Non-annual tree rings in a climate-sensitive *Prioria copaifera* chronology in the Atrato River, Colombia

David Andrés Herrera Ramírez

Universidad Nacional de Colombia
Facultad de ciencias agropecuarias, Departamento de Ciencias Forestales
Medellín, Colombia
2015

Non-annual tree rings in a climate-sensitive *Prioria copaifera* chronology in the Atrato River, Colombia

David Andrés Herrera Ramírez

Tesis o trabajo de investigación presentada(o) como requisito parcial para optar al título de:

Magister en Bosques y Conservación Ambiental

Director :
Doctor Jorge Ignacio del Valle Arango
Codirectora:
Ph.D. Laia Andreu Hayles

Línea de Investigación:
La Dendroclimatología Tropical como Herramienta para Conocer los Efectos del Cambio Climático en el Trópico
Grupo de Investigación:
Bosques y Cambio Climático

Universidad Nacional de Colombia
Facultad de Ciencias Agropecuarias, Departamento de Ciencias Forestales
Medellín, Colombia
2015

Todo en el universo tiene su historia, hay que aprender a escuchar de forma consciente.

Dedicada a todos quienes amorosa y sabiamente han compartido este camino conmigo

Cover Letter

Please, find enclosed an original manuscript, presented by David Herrera Ramirez for considering as a thesis to obtain the Master degree in Bosques y Conservación Ambiental, entitled "Non-annual tree rings in a climate-sensitive *Prioria copaifera* chronology in the Atrato River, Colombia". We investigated the annual nature of tree rings in *P. Copaifera* trees that grow over the Atrato River floodplains, in Colombia. Despite we developed a statistically reliable chronology and we detected climate signals on it, we found discrepancies with the ^{14}C measurements.

This work address as a main question: What are the implications to have intra-annual growth structures impossible to differentiate from annual tree rings, given the development of a statistically reliable chronology with significant climate signals in the tropical species *Prioria copaifera* Griseb.?

This work advances our current understanding in tropical dendrochronology. Detecting non-annual tree rings in a climate-sensitive chronology gives us a big alert about applying dendrochronological foundations, as crossdating and climate signal detection, to evaluate the annual nature of the tree rings in tropical species with very common anomalies in tree ring formation. To use proper methodologies for evaluating annual growth periodicity in those tree species is fundamental to spread out the dendrochronology over the tropics, and to improve the understanding of their ecology.

Contents

Pág.

Abstract

Dendrochronology can assign exact calendar years to tree rings. In temperate climates, tree growth dormancy due to low temperatures during winter ensures that the observed tree rings are annual. Thus, it is common practice to assume annual periodicity when: (1) there is common tree growth variability shared among trees; (2) significant correlations with meteorological records with annual resolution are found. Here, we show how these criteria are not valid for trees of the tropical species *Prioria copaifera* Griseb., located at the Atrato River in Colombia (~ 5°N). Using dendrochronological procedures, we were able to generate a reliable tree ring-width chronology that correlated significantly with several environmental variables from the region. However, 24 radiocarbon measurements from three trees demonstrated offsets of up to 40 years that indicates that *P. copaifera* can produce more than one ring in certain years. This led to the conclusion that anatomical features defining tree rings were not distinguishable as being either annual or sub-annual. Results derived from a growth model and the instabilities found in the climate-growth relationship suggest that the climatic signal found may be due to the fact that some of the trees show annual rings for the last years when analyses were performed, however, spurious significant correlations cannot be discarded. Radiocarbon measurements done before and after the bomb spike in multiple trees are an useful and independent method to validate the identification of annual tree rings when tropical species show challenging anatomical features defining the boundaries of the growth layers.

Key words: Tropical dendrochronology, ^{14}C, annual and sub-annual tree rings, climate signals, growth model

RESUMEN

La dendrocronología asigna fechas calendario exactas a la formación de los anillos de crecimiento en los árboles. En zonas templadas, los árboles paran de crecer debido a las bajas temperaturas durante el invierno asegurando que los anillos observados sean anuales. Así, es común asumir que los anillos tienen periodicidad anual cuándo: 1) hay una variabilidad común en el crecimiento de los árboles; y 2) se encontraron correlaciones significativas con los datos meteorológicos con resolución anual. Nosotros mostramos que estos criterios no son válidos para la especie *Prioria copaifera* Griseb., localizada en el bajo río Atrato en Colombia (~ 5°N). Usando procedimientos dendrocronológicos generamos una cronología de ancho de anillos confiable que correlacionó significativamente con varias variables ambientales de la región. Sin embargo, 24 medidas de radiocarbono de 3 árboles mostraron diferencias de hasta 40 años respecto a las fechas asignadas, lo cual indica que *P. copaifera* puede producir más de un anillo en ciertos años. Esto llevó a la conclusión que las características anatómicas que definían los anillos no permitían distinguir si los anillos eran formados de forma anual o sub-anual. Resultados derivados de un modelo de crecimiento y de detección de inestabilidades mostraron que la relación clima-crecimiento sugiere que la señal climática encontrada puede ser debida al hecho de que la mayoría de los árboles mostraron anillos anuales durante los últimos años, sin embargo, correlaciones espurias no pueden descartarse. Las medidas de radiocarbono hechas antes y después del pico en varios árboles son un método independiente muy útil para validar la identificación de los anillos anuales.

Palabras claves: Dendrocronología, C^{14}, Señales climáticas, Modelo de crecimiento

Introduction

The identification of ring boundaries defining the annual nature of tree rings is essential for developing reliable chronologies. Dendrochronology is a powerful, inexpensive and relatively fast methodology used to study ecology and growth of tree species that form annual rings and the climate of the region where those trees are growing (Brienen and Zuidema 2006; Rozendaal and Zuidema 2011). Tree-ring research can extend climate records and fill information gaps in areas where climate data are scarce (Fritts 1976), such as in most tropical and subtropical regions. Despite a rapid increase of dendrochronological studies in the tropics (Rozendaal and Zuidema 2011; Villalba et al. 2011), major efforts are still needed for its widespread application.

The crossdating technique, a fundamental dendrochronological principle, is the matching of growth patterns between tree-ring samples from the same tree and between trees in a given area, that guarantees the absolute calendar year to each individual tree ring. While in temperate regions, statistically significant crossdating has been accepted as sufficient proof for the identification of annual rings (Stahle et al. 1999), in the tropics the annual periodicity of tree growth cannot be taken for granted. Nonetheless, even in wet tropical forests, tree species with very well-defined annual rings have been identified, probably due to species genetics and/or to the existence of a season with unfavorable environmental conditions (Fichtler et al. 2003; Rozendaal and Zuidema 2011). Evidences of annual tree-ring formation in several tropical species have been proven by successful crossdating and correlation with climate data (Brienen and Zuidema 2005; Schöngart et al. 2005; Soliz-Gamboa et al. 2011; Worbes 1999) and by ^{14}C bomb peak dating (Groenendijk et al. 2014; Soliz-Gamboa et al. 2011; Wils et al. 2011; Worbes and Junk 1989). Back in the early 1950s, above ground atomic weapon tests produced excess of ^{14}C atoms 100 percent higher than the so call ^{14}C natural levels, tagging all living organisms on Earth (Naegler and Levin 2009). Following the 1963 Treaty Banning Nuclear Weapon Tests, the excess of ^{14}C in the atmosphere started decreasing, but its signature stored within world-wide trees growing in year 1954 onward can still be used today as a precise chronological time marker of its carbon fixation and tissue formation (Hua 2009). Bomb peak dating using ^{14}C has been successfully conducted not only in temperate (Biondi et al. 2007; Pearson et al. 2011) and subtropical regions (Biondi and Fessenden 1999; Boninsegna et al. 2009), but also in trees and shrub species from the tropics (Fichtler et al. 2003; Groenendijk et al. 2014; Ramírez and del Valle 2011; Worbes and Junk 1989). Radiocarbon dating provides an independent validation of the frequency of tree-ring formation and allows testing the synchrony of ring patterns when rings from several trees are analyzed, which is fundamental to ensure correct annual tree-ring identification (Biondi et al. 2007).

The development of long and reliable chronologies in the tropics has been hampered by issues such as indistinct growth rings (Anchukaitis and Evans 2010; Groenendijk et al. 2014; Wils et al. 2009); partially absent or ‘missing’, false, and wedging rings (Brienen and Zuidema 2006; Krepkowski et al. 2012; Rozendaal and Zuidema 2011; Worbes 2002); crossdating problems (Wils et al. 2009); lack of a significant relationship with climate data (Trouet et al. 2010); lack of information regarding tropical tree ages (López and Villalba 2011; Worbes 1999); and high decay rate of dead wood (Trouet et al. 2001). These kind of issues have been associated with drought stress, growth-suppressing conditions, intense competition (Schweingruber 1996), flooding (Junk et al. 2010;

Schöngart et al. 2002), and/or changes in topography (López and Villalba 2011). In these cases, a simple ring count at the stem base or the apparent root collar often did not reveal the true age of an individual (López and Villalba 2011; Wils et al. 2010). These difficulties obstruct the correct identification of annual growth layers, which is fundamental to develop reliable tree-ring chronologies and climate reconstructions for future advances in tree-ring research globally.

A tree ring width chronology from *Prioria copaifera* Griseb. (Leguminoceae) was developed by Herrera and del Valle (2011). *P. copaifeara*, also known as cativo, is an evergreen species that dwells in the Atrato River floodplains. At this location, cativo trees are exposed to high flooding levels over more than 8 months per year, with a shorter periods of low streamflow that can be an environmental pace-marker of growth inter-annual fluctuations for this species (Grauel 2004; Herrera and del Valle 2011). Therefore, a reliable *P. copaifera* chronology may be used to reconstruct the Atrato streamflow and to study its long-term variability. This information may be highly valuable because the Atrato River crossed major Colombian wet Pacific forest, identified as a highly endangered biodiversity hotspot (Myers et al. 2000), and this region has poor climatic records. Nonetheless, climate over this region is strongly related with regional climate phenomena as the El Niño Southern Oscillation (ENSO) and low-level westerly jet (“Chocó”) that influences the climatic variability over a big part of the planet. Thus, the finding of a climatic signal in the anatomically visible tree rings of *P. copaifera*, a species with relatively big populations in northern South America, may aid to understand past climate variability over the region if a reliable chronology can be built.

