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## A new chronology of *Cedrela fissilis* (Meliaceae) for Southern Brazil: Combining classical dendrochronology and radiocarbon dating

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### ABSTRACT

*Cedrela fissilis* is a tree species widely distributed in the tropical biomes of South America. This species has visible annual growth rings and can live for several centuries. The present study aims to (i) develop a chronology of *C. fissilis* to the Southern Brazilian Plateau using traditional dendrochronological methods, (ii) validate the dendrochronological dating using the radiocarbon (<sup>14</sup>C) bomb pulse method, and (iii) determine the influence of temperature and precipitation variations and their teleconnections with the tropical Pacific Ocean temperatures on the annual radial growth of this species. The ring width chronology was developed using 24 *C. fissilis* trees. The Schulman years of 1957, 1962, 1963, 1966, 1969 and 1974 were independently dated using the <sup>14</sup>C bomb pulse methodology by accelerator mass spectrometry (AMS). Tree-ring indices were compared with temperature and precipitation records from stations around the study forest. The chronology covers the period 1907–2018 (111 years) and is well replicated (> 10 trees) from 1941 onwards. Statistics commonly used in dendrochronology indicate that the chronology is highly reliable and of good quality (mean series intercorrelation  $r = 0.49$ ;  $R_{bar} = 0.30$ ;  $EPS = 0.86$ ;  $MSI = 0.40$ ). The <sup>14</sup>C bomb pulse of selected calendar years showed that the trees were accurately dated using the classical cross-dating approach. Precipitation from November to December (wet period) is positively correlated with tree growth ( $r = 0.36$ ,  $n = 49$ ;  $p < 0.05$ ). In addition, variations in temperature from May to July are positively correlated with ring width ( $r = 0.39$ ,  $n = 49$ ;  $p < 0.05$ ), suggesting that *C. fissilis* growth is favored by abundant rainfall during the growing season and above-average winter temperatures. Interannual variation in the chronology is partially modulated by El Niño 3.4 (East Central Tropical Pacific Sea Surface Temperature) during Oct-Dec ( $r = 0.27$ ,  $n = 68$ ,  $p < 0.05$ ). The growth of *C. fissilis* trees is directly dependent on climate variability, suggesting that more abundant precipitation and higher winter temperatures, as projected for the future climate of southern Brazil, will have a positive effect on tree growth. However, prolonged droughts and high temperatures during the growing season will have a negative impact on tree growth, even in humid forests with high soil moisture content.

### 1. Introduction

Most of the climate records in southern Brazil began to be compiled in 1970 s (Instituto Nacional de Meteorologia - INMET, 2023). This relatively short period is not sufficient to properly understand the atmospheric circulation processes related to recent climate changes. Long-term climate records are needed to obtain a comprehensive view of

present and future climate variations. One way to extend the instrumental climatic records is through the use of proxies or paleoenvironmental records such as ice cores collected at high-latitude glaciers (Schwikowski et al., 2004), sedimentary samples from peat bogs (Behling, 1995), speleothems from caves (Trindade et al., 2018) and growth rings from woody plants (Fritts, 1976). The latter can be achieved through the use of dendrochronology, a paleoenvironmental technique

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that takes advantage of the wide distribution of woody plants on the planet. In addition, the low cost of equipment and analysis, and the application of well-established standard methods, allow dendrochronology to provide centennial to millennial-long records with annual resolution around the world.

Species of the genus *Cedrela* can live over 200 years (Brienen and Zuidema, 2005; Espinoza et al., 2014; Granato-Souza et al., 2019; Villalba et al., 1992). Among them, *Cedrela fissilis* is widespread in the tropical forest biomes of South America (see <https://www.gbif.org/species/7107974>). The annual growth rings of *C. fissilis* (Baker et al., 2017; Marcati et al., 2006) are demarcated by a band of marginal parenchyma and the semi-circular arrangement of its vessels, larger and more abundant pores in the earlywood (InsideWood, 2004-onwards, 2004; Marcati et al., 2006; Wheeler, 2011). Due to its longevity, wide distribution, and well-demarcated annual rings, *C. fissilis* has been widely used in tropical dendrochronological studies with applications to various research objectives (Andreacci et al., 2014; Assis-Pereira et al., 2018; Blagitz et al., 2019; Dünisch, 2005; Ortega-Rodriguez et al., 2023; Paredes-Villanueva et al., 2016; Tomazello-Filho et al., 2000).

As trees are able to record climatic variations in their annual rings, long-lived trees have been studied as climatic and ecological proxies of past environmental changes (Fritts, 1974; Schweingruber, 2007). However, dating growth rings of long-lived species in tropical-subtropical regions can be complex due to the presence of intra-annual density variations, which can often be confused with annual rings (De Micco et al., 2016). Furthermore, in years with extreme limiting conditions for tree growth, annual rings are not formed or are only partially formed in some sectors of the stem (Larson, 1994). An extreme situation was reported by Dos Santos et al. (2015) for unmanaged plantations of another subtropical species, *Ocotea porosa*, established in 1967, where up to 29 rings were missing in suppressed, dominated trees. On the other hand, in regions with two intrannual precipitation peaks, radiocarbon ( $^{14}\text{C}$ ) dating has shown that *Cedrela* trees can form two rings per year (Baker et al., 2017). In this context, multiproxy approaches can assist in the identification and correct dating of annual rings, adding robustness to chronologies. Accurately dated tree ring records can later be used in several other studies, such as forest management, species conservation, and as a reference for validating other chronologies in tropical-subtropical regions of Brazil.

Based on the premise that the genus *Cedrela* forms annual tree-rings in tropical Brazil (Baker et al., 2017; Santos et al., 2024, 2021, 2020), this study aims to develop a chronology of *C. fissilis* trees growing in southern Brazil under a subtropical climate regime. This region experiences well-distributed precipitation throughout the year and variations in summer/winter temperatures (Nimer, 1989). The goal of the current study is to investigate the potential of this species in reconstructing past climate variability in subtropical Brazil. In this context, the study has the following objectives: i. To investigate whether trees (70–110 years old) of *C. fissilis* form synchronous rings that can be properly cross-dated using traditional dendrochronological techniques; ii. To validate the dating of the tree ring series using the carbon  $^{14}\text{C}$  bomb pulse method; and iii. To determine the influence of temperature and precipitation variations and their teleconnections with the tropical Pacific Ocean temperatures on the annual radial growth of this species. If tree-ring variations demonstrate a robust common signal among trees and a significant relationship with local climate and tropical Pacific sea surface temperature (Niño 3.4), it may be feasible to leverage *C. fissilis* chronologies to reconstruct the region's historical climate patterns and their teleconnections with the El Niño-Southern Oscillation.

