

ON THE SUITABILITY OF *CARINIANA ESTRELLENSIS* (RADDI) KUNTZE FOR DENDROCLIMATIC STUDIES: THE PROBLEM OF CHRONOLOGY BUILDING AND TRENDS IN LIFETIME GROWTH TRAJECTORIES

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With 9 figures and 2 tables

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Summary: A tropical tree-ring study is presented using 36 specimens of *Cariniana estrellensis* from the Mata Atlântica Biome within the State of São Paulo: Caetetus and Carlos Botelho. We aimed to assess the suitability of this species for chronology building, as well as for dendroclimatological studies, with the help of its lifetime growth trajectories. *Cariniana estrellensis* forms visible tree rings with a dense sequence of parenchyma bands at the end of the latewood, followed by a relatively distant sequence of parenchyma bands in the subsequent early wood of a tree ring. However, it was impossible to establish a chronology, solely by tree-ring width measurements and crossdating, for a number of reasons, including sequences of problematic wood anatomy, abundance of wedging rings and probably missing rings. Therefore, building a robust chronology for this species requires a multi-parameter approach, however, no experience is currently available. Therefore, to reveal possible climate-growth relationships for *Cariniana estrellensis* at both sites, we tested to correlation analyses of microclimatic conditions with tree growth and investigated patterns of lifetime growth trajectories. Annual precipitation is over 1300 mm at both sites, with the dry season primarily between June and August. Both sites showed clear differences in their microclimatic regime and topography. Overall, light availability is the most likely crucial factor for the studied species. A significantly lower photosynthetic active radiation and daily photoperiod was found at Carlos Botelho by the strong influence of orographic rainfall, foggy conditions and shade caused by the adjacent mountain chain. Consequently, trees at this site generally showed a lower average annual growth rate as compared to the Caetetus site with differences between juvenile and mature growth phases remaining nearly constant throughout their lives. In contrast, trees from Caetetus had less consistent growth phases, with increased growth after the juvenile growth phase. Thus, it can be concluded that dendroclimatological studies using growth characteristics have the potential to clarify the generally complex stand dynamics of *Cariniana estrellensis*. However, the development of tree-ring chronologies, based on tree-ring width analyses of cores or discs is nearly impossible.

Zusammenfassung: Eine tropische Baumringstudie wurde mit Hilfe von 36 Individuen von *Cariniana estrellensis* an den Standorten Caetetus und Carlos Botelho im Atlantischen Regenwald des Bundesstaates São Paulo (Brasilien) durchgeführt. Ziel war es, die Eignung von *Cariniana estrellensis* zur Erstellung exakter Jahrringchronologien zu überprüfen sowie die Eignung für dendroclimatologische Untersuchungen mit Hilfe von lebenslangen Wachstumsverläufen zu bewerten. *Cariniana estrellensis* bildet optisch sichtbare Jahrringgrenzen aus, die durch den Wechsel von eng aneinandergereihten Parenchymbändern im Spätholz, gefolgt von weniger dicht gestaffelten Parenchymbandabfolgen im Frühholz gekennzeichnet sind. Jedoch war es aufgrund von Sequenzen mit unklaren holzanatomischen Strukturen, sowie dem häufigen Auftreten von auskeilenden und vermutlich fehlenden Jahrringen nicht möglich, mit Hilfe der Jahrringbreitenmessung und der ‚Crossdating‘ Methode eine Chronologie zu erstellen. Möglich wäre dies ggf. nur auf der Basis eines ‚Multi-Parameteransatzes‘. Um Klima-Wachstums Beziehungen von *Cariniana estrellensis* an beiden Standorten zu verifizieren, wurden mikroklimatologische Daten herangezogen und mit den lebenslangen Wachstumsverläufen der beprobten Individuen verglichen. An beiden Standorten beträgt der durchschnittliche Jahresniederschlag über 1300 mm, wobei die Trockenzeit im Wesentlichen jeweils zwischen Juni und August liegt. Jedoch zeigen beide Untersuchungsstandorte deutliche Unterschiede in ihrem mikroklimatischen Regime als auch in ihren topographischen Gegebenheiten. Auf Basis der mikroklimatischen Bedingungen scheint an den beiden untersuchten Standorten die Lichtverfügbarkeit der wichtigste Einflussfaktor für das Wachstum von *Cariniana estrellensis* zu sein. Die Auswertungen ergaben, dass Carlos Botelho im Vergleich zum Standort Caetetus deutlich geringere Werte der photosynthetisch aktiven Strahlung, sowie der täglichen Einstrahlungszeit aufweist. Dies ist auf den hohen Einfluss von Steigungsregen, nebligen Bedingungen und dem Schattenwurf der umliegenden Berge zurückzuführen. Die beprobten Bäume des Standorts Carlos Botelho zeigten im Allgemeinen geringere durchschnittliche Wachstumsraten. Dabei ergaben sich kaum Unterschiede zwischen dem Wachstum im juvenilen Stadium und späteren Phasen. Am Standort Caetetus zeigten die beprobten Individuen hingegen eine Tendenz zu erhöhten Wachstumsraten, speziell nach dem juvenilen Stadium. Wir schlussfolgern, dass dendroclimatologische Untersuchungen mittels *Cariniana estrellensis* das Potential besitzen, komplexe Standortdynamiken zu verifizieren und damit aufzudecken, jedoch die Erstellung exakter Chronologien auf Basis der holzanatomischen Gegebenheiten nahezu unmöglich erscheint.

Keywords: Tree rings; light availability; microclimate; jequitiba; radial growth

1 Introduction

Tropical forests play a pivotal role in terrestrial carbon and water cycle (HUNTINGFORD et al. 2011), especially with regard to climate change, since trees act as major carbon sinks and carbon sources on a global scale (PAN et al. 2011). Despite advances made to understand the impact of climate change on tropical forests (LEWIS et al. 2009), especially by dendrochronological studies and investigations at leaf level (HUANG et al. 2007; CERNUSAK et al. 2011), changes that involve altered growth patterns in tropical forests remain poorly understood. However, it is also true that only a small part of the widely distributed tropical regions have so far been studied and that knowledge about suitable species for fundamental investigations on tree growth is still fragmentary. Especially, spatial studies, which have the potential to reveal different growth dynamics, are still sparse in tropical regions.

For more than half a century, a link has been assumed between tree-ring width and growth (FRITTS 1976). This has been confirmed by many dendrochronological investigations in various forest ecosystems, including the tropics (WORBES 2002). Although the detection of trends in tree growth is not wholly straightforward, especially outside of permanent sample plots, tree rings could have enormous potential for a better understanding of climate-growth relationships (BOWMAN et al. 2012).

In the tropics, various studies have described the annual character of tree rings with the help of radiocarbon dating (WORBES and JUNK 1989) and/or the relationship between tree rings and climate (DÜNISCH and MONTÓIA 2003; BRIENEN and ZUIDEMA 2005; BRÄUNING et al. 2009; LOCOSSELLI et al. 2013), resulting in several tree-ring chronologies (BIONDI 2001; ENQUIST and LEFFLER 2001). Although it is known that annual tree rings exist for some tree species in different tropical climates (WORBES 1999), species potentially useful for dendroclimatology are limited (ALVES and ANGYALOSSY-ALFONSO 2000). Compared to temperate forests, it is vastly more challenging to date tree rings of tropical forests, due to high frequencies of indistinct, missing, false and wedging rings (HEINRICH and BANKS 2006a). The sparse distribution of many tropical tree species within a highly biodiverse community makes it difficult to reach a statistically significant sample number. In order to minimize such complications, most tropical tree-ring studies have focused on sites of one single climate type and with a pronounced dormancy of tree growth (SCHÖNGART et al. 2002; THERRELL et al. 2006; WILS et al. 2011).