The objective of this work is to evaluate the annual nature and the climate signal of tree rings in *P. copaifera* by: (1) generating a reliable tree-ring width chronology from the low Atrato River in northwestern Colombia using standard dendrochronological techniques; (2) assessing the climate signal recorded by the tree-ring records; and (3) evaluating some of standard proceedings used for the assessment of annual tree-ring periodicity in tropical species.

Materials and methods

Site description and climate variability. --- We collected 15 cross-sections from *P. copaifera* trees, the dominant species in a tropical wetland forests in the floodplains of the low Atrato River (7°20’N, 76°57’W, Fig. 1), Colombia. *P. copaifera* is found in the tropical moist forest (2000 to 4000 mm rainfall year^{-1} *sensu* Holdridge (1947)), life zone at elevations between 0 and 150 m a.s.l. and from eastern Nicaragua into northwestern South America (Holdridge 1978). This type of forest develop on loamy soils, as found in river banks and swamps usually flooded during 9 months of the year (Grauel 2004). In Colombia, the soil fertility of these sites ranges from low to fertile (González et al. 1991; Londoño and González 1993), with a pH from 5.1 to 6.0 and poor drainage (Escobar 1987; Lopez and Kursar 2007). *P. copaifera* growth and ecology has been relatively well studied due to its commercial value, but his growth phenology and some ecological-climatic relationships are still unknown (Condit et al. 1993; del Valle 1986; Giraldo and del Valle 2011; Grauel 2004; Linares 1988; Lopez and Kursar 2007)

There is no clear transition from sapwood to heartwood in *P. copaifera*. Its wood shows a diffuse-porous anatomy (Fig. 2). The growth ring boundaries are distinct, defined by marginal parenchyma, without a distinct earlywood-latewood transition. The vessels are diffuse, solitary or in radial multiples of 2-3 vessels, <5 vessels per square mm, medium, just visible to the naked eye, 132±25 µm (López et al. 2014). The parenchyma is distributed in vasicentric and banded parenchyma (López et al. 2014).

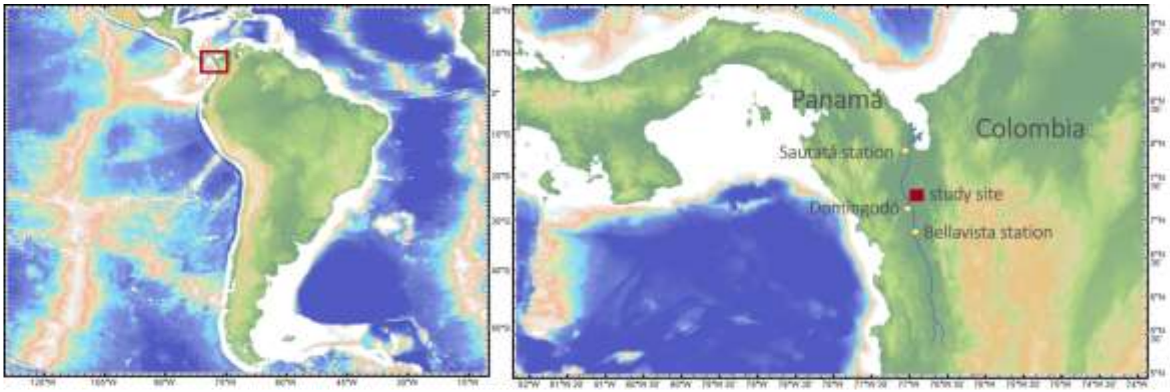

Fig. 1. Low Atrato River in the Darien region and its adjacent floodplains where the 15 cross-section of *P. copaifera* were collected (7°20’N, 76°57’W). Yellow points depict the hydroclimatic stations: Domingodó Station (1110002, 77°02’N, 7°10’ W; Precipitation and water levels), Sautatá Station (1113501, 77°07’N, 7°51’W; temperature) and Bellavista Station (1107701, 76° 57’N, 5° 57’W; streamflow). This map was generated using GeoMapApp (URL: http://www.geomapapp.org)

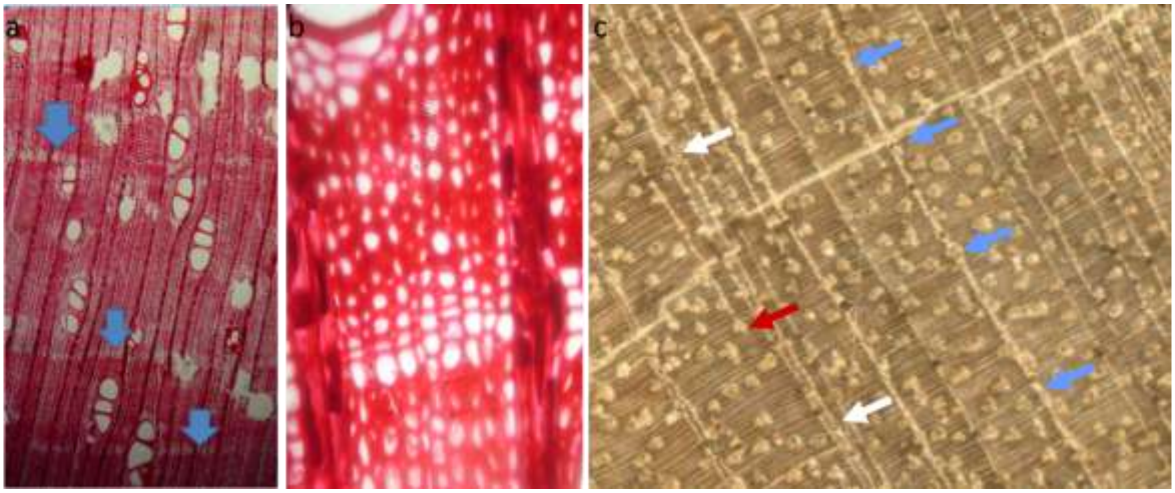

Fig. 2. Anatomical detail of *P. copaifera* tree rings: A) image at 75x B) image at 100x, and C) image at 40x. Blue arrows show the tree ring identified as real, white arrows show wedging rings and red arrow shows false rings.

The hydroclimatic records for the study region were provided by the Colombian Institute of Hydrology, Meteorology and Environmental Studies (IDEAM, Table 1). The seasonal cycle of precipitation shows a period of higher than normal precipitation from May to November and lower precipitation from December to April, and it can reach an a total precipitation of 4000 mm per year. (Fig. 3a). The amplitude of the seasonal cycle of temperature is 1°C and ranges from 26.5 to 27.5°C (Fig. 3a). . Streamflow variability drives flooding in the low Atrato River, keeping the floodplains under water from May to January, whereas from February to April the site experiences a decrease in the river water levels, due to the precipitation decrease over the entire watershed (Fig. 3a). The streamflow can reach up to 3000 m^3s^{-1} in November–December. The climate variability of this watershed is strongly affected by El Niño-Southern Oscillation (ENSO; Fig. 3a). Other regional phenomena, such as the low-level westerly jet (“Chocó”), also have a strong influence on the variability of the Western and Central Colombian regions (Poveda 2004; Poveda et al. 2001; Poveda and Mesa 1999; Rueda and Poveda 2006).

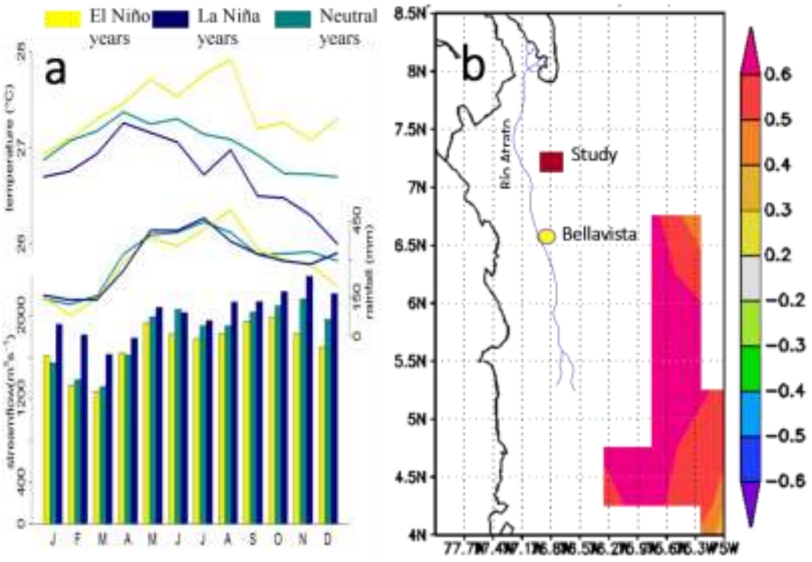

Fig. 3. Right panel: Seasonal cycle of temperature (upper panel), precipitation (middle panel) and streamflow (lower panel) for distinct ENSO phases: La Niña; neutral and El Niño ENSO. The Colombian Institute of Hidrology, Meteorology and Environmental Studies (IDEAM) provided the hydroclimatic data: temperature from 1972-2005 (Sautatá 1113501), rainfall from 1967-2006(Domingodó 1110002) and streamflow from 1965-2002 (Bellavista 1107701). Left panel: Simultaneous correlation between the annual average streamflow (Bellavista 1107701) and annual average GPCC V6 0.5 precipitation for 1965-2002 period, in the Atrato watershed (4-8.5°N, 78-75°W). The magnitude of the correlation is shown in the scale bar at right side. This map was generated using the Netherlands Meteorological Institute (KNMI) Climate Explorer (URL: http://climexp.knmi.nl/)

Sample description and dendrochronological procedure. --- In 2007, we collected 15 cross-sections from *P. copaifera* trees that were logged by local people in the Low Atrato River from a location known as '*Caño Pedeguita*'. Those cross-sections were transported to the Forest and Climate Change Laboratory at the *Universidad Nacional de Colombia* at Medellín. Herrera and del

Valle (2011) developed a preliminary tree ring-width chronology using 10 of these trees. The chronology was statistically reliable and one radiocarbon measurement was done in a single year in three trees to confirm the annual periodicity of the growth bands (Fig. 4). For the work presented here, the 10 samples used by Herrera and del Valle (2011) were re-processed, crossdated and measured again, and the rest of the samples (5) were added in order to make the chronology more robust. The samples were progressively polished with 80 to 2000 grain sand paper. To unambiguously mark the tree rings, we evaluated the continuity of the growth layer around the entire circumference, and the wedging rings were marked as true rings; thus, we identified in which part of the circumference the tree rings were locally absent. False rings were identified by the presence of discontinuous parenchyma bands and subsequent crossdating. The tree rings were visually crossdated each 10 years using Yamaguchi method (Yamaguchi 1991), pointer years (Schweingruber 1988) and images analysis in WinDendro (Version 2009b, Regent Instruments, Canada). The crossdated tree rings were identified using the anatomical features observed under a Meiji stereo zoom at 40x magnification. Once all the tree rings were identified along the entire circumference of the cross section, we follow a straight pathway from the center of the sample to the outermost tree ring to measure the them. The tree rings widths were measured on scanned images of each cross-section using the software WinDendro. For scanning, we used a resolution of 2400 dpi on a flatbed scanner calibrated by Regent Instruments (Epson Expression 10000XL). This guaranteed a precision of 0.01 mm in the measurements.