## 2. Material and methods

### 2.1. Study area

The study area is in the Brazilian Southern Plateau, a subtropical region in the mid-western part of the state of Santa Catarina, in a

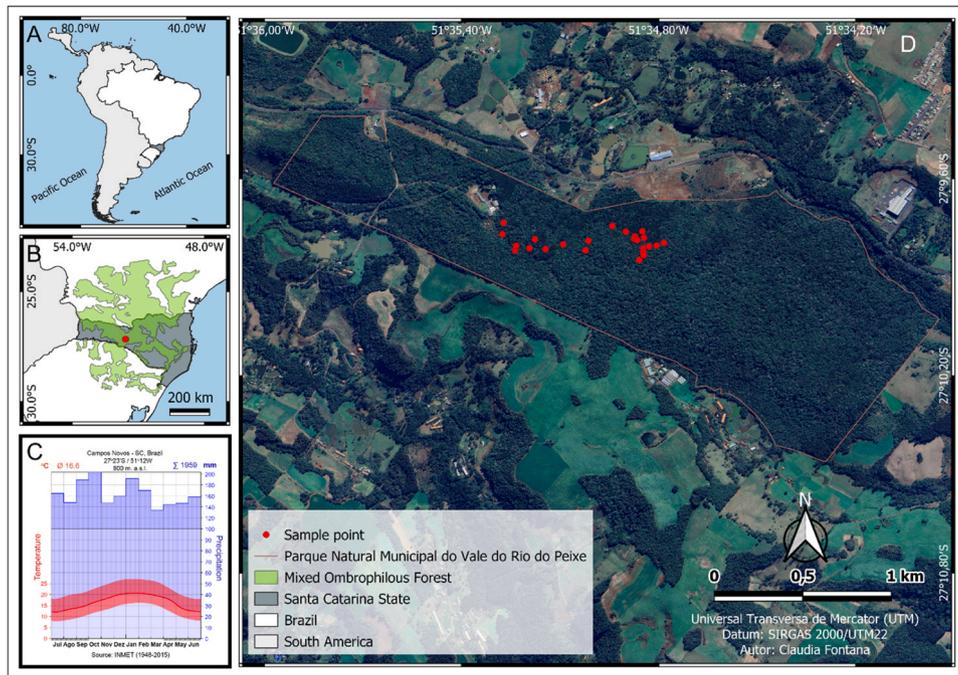
protected area called Parque Natural Municipal do Vale do Rio do Peixe (PVRP) (27° 9.908'S and 51° 34.639'W) (Fig. 1). This protected site covers an area of 250.82 ha and is located approximately 10 km from the center of Joaçaba, in the state of Santa Catarina. The mean elevation is 810 m a.s.l. The dominant vegetation cover is the Mixed Ombrophilous Forest (Instituto Brasileiro de Geografia e Estatística, 2012), also called Araucaria Forest due to the presence of the emblematic conifer *Araucaria angustifolia* in the landscape (Klein, 1978). The average annual temperature is 16°C and the total annual rainfall is around 2000 mm (Nimer, 1989), with higher precipitation in the spring (September to December; Klein, 1960) (Fig. 1C). Frost can occur from May to September with a frequency of about 10 days/year (Nimer, 1989). The main atmospheric systems influencing precipitation in this region are cold fronts, cyclonic vortices, mid-level depressions, and tropical convection associated with the South Atlantic Convergence Zone (SACZ) and maritime circulations (Monteiro, 2001).

### 2.2. *Cedrela fissilis* (Vell.) - a brief review

The neotropical genus *Cedrela* P. Browne (Meliaceae) comprises 17 species distributed across Central and South America (Muellner et al., 2010; Pennington and Muellner, 2010). In Brazil, there are two native species of this genus: *Cedrela fissilis* VELL. and *Cedrela odorata* L. (Flores, 2020). *Cedrela fissilis* is widely distributed and occurs in Argentina, Brazil, Bolivia, Colombia, Costa Rica, Ecuador, Panama, Paraguay, Peru, Suriname, Uruguay, and Venezuela (Backes and Irgang, 2009; Carvalho, 2003; Tomazello-Filho et al., 2000), inhabiting both humid and mesic tropical forests (Muellner et al., 2010). In Brazil, *C. fissilis* is found in several phytogeographies (Flores, 2020), especially in semideciduous and wet-evergreen Atlantic forests (Lorenzi, 2002). It is one of the most widely dispersed trees in the Brazilian southern states of Brazil (Klein, 1984), ranging from the Atlantic coast at the sea level to the montane ranges in the south and southeast at elevations of up to 1800 m (Carvalho, 2003). In Santa Catarina, *C. fissilis* is distributed throughout the Deciduous Forest formation, being more frequent at elevations below 1000 m (Vibrans et al., 2013), especially between 500 and 800 m (Gasper et al., 2018; Klein, 1984).

*Cedrela fissilis* is an emergent, dominant tree in the few remaining patches of the pristine forests (Backes and Irgang, 2009). Classified as a light demanding tree, it reaches 20–35 m in height and 60–90 cm in diameter (Lorenzi, 2002). Some trees as tall as 40 m and up to 3 m in diameter have been reported (Klein, 1984). Following major disturbances such as fires and selective logging during agricultural expansion (Backes and Irgang, 2009), *C. fissilis* is a pioneer species in “capoeiras” (Lorenzi, 2002) and a conspicuous component in mature forests (Carvalho, 2003). Across its distribution in Brazil, total annual rainfall ranges from 750 mm (Bahia) to 3700 mm (São Paulo mountains). Trees are found in regions with almost no seasonal water deficits (south of Brazil), moderately deficits with a dry season of up to 3 months (Midwest) to sites with severe water stress recording a dry season of up to 6 months (north of Minas Gerais) (Carvalho, 2003). *C. fissilis* can tolerate temperatures ranging from regions with a minimum average temperature of below 6°C in the coldest month (Santa Catarina) (Nimer, 1989) to regions where the average temperature of the hottest month can reach 27.7°C (Pará) (Carvalho, 2003).

*Cedrela fissilis* has visible growth rings due to the particular arrangement of vessels and parenchyma in the wood. Vessels show a semicircular to circular porosity with numerous solitaires or multiple large vessels at the beginning of the growing season. In addition, tree rings are delimited by a conspicuous marginal parenchyma band (López and Villalba, 2016), which facilitates ring identification (InsideWood, 2004-onwards, 2004; Wheeler, 2011). The dormancy of the cambial meristem is from June to August and its full reactivation occurs in October (Andreacci et al., 2017). In the region of Santa Catarina, blooming typically occurs from September to December, while fruit ripening occurs after leaf fall in July and August (Carvalho, 2003; Klein,



**Fig. 1.** Characteristic of the study area. Location of Santa Catarina State in South America (A); location of Santa Catarina State in the subtropical region of Brazil (B); location of the study area in the Midwest region of Santa Catarina (C), climo-diagram of the study region (D).

1984). The wood varies from light to moderately heavy, with a density between 0.47 and 0.61 g/cm<sup>3</sup> (Backes and Irgang, 2009; Carvalho, 2003; Lorenzi, 2002). In Brazil, its wood has a wide range of uses and is surpassed in its applications only by the wood of *Araucaria angustifolia* (Mainieri and Chimelo, 1989).

In plantations, *C. fissilis* shows a fast radial growth and the fruit production starts at the age of 10–15 years (Carvalho, 2003). It is suitable for the restoration of degraded areas (Backes and Irgang, 2009; Carvalho, 2003; Lorenzi, 2002; Reitz, 1978). According to Reitz (1978), it was one of the most abundant and economically significant trees in Santa Catarina. The tree was heavily exploited due to the value of its wood (Backes and Irgang, 2009).

### 2.3. Sampling and sample preparation

We sampled 33 trees of *C. fissilis* at heights ranging from 1.00 to 1.30 m from the ground. Two to four cores were collected per tree using manual increment borers of 5.1 mm in diameter. The diameter at breast height (DBH) was measured with a tape and the height with an electronic clinometer (Haglöf). The samples were mounted on wooden supports with carpenter's glue and polished with sandpapers with different grit sizes (80–1500 grit). Subsequently, each sample was dated under stereomicroscopy following the Southern Hemisphere (SH) convention (Schulman, 1956). Annual rings were assigned to the year in which the wood formation began. Scan high-resolution images (1200 DPis, Epson 12000XL scanner) were employed to measure the growth rings using imaging-analysis software with an accuracy of 0.001 mm (CooRecorder®, version 9.8.1, Larsson, 2014a).

