

Climatic signal in growth-rings of *Copaifera lucens*: An endemic species of a Brazilian Atlantic forest hotspot, southeastern Brazil



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ABSTRACT

In this study, we present the first tree-ring chronology for the tropical tree species *Copaifera lucens* and its climatic signal in southeastern Brazil. Tree-ring width series were compared with local climate indices using a drought index (Standardized Precipitation Evapotranspiration Index —SPEI), in monthly, bi-monthly and four-monthly scales. We also calculated negative pointer years over the time-span of the tree-ring width. The radial growth of *C. lucens* showed a positive correlation with the SPEI of the current summer and autumn in all the three analyzed time scales, while the negative pointer years matched with drier years. The species was highly sensitive to very low summer precipitation, which may lead to a 49% reduction in growth. We conclude that the long-living *C. lucens* has a great potential for dendrochronological studies as it shows a marked climatic signal. Our study also reinforces the importance of rainfall in regulating radial growth in tropical forests and sheds light on the local climate influence on tree growth in recent decades.

1. Introduction

Forests play multiple roles related to ecological systems, species, economy, culture, aesthetics, human health, among others (Hassan et al., 2005). In addition, forests influence global climate through physical, chemical, and biological processes that affect the hydrologic cycle and atmospheric composition (Bonan, 2008; Shukla et al., 1990; Wagner et al., 2016). On the other hand, the performance of forests is influenced by climate conditions (Fritts, 1976; Schweingruber, 1988; Speer, 2010), making up a complex feedback loop between climate and forests. Considering the evidence on current environmental and climatic changes (IPCC, 2014), as well the importance of such a feedback loop, it is relevant to investigate how plants react to changes in climate conditions (Bazzaz, 1996).

In this sense, tree-ring analysis provides accurate information on the magnitude and frequency of variations in past climate patterns (Cook, 1987; Fritts, 1976; Jacoby, 1989). In favorable climatic years to plant growth, the tree rings are wider, whereas in years subject to climatic

stress, such as water excess or water deficit, or even extreme temperatures, produce narrow rings (Schongart et al., 2004; Speer, 2010; Stokes and Smiley, 1996). Due to this, dendrochronology has been used as a proxy to reconstruct the climatic past and to access information about the plants' responses forward over time (Cherubini et al., 2003), e.g., growth rates, wood production, rotation times and to estimate changes in the C-stocks of above-ground wood biomass (Fichtler, 2015; Jacoby, 1989; Schöngart et al., 2011).

Many dendrochronological studies have contributed to the understanding of climate changes in tropical ecosystems. Brienen et al. (2010) analyzed the tree-rings of *Mimosa acantholoba* (Willd.) Poir in dry forests of southern Mexico and Central America, finding a negative effect of El Niño years on tree growth by as much as 37%. Callado and Guimarães (2010), studying *Schizolobium parahyba* (Vell.) S.F. Blake in Atlantic Forest also noted that the rings were narrower in years under El Niño influence and wider in years under La Niña influence. Dünisch (2005) points out that in his study 57% of variability of the annual increment of *Cedrela fissilis* Vell. in Amazon was due to temperature and

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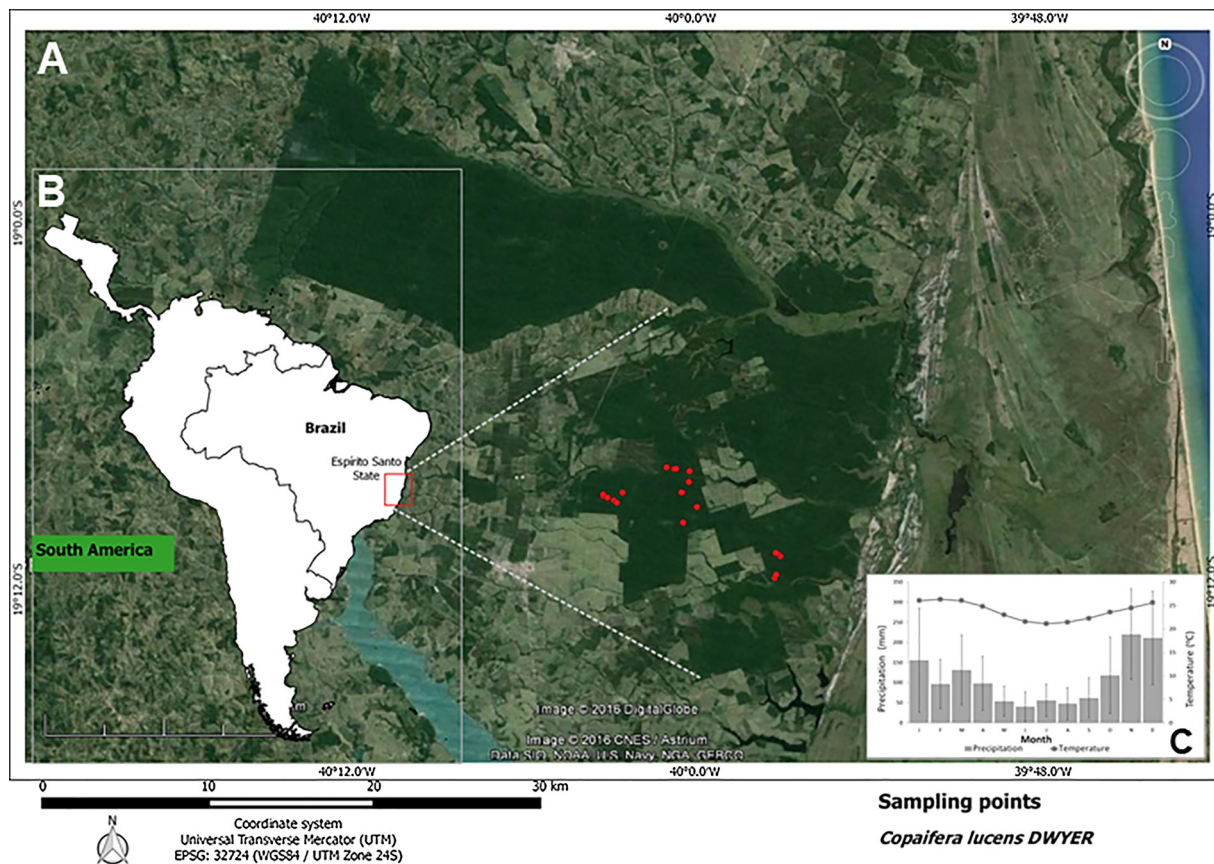