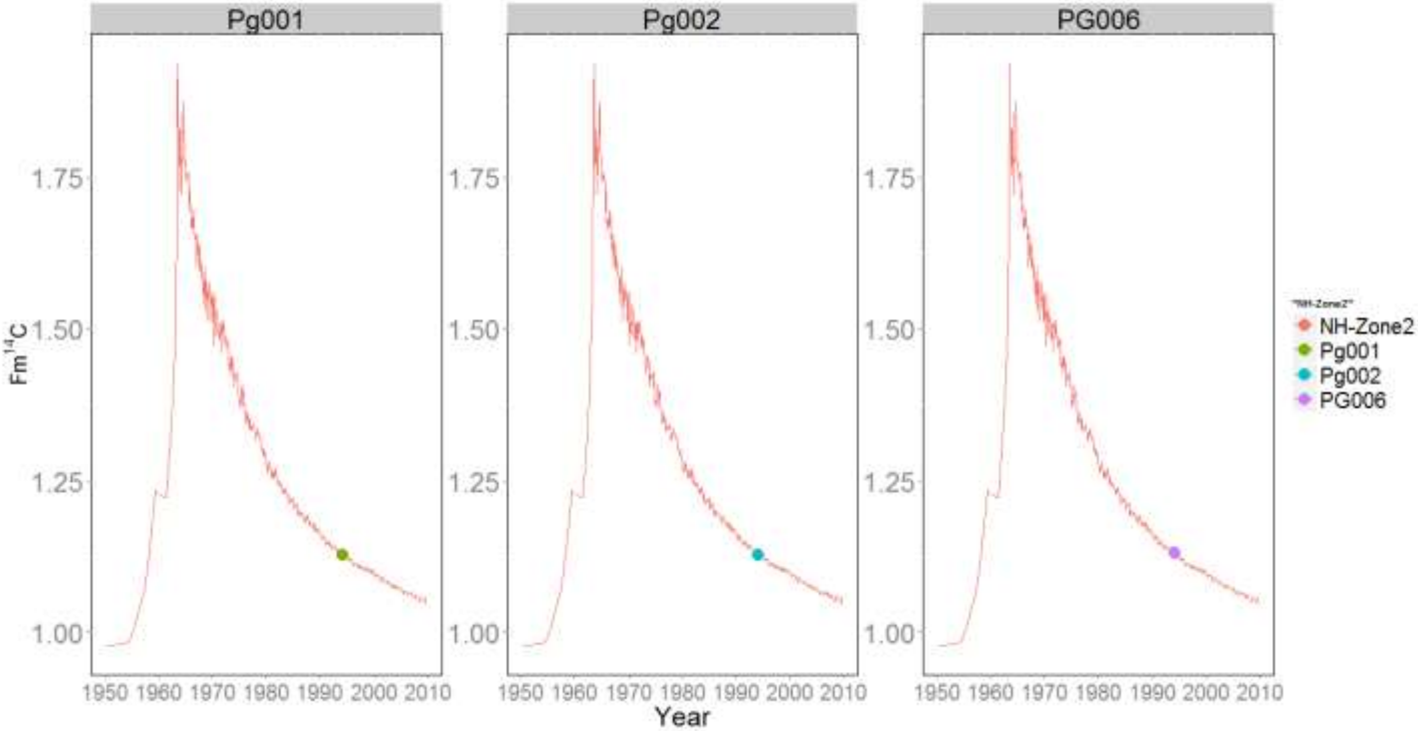

Fig. 4. Radiocarbon measurements from (Herrera and del Valle 2011) for the trees: Pg001, Pg002 and Pg006.

A total of 31 ring width series resulted from measuring 2 or 3 radii from each of the 15 coss-sections collected. The visual crossdating was performed by matching tree growth patterns among the ring-width series measured within individual (from the same tree) and among individuals (from different trees), and it was validated using the statistical software COFECHA (Grissino-Mayer 2001; Holmes 1983). COFECHA examines the series identifying possible errors committed in the visual crossdating, correlating by running segments each tree ring series with a master chronology. This chronology is developed as the average of the standardized tree ring series fitted by a cubic splines that filter the low frequency variability due to the aging process (Holmes 1983).

COFECHA is an independent tool to confirm the accuracy of the dating and measuring with a 99% of statistical confidence (Grissino-Mayer 2001). Only the samples that went through the both process visual crossdating and COFECHA, were considered well-dated and were selected. A mean chronology was calculated using a biweight robust mean over all the standardized crossdated ring-width series to avoid biases due to outlier values (Cook and Kairiukstis 1990). The standardization involves fitting the observed ring-width series to a curve or a straight line and computing an index of the observed ring widths divided by the expected value. Different standardization methods such as linear regressions, negative exponential and cubic splines were tested, and the method that produces the best statistics was chosen (Cook and Kairiukstis 1990). The final chronology was obtained fitting a cubic spline with a 50% frequency response at 60 years. A residual chronology, that yields a white noise chronology where no special frequency dominates its variance and has no serial autocorrelation, was also calculated. This procedure was performed in the software R using the library dplR (Bunn et al. 2014; Bunn 2008; Bunn 2010; R Core Team 2013).

Climate signals. --- We used the residual chronology in order to avoid autocorrelations issues comparing the high-frequency variability of climate and tree growth. We used correlation analysis to evaluate the relationship between the developed chronology and local and regional climate. The variables used to evaluate the influence of climate on *P. copaifera* growth were annual precipitation and mean streamflow, temperature, Oceanic El Niño Index (ONI) (Smith et al. 2008), and the Chocó reanalysis records. We constructed the Chocó index using the reanalysis data NCEP/NCAR (Kalnay et al. 1996) as the product of the zonal wind at 925 hPa and the specific humidity in the geographic domain 4-6°N and 78-80°W (Poveda and Mesa 1999). For further analyses, we only used time-series that overcome the normality, trend and homogeneity in order to avoid spurious correlations. We also used gridded precipitation data from GPCC V6 0.5° (Schneider et al. 2011) and HaddlSST1 1° Sea Surface Temperature (SST) (Kaplan et al. 1998). The correlations were calculated for the annual (Apr-Mar) average gridded series of precipitation and SST, and the periods of September-November and November for precipitation only. These analyses were perform to assess the relationship between climatic and the *P. copaifera* growth, as well as the strength of their signals.

Radiocarbon dating. --- The application of ^{14}C bomb peak dating of selected tree rings can be used as an independent procedure to confirm the annual nature of growth rings (Worbes and Junk 1989). This method is based on the spike of ^{14}C in the atmosphere caused by above-ground atomic weapons tests between 1954 and 1963 (Groenendijk et al. 2014; Hua et al. 2013), as mentioned earlier. Despite the ^{14}C results and the climatic signals obtained by (Herrera and del Valle 2011) that provide evidence for annual tree ring formation in the latter decades, here we implement a more rigorous evaluation of the annual nature of the tree rings for longer time periods. We selected 3 different trees to verify the annual character of tree-ring formation when applying the ^{14}C bomb peak dating method coupled with high-precision Accelerator Mass Spectrometry (AMS) (Beverly et al. 2010). Pg025 tree was randomly selected and the other Pg020 and Pg011 trees were selected due to their high correlation with the master chronology. We tested 8 tree rings in each tree spaced 10 rings apart to capture the ^{14}C bomb spike in the tropics around 1965 and to avoid ambiguities in the calibration process. By analyzing samples from different years per individual, it is possible to identify where errors in ring counting might have taken place. If all dates coincide between pre-dated rings and ^{14}C measurements (margin error ±1 year), then the rings are formed annually and, no pre-dated and measurement errors occurred. If discrepancies were observed, they could be attributed to the identification of non-annual rings or to ^{14}C sample processing and measurement errors.

From the 24 rings selected, we collected 35-50 mg of wood to determine ^{14}C concentrations. A holocellulose fraction was then isolated from the original wood samples by temperature-controlled aqueous baths of acid and alkaline solutions followed by sodium chlorite treatment, as detailed in Andreu-Hayles et al. (2015). Holocellulose extracts were converted to graphite targets, and then measured by ^{14}C-AMS technology. High-precision ^{14}C-AMS measurements were performed at the Keck Carbon Cycle accelerator mass spectrometry (KCCAMS) facility (Beverly et al. 2010). The ^{14}C data were mass-dependent isotopic fractionation corrected using the online δ^{13}C values measured by the spectrometer. Wood blank and reference samples subjected to the holocellulose extraction were also analyzed alongside with tropical tree-ring samples to aid on accuracy and precision, following established protocols (Santos et al. 2010). Measured ^{14}C values are given using the fraction modern carbon (FmC) notation (Stuiver and Polach 1977). Uncertainties smaller than 0.3% were calculated based upon counting statistics, spectrometer isotopic fractionation and background corrections, and the scatter of results from primary and secondary standards, following the data analysis described in Santos et al. (2007). Finally, we compare the FmC (±sd) value of the samples with the ^{14}C calibration curve NH-zone 2 (Hua et al. 2013).

***Age model based on the tree-ring records dated with radiacarbon measurements.* ---** We fitted a model of cumulative growth from bark to pith based on the 3 trees subjected to ^{14}C measurements. Using the correct calendar dates provided by the ^{14}C ages of the 24 dated tree rings, we generate the cumulative tree growth model. Then, the cumulative growth curves of the 31 raw ring-width series pre-dated with dendrochronological techniques were compared with the 95% confidence interval of the cumulative growth model to assess the series falling inside or outside the model's confidence interval. This approach attempts to identify series showing similarities or discrepancies with the cumulative growth pattern of the well-dated series. While series showing small differences with the model would probably imply a correct identification of annual rings and/or a low level of mismatching, big discrepancies may be the result of an erroneous attribution of growth layers to annual growth.