### 2.4. Cross-dating and chronology building

After dating the samples, the software C dendro® (Larsson, 2014b) was used to select the radius showing the highest mean correlation coefficient with the other radii from the same tree. Only samples showing correlations greater than  $r \geq 0.5$  (T test  $\geq 4.0$ ), and overlap  $\geq 40$  years were retained to develop the main chronology. This selection procedure resulted in 10 well-correlated trees showing a consistent common

pattern of tree growth. The final cross-dating was checked using the program COFECHA (Holmes, 1986), considering the Pearson critical correlation (99% confidence level;  $r = 0.3665$ ) for analysis windows of 40 years overlapped every 20 years, and a 32-year spline. This main chronology was used as a reference series to correct the remaining samples. At the end of the cross-dating process, the final chronology included 24 of the 33 sampled trees.

After cross-dating, the ring-width series were standardized to filter out non-climate related growth variations using the program ARSTAN (Cook, 1985; Cook and Holmes, 1986). A Cubic Smooth Spline Function (SPL 50% variance cutoff at 30 years segment length) was fitted to the original series to calculate the ratios between observed and predicted values for each year resulting in nondimensional ring-width indexed (RWI) series. Finally, these series were integrated into a main standard chronology (STD) using a robust bi-weighted averaging function. The autocorrelation of the RWI series was filtered out by autoregressive modeling, and the resulting series integrated into a residual chronology (RES) also using a bi-weighted robust averaging function (Cook, 1985). The statistics used to characterize the quality of the chronologies were: mean and standard deviation (SD), mean sensitivity index (MSI), mean autocorrelation (AC), mean intercorrelation ( $r_{int}$ ), mean inter-series correlation ( $r_{bar}$ ), and the expressed population signal (EPS) (Fritts, 1976; Speer, 2010; Wigley et al., 1984). The  $r_{int}$  and MSI indices were calculated using the program COFECHA (Holmes, 1983) whereas the other dendrochronological statistics were estimated using the program ARSTAN (Cook and Krusic, 2005).

### 2.5. Annuality of growth rings

We applied <sup>14</sup>C bomb pulse dating to validate dates on the tree ring width chronology developed by classical dendrochronological methods. The approach was chosen as a means to validate our dendrochronology results, especially considering that chronology building based on manual increment borers from tropical and subtropical species is recognized as technically challenging.

We selected, following the Schulman convention (Schulman, 1956), the (t) years of 1957, 1962, 1963, 1966, 1969, and 1974. However,

post-bomb  $^{14}\text{C}$  levels tend to yield calendar years plus smaller units of time, such as months. Thus, we expect that those selected tree ring Schulman (t) years would grant  $^{14}\text{C}$  signatures in close proximity to the beginning of 1958, 1963, 1964, 1967, 1970, and 1975. Those latter times cover the period showing the largest differences in atmospheric  $^{14}\text{C}$  between consecutive calendar years during the past 70 years (Levin et al., 2022) as most aboveground nuclear tests during the bomb era were concentrated during 1955–1965 (Enting, 1982). Moreover, since the tests were largely concentrated in the North Hemisphere (NH), air circulation carrying bomb-derived  $^{14}\text{C}$  created a latitudinal gradient of this radioisotope. Current atmospheric  $^{14}\text{C}$  concentrations are divided into five geographical zones: NH1, NH2, and NH3 for NH, and SH1–2 and SH3 for those in SH (Hua et al., 2022). Since bomb  $^{14}\text{C}$  radioisotopes have been incorporated into all living organisms producing tissue directly from carbon dioxide (i.e., photosynthesis), tree rings can mirror the atmospheric  $^{14}\text{C}$  signal at the time the tissue was formed. The replication of  $^{14}\text{C}$  signatures at a given geographical zone using known aged tree rings is a robust way to validate dendrochronology dates (Santos et al., 2024, 2021, 2020). The  $^{14}\text{C}$  concentration in the rings of a dendrochronologically-dated specimen in particular, when compared with atmospheric  $^{14}\text{C}$  record from a distinctive geographic region can yield calendar years within < 1 year. Notably, high precision and accuracy are possible when the calendar years selected for tests show high atmospheric  $^{14}\text{C}$  activity levels, as those selected in this study.

Wood material weighing 20–30 mg was collected from each selected ring based on the marginal parenchyma as the border between rings, not including material from neighbor rings. Labeled samples were shipped to the Keck Carbon Cycle AMS (KCCAMS) facility at University of California, Irvine (UCI) for chemical extraction of  $\alpha$ -cellulose, graphite target processing, and  $^{14}\text{C}$  analysis. At KCCAMS/UCI,  $\alpha$ -cellulose was isolated following from Santos et al. (2023). This chemical method, which does not make use of any organic solvents to remove extractives, has been rigorously tested on a large array of  $^{14}\text{C}$  aged woods including post-bomb ones across the Pantropical region (Biondi et al., 2023; Santos et al., 2024, 2022, 2021). Here, wood material was chemically processed alongside of reference materials whose  $^{14}\text{C}$  values are well known, e.g., FIRI-J barley (post-bomb) and AVR wood-blank ( $^{14}\text{C}$ -free wood). Other reference materials added to this wood batch are combustible materials (NIST HOx2 SRM-4990 C) and ANU-sucrose designed to evaluate measurement performance. All samples were heated at 900°C in quartz sealed tubes per 3 hours to evolve  $\text{CO}_2$ , follow by reduction to filamentous graphite using the Zn method (Santos and Xu, 2017). Graphite targets were pressed into aluminum target holders and then measured at a modified compact accelerator mass spectrometer (AMS) system (NEC 0.5 MV 1.5SDH-1) with  $^{12}\text{C}$  and  $^{13}\text{C}$  measurement capabilities (Beverly et al., 2010). Radiocarbon data are reported as  $F^{14}\text{C}$  (according to recommendations of Reimer et al., 2004) after normalization to primary standard (NIST HOxI SRM 4990B), isotopic fractionation corrections using online- $\delta^{13}\text{C}$ , and the subtraction of the in-house wood processed blank (AVR) (Santos et al., 2007; Stuiver and Polach, 1977).

Results of tree ring  $F^{14}\text{C}$  and uncertainties were converted to calendar years using the online CALIBomb software (<http://calib.org/CALIBomb/>), which allowed us to derive the most likely timing of tissue formation associated with the tree rings measured. Dendrochronology dates and calibrated  $^{14}\text{C}$  calendar years were then compared to evaluate the annual periodicity in tree-ring formation. We chose to compare our data to two geographical zones from SH, i.e., SH1–2 and SH3 (Hua et al., 2022), because the tropical low-pressure zone over South America reaches its southernmost position during the austral summer (Hogg et al., 2020).