However, for a better understanding of tropical forests under global change, studies must not be restricted to permanent plots since most investigations confined to permanent plots are not able to fully represent forest dynamics of primary sites (ZUIDEMA et al. 2013). Therefore, as the first step, it was suggested to intensify research in pristine forests using tree-ring studies to elucidate fundamental dynamics of tree growth at decadal to centennial scales. Tree growth can be measured in different ways using diameter or stem basal area increment along the lifespan of a tree (WEISKITTEL et al. 2011). All of these parameters show quite similar patterns for each individual, but vary among individuals at the same site due to different growth conditions (HÉRAULT et al. 2010; BOWMAN et al. 2012). In general, such differences are enhanced when comparing different species at the same site because of genetic dissimilarities in growth patterns. Consequently, it is necessary to detect and separate growth from environmental influences versus those inherent within specific species.

Light availability is one of the most limiting factors of tree growth, thus shade tolerance and performance are essential to understand growth dynamics (CANHAM et al. 1990; ROZENDAAL et al. 2009; ALTMAN et al. 2016). In general, tropical forests differ in light availability between dry and moist forests (TABARELLI and MANTOVANI 1997; TABARELLI et al. 1999; BRIENEN et al. 2010). In moist forests, the juveniles are subject to low light conditions within the forest understory, leading to suppressed growth. By assessing canopy levels, increased light conditions may lead to a sustained release in growth rates (ALTMAN et al. 2014; BAKER and BUNYAVEJCHEWIN 2006). Consequently, lifetime growth trajectories of trees from the same species, but different sites, might reflect different light conditions (POORTER et al. 2005). Moreover, canopy disturbances caused by competition of trees and branch falls seem to have an important impact on growth patterns of juvenile trees (BRIENEN and ZUIDEMA 2006). In other words, several intra- and inter-specific influences characterize the growth of an individual, or even a population, throughout its lifespan.

The present study focuses on the dendroecological potential of *Cariniana estrellensis* and, in particular, its growth behaviour in response to various environmental impacts. The study covers approximately one and a half centuries, which have seen the most dramatic environmental changes, mainly from anthropogenic activities. In this study, we aimed to answer the questions 1) if *Cariniana estrellensis* would have the dendrochronological potential required to build an exact chronology and 2) what might drive

the long-term growth rates of this species based on different site conditions within the biome of Mata Atlântica, Brazil.

The selection of *Cariniana estrellensis* is based on the assumption that this species is long lived, and that it is a canopy-to-emergent tree, ideal to record climatic influences within tree rings. Mata Atlântica is of special interest because it is the second largest tropical forest in South America. Even though it is significantly downscaled and fragmented as a result of deforestation, this area still enables investigations on tree growth almost comparable to those conducted in genuine forests.

2 Methods

2.1 Study area and climate

The Atlantic Rainforest in the State of São Paulo, Brazil (Fig. 1a, b), is the second largest moist-forest in South America, despite its high fragmentation and reduction to approximately 11 % of its original distribution (RIBEIRO et al. 2009). The biome structure is highly heterogeneous and can be divided into differ-

ent vegetation types because of its latitudinal range, relief, soil, and climate conditions (EISENLOHR and OLIVEIRA-FILHO 2015).

In order to take advantage of such heterogeneity, this study was conducted in two different phyto-geographic areas of the Atlantic Forest. Two protected areas, Parque Estadual de Carlos Botelho (State Park) and Estação Ecológica de Caetetus (Ecological Station), were chosen as being representative of evergreen and semi-deciduous forests, respectively (Tab. 1).

Carlos Botelho State Park belongs to the ombrophilous dense forest and is located in the south of the State of São Paulo, about 60 km away from the Atlantic coast (24°00′-24°15′S and 47°45′-48°10′W). The topography at Carlos Botelho is mainly mountainous with steep slopes and small brooks.

Caetetus Ecological Station lies within the semi-deciduous forest in the interior of the State of São Paulo, one of the most transformed subregions of the Atlantic Rainforest (RIBEIRO et al. 2009). It is located about 290 km west of Carlos Botelho and 350 km away from the sea, in southwestern São Paulo State (22°20′-22°30′S and 49°40′-49°45′W). In contrast to Carlos Botelho, slopes are gentle with inclinations of less than 6 %.

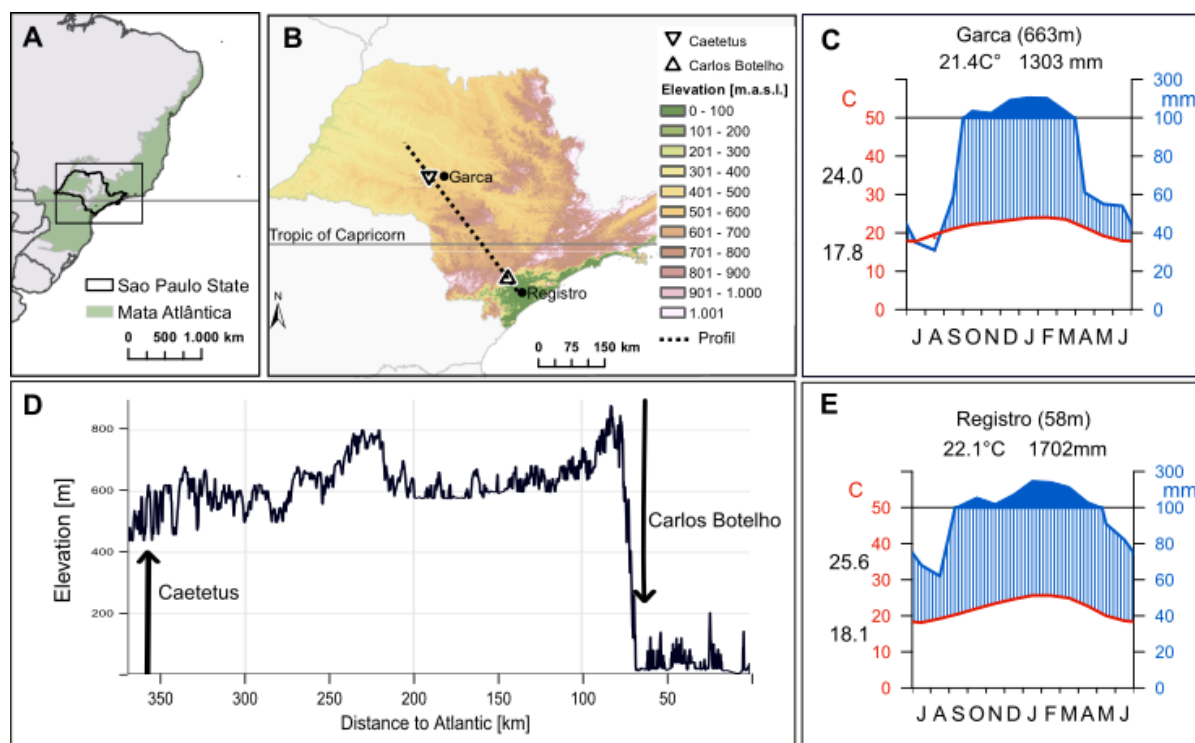


Fig. 1: Distribution of the Mata Atlântica biome along the eastern coast of Brazil (A); hypsographic map of the State of São Paulo and location of the two study sites, Estação Ecológica de Caetetus and Parque Estadual de Carlos Botelho (B); elevation profile between Caetetus and Carlos Botelho (C); climate diagrams showing long-term average values (1970-2000) of temperature and precipitation for Garca (D) and Registro (E), the two stations nearest the study sites, respectively.