The cumulative growth model fitted is a log-log model:

$$\ln(years) = a + b*\ln(distance)$$

of the years counted from the bark as a function of the distance measured from the bark. Where the years to the bark were determined by ^{14}C measurements in the tree rings and, the distances to the bark were measured in the cross-sections of the trees submitted to the ^{14}C analysis. The log transform was fitted to attempt linearity in the relationship.

Assessment of the stability between climate and the tree-ring records. --- We implemented a stochastic response function model based on the application of a sub-model from the class of the so-called structural time series models (STMs) to detect and visualize the instabilities in the relationship between the ring-width chronology and both the streamflow records (Bellavista station 1107701) from 1965 to 2002 and the ONI index from 1950 to 2006. We selected both series with the aim to evaluate the instabilities in the chronology-climate relationship at regional and local scale. The methodology proposed by Visser et al. (2010) follows the model:

$$I_t = \mu_t + \alpha_t * X_t + \varepsilon_t$$

Here, the "intercept" μ, which is traditionally a constant, is replaced by a slowly bending trend model μ_t (the integrated random walk (IRW) model). We replaced the constant response weight α by a stochastic counterpart α_t based on random walk models for individual climate variables. Both trend and response weights were estimated using the discrete Kalman filter (Harvey and Shephard 1993; Visser and Molenaar 1988); this filter is ideal in the sense that it yields the minimum mean square error estimates (MMSE, normally distributed noise processes) for μ_t and α_t along with maximum likelihood estimates for unknown noise variances (Visser et al. 2010). This analysis allows us to verify whether the relationship between the variables is stable in the entire window of time analyzed or if it is stable in a shorter period and, whether the short period of stability is shared by both climate variables: ONI and streamflow. The explained variance used here was computed as:

$$Var_{explained} = \left[1 - \left(\frac{var(Y_t - \hat{\mu}_t - \hat{\alpha}_t * X_t}{var(Y_t - \hat{\mu}_t)}\right)\right] * 100$$

and it can be understood as the measure of the explanatory power of adding X_t to the model, in other words, how much of the phenomena is explained by adding and explanatory variable instead of only using the slowly bending trend $\hat{u}_{t.}$

Results

Tree-ring chronology. --- The tree-ring width chronology based on 31 series from 15 trees was successfully crossdated and spans from 1830 to 2006 (Fig. 5). The mean correlation among the series, calculated with COFECHA, was significant (r = 0.49, p < 0.01). The successful crossdating along the entire time span was supported by the finding of significant correlations between each series and the master series, performed over segments of 20 years lagged by intervals of 10 years. For a total of 372 segment correlations, 320 (85%) were statistically significant at 99% confidence. The resulting standard chronology has a slightly significant first order negative autocorrelation (r= -0.20, p <0.05), which was removed in the residual chronology for the subsequent climate analysis. From 1910 to 2006, the Expressed Population Signal (EPS) was above the arbitrary threshold widely used to determine the reliability of tree-ring chronologies (EPS > 0.85; (Wigley et al. 1984)), which indicates that the chronology is statistically reliable from 1910 to 2006.

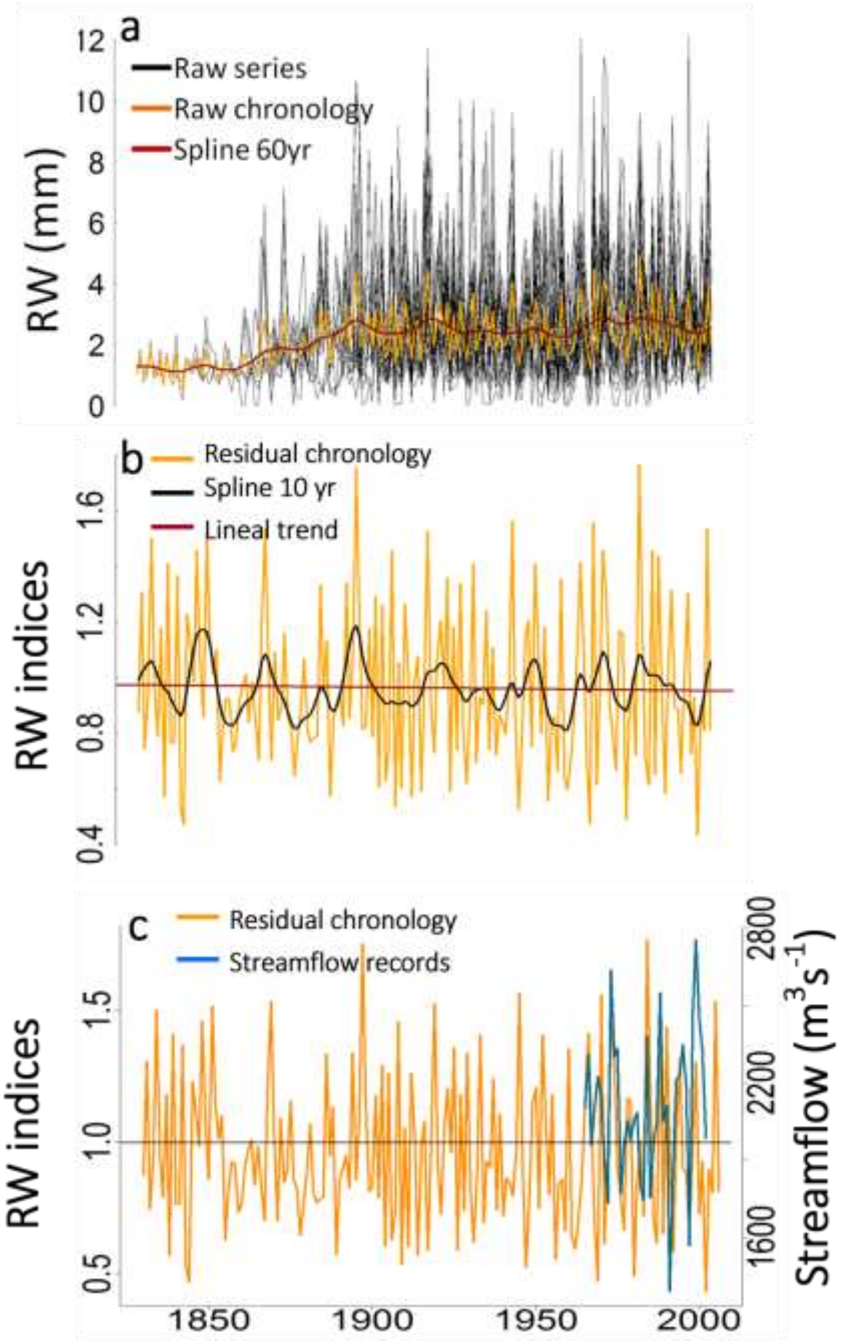

Fig. 5. A) 31 raw tree-ring series from 15 trees of *P. copaifera*. B) The *P. copaifera* residual tree-ring chronology spanning from 1830 to 2006. C) The *P. copaifera* residual tree-ring chronology versus the streamflow series from 1965 to 2002.

Climate signal in the tree-ring chronology. --- We assessed the climate signals recorded in the *P. copaifera* tree-ring chronology performing correlations with temperature, precipitation, water levels, streamflow records, the Chocó index, and the ONI (Table 1). The highest positive correlations were found with annual streamflow, and followed by Chocó and ONI records that also show a significant positive and negative relationship, respectively (Table 1). Correlations between annual precipitation and streamflow showed that the streamflow in the low Atrato River is highly dependent on the upstream watershed precipitation (Fig. 3b). A significant positive relationship was also found between the cativo chronology and the precipitation in the upper part of the river basin. For the period from 1965 to 2002 (Fig. 6a-c), cativo growth correlated strongly positive with the average gridded precipitation from April of the current year to March of the next year, September to November (rainy season) and November (the rainiest month). Field correlations between our chronology and SST (Kaplan et al. 1998) for the period from 1965 to 2006 showed negative correlations across the tropical Pacific Ocean (Fig. 6D). Overall, these results show a coherent signal in the relationship between the cativo chronology and the regional climate. SST and ONI correlations, together with the observed relationships with gridded precipitation, are consistent with the known influence of the ENSO phenomenon over the region. The La Niña event generally leads to above normal precipitation in the basin (Poveda 2004), which in turn leads to above normal streamflow and enhanced tree growth; whereas the opposite is expected during an El Niño event.