Fig. 1. A – Map of the study area in the state of Espírito Santo, in southeastern Brazil. Red points indicate the georeferenced locations of the sampled trees. B – Study area location in South America and Brazil. C – Climatic diagram of the study area. Bars show standard deviation. Data provided by Instituto Capixaba de Pesquisa, Assistência Técnica e Extensão Rural (INCAPER) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

precipitation related to El Niño. Schongart et al. (2004) present a more than 200-year long chronology of *Piranhea trifoliata* (Baill.) in the Amazon and showed a general trend of increase of El Niño events from the 19th to the 20th. These examples highlight the importance of dendrochronology to understand the effects of climate change on forest growth and carbon stocks in several ecosystems.

Tropical forests store between 25% and 54% of the terrestrial biosphere carbon and 33% of the primary terrestrial net production (Bonan, 2008; Liu et al., 2015). However, these stocks are at risk due to anthropogenic deforestation and possibility of release of carbon driven by climate change (Cramer et al., 2004). The Brazilian Atlantic Forest is considered one of the richest hotspots in biodiversity (Myers et al., 2000), containing more than 19,000 plant species (Forzza et al., 2012). However, deforestation has already reached 88.27% of its original area (Ribeiro et al., 2009) making this ecosystem among the most vulnerable to climate changes (Bellard et al., 2014). Despite the great diversity, dendroclimatological studies are still scarce in the Atlantic forest.

The “Tabuleiros” Atlantic Forest (TAF), located in southeastern Brazil, presents a floristic mixture of Amazonian and Atlantic elements (Garay et al., 2003; Jesus and Rolim, 2005; Peixoto and Gentry, 1990; Rizzini, 1963; Siqueira, 1994; Veloso, 1991) and is considered to have the highest trees species density per hectare in the globe (Thomas et al., 2008). Within a broader vegetation scheme, TAF is within the “Lowland Dense Ombrophilous Forest” and the “Lowland Semideciduous Forest” (IBGE, 2012; Veloso, 1991). The contribution of organic material to the soil is another evidence of the seasonality in this forest, which shows a temporal rhythm modulated essentially by precipitation (Louzada et al., 1997). Total litter fall of many plant species shows irregularity in years with climatic anomalies, triggering changes in the community patterns

(Engel, 2001).

The wood of *Copaifera* L. (Leguminosae) is characterized by intercellular canals (secretory canals), which are distributed in concentric bands along the marginal axial parenchyma that delimits the growth rings (Alencar and da, 1982; Barbosa, 1982; Grandis et al., 2010; Martins-da-Silva et al., 2008; Metcalfe and Chalk, 1950). Yet, application of dendrochronological techniques in these species may be challenged by the presence of both false rings and confluent rings, as it was reported for *Copaifera multijuga* Hayne and *Copaifera langsdorffii* Desf. (Medeiros and da, 2016; Melo-Júnior et al., 2011). *Copaifera lucens* DWYER is an endemic species that occurs in northeastern and southeastern Brazil (Costa, 2017). In *C. lucens*, the main marker of the growth rings is also the axial marginal parenchyma associated with the secretory canals (Barbosa, 1982).

A first step in predicting forest resistance and resilience to climate change is to know how it performed in relation to past climatic conditions. To investigate this issue by dendrochronological methods, it is necessary to identify which species are sensitive to the climate to the point of triggering annual growth rings. In this context, our goal was to explore the dendrochronological potential and to assess climate influence on radial growth in *C. lucens*, the endemic species forming growth rings in seasonal tropical lowland Atlantic Forest. Since the markedly seasonal rainfall regime prevailing over its geographic range is deemed to play a major role in controlling growth rhythm, we hypothesize that growth rings of *C. lucens* are formed on an annual basis. Likewise, we expect to find a common signal among ring-width series of trees in a site, as well as a positive association between ring width and water availability.

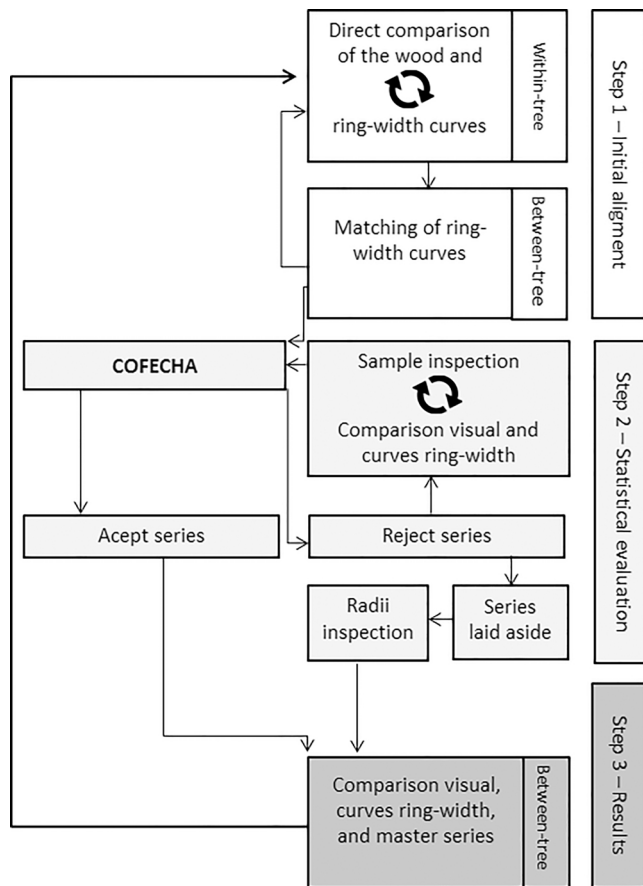


Fig. 2. Scheme of the steps followed for crossdating. Adapted from Wils et al. (2011).