Tab. 1: Site characteristics of Caetetus and Carlos Botelho

| Site | Caetetus | Carlos Botelho |
|--|--------------------|-------------------|
| Covered area | 2.200 ha | 40.000 ha |
| Altitude (at sampling site) | 520 – 580 m a.s.l. | 30 - 100 m a.s.l. |
| Mean annual temperature | 21.4 °C | 22.1 °C |
| Annual precipitation | 1100–1700 mm | 1200–2400 mm |
| Dry season (<100mm/month) | Mar-Aug | Jun-Aug |
| Vegetation type | Semi-deciduous | Evergreen |
| <i>Cariniana estrellensis</i> characteristics | | |
| Adult stature | Canopy/emergent | Canopy |
| Number of trees | 24 | 12 |
| Recorded years of trees | 52–155 | 72–212 |
| Tree diameter (cm) | 42–95 | 28–86 |
| Tree height (m) | 13.5–36.0 | 16.5–28.0 |

Climate stations closest to the sampling sites are located in the municipalities of Garça (Caetetus) and Registro (Carlos Botelho), showing a characteristic precipitation pattern with wet summer and dry winter seasons (Fig. 1d, e). Annual rainfall is higher and cloud cover is thicker at Carlos Botelho as compared to Caetetus because of orogenic rainfall caused by the occurrence of tradewinds from the Atlantic Ocean. Local climate data from Carlos Botelho (kindly provided by P. Sentelhas), although unsteady and incomplete, suggest a vastly higher annual precipitation with values of over 3000 mm (Fig. 2).

To detect microclimatic conditions at both sites, we analysed mean temperature, temperature range, precipitation, relative humidity, photosynthetically active radiation (PAR) and photoperiod. All data were originally gathered by Paulo Sentelhas between 1 November 2003 and 30 September 2004 in intervals of 15 minutes (Fig. 2). Daily and monthly means for all categories were calculated and then the Wilcoxon signed-rank sum test (WILCOXON 1945) was applied to test if the means differed from each other, with the help of R (R CORE TEAM 2016).

2.2 Tree species

Samples of *Cariniana estrellensis* (Raddi) Kuntze were collected, locally known as “jequitibá-branco” (Tab. 1); a species which is part of the Neotropical genus in the pantropical family Lecythidaceae

(HUANG et al. 2008). This species is widespread in the biome of the Mata Atlântica in southeastern Brazil and is the only species of *Cariniana* commonly found south of the Tropic of Capricorn (Fig. 3). It is brevi-deciduous, and forms visible tree rings marked by fibrous zones. LISI et al. (2008) verified the annual character of the growth rings by combining monthly dendrometer measurements with the “window method” described by DÉTIENNE and MARIAUX (1977). *Cariniana estrellensis* is relatively light-demanding in the juvenile phase (DURINGAN et al. 2000) and belongs to the late secondary growth succession stage (LEITE 2007). At both sites, individuals were selected as either canopy or emergent trees.

2.3 Sample collection and laboratory work

Samples from 24 and 12 trees were taken at Caetetus and Carlos Botelho, respectively, from August to September 2013. Since both sites are naturally protected areas, only increment cores (2 per tree) from living individuals could be taken. Whenever possible, samples were taken at breast height. As such, we analysed 72 radii.

We employed a gasoline-powered drilling machine to take cores 15mm in diameter and up to 1m in length (KROTTENTHALER et al. 2015). To minimize a possible invasion of insects and fungi, we treated the boreholes with a fungicide composed of

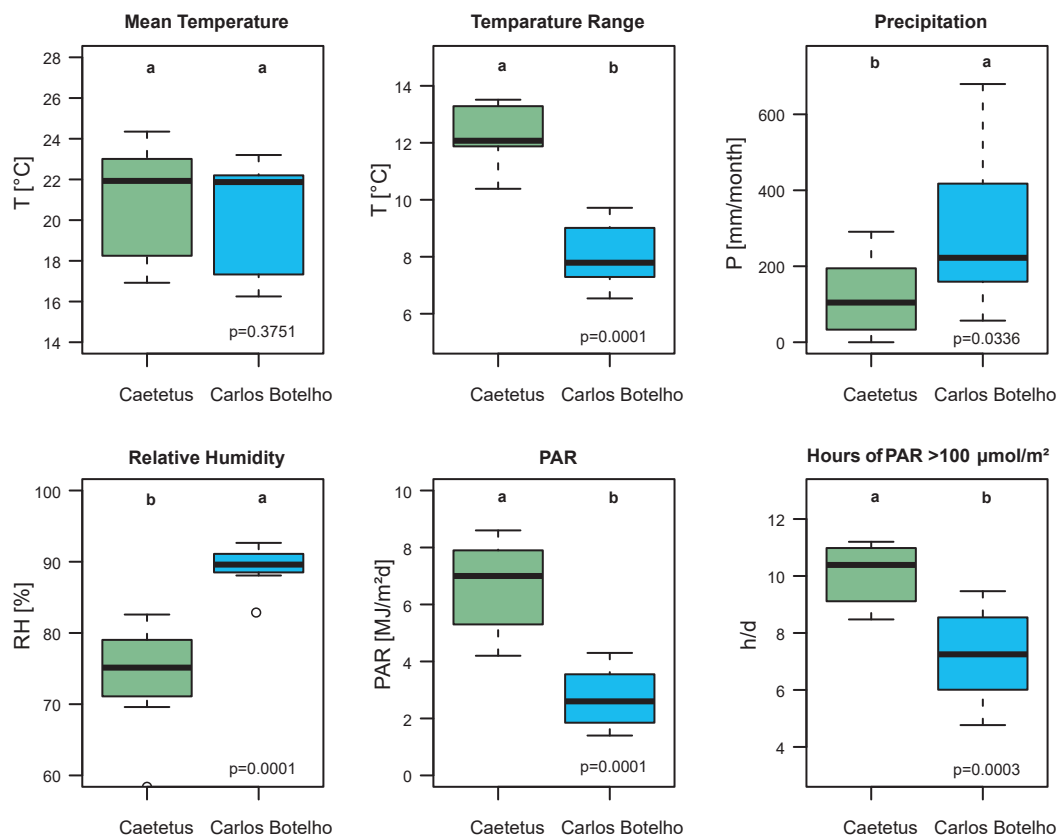


Fig. 2: Mean temperature (°C), temperature range ($T_{\max} - T_{\min}$), precipitation (mm), relative humidity (%), photosynthetically active radiation (PAR) ($\text{MJ}/\text{m}^2\text{d}$) and photoperiod ($\text{h}/\text{d} > 100\mu\text{mol}/\text{m}^2$) at Caetetus and Carlos Botelho. The thick black bar indicates the median of each dimension. All values are monthly means of *in situ* measurements at 15-minute intervals from 2003–2004. Boxes sharing the same letter are not significantly different at $P < 0.05$. (Data Source: P. Sentelhas).

a saturated solution of copper (II) sulphate CuSO_4 and slacked lime (calcium hydroxide) $\text{Ca}(\text{OH})_2$ in a 1:1 ratio. Afterwards, the boreholes were sealed with a cork to prevent insect entrance or rainwater intrusion.