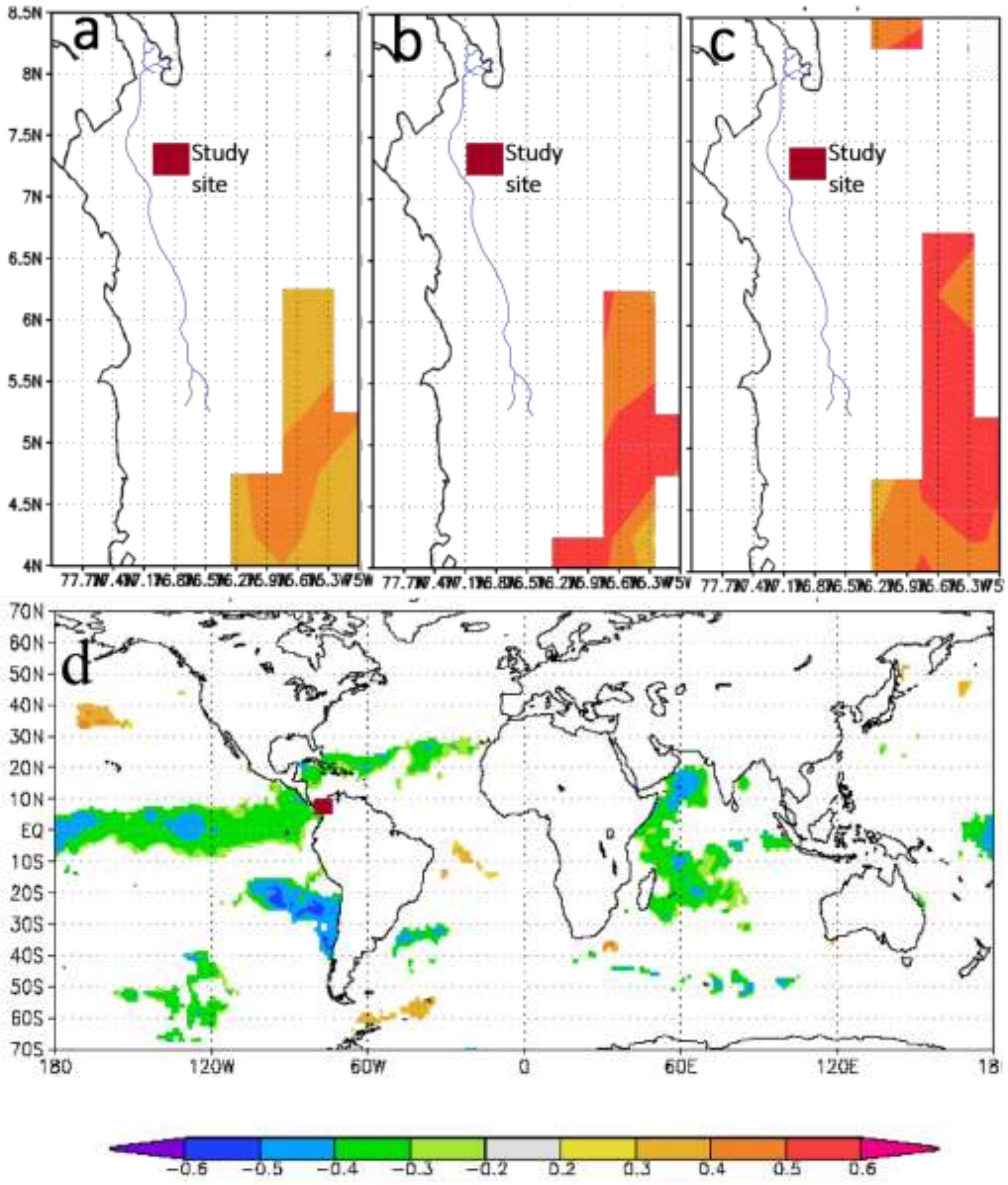

Fig. 6. Spatial correlation coefficients between the *P. copaifera* chronology and : A) Apr-Mar average GPCC V6 0.5 precipitation 1965-2002, B) Sept-Nov average GPCC v6 0.5 precipitation 1965-2002, C) Nov GPCC V6 0.5 precipitation 1965-2002 and, D) Apr-Mar HaddlSST1 SST 1965-2006. These maps were generated using the Netherlands Meteorological Institute (KNMI) Climate Explorer (URL: http://climexp.knmi.nl/)

Table 1. Mean Pearson correlations (r) between the *P. copaifera* tree-ring width chronology and the annual climatic variables for the maximum time span of available records and for a shorter period from 1980 to 2006. Significant correlations are indicated by * ($p < 0.05$)

Climatic station	Climatic Variable	R	Time Span	R	Time Span
Domingodó Station	Annual Precipitation	0,06	1967-2006	-0,06	1980-2006
Sautatá Station	Annual mean Temperature	-0,22	1972-2005	-0,23	1980-2005
Domingodó Station	Annual Water Levels	0,31	1979-2003	0,3	1980-2003
Bellavista Station	Annual Streamflow	0,4*	1965-2002	0,51*	1980-2002
NCEP/NCAR	Chocó index	0,38*	1950-2006	0,41*	1980-2006
NOAA	ONI index	-0,25*	1950-2006	-0,39*	1980-2006

Radiocarbon analysis. ---The 24 ^{14}C measurements done in this study in 3 different trees show different calendar dates than those obtained using dendrochonolgy methods (Fig. 7). Two trees, Pg011 and Pg020, match with the NH-zone 2 ^{14}C curve (NHzone 2, Hua et al. 2013) from 1975 to 2006, while the third one, Pg025, match only for 2000 onwards. Therefore, a total of 13 radiocarbon measurements (including those from Herrera and del Valle (2011)) perfectly match the NH-zone 2 calibration curve during the last decades of the 20th century (Fig 4 and Fig 7). Thus, radiocarbon measurements demonstrated that from 1990 to 2006 all the trees analyzed show annual ring, and even some of them (e.g. Pg011, Pg020) diverge from the calibration curve after 1975.

This indicates that for some years more than one ring was detected and measured using the standard dendrochronological techniques described in the methodological section. . For the period from 1962 to 1980, 4.25±2.9 annual tree rings more were identified per decade in Pg011, resulting in a maximum mismatch of 17 rings by 1962. The Pg025 ring-width series resulted in 5.4±2.2 misidentified tree rings per decade from 1973 to 2005, resulting in an offset of approximately 40 years by 1973. Finally, 4 tree rings were not identified in Pg020 from 1988 to 1974 and 3 additional rings were detected from 1974 to 1964, resulting in a cumulative mismatch of 7 rings by 1964. Note that these intra-annual growth bands presenting a sub-annual resolution were anatomically indistinguishable from annual rings after the macroscopic evaluation.

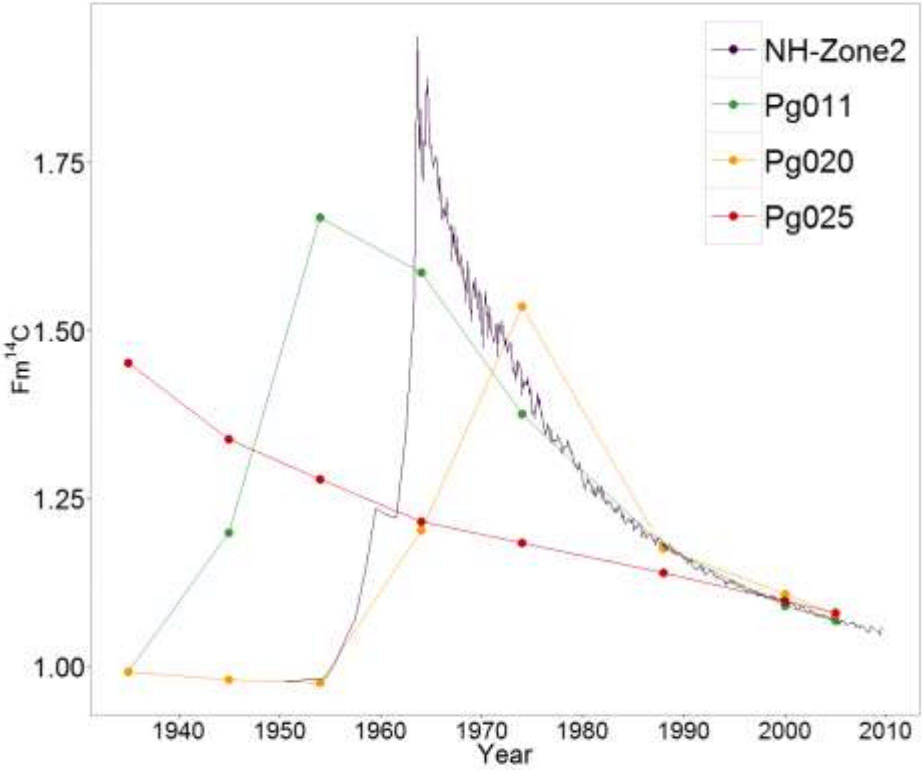

Fig. 7. The fraction modern carbon (Fm14C) values of the analyzed samples of *P. copaifera* selected from three different trees (Pg011, Pg020 and Pg025) are plotted against the atmospheric record compilations for NH-Zone2 (solid dark purple line) from 1950 to 2010 (Hua et al. 2013).

Given the non-systematic mismatches in the identification of annual tree ring in time and among individuals reported by the ^{14}C analysis, the reliability and suitability of the hydroclimatic signals recorded by the *P. copaifera* tree-ring chronology were difficult to understand and further analyses were done. Specifically, (1) a growth model was generated based on the 3 well-dated series by ^{14}C, to detect which trees shared this growth pattern, and (2) the stability of the relationship between tree-ring growth and the hydroclimate variables was assessed.

Fitting of tree-ring series to the growth model. --- The cumulative growth model resulting from the 24 ^{14}C ages suggests the expected cumulative growth patterns if the correct dates would have been successfully assigned to the tree-ring series by dendrochronological methods. The cumulative series above the upper limit of the model's confidence interval display lower than normal growth rates for 6 trees and thus, probably these trees also has the highest age overestimations, as Pg025 (Fig. 8). It is also likely that these series would show large tree-ring offsets if ^{14}C investigations had been performed, such as in Pg025 and Pg011 (Fig. 7). The rest (9 series) did not show significant differences with the cumulative growth model, remaining within the gray band in Fig. 8 and may be having low mismatching rate. Specifically, Pg025 (red lines in Fig. 8) have the highest growth rates and consequently, the highest disagreement with ^{14}C measurements; Pg011 (green lines in Fig. 8) is also outside of the confidence interval, with a 17-year offset found by ^{14}C dating (Fig. 7); and Pg020 (orange lines in Fig. 8) is within the model's confidence interval, indicating lower presence of intra-annual growth variations, resulting in ±3 years offset. The three series subjected to ^{14}C analysis by (Herrera and del Valle 2011) (i.e. Pg001, Pg002 and Pg006) are within the confidence limits and thus, are not significantly different from the growth model nor Pg020. This validates the suitability of the model to evaluate the annual tree ring identification in the dendrochronological series.