## 2.6. Dendroclimatic signals

The local climate data (mean monthly temperature and total monthly precipitation) was obtained from the Instituto Nacional de

Meteorologia (INMET, 2023; <https://bdmep.inmet.gov.br/>). Temperature and precipitation series from two conventional weather stations located at Joaçaba and Campos Novos (~60 km away from the study area), represent the longest (1969–2018) and most complete climate records for the region. In order to increase the reliability and representation of the meteorological data, the Campos Novos and Joaçaba climate records were compared to create a single homogeneous record. Based on this information, regional composite records based on the means from the SDs were developed for temperature and precipitation. To determine the relationships between variations in climate and annual radial growth, correlation analyses were used based in InfoStat software (Balzarini et al., 2008). A simple method for comparing variations in climate and tree growth is the correlation function (Blasing et al., 1984), which examines the statistical relationships between ring width and climate over the common period, in our case 1969–2018 (49 yr). Because tree growth in a given year may be influenced by climate conditions in previous years, the comparison period analyzed comprised a sequence of 16 months for both temperature and precipitation, starting in January from the previous growing season and lasting until April at the end of the current growing season. Since the interannual variability of precipitation in the subtropical region of Brazil is strongly influenced by the Southern Oscillation (Montecinos et al., 2000), the chronology of *C. fissilis* was compared over 68 years (1950–2019) with Niño 3.4 Sea Surface Temperature (SST) anomalies in the tropical Pacific (<https://www.cpc.ncep.noaa.gov/data/indices/ersst5.nino.mth.91-20.ascii>). Finally, we estimated the spatial patterns of correlation between *C. fissilis* tree-ring chronology, regional precipitation, and ERA5 Near-Surface Air Temperature (T2m) over South America and the tropical Pacific Ocean using the facilities provided by Koninklijk Nederlands Meteorologisch Instituut (KNMI) Climate Explorer (<https://climexp.knmi.nl/start.cgi>). The ERA5-T2m record was chosen because it encompasses the entire global surface temperature, allowing for more accurate testing of simulations worldwide (Scafetta, 2022). If the growth of *C. fissilis* is influenced by ENSO events, our chronology should show temporal variations that align with those observed in ENSO 3.4. Additionally, the spatial pattern of correlation between our chronology and surface temperatures (T2m) should be consistent with that resulting from comparing regional precipitation with T2m.

## 3. Results

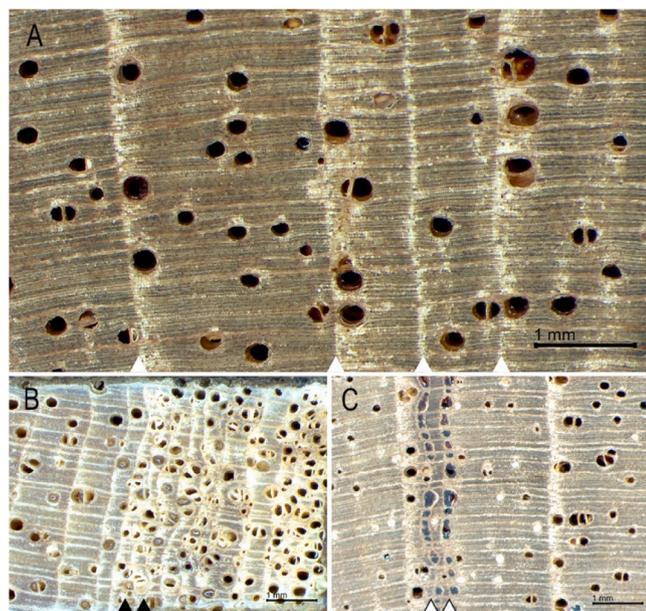
### 3.1. Wood anatomy and growth rings

Growth rings in *C. fissilis* are visible to the naked eye, even before conducting a careful polishing of the samples. The *C. fissilis* wood exhibit semicircular to circular porosity with numerous, large solitary or multiple vessels in the earlywood. A conspicuous marginal parenchyma band is regularly used to determine the separation between annual rings (Fig. 2). This light-color parenchyma, frequently surrounding the large vessels at the beginning of the earlywood, contrasted with the darker latewood dominated by small vessels and a larger proportion of fibers (Fig. 2A). As trees increased in diameter, growth rings usually became narrower making ring counting more difficult. In cluster of micro-rings, the marginal parenchyma from contiguous rings tends to merge, making ring determination problematic (Fig. 2B). Wedging rings were occasionally recorded in *C. fissilis*. Occasional traumatic canals were observed along individual growth rings or randomly located within the rings (Fig. 2C).

Based on the tree-ring width measurements from the 24 cross-dated tress of *C. fissilis*, the mean diametric growth is 0.49 cm/year (111 years), reaching maximum and minimum means of 0.98 cm and 0.13 cm for the years 1915 and 1956, respectively.

### 3.2. Crossdating and chronology building

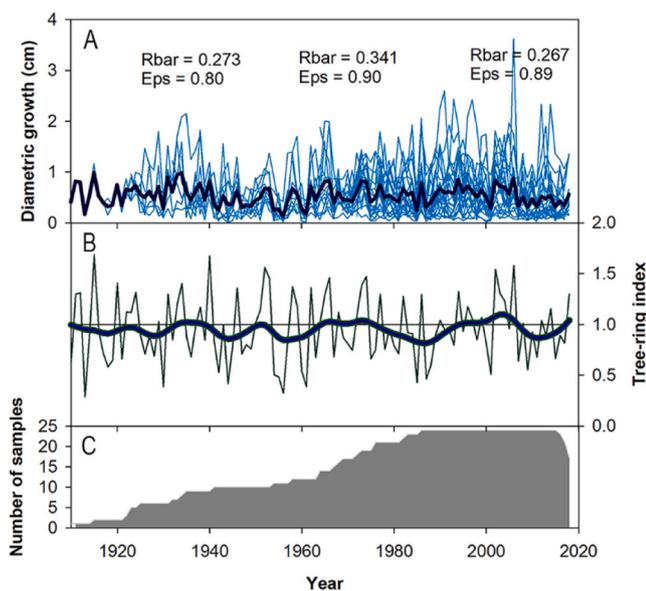
The *C. fissilis* chronology is based on 24 out of the 33 collected trees,



**Fig. 2.** Transversal section of *Cedrela fissilis* wood. Well-marked annual rings delimited by axial marginal parenchyma and semi-ring-porous (white arrowheads) (A). Micro-rings (black arrowhead) (B). Traumatic canals (arrowheads filled white) (C). Bars = 1 mm.

covers the period 1907–2018 (111 years) and shows a good replication from 1941 onwards (> 10 trees, Fig. 3). Statistics commonly used in dendrochronology to evaluate the quality of tree ring records indicate that the chronology of *C. fissilis* is highly reliable and of good quality (Table 1).

The chronology shows a marked inter-annual variability in growth rates (MSI = 0.585), with contrasting periods of low and high radial growth (Table 1). Periods of above-average tree growth are recorded from 1964 to 1974 and particularly during the interval 1998–2006. In



**Fig. 3.** Annual variations of tree-ring width per tree (blue lines) with mean (dark blue line, top graph) and residual tree-ring chronology (middle graph) of *Cedrela fissilis* collected in the Parque Natural Municipal do Vale do Rio do Peixe, Brazil (A). In order to highlight long-term interannual variations, the chronology was smoothed with a cubic spline (dark line) that highlights low-frequency variations in 15-year intervals (Cook and Peters, 1981) (B). The variation in sample size over time is presented in C.