For all individuals, tree height and surrounding canopy height were measured with a clinometer (Haglöf© EC II). The circumference of each tree was quantified with a measuring tape at breast height.

After air-drying, all samples were polished mechanically with sandpaper, (grit 80 to 1200). Afterwards, a pressure washer with 100 bar was used to remove the dust from the vessels. All visible rings were counted and marked with the help of a 40x10 stereomicroscope (Novex© AR Zoom). Cores were scanned at a resolution of 2400 dpi with a desk scanner (Epson© Perfection V370 Photo). The measurement of tree-ring widths was performed with scanned images of the cores using CooRecorder (Cybis Elektronik & Data AB, Saltsjöbaden, Sweden).

If ring boundaries could not be easily detected, thin sections were used, often dampened to improve visibility, together with incident light of the stereomicroscope. A thin section (0.9–1.1mm) of the polished surface was cut from all cores using a modified water-cooled Buehler© IsoMet 5000 saw with a diamond cutting disc 0.5 mm in thickness rotating at 4000 rpm. The saw produces a high-quality cut surface.

Since some increment cores did not hit the pith, we had to estimate the number of missing juvenile rings by using the estimation feature of CooRecorder.

2.4 Crossdating

Crossdating is a dendrochronological technique to match growth patterns of radii from the same tree and/or from different trees by comparing patterns of wide and narrow rings (YAMAGUCHI 1991). This allows assigning a calendar year to each de-

Tab. 2: Average growth rates (AGR) (with SD) based on mean diameter of *Cariniana estrellensis* at Caetetus and Carlos Botelho. Percentage of AGR in each Phase indicates the respective relative growth compared to the overall AGR at each site. Results of the Kruskal-Wallis test comparing the growth phases among each population's growth phases are also provided. The group's letters indicate if the growth phases are statistically different (different letters) or not (equal letters) based on the results of the Dunn's test.

| | Caetetus | | Carlos Botelho | |
|-------------------------------------|--|-------|---|-------|
| Kruskal-Wallis | $p < 0.0001$, $DF = 2$, $\chi^2 = 35.41$ | | $p = 0.007$, $DF = 2$, $\chi^2 = 10.02$ | |
| Period | Mean \pm SD | Group | Mean \pm SD | Group |
| Juvenile Phase I (1 – 20 years) | 0.22 \pm 0.11 | C | 0.26 \pm 0.22 | B |
| (% of AGR) | (46%) | | (81%) | |
| Juvenile Phase II (1 – 50 years) | 0.42 \pm 0.26 | B | 0.28 \pm 0.16 | B |
| (% of AGR) | (88%) | | (88%) | |
| Mature Phase (51 – sample age) | 0.54 \pm 0.17 | A | 0.35 \pm 0.13 | A |
| (% of AGR) | (113%) | | (109%) | |
| Wilcoxon | $p < 0.0064$, $DF = 1$, $\chi^2 = 7.43$ | | | |
| Overall | 0.48 \pm 0.17 | A | 0.32 \pm 0.13 | B |
| (% of AGR) | (100%) | | (100%) | |
| SD/AGR (%) | 35% | | 40% | |

tected ring. A first visual crossdating was applied by matching ring-width patterns. Statistical programs were used to validate the preliminary results, and additional support was based on TSAPWin (RINN 2005) and COFECHA software (HOLMES 1983; GRISINO-MAYER 2001). These techniques allow the identification of false and missing rings, which are a well-known problem in tropical trees. Crossdated ring-width series of individuals of the same species indicate common external factors, such as temperature or precipitation, influencing radial growth (WORBES 1995).

2.5 Determination and bias of growth patterns and ages

In order to investigate growth patterns and trends, annual increments were calculated by averaging the corresponding increments of both radii of a tree. To make differences visible, we calculated diameter average growth rates (AGR) for both sites by taking the mean AGR value for each year of

cambial age (Fig. 4). We estimated AGR values over the whole lifespan and for the first 20 and 50 years, respectively (Juvenile Phase I and II), to detect possible juvenile growth patterns, as well as the 51st year to coring age of cambial age (Mature Phase). Statistical operations were performed with the help of the Kruskal-Wallis test and Dunn's test (DINNO 2014).

Over- or underestimations of AGR are possible due to different sampling biases (BOWMAN et al. 2012). Additionally, whenever the pith was rotten, or not reached, the missing years had to be estimated. As a consequence of different growth behaviour of trees in the juvenile phase, two different methods to estimate the juvenile rings were applied. For linear growth behaviour, we calculated the number of missing rings (R_m) based on the available core length (C_p), the measured years (R_p) and the missing distance to the core (C_m), which was calculated with the help of the measured circumference. The calculation is based on the fact that the ratio of the number of unknown rings to the length from the pith to the start of the core is equal to the number of

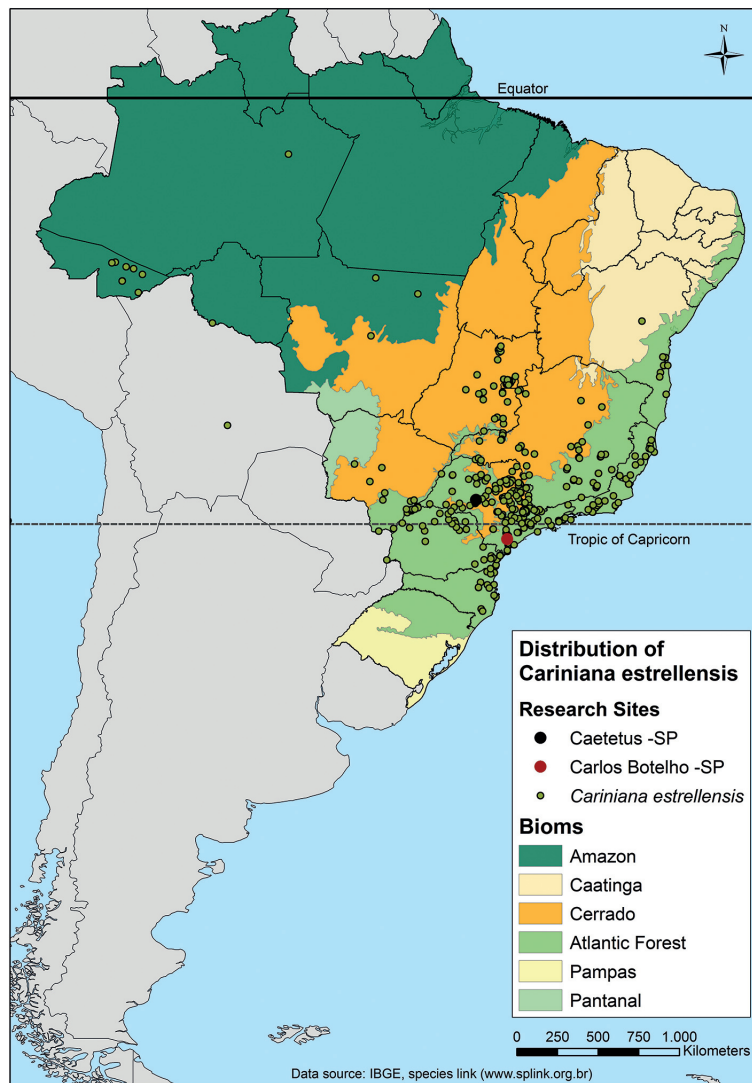


Fig. 3: Distribution of *Cariniana estrellensis* in Brazil and location of the sampling sites of the study.

measured rings divided by the corresponding length of the core, *i.e.*, $R_m/C_m = R_p/C_p$. This leads to the equation for the number of missing rings:

$$R_m = \frac{C_m * R_p}{C_p} \quad (1)$$

The second method uses the integrated calculator of CooRecorder to estimate the number of missing rings to the pith. In trees with a slow-growing juvenile phase, the mathematical calculation would underestimate the missing years more than the software-based calculation. Consequently, the estimated age of each tree differs slightly (around 10–15%), depending on the calculation method employed (Fig. 5).