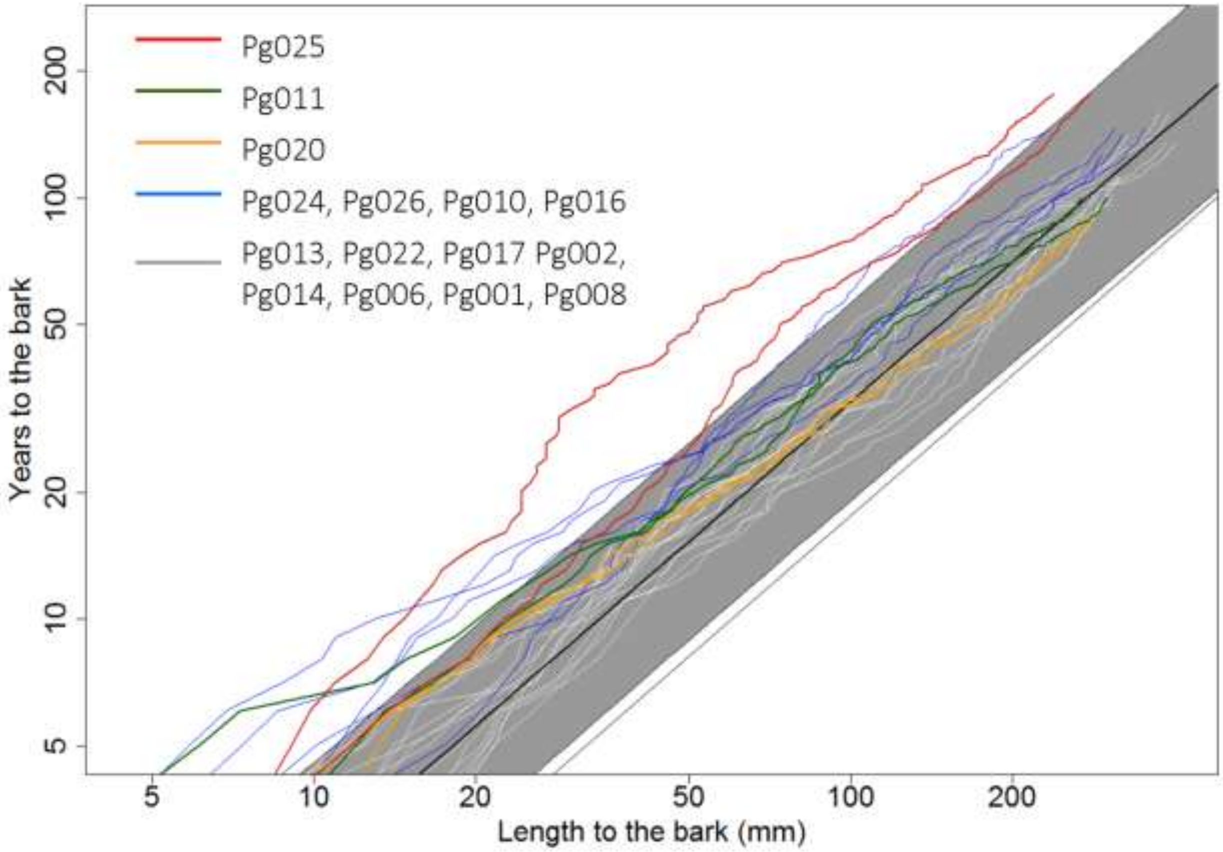

Fig. 8. Age model ln(^{14}*C age*) = -0.7683 + 0.9232ln(*length to the bark*) depicted by the black line, the gray zone represent 95% confidence interval. The lines show the dendrochronological ages from bark to pith and distance to the bark. The grey and orange lines did not differ significantly with the accumulated age model. The blue, red and green lines differ significantly with the age model and may be the most incorrect dated tree ring series with large overestimations of the real age of the trees.

Instability in the relationship between cativo growth and environmental variables. --- The correlations between the ring-width chronology and annual streamflow, Chocó and ONI records were higher when a shorter period from 1980 onwards was used instead of the maximum time span available of climatic records (Table 1). This behavior only occurred with the climate variables significantly correlated with the tree-ring chronology, while the other climate series did not show any improvements (Table 1). This is in agreement with the results obtained applying structural time series models that allow the identification of instabilities in the relationship between the climate series and the chronology. The models were calculated for streamflow and ONI as dependent variables, and they can explain 97% of the variance for streamflow and 21% for ONI (Fig. 9). Although the growth-climate relationship shows an early period of instability in the estimators α (stochastic response weight) and μ (the bending trend), both α and μ become constant from about 1980 to 2006 (Fig. 9). This means there is a stable response after 1980 for both variables ONI and streamflow. In the relationship growth-streamflow, the stochastic response weight α_t is stable from 1970 to 2006, whereas the trend component μ_t becomes stable after 1980. For ONI, both α_t and μ_t become stable at approximately 1980 and stay stable until the last year, 2006 (Fig. 9). Before 1980, the behavior of the time-dependent parameters is random and completely unstable.

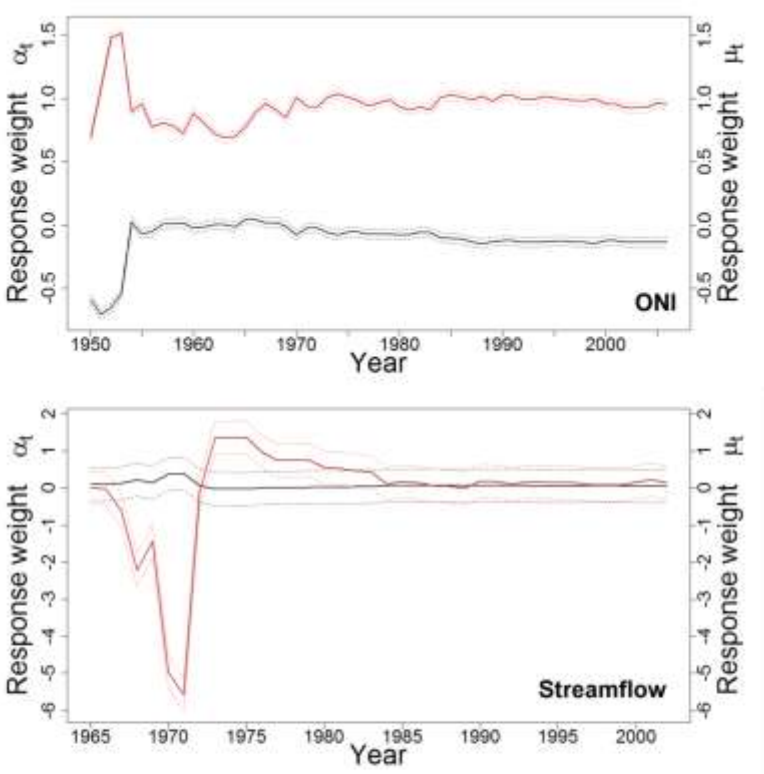

Fig. 9. Stochastic response function estimates, derived from a structural time series model, between the tree-ring chronology and streamflow from 1965 to 2002 (upper panel) and ONI from 1950 to 2006 (lower panel). Red lines show the estimated integrated random walk trend μ_t and the black line shows the response of $\alpha_{t.}$ Both relationships were time dependent until 1980, and become stable from 1980 to 2006. Dotter lines denote 95% confidence limits.

Discussion

Although the *P. copaifera* ring-width chronology generated in this study contains enough common information to be considered a reliable chronology for the period from 1910 to 2006 (EPS > 0.85) and shows a statistically significant relationship with the climate over the region (Fig. 6, Table 1), the ^{14}C results demonstrated a lack of annual tree growth periodicity in 3 of the trees composing the chronology (Fig. 7). The disagreement between the dendrochronological dates and the ^{14}C atmospheric signal of the tree rings of *P. copaifera* cannot possibly be attributed to incomplete removal of extraneous substances during chemical pretreatment. Our holocellulose extraction procedure is robust, and has proven to produce a perfect tree-ring/^{14}C crossdating match in subtropical tree species, when 71 consecutive tree rings were processed and measured (Santos et al. 2015). In addition, the targets produced here from the tree Pg025 were processed and ^{14}C-AMS measured together with another set of tropical wood samples independently validated by us, and that shows perfect annual frequency of tree-ring formation (Andreu-Hayles et al. 2015). It is possible that problematic anatomic features, such as vague rings, discontinuous rings, missing and false rings may be hindering the correct identification of tree-ring boundaries since these kinds of issues are very common in tropical species (Brienen and Zuidema 2005), and in particular, very difficult to identify in *P. copaifera*. However, we believe that this large offset in the ^{14}C dates is due to the presence of intra-annual parenchyma bands formation that lead to rings with sub-annual resolution, that in many cases are very difficult or even impossible to differentiate from annual rings. Therefore, *P. copaifera* trees may have produced one or more rings per year, without a constant frequency, as suggested before by Grauel (2004). The formation of sub-annual rings could be the response to strong intra-annual variability in growth during a given year. Thus, it would be impossible to anatomically differentiate annual rings from sub-annual rings in certain years in which the limiting factors (e.g streamflow in *P. copaifera*) vary very strongly. These results imply some important limitation to use the *P. copaifera* ring-width chronology for reconstructing the climate over the low Atrato River. Nevertheless, due its ubiquity and long time span further investigations and resources should be consider in order to develop a reliable chronology.

A reconstruction of the water levels of the Atrato river was generated from a tree-ring chronology based on 10 of the trees evaluated here (Herrera and del Valle 2011), in which the annual resolution was proven based on three ^{14}C measurements over the tree rings corresponding to 1994. McKenzie (1972), based on the periodic cambial wounding technique over 23 trees, also described the *P. copaifera's* tree-ring frequency formation as annual, whereas Giraldo and del Valle (2011) also provided evidence of the annual nature in *P. copaifera* tree rings by examining ^{14}C signature in a single ring of the recent period. Thus, particular ^{14}C analysis over the last years would probably lead to erroneous conclusions about the identification of annual tree rings over an entire chronology. This alerts about the danger of generating erroneous climate reconstructions in the tropics based on tree-ring chronologies without annual resolution, as seen in Herrera and del Valle (2011), if a proper independent validation of the annual nature of the tree rings is not performed.

Few studies in the tropics have proven the annual tree-ring formation by independent validations, rather most of them are based on anatomical descriptions and crossdating (Fichtler et al. 2003; Groenendijk et al. 2014; Trouet et al. 2001; Worbes and Junk 1989). Although obtaining multiple high-precision ^{14}C-AMS dates using ^{14}C is still expensive, it seems to be a good approach for the validation of the successful identification of annual tree rings in species with anatomical problems or species never used before in dendrochronological works (Andreu-Hayles et al. 2015; Santos et al. 2015). Measurements before and after the bomb-spike can be done in order to obtain a precise assessment of the annual tree-ring identification over the entire chronology, especially in certain species that show complex anatomical features that can potentially introduce dating uncertainties, as is the case of many tropical species. Besides the ^{14}C analyses, there are other independent validation procedures that can be considered such as periodic dendrometric measurements (Callado et al. 2013), periodic cambial wounding (Mariaux 1967), successive micro-sampling for evaluations of cambial activity throughout a given period (Braüning et al. 2008; Krepkowski et al. 2011), or counting rings in trees of a known age (Dünisch et al. 2003).