2. Material and methods

2.1. Study area and species

The study was carried out in the Reserva Natural da Vale, an area of 23,000 ha covered by a well-preserved tropical seasonal forest called “Tabuleiros” Atlantic Forest. It is located in the state of Espírito Santo, in the southeastern region of Brazil (19°S - 19°14'S, 39°12'W - 40°W), between 30 and 80 m a.s.l., approximately 30 km off the coast of the Atlantic Ocean (Fig. 1).

The climate in the area is classified as a seasonal tropical with a dry season (Koeppen, 1948), and has an average annual precipitation and temperature of 1230 mm and 23.8°C. The monthly precipitation averages of the warmer and wetter season vary between 130 to approximately 200 mm from October to April during which 72% of precipitation occurs (Rolim et al., 2016). Precipitation during the drier and cooler season does not exceed 25% of the totals annual, being below 60 mm from April to September (Víncens et al., 2003). The average temperature ranges between 19.7°C in July to 28°C in February (Fig. 1C). Severe droughts are related to strong “El Niño-Southern Oscillation” (ENSO) events (Rolim et al., 2016). Evapotranspiration is an important climate component in this region, attaining in average 1246 mm per year, with maximum values in summer and frequently exceeding precipitation in winter (Víncens et al., 2003).

Soils in the sampling area are predominantly yellow podzolic (yellow, tertiary argisol), dystrophic, with a drastic difference in grain size according to depth, presenting low fertility and low cation-exchange capacity (Garay and Silva, 1995; Louzada et al., 1997). Mull humus is present ($\sim 3.9 \text{ t} / \text{ha}^{-1}$), with rapid decomposition of organic inputs (~ 9 months), being the main soil nutrient reservoir (Garay and

Silva, 1995; Louzada et al., 1997).

Data cataloged from the herbarium material of the Reserva Natural da Vale shows that *C. lucens* is semideciduous (losing $\sim 80\%$ of the leaves in winter), flowering from February to June and fruiting in May (immature fruits) and June. Species of this genus are large and slow-growing trees, ranging from 25 to 40 m in height, found in late secondary and climax forests (Carvalho, 2003; Lorenzi, 2002).

2.2. Sample collection, preparation and tree-ring analysis

For tree rings analysis, we selected 20 trees without external evidence of trunk and crown injuries distributed in a mature stand (Fig. 1). Mean trunk diameter at breast height in sampled trees was 53 cm (20–85 cm) and mean height 29 m (24–34 m). All individuals were georeferenced. For each tree, we collected up to three transversal wood cores (radii) at breast height, using a 5-mm diameter increment borer. We treated the injuries inflicted on sampled trees with a mix of 15 g of copper sulfate and 15 g of whitewash dissolved in 2.5 l of water. Wood cores were air-dried and then glued to wooden holders. After that, cross-sections were polished with sandpaper, with progressively finer grades, from 80 to 600 grits, until the anatomical characteristics of the ring boundaries were clearly identifiable.

The obtained cross-sections were visually examined under a stereomicroscope (Zeiss MZ8, $\times 10$ magnification) and the growth-layers boundaries were identified and marked. Beside growth layers, wood anomalies were considered as possible time markers (Wils et al., 2011, 2009), such as deformed or colored filled cells (probably with oil-resin), false or indistinct rings, vessel distribution and fiber wall thickness. Wood cross-sections were then scanned with a high resolution at 1200–2400 dpi (Epson Perfection V750 PRO) with a reference scale, and the tree-ring widths measured using the Image Pro Plus software, version 4.5.0.29 (Media Cybernetics, 2001).

We took some images (camera Canon DS126311) to macroscopically characterize the main difficulties in dating *C. lucens* growth ring.

2.3. Crossdating and chronology building

Crossdating cores proved to be very difficult, especially in the inner part of the core segments showing narrower growth layers. Thus, only the last ~ 50 growth rings of each tree were analyzed, taking into account that the minimum time-span indicated for crossdating is around 30–50 years (Briffa and Jones et al., 1990; Pilcher, 1990; Stahle et al., 1999), and because the local meteorological series available to explore climatic signals were recent (see below).

Crossdating quality was checked with the software COFECHA (Holmes, 1986, Holmes, 1983), following a stepwise process (Fig. 2). First of all, we crossdated series within trees with the software COFECHA. Then, after the crossdating was satisfactorily performed within-trees, mean tree-ring widths series for each tree were obtained through a bi-weighted robust mean function, in ARSTAN software (Cook, 1985; Cook and Holmes et al., 1996). With the average series of each tree, we checked the crossdating among trees in COFECHA again. Two of the trees had high correlation and were then compared with the remnant mean tree series and testing also with the individual cores of the remnant trees. If changes were feasible according to the re-inspection of wood-anatomical features, dating adjustments were made and the series aggregated in the master chronology subset, given that its inclusion did not impair the master's overall intercorrelation. Higher correlations were established with the best cores of each tree (whose rings are well defined and easily dated) than with the mean radii of the trees. The process finished once no more inclusion of tree cores series was possible due to poor visibility of ring boundaries in some samples. Therefore, 14 trees composed the master chronology, being two composed by mean series and 12 by one core per tree.