3 Results

3.1 Tree-ring structure and crossdating potential

Differences between years vary significantly within the cores, despite the visible tree-ring boundaries in *Cariniana estrellensis* at both sites. Sequences which are easy to analyse have clear boundaries where parenchyma bands are very dense at the end of the latewood, followed by relatively distant parenchyma bands in the following earlywood (Fig. 6a), delimiting the so-called fibrous zones, sometimes also exhibiting a darker tissue at the surroundings. Other features such as xylem colouring or diffuse porous vessels did not indicate tree-ring boundaries and can sometimes be misleading when trying

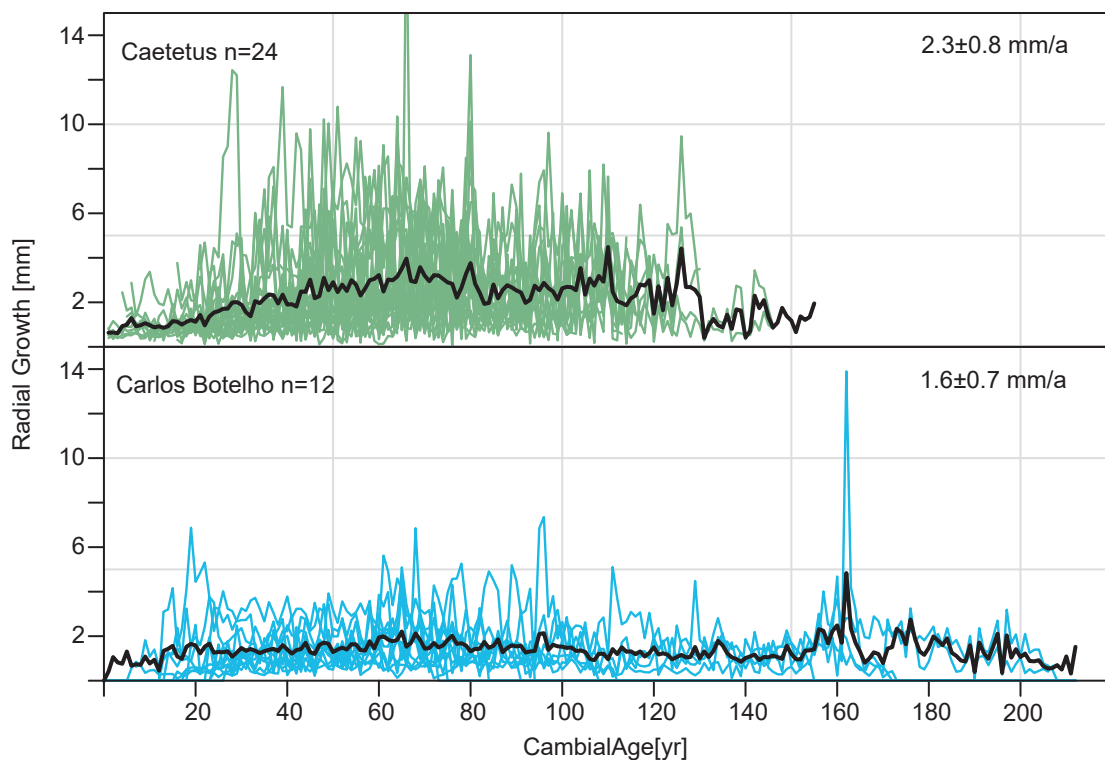


Fig. 4: Average growth rate (AGR) of cambial age of *Cariniana estrellensis* at Caetetus and Carlos Botelho. The bold black line shows the average, while the green and blue lines show the curves of all investigated individuals at each site.

to detect borders. In contrast, while problematic sequences of tree rings (Fig. 6b) of *Cariniana estrellensis* also have visible rings, they are lined up very closely, featuring tree-ring widths of 1 mm, or even less, indicating a pattern of successively narrow and wider parenchyma bands. Unfortunately, the corresponding differences can be very hard to detect, especially if rings are extremely narrow. In this case, vessels are densely packed, making it extremely difficult to identify boundaries. Some areas are particularly ambiguous, where parenchyma bands vary only slightly within a tree ring, as indicated by the upper arrows of Figure 6b. These fluctuations are considered to be intra-annual growth variations. In general, narrow sequences appear in all investigated individuals. This is particularly true for the juvenile phase, for periods of growth suppression, and in older individuals with large stem diameters, where yearly growth already shows a geometric trend that tends toward smaller rings.

Another problem is the presence of wedging and missing rings. In principle, they can be found anywhere between pith and bark. They are especially abundant in the juvenile phase, where boundaries are, in general, less pronounced and during slow-growing phases. Even in the fastest-growing

individuals, this study shows that about 10% of wedging rings were detected for *Cariniana estrellensis* at both sites, but further undetected wedging and missing rings are possible. We are, therefore, aware that the correct combining, i.e., crossdating, of two cores from a tree poses tremendous problems.

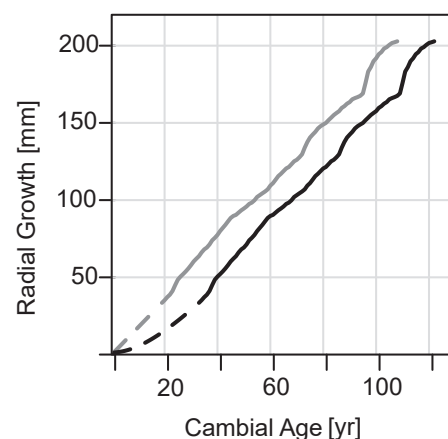


Fig. 5: The resulting differences of lifetime growth trajectories, according to two different methods of calculating the pith offset for an individual at Carlos Botelho. The grey line and dots show the Coo estimation; the black line and dots show the linear estimation.

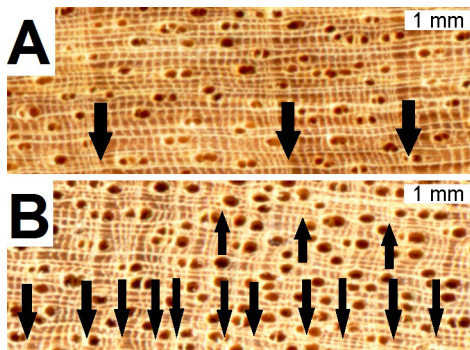


Fig. 6: Tree-ring boundaries of *Cariniana estrellensis* from Caetetus. Two sections with a sequence of clear and wide tree rings (A) and a sequence of narrow tree rings and problematic ring boundaries (B). Arrows from the top indicate clear tree rings; arrows from the bottom mark intra-annual growth variations. The growth direction is from left to right.