Despite the discrepancies between the dendrochronological dates and the ^{14}C dates, the climate signals detected in the tree-ring chronology seem to be plausible and not accidental, providing insights of how *P. copaifera* growth responds to climate. Here, we find that *P. copaifera* grows more producing wider rings during years with higher precipitation and streamflow, such as during La Niña years; and grows less forming narrower rings in drier conditions, such as during the El Niño phase of the ENSO. Grauel (2004) and Clark et al. (2003) reported that *P. copaifera* growth is highly variable, but diminished during the El Niño of 1997-1998 and increased for the La Niña period of 1999-2000. The authors reported this behavior in flooded stands as our study site, but also in more diverse and drained forests, supporting the climate-growth relationship described here. A major growth during the flooding season, only described for very few species, could be a combination of a successful adaptation strategy to flooded environments and a shallow root system (De Simone et al. 2003; Grauel 2004; López et al. 2014) that make *P. copaifera* trees extremely sensitive to dry seasons that may be driven the periodicity of the observed tree rings.

Although spurious significant correlations cannot be discarded as the cause for the detection of hydroclimate signals in the cativo chronology (Fig. 5 and Fig.6), they are unlikely to occur. other feasible explanations may be suggested. First, the agreement between the ^{14}C measurements from 2 trees used to generate the growth model and the ^{14}C curve NH-zone 2 (Hua et al. 2013) from 1980 onwards (Fig. 7) suggest a correct identification of annual tree rings during the last 26 years for these 2 ring width series. Nevertheless, as the bomb pulse curve becomes attenuated in this period, incorrect dendrochronological age assessments are harder to be detected when they have about 1 to 2 years offset (e.g. absolute certainty for the period will only be achieved by measuring every single ring). Thus, we hypothesize that during those most recent years, simultaneous correlations, or correlations with 1 to 2 year lags between the chronology and climate series, may have occurred. This small lagging in the series could still lead to significant correlations due to the capture of an average association.

Second, the comparison of the individual cumulative growth series with the age model shows that: (a) 6 of the 15 trees (blue lines in Fig. 8) differ significantly from the cumulative growth curves based on the ^{14}C analysis (note that 2 of 6 were analyzed by ^{14}C-AMS); (b) 9 of the 15 trees (gray lines in Fig. 8) may have a low amount of sub-annual tree rings, thus the cumulative effect may not so strongly affect the significance of the correlations (Fig. 8 and Fig. 9). We hypothesize that the climatic signals and their coherence with previous works (Clark et al. 2003; Grauel 2004) may be due to a low occurrence or absence of sub-annual tree rings in most of the series contributing to the mean chronology (i.e. at least 9 of the 15 trees analyzed), at least for the period 1975-2006, since their growth pattern did not differ from the mean growth/age trend estimated by the model (i.e. ring-width series within the confidence interval; Fig. 8) and is not different from the series that show annual tree rings for the recent years. *P. copaifera* trees may have different rates of sub-annual ring formation. The fact that most of the trees may be forming fewer sub-annual rings, specially over the recent period may be due to the age of the trees: older trees have a lower rates of intra-annual structure formation (Dünisch et al. 2003); stand/crown position: trees under suppressed growth conditions tend to form more intra-annual structures (Groenendijk et al. 2014); and/or physiological factors as root depth or less susceptibility to insect attacks (Copenheaver et al. 2006).

Third, from about 1980 onward higher correlations with streamflow, Chocó and ONI (Table 1) and stable relationships between the chronology and both streamflow and ONI (Fig. 9) support the hypothesis that the *P. copaifera* chronology is capturing a 'true' climatic signal for the most recent period. The instabilities found before 1980 indicate that most of the marked rings were not annual and the cumulative effect of that misidentification led to an unstable relationship between the chronology and the climate variables. Therefore, since the climate series cover the last 24 or 37 years, the climate signal found is likely to be the result of climate simultaneous correlations between hydroclimate variables and the cativo chronology that runs stable over that period (Fig. 6 and Fig. 9).

Conclusions

Our study shows that crossdating and climate signal detection are not sufficient to evaluate the annual nature of tree-ring formation in some species when there is high occurrence of intra-annual growth bands not anatomically distinguishable from annual rings. Multiple high-precision ^{14}C-AMS dates before and after the bomb spike in multiple individuals (Fig. 7), age models (Fig. 8) and assessing the stability in the growth-climate relationship (Fig. 9) are appropriate methods for evaluating annual growth periodicity in tree-ring series and thus, their suitability for reconstructing climate and/or for studying ecological relationships of the targeted species. Considering that the frequency of tree-ring formation may be distinct for the same species growing in different environments (Groenendijk et al. 2014; Pearson et al. 2011), it would be advisable to conduct similar studies targeting *P. copaifera* in different locations to gain more information about its tree-ring frequency formation. The wide range of results reported by different dendrochronological studies in relation to the ^{14}C analysis lead to the recommendation to conduct multiple ^{14}C measurements per tree (ideally on wood tissues belonging to the sharp ascending and descending portions of the ^{14}C bomb curve) and in more than one tree (when attempting to corroborate the annual nature of the tree-ring formation). We also recommend testing the stability of the climate signal recorded by the tree-ring chronologies before the development of climate reconstructions or other applications requiring high precision dating. Larger sampling replication and longer, reliable climatic records may also aid towards the generation of more reliable chronologies and climate reconstructions in tropical regions.

Aknowledgements

This research was partially supported by the Department of Forest Sciences of the Universidad Nacional de Colombia, by the KCCAMS facility, University of California, Irvine, and the Lamont-Doherty Earth Observatory Climate Center. The hydroclimatic data was provided by the Colombian Institute of Hydrology, Meteorology and Environmental Studies (IDEAM). We give special thanks to Caroline Leland and Javier Martin-Fernandez for their help. LAH was supported by the Marie Curie International Outgoing Fellowship PIOF-GA-2009-253277 grant within the FP7-PEOPLE-2009-IOF program.

References

Anchukaitis KJ, Evans MN (2010) Tropical cloud forest climate variability and the demise of the Monteverde golden toad. Proceedings of the National Academy of Sciences 107:5036-5040. doi: 10.1073/pnas.0908572107

Andreu-Hayles L et al. (2015) Perfect matching between the Southern Hemisphere 14C curve and dendrochronological dates from a Bolivian tropical tree species. Radiocarbon 57:In Press. doi: 10.2458/azu_rc.57.18192

Beverly RK et al. (2010) The Keck Carbon Cycle AMS Laboratory, University of California, Irvine: Status Report. Radiocarbon 52:301-309

Biondi F, Fessenden JE (1999) Radiocarbon analysis of Pinus lagunae tree rings; implications for tropical dendrochronology. Radiocarbon 41:241-250

Biondi F, Strachan SJ, Mensing S, Piovesan G (2007) Radiocarbon Analysis Confirms the Annual Nature of Sagebrush Growth Rings. Radiocarbon 49:1231-1240

Boninsegna JA et al. (2009) Dendroclimatological reconstructions in South America: A review. Palaeogeography, Palaeoclimatology, Palaeoecology 281:210-228

Braüning A, von Schnakenburg P, Volland-Voigt F, Peters T (2008) Seasonal growth dynamics and its climate forcing in a tropical mountain rain forest in southern Ecuador TRACE - Tree Rings in Archaelogy, Climatology and Ecology, vol. 6. Postdam, Erlangen, Germany, pp 27-30

Brienen RJW, Zuidema PA (2005) Relating tree growth to rainfall in Bolivian rain forests: a test for six species using tree ring analysis. Oecologia 146:1-12

Brienen RJW, Zuidema PA (2006) Lifetime growth patterns and ages of Bolivian rain forest trees obtained by tree ring analysis. Journal of Ecology 94:481-493

Bunn A et al. (2014) dplR: Dendrochronology Program Library in R. R package version 1.6.0

Bunn AG (2008) A dendrochronology program library in R (dplR). Dendrochronologia 26:115-124. doi: http://dx.doi.org/10.1016/j.dendro.2008.01.002

Bunn AG (2010) Statistical and visual crossdating in R using the dplR library. Dendrochronologia 28:251-258. doi: http://dx.doi.org/10.1016/j.dendro.2009.12.001

Callado CH, Roig FA, Tomazello-Filho M, Barros CF (2013) Cambial Growth Periodicity Studies of Shouth American Woody Species- A Review. IAWA Journal 34:213-230. doi: doi:10.1163/22941932-00000019

Clark DA, Piper SC, Keeling CD, Clark DB (2003) Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during

1984–2000. Proceedings of the National Academy of Sciences 100:5852-5857. doi: 10.1073/pnas.0935903100

Copenheaver CA, Pokorski EA, Currie JE, Abrams MD (2006) Causation of false ring formation in Pinus banksiana: A comparison of age, canopy class, climate and growth rate. Forest Ecology and Management 236:348-355. doi: http://dx.doi.org/10.1016/j.foreco.2006.09.020

De Simone O, Junk WJ, Schmidt W (2003) Central Amazon Floodplain Forests: Root Adaptations to Prolonged Flooding. Russian Journal of Plant Physiology 50:848-855. doi: 10.1023/B:RUPP.0000003285.70058.4c

Dünisch O, Ribeiro Montóia V, Bauch J (2003) Dendroecological investigations on Swietenia macrophylla King and Cedrela odorata L. (Meliaceae) in the central Amazon. Trees 17:244-250

Escobar JA (1987) Caracterización de tipos de cativales. B.Sc., Universidad Nacional de Colombia sede Medellín Medellín

Fichtler E, Clark DA, Worbes M (2003) Age and Long-term Growth of Trees in an Old-growth Tropical Rain Forest, Based on Analyses of Tree Rings and 14C. Biotropica 35:306-317. doi: 10.1646/03027

Fritts HC (1976) Tree ring and climate. Academic Press, London

Giraldo JA, del Valle JI (2011) Estudio del crecimiento de Prioria copaifera (Caesalpinaceae) mediante técnicas dendrocronológicas. Revista de Biología Tropical 59:1813-1831

González H, Gómez HF, Arteaga FJ (1991) Aspectos estructurales de un bosque de cativo en la región del bajo Atrato, Colombia. Revista Facultad Nacional de Agronomía 44:3-50

Grauel WT (2004) Ecology and management of wetland forests dominated by Prioria copaifera in Darien, Panama, University of Florida, Florida

Grissino-Mayer HD (2001) Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. TreeRing Research 57:205-221

Groenendijk P, Sass-Klaassen U, Bongers F, Zuidema PA (2014) Potential of tree-ring analysis in a wet tropical forest: A case study on 22 commercial tree species in Central Africa. Forest Ecology and Management 323:65-78. doi: http://dx.doi.org/10.1016/j.foreco.2014.03.037

Harvey AC, Shephard N (1993) Structural Time Series Models In: Maddala GS, Rao CR, Vinod HD (eds) Handbook of statistics. Elsevier Science Publishers pp 261-302