After the crossdating process, ring-width series were standardized to

filter non-climate-related growth variations. For each tree, we fitted a Cubic Smoothed Spline Function (50% variance cutoff in 21 years segment length) and computed ratios between observed and predicted values, obtaining indexed ring-width (RWI) series that were combined in a Standard site chronology (STD) through a bi-weighted robust mean function. Therefore, the autocorrelation of RWI series was filtered by autoregressive modeling and the resulting series combined in a Residual site chronology (RES chronology) using a bi-weighted robust mean function (Cook, 1985). The following statistics were used to describe the resulting chronologies: average and standard deviation (SD) of tree-ring widths, mean sensitivity index (MSI), mean autocorrelation (AC), mean intercorrelation (rint), mean correlation between series (\bar{r}) and mean expressed population signal (EPS) (Fritts, 1976; Speer, 2010; Wigley et al., 1984). These calculations were performed on ARSTAN software (except rint, calculated on COFECHA).

2.4. Detection of dendroclimatic signals

To explore radial growth responses to climatic conditions, we considered monthly total precipitation and mean temperature data recorded in a nearby meteorological station, 10 km away from the study site, carried by the Instituto Capixaba de Pesquisa, Assistência Técnica e Extensão Rural (INCAPER). The monthly meteorological series covers the period from 1976 to 2012, with few data gaps (12 for precipitation; 16 for temperature) that were filled with the respective month average (Fig. 3).

Based on these, we estimated the Standardized Precipitation Evapotranspiration Index – SPEI (Fig. 3). This is a drought index, sensitive to global warming and based on a simple climatic water balance that takes into account the evapotranspiration. SPEI values close to zero indicate a normal monthly water balance for a given timescale (monthly or seasonal basis, for instance), while negative (or positive) values indicate drier (or wetter) than expected conditions for that timescale (Vicente-Serrano et al., 2010).

Climatic data were analyzed according to the growing season in order to determine the SPEI time scales. Precipitation below 60 mm was considered as a dry month, because this precipitation threshold may affect the growth of tropical trees (Worbes, 1995). Most years had drought events (< 60 mm of precipitation) that range from one (62%) to two months (18%) during the growing season. Four consecutive months of drought in one growing season is a rare event in the analyzed series (only one year), whereas there were years with no dry months during the growing season (18% of years). In this way, we tested monthly SPEI series, calculated in monthly (SPEI1), bi-monthly (SPEI2) and four-monthly (SPEI4) scales.

Afterward, we used Correlation Function Analysis (Blasing et al. 1984) to test the existence of dendroclimatic signals in *C. lucens* by comparing the RES chronology to monthly SPEI series, calculated in monthly (SPEI1), bi-monthly (SPEI2) and four-monthly (SPEI4) scales. We considered possible radial growth responses to climatic conditions through the previous and current growth year by correlating the RES chronology to SPEI series from October (spring) of the previous growth year to April (autumn) of the current growth year. The statistical significance of the correlation coefficients was addressed on a 95% confidence interval obtained by bootstrap resampling (Biondi and Waikul, 2004). SPEI estimates and Correlation Function Analyses were performed on R program (R Studio Team, 2016), respectively in packages SPEI (Beguería and Vicente-Serrano, 2017) and bootRes (Zang and Biondi, 2013).

Pearson's correlations were calculated to verify the agreement between SPEI1 (most frequent event) and RES chronology. To verify the match between RWI and SPEI1 over time-span, negative pointer years were highlighted. Pointer years were considered to occur when RWI was at least 25% below the average of the previous four years (Oliveira et al., 2016).

3. Results and discussion

3.1. Tree-ring characteristics

The species has an eccentric growth that makes crossdating difficult, with many false and wedging rings, especially near the pit, while the recent rings are better marked (Fig. 4). These characteristics are frequent in the genus, being observed up to seven false rings in a year in *C. langsdorffii* (Medeiros, 2016; Melo-Júnior et al., 2011).

The average annual tree-ring widths ranged from 1.54 to 3.44 mm yr^{-1} with an average value of 2.25 mm yr^{-1} (Table 1). Costa et al. (2015) found in *C. langsdorffii* an annual mean tree-ring widths of 4.7 mm yr^{-1} , but they carried out the study in a young experimental plantation (30 years) under full sunlight conditions, which justifies the greater growth rate.

Previous studies describing different ecological aspects of the genus *Copaifera* mentioned the individuals could live up to an age of ~ 400 years (Araújo-Júnior et al., 2005; Veiga-Junior and Pinto, 2002). Based on the total number of tree-rings identified (without crossdating), we estimated that the sampled trees are between 90 and 200 years old (average = 134, DP = ± 34). We carried out our study in the best-preserved area of the *C. lucens* distribution, where the oldest trees of this species are probably found. According to Brienen et al. (2016), tropical tree species rarely attain ~ 500 years, with a typical average age being about 200 years. Since many species of *Copaifera* are considered long-lived climax species, ~ 200 years old is a feasible lifespan for this species.

3.2. Crossdating and chronology building

We crossdated the last 47 years of 20 trees, with six trees being poorly correlated with the master chronology. We used 70% of the trees (14 out of 20) to build the chronology and the mean correlation within trees was $\text{rint} = 0.52$ (Table 1). Beside this, we could use only the internal mean of two of these trees, and for 12 of them we had sufficiently high correlations with the master chronology using only one core per tree (Fig. 5). Brienen and Zuidema (2005) also rejected a rather high percentage of series to manage quality control in a study carried out in the Bolivian rainforest. We expected to enhance the chronology variance related to changes in climatic conditions by selecting the best radii correlations and sensitivity.