To compare the quality of cores from individuals against one another, i.e., how they match, we first crossdated radii within individual trees. All trees revealed several core positions where the intra-tree curves did not really fit together throughout all growth phases (Fig. 7a). Consequently, missing years were added at statistically significant points, where

wood anatomical conditions (i.e. distinct latewood patterns) supported this measure. Similarly, questionable ring boundaries and intra-annual growth variations were reassessed. As a result, within tree intercorrelation rose significantly from $r=0.20$ (GLK $\approx 52\%$, 143 years) to $r=0.48$ (GLK $\approx 65\%$, 156 years, Figure 7b); an average of 13 years per tree were added as missing rings. These measures indicate that it is largely impossible to find all wedging and missing rings, even if a statistically trustworthy record deduced from two cores per tree is used. Wedging and missing rings may even be impossible to find, even if four or more cores are used, in addition to the increased workload required.

Confronted with these problems, we were not able to crossdate all individuals of both sites because of rot, broken or damaged cores, buttress influence or one-sided suppressed growth. Therefore, building a chronology based on tree-ring width is currently not possible for this species at these locations, essentially because the common growth signal is too weak to synchronize mean curves of different individuals. We further assume missing rings that could not be located in any of the cores, at least for some of the trees.

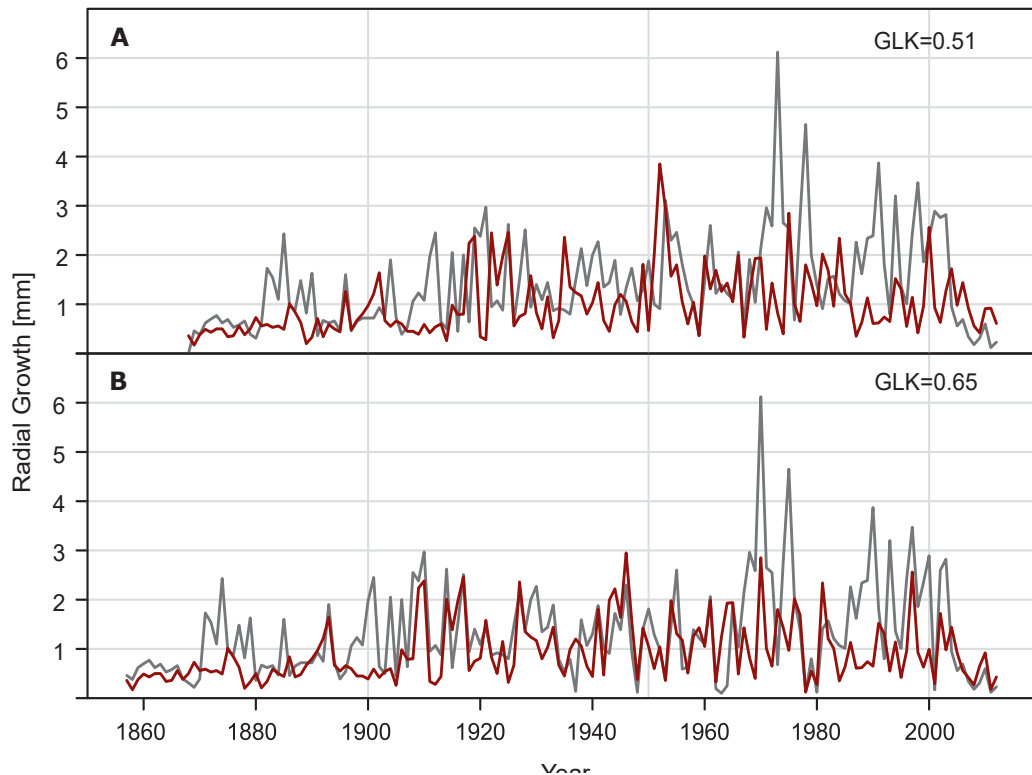


Fig. 7: Tree-ring width curves of two radii (brown and grey lines) of *Cariniana estrellensis* at Carlos Botelho. The upper chart (A) shows the matching after raw measurements ($a = 143$; GLK = 51%; $r = 0.20$), while the lower chart (B) presents crossdated curves with inserted wedging rings ($a = 156$; GLK = 65%; $r = 0.48$).

3.2 Stand structures and microclimatic observations

Results show that the studied trees from both sites had comparable tree heights and median ages, which favours the comparison within the present study (Fig. 8). Despite the fact that the tallest tree at Caetetus reached 36.2 m and in Carlos Botelho only 27 m, no statistical difference exists in tree height between these two sites, with average values of 22.1 m and 21.8 m, respectively. This was also true for the diameter at breast height (DBH) of the same trees, with average values of 58.3 cm and 46.6 cm, respectively. Moreover, we found no statistical difference between the ages of the trees from the two sites, with average values of 84.3 years and 112 years, respectively. We only found a statistical difference between the canopy height of these two sites, with average values of 15.3 m and 17.8 m, respectively; on average, canopy height of 2.5 m was higher at Carlos Botelho.

With regard to microclimate conditions (Fig. 2), the mean annual temperature did not differ statistically between the two sites (average values of 20.9°C and 20.2°C at Caetetus and Carlos Botelho, respectively (see also Fig. 1). All other parameters showed significant statistical differences: Temperature range (average values of 12.9°C and 8.1°C), precipitation (average values of 124 mm and 291 mm), relative humidity (average values of 72.4 % and 89.5 %), PAR (average values of 6.6 MJ/m²d and 2.7 MJ/m²d) and photoperiod (average values of 10.0 h/d and 7.3 h/d).

3.3 Growth patterns and ages

Significant differences in *Cariniana estrellensis* growth rates and lifetime growth trajectories were apparent between Caetetus and Carlos Botelho. Though only 12 trees at Carlos Botelho, and 24 trees at Caetetus (Tab. 1) were sampled, 4