**Table 1**

Statistics for the residual ring-width chronology of *Cedrela fissilis* in the Parque Natural Municipal do Vale do Rio do Peixe, Brazil.

| Parameter  | Values  |
|--|---|
| Crossdating period                               | 1907–2018 (111 years)                         |
| Mean length of series (year)                     | 68 (Min = 33; Max = 111; SD = 22)             |
| Trees / trees dated / cores crossdated           | 33 / 24 / 24                                  |
| <b>Individual series statistics</b>              |   |
| Diametric growth (cm)                            | 0.49 (Min = 0.13 Max = 0.98; SD = ±0.83 cm)   |
| Mean sensitivity index (MSI)                     | 0.585 (Min = 0.395; Max = 0.729; SD = ±0.079) |
| Intercorrelation between tree-ring series (rint) | 0.470 (Min = 0.343; Max = 0.607; SD = ±0.05)  |
| <b>Standardized chronology statistics</b>        |   |
| Mean correlation between series (rbar)           | 0.229 (Min = -0.20; Max = 0.75; SD = ±0.15)   |
| Standard error (SE)                              | 0.009   |
| Mean expressed population signal (EPS)           | 0.86  |
| Mean sensitivity index                           | 0.405   |

contrast, periods with below-mean radial growth were recorded in 1911–1932, 1939–1949, 1951–1963, in the 1980–1990 s, and from 2006 to 2016 (Fig. 3).

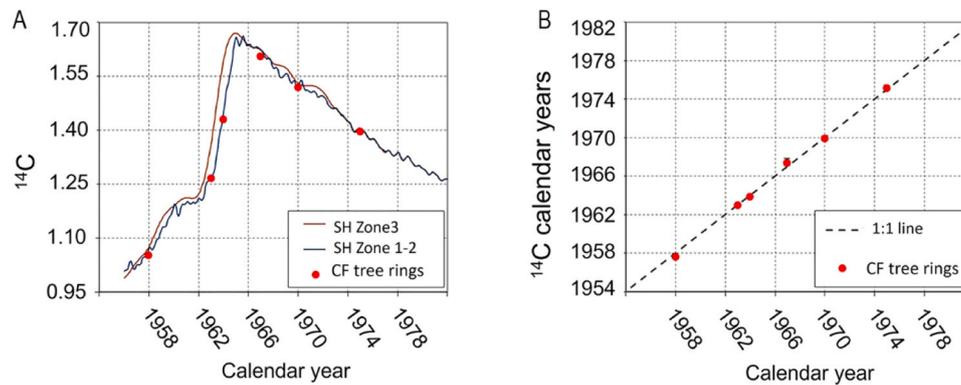
### 3.3. Annuality of growth rings

Following the visual dating of the growth rings and its control by the program COFECHA, we pursue an additional checking of the dates by means of the  $^{14}\text{C}$  calibration curve using the datasets of geographical zones SH1–2 and SH3, according to Hua et al. (2022) (Fig. 4). The  $F^{14}\text{C}$  associated value of each calendar year's individual tree rings were plotted alongside the atmospheric  $^{14}\text{C}$  calibration curves (Fig. 4A). We also plotted the relationship between the dendrochronology date and calibrated  $^{14}\text{C}$  dates (Fig. 4B), using the  $^{14}\text{C}$  calendar years derived from the SH1–2 curve. Since tree growth of *C. fissilis* in this study was found to be positively correlated with precipitation running from November to January, the dendrochronological dates (or Schulman years (t)) in Figs. 4A and 4B were adjusted by the addition of 0.95 (December 15). While whole rings may take 3 months in total to reach completion, starting growing wood cells at the preceding year and reaching cessation in the next, we assume that it would be appropriate to use an average monthly correction of 0.95 for dendrochronological dates.

The  $F^{14}\text{C}$  of selected tree-rings of *C. fissilis* is in perfect synchronization with the bomb SH1–2 curve (Fig. 4A, B). The highly consistent dating pattern between traditional and radiometric methods, indicates that the growth rings are annually formed, but most importantly, well dated. *Cedrela fissilis* calendar ages and their variations (shown in Table 2) are better lined up with those of SH1–2, as all  $F^{14}\text{C}$  values yielded calendar years within the wetter season over the southernmost region of Brazil. As such, we also confirm that most (if not all tree species) in the Vale do Rio do Peixe are most likely primarily sensitive to changes in air parcels geographical provenances carrying  $^{14}\text{C}$  originated at middle to higher SH latitudes, as other tree species in the SH1–2 large geographical zone (Hua et al., 2022). Radiocarbon results, as  $F^{14}\text{C}$  and calibrated  $^{14}\text{C}$  ages, are detailed for each of the tree rings analyzed in Table 2.

### 3.4. Climate-tree growth relationships

The radial growth of *C. fissilis* in the South Atlantic Forest is favored by rainfall during the wet season (Fig. 5 upper right). Radial growth is significantly related to spring-summer rainfall, specifically to November rains during the current growing season. In addition, radial growth is positively related to temperature during the coldest winter months. The correlation coefficients are significant during June–July in the winter previous to the growing season (Fig. 5 upper left), that represent the



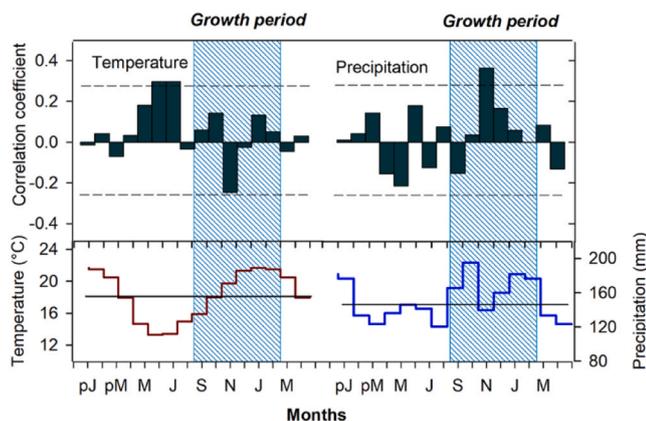
**Fig. 4.** Radiocarbon values of dendrochronological dated tree ring samples from *Cedrela fissilis* (red circles) are shown as (A)  $F^{14}C$  values against the current atmospheric  $^{14}C$  records of Southern Hemisphere (SH1-2 and SH3; Hua et al. 2022); and (B) dendrochronological dates versus calibrated  $^{14}C$  derived dates using CALIBomb and the SH1-2 dataset. Individual results for each  $F^{14}C$  value and associated  $^{14}C$  calendar year upon calibration are shown in Table 2. Uncertainties were calculated according to the range of the age interval that best fit expected results, and they are mostly shadowed by symbols. R-squared of 0.9988 was obtained from dated years and  $^{14}C$  calendar years relative to 1:1 dashed line.

**Table 2**

Radiocarbon results as F14C (Fraction Modern Carbon) from selected tree rings of the *Cedrela fissilis* at Parque Natural Municipal do Vale do Rio do Peixe, Brazil. Averaged 14 C calibrated years using CALIBomb, centered on the datasets of SH1-2 and SH3 and 95% confidence are also shown.

| UCIAMS# | Sample name   | Schulman years (t) | Corrected years (t+0.95) | $F^{14}C \pm 1\sigma$ | Av. $^{14}C$ cal. yr (SH1-2) | Av. $^{14}C$ cal. yr (SH3) |
|---------|---------------|--------------------|--------------------------|-----------------------|------------------------------|----------------------------|
| 278366  | CF(6-68c)1957 | 1957               | 1957.95                  | $1.0530 \pm 0.0018$   | $1957.7 \pm 0.3$             | $1957.5 \pm 0.3$           |
| 278367  | CF(5-68c)1962 | 1962               | 1962.95                  | $1.2682 \pm 0.0018$   | $1963.0 \pm 0.1$             | $1962.5 \pm 0.1$           |
| 278368  | CF(4-68c)1963 | 1963               | 1963.95                  | $1.4320 \pm 0.0019$   | $1963.9 \pm 0.1$             | $1963.3 \pm 0.1$           |
| 278369  | CF(3-68c)1966 | 1966               | 1966.95                  | $1.6064 \pm 0.0021$   | $1967.5 \pm 0.4$             | $1967.4 \pm 0.3$           |
| 278370  | CF(2-68c)1969 | 1969               | 1969.95                  | $1.5215 \pm 0.0021$   | $1969.9 \pm 0.2$             | $1970.9 \pm 1.3$           |
| 278371  | CF(1-68c)1974 | 1974               | 1974.95                  | $1.3970 \pm 0.0021$   | $1975.2 \pm 0.3$             | $1975.2 \pm 0.3$           |

UCIAMS# - reference code associated to each individual 14 C result produced by the KCCAMS/UCI facility.