The mean correlation between trees was $\text{rint} = 0.45$. Grissino-Mayer (2001) suggested a threshold for inter-series correlations above $\text{rint} = 0.50$, but this implies considerations such as species, geographic location, and regional climate. In the case of lowland tropical forests, trees show less climatic sensitivity when compared with boreal and temperate forests (Payette and Filion, 2010; Perone et al., 2016; Schweingruber, 1988). Therefore, the inter-series correlation found in this study may be enough to emphasize the synchronism between trees of the same site. MSI above 0.40 also highlights the climate sensitivity (Grissino-Mayer, 2001). Similar values to correlation ($r = 0.49$) and MSI (0.47) was found to *C. langsdorffii* in the same site (Costa et al. 2015), which may represent the dendrochronological characteristic of the genus in this region. A MSI value of 0.47 in our study (Table 1) shows high sensitivity and high-frequency variability, which greatly increases the difficulty in dating because of the frequency of micro rings next to very wide rings (Pumijunnong et al., 1995; Speer, 2010). The fact that both wide and narrow ring matched between trees underpin the climatic control on radial growth for *C. lucens*, although non-climatic factors cannot be discarded given that we also observed sequences of wide rings, which are likely related to changes in stand competition levels (Fritts, 1976). The numeric parameters for the STD and RES individual series chronologies were similar, except for autocorrelation, which was removed successfully in the RES chronology (Table 1).

After standardization, the average correlation coefficient between

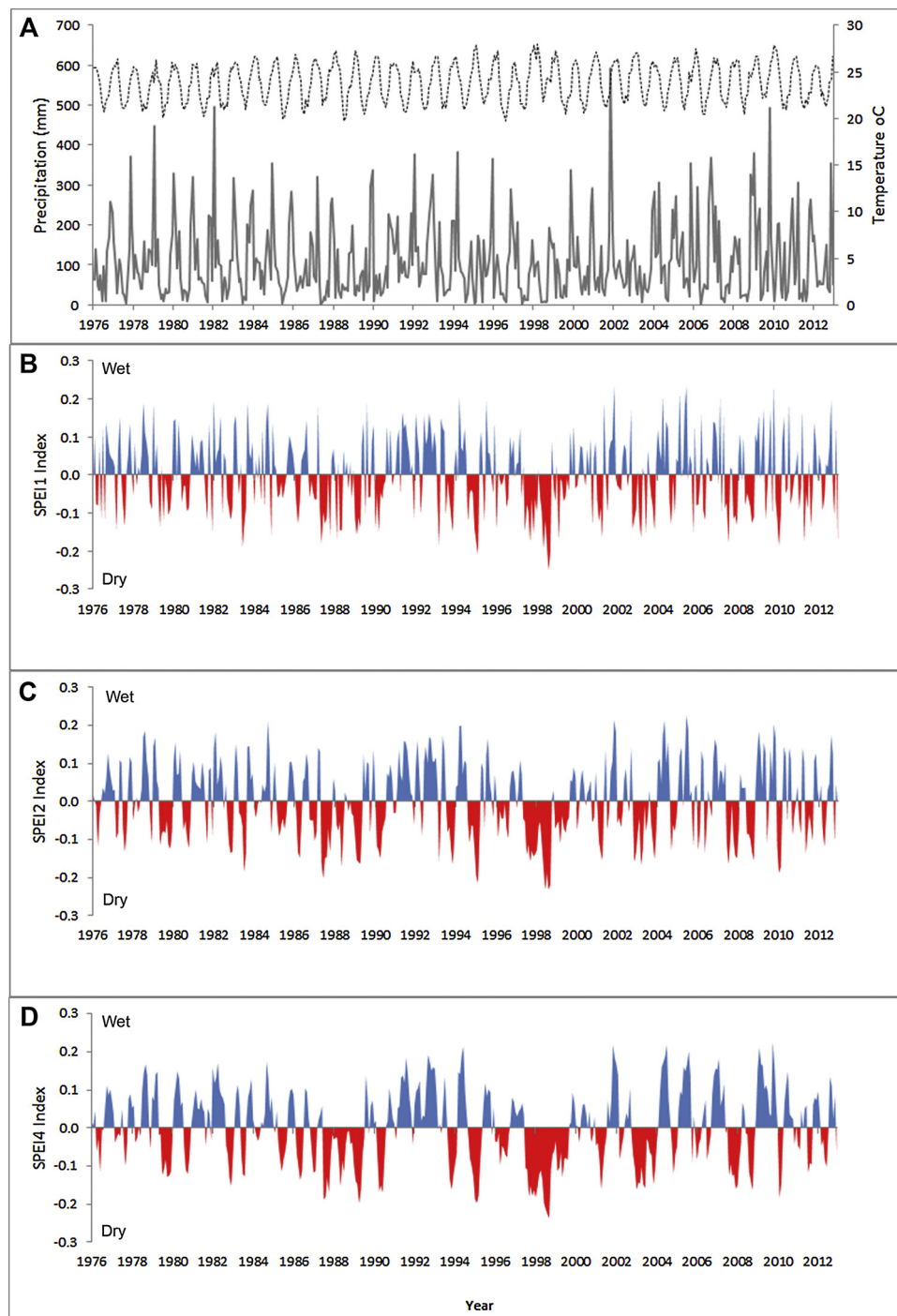


Fig. 3. A – Monthly data for temperature (dashed line) and precipitation (full line) (1976–2012). B – Estimated monthly data for the Standardized Precipitation Evapotranspiration Index (SPEI) (1976–2012); C – bi-monthly SPEI and D – four-monthly SPEI.

trees and the average values for the classical parameters for the RES chronology were $r_{bar} = 0.31$, $MSI = 0.28$ and $EPS = 0.83$ (Table 1). These values varied across the tree's time span (Fig. 5). The comparison between different periods allowed us to identify the best correlation related to growth limitation due to climatic factors as opposed to site factors (Fritts, 1976). Previous correlation values found in tropical environments between trees in tropical forests ranges between 0.19 and 0.38 (Oliveira et al., 2010; Pumijumnong et al., 1995); but Stahle (1999) found values of 0.49 and 0.56 for *Pterocarpus angolensis* DC. growing in seasonal dry forests in Africa and Heinrich and Banks (2005) showed intercorrelation of 0.45 for *Toona ciliata* M. Roemer in Australia. These values show strong evidence that there are common

factors (regional climate) acting on tree growth. By comparison, the r_{bar} value we found in this study evidences a moderate growth synchronism among trees.