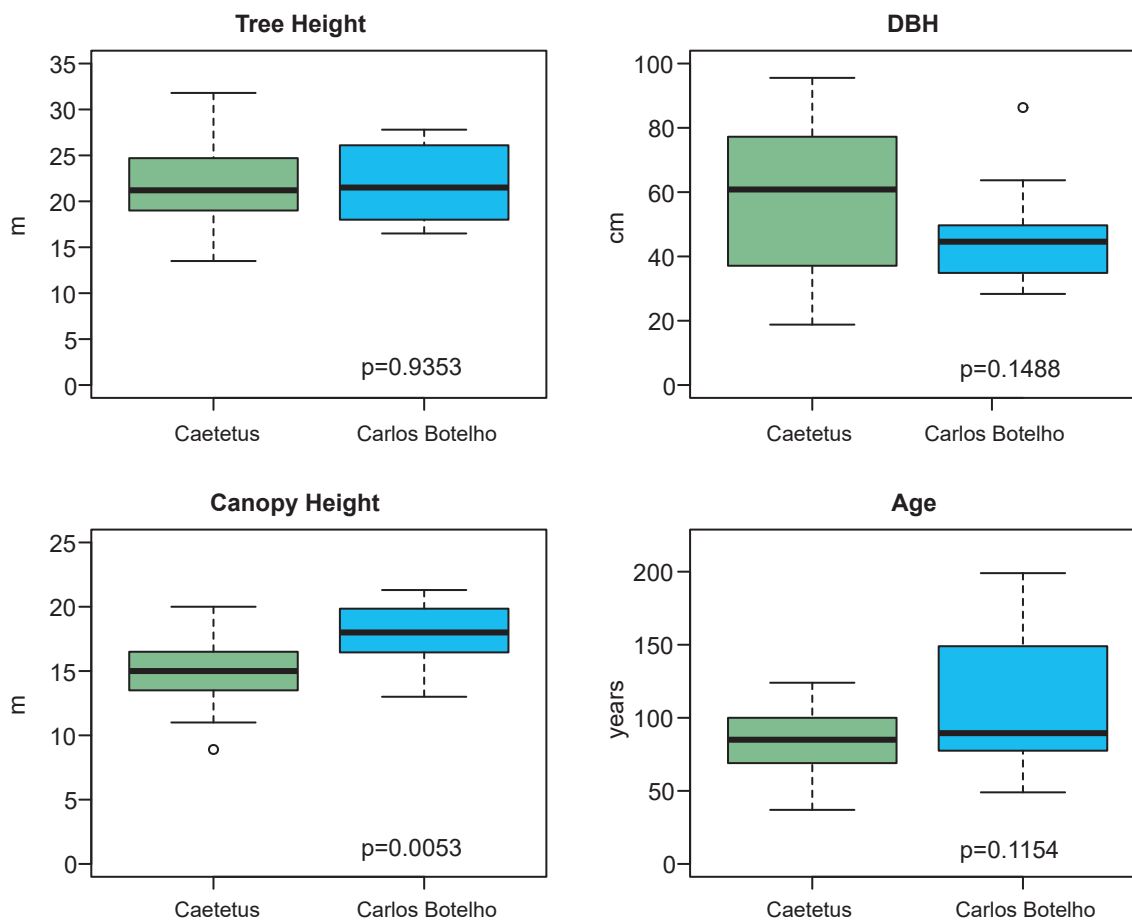


Fig. 8: Boxplots, comparing tree height, diameter at breast height (DBH), the surrounding canopy height and the ages of all sampled *Cariniana estrellensis* at Caetetus and Carlos Botelho. The thick black bar indicates the corresponding median value.

were already older than the oldest individual from Caetetus. Average growth rate (AGR) was $0.48 \pm 0.17\text{cm/yr}$ for Caetetus and $0.32 \pm 0.13\text{cm/yr}$ for Carlos Botelho (Tab. 2). Lifetime growth patterns varied between sites and lifespan, especially during the juvenile phases. The results of the Kruskal-Wallis test and Dunn's test show that all investigated AGR phases at Caetetus are statistically different. Juvenile phases at Carlos Botelho do not differ, but they are different to the mature phase. While Caetetus has growth rates of $0.22 \pm 0.11\text{cm/yr}$ and $0.42 \pm 0.26\text{cm/yr}$ for the first 20 and 50 years of cambial age, respectively, Carlos Botelho has values of $0.26 \pm 0.22\text{cm/yr}$ and $0.28 \pm 0.16\text{cm/yr}$, respectively (Tab. 2). This means that *Cariniana estrellensis* at Caetetus only displays about 46 % and 88 % of AGR in the first 20 and 50 years of cambial age, respectively, compared to the AGR of its entire lifespan. However, *Cariniana estrellensis* trees from Carlos Botelho reveal 81 % and 88 % for this reference period. Growth rates from year 51 to the coring age are approximately those of the lifetime growth rate at Carlos Botelho (109 %), whereas growth rates at Caetetus are at a higher level (113 %) during the mature phase. Thus the age at a given diameter (except for juvenile phase I) is always higher at Carlos Botelho compared to Caetetus.

In summary, *Cariniana estrellensis* at Carlos Botelho has a lower AGR throughout its lifespan compared to *Cariniana estrellensis* at Caetetus. The latter tends to have a slightly lower variation in growth trajectories within the population, as the ratio of SD/AGR (35 %) is lower than that at Carlos Botelho (40 %). Concerning growth trajectories in

general, the investigated trees at Carlos Botelho roughly tend to have a linear trend, while trees at Caetetus show a strongly restricted juvenile phase I. In addition, growth rates at Caetetus are above average for the mature phase (Fig. 9).

4 Discussion

4.1 Suitability of *Cariniana estrellensis* for tree-ring studies and chronology building

Since Raddi (1820) described *Cariniana estrellensis* (albeit under a different name), various studies have been carried out on this species. LEITE (2007) summarized the state of knowledge, including tree physiological, phenological and ecological features of this species. However, the knowledge about *Cariniana estrellensis* is still sparse, especially at semi-deciduous and evergreen sites (LISI et al. 2008). One aim of the present study was to verify the potential for building chronologies with this tree species under the given ecological conditions.

Growth rings of *Cariniana estrellensis* are generally distinguishable, but often with difficulties. Detection of wedging rings, a well-known problem in tropical trees, is the biggest challenge (TROUET et al. 2010; LOCOSSELLI et al. 2016), but the factors provoking this phenomenon are, so far, unknown. It is likely that slow growth - caused by high competition, poor light conditions and buttress - boost the occurrence of wedging rings (WORBES 2002). At both investigated sites, *Cariniana estrellensis* shows slow AGRs comparable to those of other recently

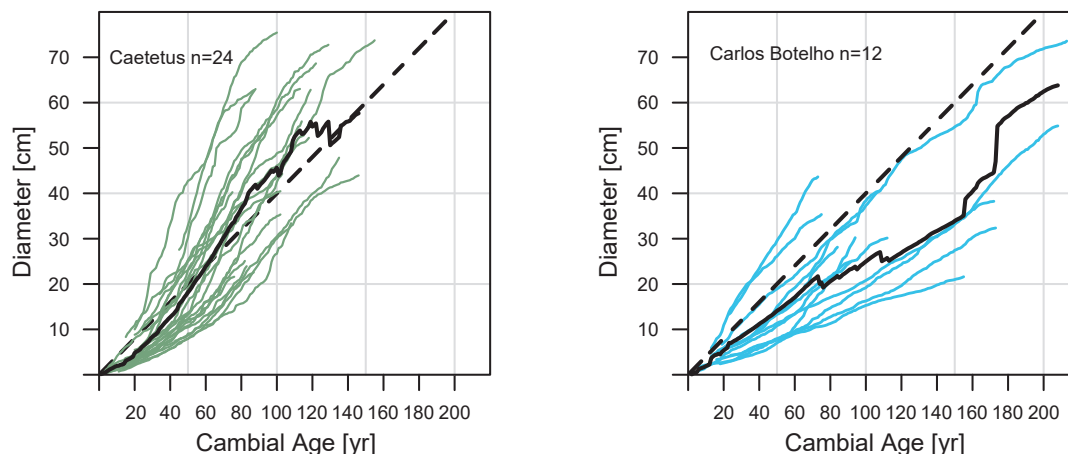


Fig. 9: Lifetime growth trajectories of cambial age of *Cariniana estrellensis* at Caetetus and Carlos Botelho. The bold black line shows the average, while the green and blue lines show the cumulative curves of all investigated individuals at each site. The thin straight line is a ledger line, which allows a comparison of the average lifetime growth trajectories of both sites.

investigated tropical tree species (DE RIDDER et al. 2013; GROENENDIJK et al. 2014). Our attempts to build a robust chronology were unsuccessful for *Cariniana estrellensis* as a direct result of undetectable wedging and missing rings in all sampled trees at both sites.