**Fig. 5.** Relationships between *Cedrela fissilis* tree growth and climate (temperature at left and precipitation at right), using a composite record from Campos Novos and Joaçaba weather stations from January of the previous season to April of the current growing season (upper). Correlations greater than  $r = 0.26$  (dashed lines) are statistically significant ( $p < 0.05$ ; period 1969–2018). The current growing season for *C. fissilis* in the study region is highlighted. Monthly variations for temperature and precipitation at the Campos Novos weather station during the comparison period (below).

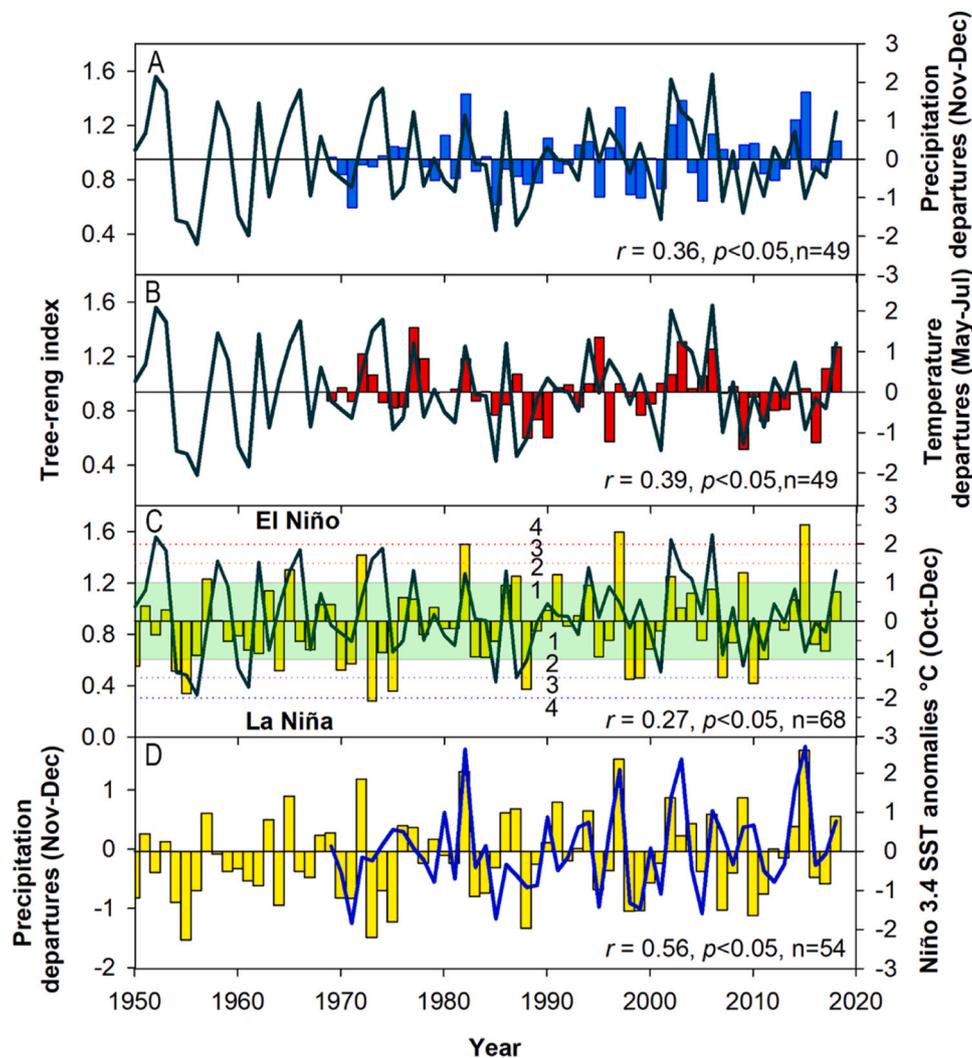
coldest months in the study region (Fig. 5 bottom). Based on seasonal periods, the interannual variations in tree growth of *C. fissilis* are significant positively correlated ( $r = 0.36$ ,  $n = 49$  years, 1969–2018) with November-December precipitation in the Vale do Rio do Peixe. In addition, interannual variations in May-July temperature and ring width are also positively correlated ( $r = 0.39$ ,  $n = 49$ , Fig. 6). Over the 68-year period from 1950 to 2018, the growth of *C. fissilis* exhibited a significant correlation with sea surface temperatures in the Central-eastern Tropical

Pacific (Niño 3.4) region during October-December ( $r=0.27$ ,  $p<0.05$ , Fig. 6, bottom). These results align with the highly significant relationships between our regional precipitation record in November-December and October-December Niño 3.4 SSTs ( $r=0.56$ ,  $n=54$ ,  $p<0.01$ ; Fig. 6). Although weaker, the spatial correlation pattern between the *C. fissilis* chronology and ERA5 T2m is similar to the correlation pattern between the regional precipitation and T2m, indicating the significant influence of SSTs over the tropical Pacific (Niño 3.4) and the tropical-subtropical sector of the Atlantic in front of South America on both regional precipitation and *C. fissilis* tree growth (Fig. 7).

## 4. Discussion

### 4.1. Wood anatomy and growth rings

The annual rings of *Cedrela fissilis* are visible due to the particular arrangement of vessels and parenchyma in the wood. Vessels exhibit a semicircular to circular porosity with numerous solitary or multiple large vessels at the beginning of growing season. In addition, tree rings are delimited by a conspicuous marginal parenchyma band. These anatomical characteristics are common in this species and were observed in trees growing in different biomes of South America, such as the mountain cloud forests of Bolivia, the Cerrado and the Atlantic Forest of Brazil (Andreacci et al., 2017; López and Villalba, 2016; Marcati et al., 2006; Paredes-Villanueva et al., 2016; Pereira et al., 2018; Quintilhan et al., 2021; Santos et al., 2021). Previous studies have indicated that traumatic resin canals may be present in up to 40% of samples (Dünisch and Baas, 2006). However, in our sample, they were only observed on an occasional basis. Traumatic canals within the Meliaceae family are linked to injuries occurring to the cambium or the formation of axial parenchyma cells (Dünisch and Baas, 2006). The gums and resins exuded via these canals are presumed to function in inhibiting invading organisms and effectively sealing the wound surface



**Fig. 6.** Comparison between year-on-year variations of regional deviations in (A) precipitation (November-December) and (B) temperature (May-July) with the growth of *Cedrela fissilis* during the common period 1969–2018. The effects of El Niño and La Niña (anomalies Niño 3.4 ST, <https://www.cpc.ncep.noaa.gov/data/indices/ersst5.nino.mth.91-20.ascii>) on the growth of *C. fissilis* in the Municipal Natural Park do Vale do Rio do Peixe (C). The numbers indicate: 1 Weak, 2 Moderate, 3 Strong and 4 Very strong El Niño/La Niña events. Strong relationships between Oct-Dec El Niño 3.4 and Nov-Dec regional precipitation (D).

for protection (Larson, 1994). In addition to mechanical injuries, traumatic canals can be triggered by other exogenous factors, such as frost (Schweingruber, 1988).