The mean MSI was approximated from that reported in studies carried out in tropical forests in Australia, Asia and South America (Chowdhury et al., 2016; Heinrich and Banks, 2005; Reis-Ávila and Oliveira, 2017). In general, the correlation value we found is considered moderate. On the other hand, Taynik et al. (2016) found MSI of 0.32 at the upper treeline sites in the Russian mountains. Species in their distribution range, especially in treelines, are theoretically the most sensitive to climate (Fritts, 1976). Considering the complexity of tropical forest (e.g., wood anatomy features, community diversity and

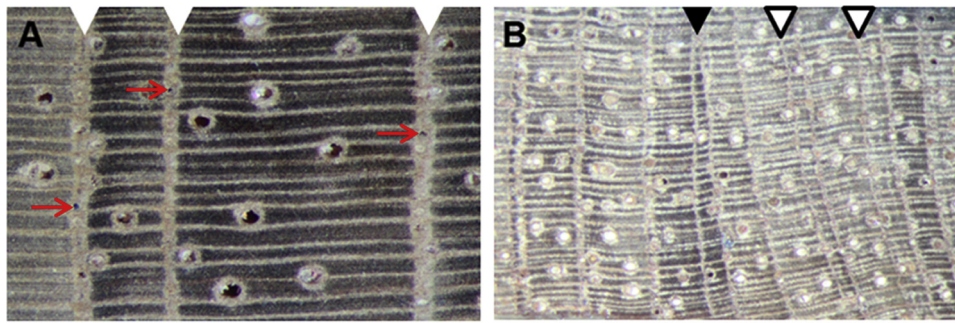


Fig. 4. Wood cross section of *Copaifera lucens*. A – Well-marked annual rings delimited by axial marginal parenchyma (white arrows heads) associated with secretory canals (thin red arrows). B – wedging rings (black arrow head) and false rings (arrow heads filled white). Magnification: A = 1.6 × and B = 1.0 ×.

Table 1

Statistical characteristics of standard ring-width index chronology of *Copaifera lucens* from Tabuleiros Atlantic Forest. STD = standard chronology; RES = residual chronology.

Parameter	Values
Time crossdating	1966-2012 (47 years)
Mean length of series (year)	35 years (Min = 23; Max = 0.47; SD = 7)
Trees/cores dated/cores crossdated	20/50/36
Trees/cores master chronology	14/16
Individual series statistics	
Mean tree ring width (mm)	2.25 (Min = 1.54; Max = 3.44; SD = ± 1.06 mm)
Mean sensitivity index (MSI)	0.47 (Min = 0.28; Max = 0.58; SD = ± 0.11)
Intercorrelation within tree-series (rint)	0.52 (Min = 0.33; Max = 0.77; SD = ± 0.19)
Intercorrelation between tree-series (rint)	0.45 (Min = 0.36; Max = 0.56; SD = ± 0.05)
Standardized chronology statistic	
STD mean correlation between series (rbar)	0.35 (Min = 0.01; Max = 0.75; SD = ± 0.16)
RES mean correlation between series (rbar)	0.31 (Min = -0.04; Max = 0.70; SD = ± 0.17)
Standard error (SE) STD/RES	0.018 / 0.018
Mean expressed population signal STD/RES	0.85 / 0.83
Mean sensitivity index STD/RES	0.30 / 0.28
Second-order autocorrelation STD/RES	0.08 (SD = ± 0.13) / -0.02 (SD = ± 0.05)

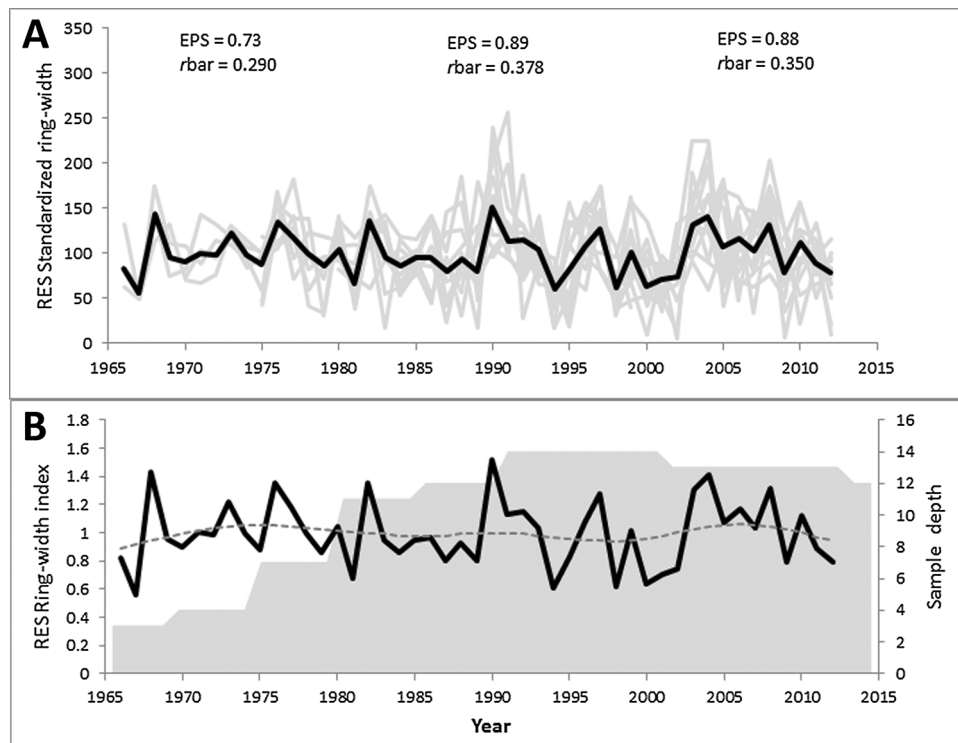


Fig. 5. A - Individual ring width series of *Copaifera lucens* (gray lines) and their mean curve (black line) from “Tabuleiros” Atlantic Forest in Brazil. B - RES chronology (black line) of *C. lucens* and 21 years smoothing curve (dotted line). The area in light gray shows sample depth over the analysis period.

competition) our results for MSI represent a relevant sensitivity.