Herrera DA, del Valle JI (2011) Reconstrucción de los niveles del río Atrato con anillos de crecimiento de Prioria copaifera. Dyna 78:121-130

Holdridge LR (1978) Ecología basada en zonas de vida. Instituto Interamericano de Ciancias Agrícolas-IICA, Costa Rica

Hua Q (2009) Radiocarbon: A chronological tool for the recent past. Quaternary Geochronology 4:378-390. doi: http://dx.doi.org/10.1016/j.quageo.2009.03.006

Hua Q, Barbetti M, Rakowski AZ (2013) Atmospheric Radiocarbon for the Period 1950–2010. Radiocarbon 55

Junk WJ, Piedade MTF, Wittmann F, Schöngart J, Parolin P (2010) Amazonian flood plain forest: ecophysiology, biodiversity and sustainable management. SpringerVerlag, Berlin

Kalnay E et al. (1996) The NCEP/NCAR 40-Year Reanalysis Project. Bulletin of the American Meteorological Society 77:437-471. doi: 10.1175/1520-0477(1996)077<0437:tnyrp>2.0.co;2

Kaplan A, Cane MA, Kushnir Y, Clement AC, Blumenthal MB, Rajagopalan B (1998) Analyses of global sea surface temperature 1856–1991. J. Geophys. Res. 103:18567-18589

Krepkowski J, Bräuning A, Gebrekirstos A (2012) Growth dynamics and potential for cross-dating and multi-century climate reconstruction of Podocarpus falcatus in Ethiopia. Dendrochronologia 30:257-265. doi: http://dx.doi.org/10.1016/j.dendro.2012.01.001

Krepkowski J, Bräuning A, Gebrekirstos A, Strobl S (2011) Cambial growth dynamics and climatic control of different tree life forms in tropical mountain forest in Ethiopia. Trees 25:59-70. doi: 10.1007/s00468-010-0460-7

Londoño LF, González F (1993) Identificación de variables relacionadas con el crecimiento en diámetro del cativo (*Prioria copaifera*). Crónica Forestal y de Medio Ambiente 8:25-34

López J, del Valle JI, Giraldo JA (2014) Flood-promoted vessel formation in Prioria copaifera trees in the Darien Gap, Colombia. Tree Physiology 34:1079-1089. doi: 10.1093/treephys/tpu077

López L, Villalba R (2011) Climate influences on the radial growth of Centrolobium microchaete, a valuable timber species from the tropical dry forests in Bolivia. Biotropica 43:41-49

Lopez O, Kursar T (2007) Interannual variation in rainfall, drought stress and seedling mortality may mediate monodominance in tropical flooded forests. Oecologia 154:35-43. doi: 10.1007/s00442-007-0821-0

Mariaux A (1967) Les cernes dans le bois tropicaux africains, nature et périodicité. Revue Bois et Forê des Tropíques 114:23-37

McKenzie TA (1972) Observations on growth and a technique for estimating annual growth in Prioria copaifera. Turrialba 22:352-354

Naegler T, Levin I (2009) Observation-based global biospheric excess radiocarbon inventory 1963–2005. Journal of Geophysical Research: Atmospheres (1984-2012) 114. doi: 10.1029/2008jd011100

Pearson S, Hua Q, Allen K, Bowman DMJS (2011) Validating putatively cross-dated Callitris tree-ring chronologies using bomb-pulse radiocarbon analysis. Australian Journal of Botany 59:7-17. doi: http://dx.doi.org/10.1071/BT10164

Poveda G (2004) La hidroclimatología de Colombia: una síntesis desde la escala inter-decadal hasta la escala diurna Revista Academia Colombiana de Ciencias 28:201-222

Poveda G, Jaramillo A, Gil MM, Quiceno N, Mantilla RI (2001) Seasonality in ENSO-related precipitation, river discharges, soil moisture, and vegetation index in Colombia. Water Resources Research 37:2169-2178

Poveda G, Mesa OJ (1999) La corriente de chorro superficial del oeste ("Del Chocó") y otras dos corrientes de chorro en Colombia: climatología y variabilidad durante las fases del ENSO. Revista Academia Colombiana de Ciencias 23:517-528

Poveda G, Mesa OJ (2000) On the existence of Lloró (the rainiest locality on Earth): Enhanced ocean-land-atmosphere interaction by a low-level jet. Geophysical Research Letters 27:1675-1678. doi: 10.1029/1999gl006091

R Core Team (2013) R: A language and environment for statistical computing. . R Foundation for Statistical Computing Vienna, Austria

Ramírez JA, del Valle JI (2011) Paleoclima de La Guajira, Colombia; según los anillos de crecimiento de Capparis odoratissima (Capparidaceae). Revista de Biología Tropical 59:1389-1405

Rozendaal DM, Zuidema PA (2011) Dendroecology in the tropics: a review. Trees 25:3-16

Rueda OA, Poveda G (2006) Variabilidad espacial y temporal del chorro del "Chocó" y su efecto en la hidroclimatología de la región del Pacífico Colombiano. Meteorología Colombiana 10:132-145

Santos GM, Linares R, Lisi CS, Tomazello Filho M (2015) Annual growth rings in a sample of Paraná pine (Araucaria angustifolia): Toward improving the 14C calibration curve for the Southern Hemisphere. Quaternary Geochronology 25:96-103. doi: http://dx.doi.org/10.1016/j.quageo.2014.10.004

Santos GM, Moore RB, Southon JR, Griffin S, Hinger E, Zhang D (2007) AMS 14C Sample Preparation at the KCCAMS/UCI Facility: Status Report and Performance of Small Samples. Radiocarbon 49:255-269

Santos GM et al. (2010) Blank Assessment for Ultra-Small Radiocarbon Samples: Chemical Extraction and Separation Versus AMS. Radiocarbon 52:1322-1335

Schneider U, Becker A, Finger P, Meyer-Christoffer A, Rudolf B, Ziese M (2011) GPCC Full Data Reanalysis Version 6.0 at 0.5°: Monthly Land-Surface Precipitation from Rain-Gauges built on GTS-based and Historic data. Global Precipitation Climatology Centre (GPCC, http://gpcc.dwd.de/) at Deutscher Wetterdienst

Schöngart J, Piedade MTF, Ludwigshausen S, Horna V, Worbes M (2002) Phenology and stem-growth periodicity of tree species in Amazonian floodplain forests. Journal of Tropical Ecology 18:581-597

Schöngart J, Piedade MTF, Wittmann F, Junk WJ, Worbes M (2005) Wood growth patterns of Macrolobium acaciifolium (Benth.) Benth. (Fabaceae) in Amazonian black-water and white-water floodplain forests. Oecologia 145:454-461

Schweingruber FH (1996) Tree rings and environment: dendroecology. Paul Haupt AG Bern, Switzerland

Smith TM, Reynolds RW, Peterson TC, Lawrimore J (2008) Improvements to NOAA's Historical Merged Land–Ocean Surface Temperature Analysis (1880–2006). Journal of Climate 21:2283-2296. doi: 10.1175/2007jcli2100.1

Soliz-Gamboa C, Rozendaal DA, Ceccantini G, Angyalossy V, van der Borg K, Zuidema P (2011) Evaluating the annual nature of juvenile rings in Bolivian tropical rainforest trees. Trees 25:17-27. doi: 10.1007/s00468-010-0468-z

Stahle DW, Mushove PT, Cleaveland MK, Roig F, Haynes GA (1999) Management implications of annual growth rings in Pterocarpus angolensis from Zimbabwe. Forest Ecology and Management 124:217-229. doi: http://dx.doi.org/10.1016/S0378-1127(99)00075-4

Stokes MA, Smiley TL (1968) An introduction to tree-ring dating University of Chicago Press, Chicago

Stuiver M, Polach HA (1977) Reporting of C-14 data - Discussion. Radiocarbon 19:355-363

Trouet V, Esper J, Beeckman H (2010) Climate/growth relationships of Brachystegia spiciformis from the miombo woodland in south central Africa. Dendrochronologia 28:161-171

Trouet V, Haneca K, Coppin P, Beeckman H (2001) Tree ring analysis of Brachystegia spiciformis and Isoberlinia tomentosa: Evaluation of the enso-signal in the miombo woodland of eastern Africa. IAWA JOURNAL 22:385-399

Villalba R et al. (2011) Dendroclimatology from Regional to Continental Scales: Understanding Regional Processes to Reconstruct Large-Scale Climatic Variations Across theWestern Americas. Dendroclimatology, vol 11, Hughes, Malcolm K. and Swetnam, Thomas W. and Diaz, Henry F. edn. Springer Netherlands, Netherlands, pp 175-227

Visser H, Büntgen U, D'Arrigo R, Petersen AC (2010) Detecting instabilities in tree-ring proxy calibration. Clim. Past 6:367-377. doi: 10.5194/cp-6-367-2010

Visser H, Molenaar J (1988) Kalman Filter Analysis in Dendroclimatology. Biometrics 44:929-940

Wigley TML, Briffa KR, Jones PD (1984) On the Average Value of Correlated Time Series, with Applications in Dendroclimatology and Hydrometeorology. Journal of Climate and Applied Meteorology 23:201-213. doi: 10.1175/1520-0450(1984)023<0201:otavoc>2.0.co;2

Wils TG, Robertson I, Eshetu Z, Touchan R, Sass-Klaassen U, Koprowski M (2011) Crossdating Juniperus procera from North Gondar, Ethiopia. Trees 25:71-82. doi: 10.1007/s00468-010-0475-0

Wils TH, Gm. et al. (2010) Dendrochronology in the dry tropics: the Ethiopian case. Trees 25:10

Wils THG, Robertson I, Eshetu Z, Sass-Klaassen UGW, Koprowski M (2009) Periodicity of growth rings in Juniperus procera from Ethiopia inferred from crossdating and radiocarbon dating. Dendrochronologia 27:45-58. doi: http://dx.doi.org/10.1016/j.dendro.2008.08.002

Worbes M (1999) Annual growth rings, rainfall-dependent growth and long-term growth patterns of tropical trees from the Caparo Forest Reserve in Venezuela. Journal of Ecology 87:391-403

Worbes M (2002) One hundred years of tree-ring research in the tropics: a brief history and an outlook to future challenges. Dendrochronologia 20:217-231

Worbes M, Junk WJ (1989) Dating tropical trees by means of 14C from bomb test. Ecology 70:503-507