It is common to observe that as the *C. fissilis* trees increase in diameter, the growth rings become narrower, making more difficult to count and date the year of ring formation accurately (Boninsegna et al., 1989; Villalba et al., 1987). In sectors with numerous micro-rings, the parenchyma is more abundant, making it difficult to precisely delimit the growth rings. The frequent presence of micro-rings limited the accurate dating of the rings and made much more difficult to develop chronologies based on a common pattern of interannual variability in tree growth (López et al., 2012; Villalba et al., 1985). In order to confirm the dating precision, and consequently the annual nature of tree rings in tropical and subtropical species, post-bomb  $^{14}\text{C}$  dating are frequently used (Baker et al., 2017; Dezzeo et al., 2003; Hammerschlag et al., 2019; Santos et al., 2021, 2020). Although the annuality of growth in *C. fissilis* has already been confirmed for different biomes by visual dating and cross-dating (Holmes, 1986; Schöngart et al., 2017), in this study we used  $^{14}\text{C}$  analysis to verify the initial dating using traditional dendrochronological techniques.

The post-bomb  $^{14}\text{C}$  analysis confirmed the annual nature of growth ring formation in *C. fissilis* by direct comparison of selected calendar

years with their respective  $\text{F}^{14}\text{C}$  values obtained by  $^{14}\text{C}$ -AMS, once the former were either directly compared to compiled atmospheric  $^{14}\text{C}$  datasets for the SH (Hua et al., 2022) or after  $\text{F}^{14}\text{C}$  calibration using the CALIBomb software. In this context, the dendrochronological record developed in this study for the Atlantic Forest in southern Brazil, represents the first *C. fissilis* chronology in which the traditional dating method have been confirmed with  $^{14}\text{C}$  dates. In turn, this  $^{14}\text{C}$  analysis supports the idea of adding species from non-seasonal environments, such as the Atlantic or tropical rainforests, to the current network of chronologies in the tropics. In addition, the correctly-dated growth rings in *C. fissilis* represent a solid proxy indicator of regional climate variability and provide short-term, precise information on atmospheric  $^{14}\text{C}$  values for the Southern Hemisphere.

Our dendrochronological study of *C. fissilis* trees at the Parque Natural Municipal do Vale do Rio do Peixe, provide precise information on the current diametric growth rate of the species over an interval of 111 years (1907–2018). This mean rate of growth is within the reported ranges *C. fissilis* (0.37–0.53 cm) for the states of Santa Catarina and Paraná in southern Brazil (Stepka et al., 2021). For the Cerrado and some tropical rainforests, similar rates of annual growth (0.38–0.60 cm/year) have also been reported for *C. fissilis* with small differences attributed to the amount and seasonality of moisture in the

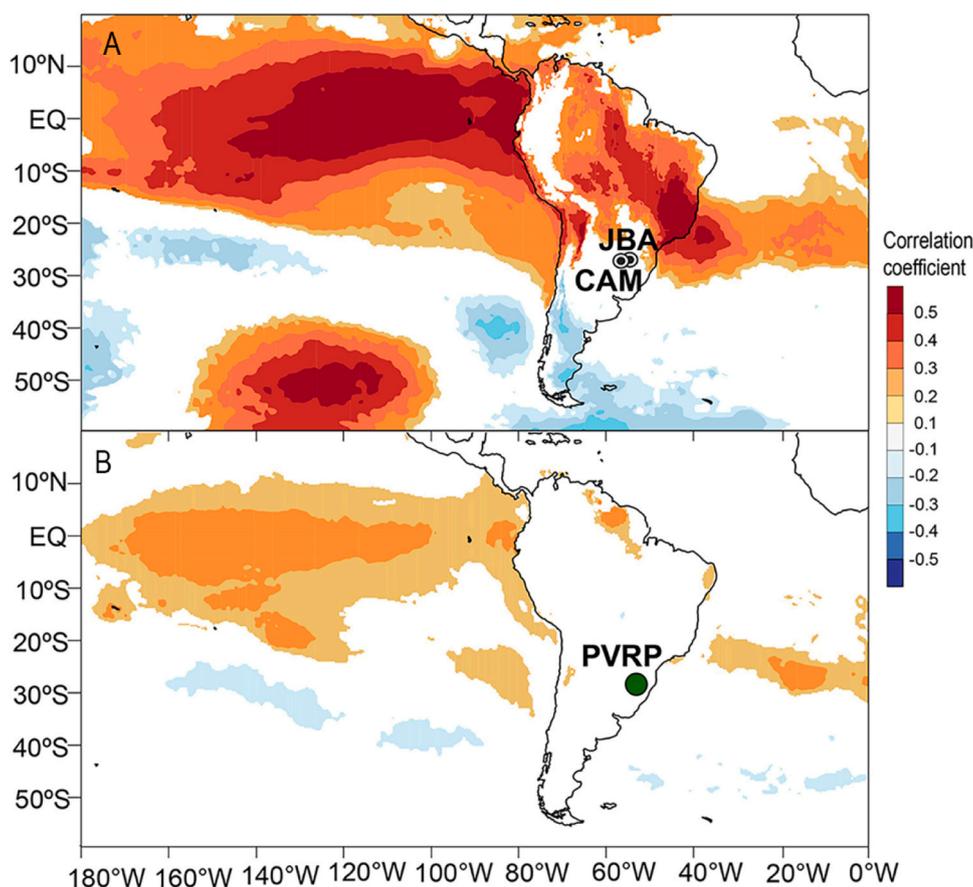


Fig. 7. Spatial correlation patterns between (A) October-December regional precipitation and October-December ERA5 surface (T2m) temperature, and (B) between *Cedrela fissilis* residual chronology at Parque do Vale do Rio do Peixe (PVRP) and November-December ERA5 surface (T2m) temperature across the Pacific and Atlantic Oceans between 20°N and 60°S latitude. The regional precipitation record is a composite from Joaçaba (JBA) and Campos Novos (CAM) weather stations.

soil, the extension of the dry period, age of the trees, and disturbance history of the sites (López et al., 2019; Marksteijn et al., 2010; Pereira et al., 2018; Worbes, 1999). While many studies carried out for this species at similar latitudes do not report the growth rates, this information provides an accurate knowledge of its growth ecology, productive capacity, and response to current environmental changes.

