.9 (0.958)	1998.9	-0.1	1965	2016	51
		Tcol71-1	1987	1.1944 ± 1.9‰	1986.6 (0.918)	1986.5 (0.907)	1986.6	-0.4			
		Tcol71-2	1990	1.154 ± 1.8‰	1990.7 (0.9)	1990.9 (0.9)	1990.8	0.8			
		Tcol71-3	1995	1.1248 ± 1.8‰	1994.5 (1.0)	1994.6 (0.94)	1994.6	-0.4	1953	2012	59

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