The mean EPS value for RES chronology was slightly below the threshold of 0.85 suggested by Wigley et al. (1984), whereas that EPS threshold was overcome (~ 0.88) for most of the period considered to assess growth-response to climatic conditions (Fig 5). Sample size affects the EPS value (Briffa and Jones et al., 1990; Cook and Kairiukstis, 1990; Fritts, 1976; Mérian et al., 2013; Speer, 2010; Wigley et al., 1984) and, for this reason, this parameter has been widely used as an indicator of sample adequacy (e.g., Brienen et al., 2010; Heinrich and Banks, 2005; Venegas-González et al., 2016). This threshold has been the subject of new discussions among dendrochronologists (Briffa and Jones et al., 1990; Buras, 2017; Mérian et al., 2013). For Briffa and Jones et al., 1990, no specific EPS value can determine whether the chronology is suitable for dendroclimatic analysis, while Buras (2017) suggested that the threshold presented by Wigley et al. (1984) actually refers to the subsample signal strength rather than the total sample size. In this regard, Campelo et al. (2007) used the subsample signal strength to establish the reliable estimate of the mean chronology, since in their study the sample depth declines in the early portions of chronology, then subsample becomes important.

3.3. Growth-response to climatic conditions

Our study showed a strong influence of the climatic regional conditions on the radial growth of *C. lucens* during the late rainy season, which extends from mid-summer (February) to early autumn (April) (Fig. 6). The correlation coefficient between the RES chronology and the SPEI1 showed high positive values for February of the current year ($r = 0.66$, Fig. 6 A), while SPEI2 for February ($r = 0.49$) and March ($r = 0.58$, Fig. 6 B), and SPEI4 for March ($r = 0.53$) and April ($r = 0.51$, Fig. 6 C). These results evidence that drought in the middle of summer (SPEI1) reduces significantly the wood production of *C. lucens*. Previous studies in tropical forests showed significant and positive correlation coefficients for the rainy season, with values ranging from 0.28 to 0.66 (Brienen and Zuidema, 2005; Chowdhury et al., 2016; Worbes, 1999). Chowdhury et al. (2016) show that the annual and monsoon precipitation mainly influence the tree growth of *Heritiera fomes* Buch.-Ham and it can be applied as an indicator for monsoon precipitation variations in Bangladesh. Strong positive and significant ($r = 0.40$) correlation with the rainy season (November to June) was also found for *Bertholletia excelsa* Bonpl. growing in a seasonal site in the Amazon (Schöngart et al., 2015). In southeastern Atlantic Forest, recent dendrochronological studies corroborated the positive association between precipitation and tree growth (Brandes et al., 2011; Latorraca et al., 2015; Souza et al., 2016), underpinning the applicability of dendrochronology in tropical regions. Our study adds to this evidence about the dendrochronological potential of tropical species and encourages that many other species to be tested. Besides the crossdating, the strong climatic signal present in the rings of *C. lucens* also supports the hypothesis of the annual nature of the growth rings (crossdating $r = 0.31$; SPEI1 $r = 0.66$ to SPEI4 $r = 0.51$).

The growing season in the TAF is presumed to extend from October to December (early growing season) and from January to April (late growing season). Most of the studies in tropical forests show the influence of rainfall in the early rainy season (Boninsegna et al., 2009; Brienen and Zuidema, 2005; Pumijumnonng et al., 1995; Worbes, 1999). Worbes (1999) considers that the cambial activity in the tropics is high during the rainy season and decreases near the end of the rainy season or immediately after the beginning of the dry season. In the case of *C. lucens*, we observed that February is the drier month in the rainy season (Fig. 1C). Moreover, flowering starts in February for this species (Reserva Natural da Vale, unpublished data), being this an activity that demands high energetic investment (Evert, 2014). In this sense, an explanation of the importance of rainfall in the middle of summer (late season) is because it matches with the initial period of flowering in *C. lucens*, which can express a tradeoff between flowering and radial