For periods of five to ten years, almost all individuals show repeated synchronous behaviour, but with chronological gaps at each site. Thus, it is possible that additional methods could further help to find missing rings (HEINRICH and ALLEN 2013). One possible approach could be to crossdate tree-ring series with the use of stable carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) isotopes (RODEN 2008). Compared to tree-ring width curves, yearly isotopic ratios have shown a better correlation between individuals. Together with the synchronous patterns of tree-ring width, wedging rings might be identified, and a chronology could possibly be established. In addition, stable isotopes can potentially reveal various environmental variables like temperature, humidity or precipitation (MCCARROLL and LOADER 2004), which could assist in calibrating the chronology with instrumental data. Recent improvements in ^{14}C -dating (WOOD 2015) may be an important additional help, but has not yet been tested on *Cariniana estrellensis*. Other possibilities would be to analyse growth patterns within full tree discs, or vastly increase the number of cores per tree. However, a number of ecological, political and logistical restrictions prevent these final alternatives from being realistic options.

Altogether, *Cariniana estrellensis* is an anatomically challenging species. Other studies have shown that this is not an exception for trees of semi-deciduous and evergreen forests, but rather the general rule (GROENENDIJK et al. 2014). Apart from these difficulties, *Cariniana estrellensis* does offer some advantages for potential tree-ring studies. First, it is a widely distributed tree species in Brazil, growing in various biomes from the seasonally dry savanna like the Cerrado to the evergreen Mata Atlântica. Second, it is a relatively slow-growing species, developing over hundreds of years and, hence, ideal for building chronologies, as supported by findings from SCHLESER et al. (2015) for a related species, namely *Cariniana micrantha*, endemic to the Amazon region. Because of the high biodiversity of tropical forests, the frequency of *Cariniana estrellensis* is low per hectare. Nonetheless, *Cariniana estrellensis* is one of the dominant species at Caetetus, with about five trees per hectare (DURINGAN et al. 2000).

4.2 Average growth rates and lifetime growth trajectories of *Cariniana estrellensis* in semi-deciduous to evergreen forests

Although both sites are part of the Mata Atlântica biome, mean AGRs and lifetime growth trajectories vary considerably. In principle, many factors influence local tree growth, such as precipitation (BRIENEN and ZUIDEMA 2005; TOLEDO et al. 2011), soil characteristics, nutrient availability (WRIGHT et al. 2011; SANTIAGO et al. 2012) and competition (COMITA et al. 2010; COOMES et al. 2011). In our case, we found that geomorphology and light availability tended to be the driving forces, significantly differing between sites. Other factors, such as competition, mean temperatures and water availability, are largely comparable at both sites.

Caetetus is part of the inland plateau region of São Paulo State; therefore, all sampled individuals grow on almost plain ground (< six degrees of inclination). On the other hand, Carlos Botelho is part of the transition zone between coastal plains and the southeastern part of the “Serra do Mar” (Fig. 1b,c). Consequently, both regions show very different global solar radiation values (Qg) at canopy level, as well as different amounts of precipitation from orographic effects at Carlos Botelho. LERF (2006) measured the values for Qg for both sites and stated that Carlos Botelho receives only half of $\text{MJ}/\text{m}^2\text{d}^{-1}$ compared to Caetetus.

Additionally, PAR measured at the canopy level of Carlos Botelho shows only around 38% of that measured at Caetetus. Generally, higher precipitation resulting from a shorter dry season and orographic rainfall resulting in higher cloud cover support the lower value of PAR at Carlos Botelho. Therefore, Caetetus is marked by a higher monthly photoperiod compared to Carlos Botelho.

The observation of Qg and PAR values, as well as the daily photoperiod, could account for the different AGRs. Various studies have shown that tree growth is highly correlated with light availability in various ecosystems (ALTMAN et al. 2013; RÜGER et al. 2011; DONG et al. 2012). Higher amounts of precipitation point to a generally thicker cloud cover and thus reduced light availability. Supporting evidence could be found assuming the actual yearly precipitation values at Carlos Botelho are significantly higher than those suggested by the closest climate station in Registro (1670 mm). Therefore, the already lower Qg ratio at Carlos Botelho compared to Caetetus is presumably even lower at canopy level. Personal experience during the field campaign with drizzle and

foggy conditions at Carlos Botelho in August and September 2013 supports this hypothesis.

POORTER et al. (2005) reported that tropical species show specific growth rates and that lifetime growth trajectories very much dependent on light availability. In general, *Cariniana estrellensis* is a light-demanding species, especially in its juvenile phase (LEITE 2007). Even though *Cariniana estrellensis* has an AGR at Caetetus more than 50 % higher than that at Carlos Botelho, both populations show a clearly lower growth rate during the first 20 to 50 years of cambial age. Throughout their juvenile phase, individuals are presumably inhibited in their growth in the understory because of reduced amounts of light at both sites. After this phase of juvenile growth, growth trajectories at both sites move apart. BRIENEN et al. (2010) state that growth trajectories of juvenile trees in moist forests are driven by light availability. In their study, 72 % of the investigated juveniles were suppressed, compared to 17 % in a dry forest. Moreover, the observed periods of suppression were significantly higher in the moist forest than in the dry forest (9 vs. 5 years).

While *Cariniana estrellensis* at Caetetus shows markedly increasing growth rates with age, the population at Carlos Botelho grows steadily throughout its whole lifespan. This could be explained by the fact that individuals at Caetetus obtain more light throughout the year after reaching the canopy and therefore experience a growth release (BRIENEN and ZUIDEMA 2006). In contrast, individuals at Carlos Botelho experience only a slight increase of growth after reaching the canopy as a result of the mostly dimmed conditions, which do not result in a marked growth release (ALTMAN et al. 2014).

4.3 Outlook and recommendations

This investigation represents the first tree-ring study of *Cariniana estrellensis*, which compares the populations of two different sites. So far, tree-ring studies in tropical climates are relatively sparse (ROZENDAAL and ZUIDEMA 2011), and knowledge about tropical dendrochronology is still minimal, but offers a great possibility for understanding long term dynamics of tropical trees. Investigations of *Cariniana estrellensis* hold a high potential for tree-ring studies. Up to now, the biggest challenge consists in solving the problem of chronology building, i.e., correct dating by only using tree-ring widths. Presumably, a multi-proxy approach would be beneficial (HEINRICH and BANKS 2006b; SIDOROVA et al.

2012) to create a robust chronology. Subsequently, this could allow the implementation of tree-ring studies outside of permanent sample plots or selective logged sites, which describe most of the studies so far (ROZENDAAL et al. 2010). In summary, each of the investigated sites in the present work is influenced by different atmospheric circulation patterns (VERA et al. 2006), leading to different amounts of rainfall and cloud cover throughout the year causing significant differences in light availability. Once dating problems have been overcome, it might be possible to obtain information about origin and composition of rainfall amounts (BRIENEN et al. 2012) and/or other climatic parameters (SCHOLLÄN et al. 2014) along the lifespan of the investigated trees.

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