#### 4.2. Chronology statistics

The *Cedrela fissilis* chronology represents one of the first accurately dated (by classical chronology and  $^{14}\text{C}$ ), well-reproduced, and statistically reliable records for the Atlantic rainforests in Brazil. Traditional statistics commonly used in dendrochronology indicate that the *C. fissilis* chronology is of good quality and contains a strong common signal in tree growth variability. The tree-series intercorrelation  $r = 0.47$ , the  $R_{\text{bar}} = 0.23$ , and the expressed population signal,  $\text{EPS} = 0.86$ , show similar values to those reported for most chronologies in the Southern Hemisphere, even for records from colder sites with marked seasonality in temperature and precipitation. The  $R_{\text{bar}}$  values for the *C. fissilis* chronologies range from 0.25 in the Atlantic forest of the state of Paraná (Marcon et al., 2022), 0.26 in the tropical rainforests, 0.28 in the dry forests of the Bolivian Cerrado (Paredes-Villanueva et al., 2016) to 0.52 in the Brazilian Cerrado (Pereira et al., 2018). The  $R_{\text{bar}}$  for our chronology is consistent with an important common signal in the tree-ring variation and considerable replication in the chronology. The  $R_{\text{bar}}$  statistic is consistent with an EPS value above the threshold of 0.85, which also indicates that the replication in the chronology is adequate, and therefore, captures a high percentage of the theoretical common signal in tree-ring variations (Briffa, 1995; Wigley et al., 1984). The

species' high sensitivity to climate variations is reflected in the mean sensitivity index ( $\text{MSI} = 0.585$ ), which is determined by the presence of micro or missing rings alternating with very wide rings (Speer, 2010). This high sensitivity ( $> 0.45$ ) was also reported by Andreacci et al. (2014) for other populations of *C. fissilis* in southern Brazil.

Although chronologies longer than 200 years have been reported for *C. fissilis* in pristine Amazonian forests (Ortega-Rodriguez et al., 2023), records similar in length to our chronology have been developed in Paraná forests (43–116 years; Marcon et al., 2022) and in the Bolivian humid tropics (84–88 years; Paredes-Villanueva et al., 2016). In this context, our chronology based on 24 trees covering the last 111 years for the remnant Atlantic forests becomes an important contribution to dendroclimatology. Moreover, considering the rarity and lack of long-lived specimens in a region where instrumental records are scarce and of short duration, this chronology is currently the most important climatic proxy source for the Atlantic forests in Brazil.

#### 4.3. Climate-tree growth relationships

The relationships between variations in the regional climate and in the radial growth of *Cedrela fissilis* identified in this study share similarities with those recorded for other emblematic species of the Atlantic forest of southern Brazil (Marcon et al., 2022). Radial growth is mostly modulated by variations in precipitation during the growing season, being highly significant during the month of November. Abundant rainfalls in October increase soil moisture content and favor the onset of *C. fissilis* tree growth. Our results are consistent with Marcati et al.'s (2006) study, which indicates that cambium division is concentrated in November and December, months with heavy rainfall, although slightly

less than in October. The correlation pattern suggest that the radial growth is modulated by the water supply during these three months in the spring-to-summer transition, which also corresponds to the warmer period of the year peaking in January. A similar response to climate for *C. fissilis* and other species of the same genus has been observed in the humid Central Brazilian Amazon and Atlantic coastal forests (Dünisch et al., 2003; Venegas-González et al., 2014). In contrast to previous studies in the region, no significant influence of previous growing season rainfall on wood production was recorded.

Based on the correlation functions, we noted that tree growth appears to be sensitive to low winter temperatures (May to July), interval concurrent with less abundant precipitation in the study region. Unlike to previous results from tropical-subtropical studies, radial growth in southern Brazil is directly related to temperature during the months of June and July, suggesting that the radial growth of *C. fissilis* in the Parque Natural Municipal do Vale do Rio do Peixe is favored by mild, not cold winter temperatures. The forests of *C. fissilis* in Vale do Rio do Peixe are located at the southern end of its wide distribution in the tropical regions of South America. Therefore, it is possible that these forests are affected by the winter temperatures in southeastern Brazil, which have lower thermal records than other regions where the species occurs.

Consistent with our results, this pattern of response has also been observed at sites near the study area, noting that maximum winter temperatures are positively correlated with tree growth (Venegas-González et al., 2018). Understanding the growth patterns of *C. fissilis* and their interactions with climate variability becomes crucial face the challenges posed by accelerating climate change. Local climate variability, sometimes induced by teleconnections with global or hemispheric climate forcing, affects tree growth rates and consequently competitive interactions among individuals in forests (Schöngart et al., 2004; Stenseth et al., 2003; Viegas et al., 2019). The Southern Oscillation, centered in the tropical Pacific, is the main mode of interannual climate variability associated with local and regional climate anomalies across the globe (Grimm and Tedeschi, 2009; Viegas et al., 2019). This phenomenon causes El Niño and La Niña events, which have a major impact on climate affecting regional and local economies in Brazil (Araújo, 2012; Berlatto et al., 2005). In southern Brazil, El Niño is associated with an increase in precipitation and higher temperatures. On the other hand, the opposite effect is often observed during La Niña events, with a tendency towards drought and lower temperatures in southern Brazil (Barros et al., 2002; Marengo and Camargo, 2008; Valente et al., 2023). Thus, climatic conditions in our study area are largely modulated by El Niño/La Niña, with intense rains and severe droughts during these events, respectively. Sea surface temperatures from October to December in the Niño 3.4 sector strongly modulate spring rainfall variations in our study region and thus interannual variations in *C. fissilis* growth (Fig. 6). The spatial correlation patterns shown in Fig. 7 clearly indicate that the forcing associated with the regional climate variability is indirectly modulating the growth of the trees in the region. Prolonged El Niño and La Niña events (two or more consecutive years), have a direct effect on tree growth.

## 5. Conclusions

The presence of trees with clearly defined annual growth rings in the threatened and heavily impacted Atlantic rainforests provides precise information to address many ecological and environmental questions that are crucial for the conservation of these forests. In the Parque Natural Municipal do Vale do Rio do Peixe, *Cedrela fissilis* shows annual tree rings, that our study was able of verifying using post-bomb  $^{14}\text{C}$  dating. The combination of two techniques, the traditional visual dating complemented with sample cross-dating and the independent verification using post-bomb  $^{14}\text{C}$  analysis, allowed us to build a solid chronology resulting from the exact and consistent dating of selected years for comparison.

Through the measure of 1596 rings from 24 trees with ages exceeding 100 years, a solid chronology of *C. fissilis* was developed for the Atlantic Forest in southern Brazil. Based on this statistically reliable and well-replicated chronology, we were able to determine that inter-annual variations *C. fissilis* growth are modulated by regional climate, mainly precipitation variations during the wet period and thermic conditions in the cold season. Indeed, the growth of *C. fissilis* is favored by abundant rainfalls in the transition from spring to early summer (October to December). In addition, above-mean winter temperatures favor tree growth. The direct dependence of *C. fissilis* tree growth on climatic variations suggests that future climatic changes in southern Brazil and variations in the frequency of prolong El Niño-La Niña events might have a major impact on tree growth, even in the Atlantic Forests where current soil moisture is not a major constraint for tree growth. Sea surface temperatures in the El Niño 3.4 sector from October to December are key in modulating spring rainfall and, consequently, the interannual growth variations of *C. fissilis*.

## CRedit authorship contribution statement

**Bruna Hornink:** Writing – review & editing, Visualization. **Guaiciara M. Santos:** Writing – review & editing, Visualization, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Ricardo Villalba:** Writing – review & editing, Visualization, Validation, Methodology, Investigation, Formal analysis, Conceptualization. **Mario Tomazello-Filho:** Writing – review & editing, Supervision, Resources, Funding acquisition. **Gabriel Assis-Pereira:** Writing – review & editing. **Fidel A. Roig:** Writing – review & editing. **Cláudia Fontana:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Lidio López:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

## Declaration of Generative AI and AI-assisted technologies in the writing process

We do not use generative artificial intelligence (AI) and AI-assisted technologies in the writing process.

## Declaration of Competing Interest

As corresponding author, representing all authors of this submission, I hereby declare that we have no financial or personal relationships with individuals or organizations that could potentially influence (bias) the integrity of this work in any inappropriate manner.

## Data availability

Data will be made available on request.

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