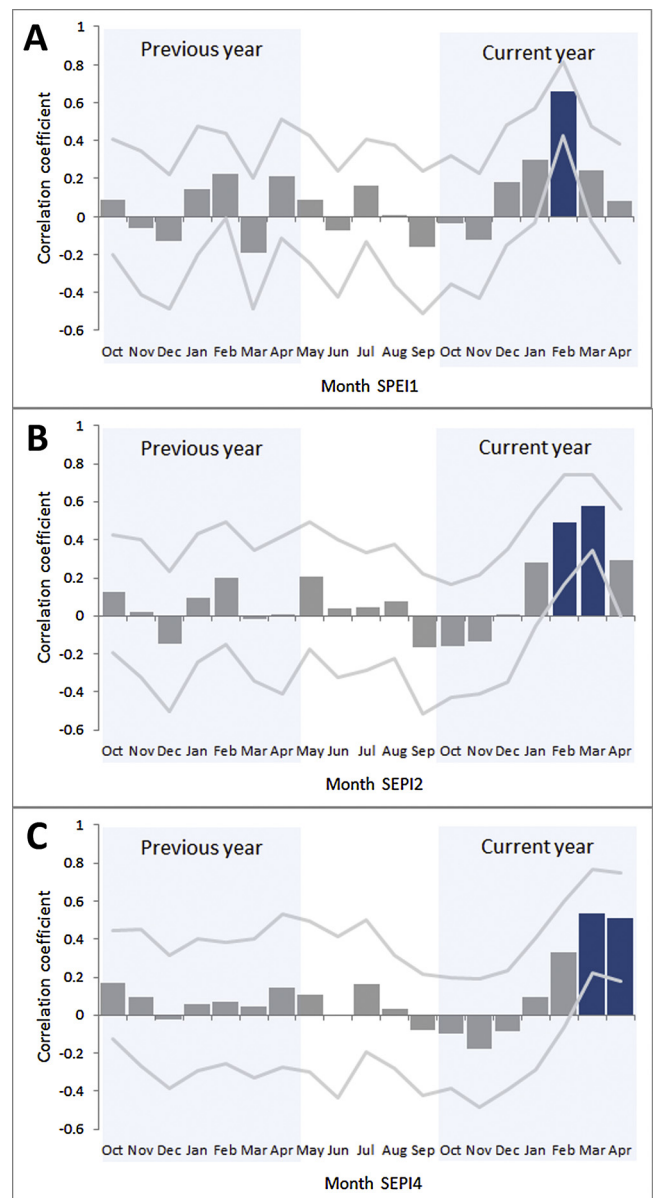


Fig. 6. Correlation between RES chronology and Standardized Precipitation Evapotranspiration Index (SPEI) (1976–2012). Correlation between tree-ring width index and –A– monthly, –B– bi-monthly and –C– four-monthly SPEI. Columns in dark blue indicate month with significance levels at $p < 0.05$. Grey lines delimit the 95% confidence interval. Light-blue rectangles show the estimated growth season period. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

growth under drought-stress, as it was previously observed by Borchert (1994). By evaluating primary production, Brando et al. (2008) also noted that wood production is the more sensitive aboveground component to water deficit. However, when considering a prolonged period of drought (SPEI4), we observed that rainfall throughout the late growing season period is the most important factor. In this regard, this species could be used as a proxy to investigate the duration of dry periods.

The strength of the linear correlation between tree growth and February SPEI1 can be observed over the time-span (Fig. 7). We noticed growth reductions in 1981 (34%), 1994 (49%), 1998 (34%), 2000 (36%) and 2009 (31%). These years matched with the SPEI1 calculated for the respective years, except for 1981, which was a wet year. Severe droughts episodes were registered at the study area in 1987 – 1989,

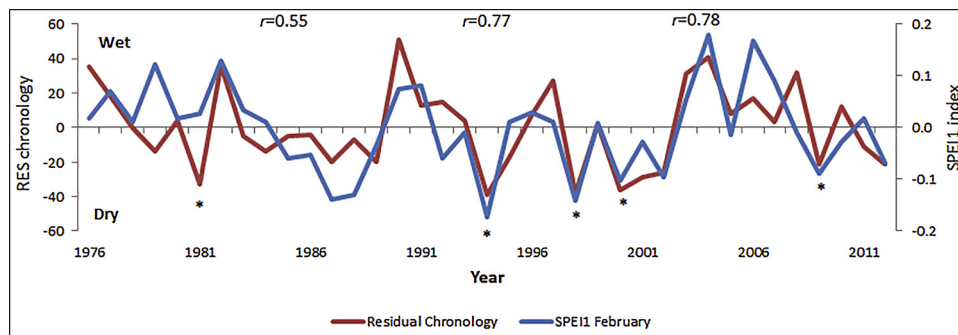


Fig. 7. RES chronology (red line) superimposed on February Standardized Precipitation Evapotranspiration Index (SPEI – 1976–2012) (blue line), considering growth-year. (*) Negative pointer years. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

1996 – 1999 and 2007 – 2008, including fires in the summer-autumn (1999) near the study site (Gazeta-online, 2015; Rolim et al., 2016; VÍncens et al., 2003). Monthly precipitation during the first periods was below 100 mm, while values up to 60 mm occurred in the subsequent ones in February. In this regard, *C. lucens* seems to be very sensitive to precipitation below 60 mm (Fig. 7). It is important to note that 1994 (the negative pointer year with the greatest reduction of growth) had a very low precipitation in January and February (4.40 and 7.20 mm, respectively). Therefore, we can conclude that *C. lucens* radial growth is sensitive to drought in cases of extreme water deficit (< 37 mm) during the late growing season, with growth reductions reaching up to 49%. One possible explanation for the pointer year that occurred under wet conditions in 1981 is that non-climatic exogenous factors acting in the community surpassed the climatic effect (Cook, 1987; Fritts, 1976).

This study presents the first chronology of growth rings for *C. lucens*, which we explored, in a pioneering way, the dendroclimatic signals in a tropical seasonal forest of the “Tabuleiros” Atlantic Forest in south-eastern Brazil. The fact that long-lived *Copaifera lucens* has annual rings hints a great potential for dendrochronological studies, which could be used to investigate past drought events in tropical regions. Moreover, low rainfall during the second half of the growing season (January–April) was found to be linked to reduced radial growth. Thus, our investigation suggests that wood production in *C. lucens* would be negatively affected in the event of decreasing precipitation regimes in South America, as it was predicted by climate change projections (IPCC, 2014). This climatic response may be similar for other wood species endemic to the Brazilian Atlantic Forest whose environmental restrictions are greater in relation to the widely distributed species. In this forest, ~ 55% of the trees are endemic (Flora do Brasil 2020, 2017), which might significantly affect the ability of this forest to sequester carbon. Yet, given the high complexity encountered during crossdating due to frequent narrow and false rings, we recommend that further investigation dealing with *C. lucens* should involve larger collected cores per tree, as well as a higher number of sampled trees.

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