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Climatic Response of Cedrela fissilis Radial Growth in the Ombrophilous Mixed Forest, Paraná, Brazil

Amanda Koche Marcon¹ , Tomaz Longhi-Santos², Franklin Galvão² Kelly Geronazzo Martins³, Paulo Cesar Botosso⁴, Christopher Thomas Blum²

¹Programa de Pós-Graduação em Engenharia Florestal, Departamento de Ciências Florestais, Universidade Federal do Paraná - UFPR, Curitiba/PR, Brasil

²Departamento de Ciências Florestais, Universidade Federal do Paraná – UFPR, Curitiba/PR, Brasil ³Departamento de Engenharia Ambiental, Universidade Estadual do Centro Oeste - UNICENTRO, Campus de Irati, Irati/PR, Brasil

⁴Embrapa Florestas, Empresa Brasileira de Pesquisa Agropecuária – EMBRAPA, Colombo/PR, Brasil

ABSTRACT

We examined the climatic response of Cedrela fissilis radial growth based on precipitation, air relative humidity, temperature and monthly thermal amplitude. It was intended to assess how the secondary growth of C. fissilis is influenced by the climatic variables and which one are the best growth predictors in Ombrophilous Mixed Forest, southern Brazil. Wood cores were processed using classical dendrochronology methodology. Principal Components Analysis, Generalized Linear Models and correlation were used to explore the relationship between radial growth and climate. Our results indicated that the best radial growth predictor is the temperature: the seasonal behavior, under well-watered conditions, seems to have a dominant effect on growth responses. Changes in tree growth corresponding to an increase in temperatures suggest a sensitivity of the species to climate changes. These results are important to help understand how the global warming may influence long-lived pioneer tree growth.

Keywords: dendrochronology; climate changes; dendroecology; Araucaria forest.

1. INTRODUCTION

Advances in understanding plant autecology across environmental gradients are directly related to the use of environmental variables linked to their growth. The particularities of each species and the environmental conditions may determine occurrence, growth patterns and competitive interactions among species (Tilman, 1985; Pausas & Austin, 2001).

As plants are sessile organisms, their development is profoundly influenced by the environment and its disturbances (Cui et al., 2014). The development patterns are characterized by endogenous rhythms, sometimes driven by environmental variation or others exogenous factors (Walter et al., 2009), where a single factor may limit growth, reproduction or distribution of a species (Billings, 1952). This understanding is also important for the analysis of the possible effects of climate changes (Cusatis et al., 2013).

Advances in the science of climate changes are providing a clearer understanding of the inherent variability of Earth's climate and its likely response to human and natural influences (Moss et al., 2010). The increase of global mean surface temperature by the end of the 21st century range from 3.7 °C to 4.8 °C, impacting on natural and human systems on all continents and oceans, according to Intergovernmental Panel on Climate Change (IPCC, 2014). From this knowledge, studies have shown that some modification in tree development triggered by drought and/or high temperatures may already be occurring in response to global climate change (Allen et al., 2010). The response of tree growth to a change in temperature may differ from different functional groups and biomes: in high latitude and altitude, for example, tree growth may be temperature-limited and thus benefit from some degree of warming, as opposed to warm-adapted species (Way & Oren, 2010).

Tree-ring chronologies are often used to detect shared signs in a population and reconstruct histories of unmeasured events in the past (Fritts, 1976; Gholami et al., 2015), displaying an important tool to the knowledge on the relationship between climatic conditions and tree growth (Cedro et al., 2013; Gebrekirstos et al., 2014). Thus, tree-ring studies might add important information about past climate variability and may potentially contribute to a better understanding of future climate patterns (Li et al., 2012).

The dendrochronological potential of Cedrela fissilis Vell. (Meliaceae) is evidenced by its distinct and conspicuous annual growth layers, due to its semi-porous rings, visible to the naked eye (López & Villalba, 2016). These rings are delimited by marginal bands of axial parenchyma and earlywood vessels with larger diameters (López & Villalba, 2016; Andreacci et al., 2017). Research this species climatic responses is relevant, considering that it has a wide geographic distribution and allows to compare responses in different climatic types. C. fissilis occurs from Colombia to Brazil, where can be found in the phytogeographic domains of Amazon Rainforest, Cerrado vegetation (Brazilian savanna) and Atlantic Rainforest, occurring in the Mixed and Dense Ombrophilous Forests, Deciduous and Semideciduous Seasonal Forests, as well as in Brazilian savanna formations (Muellner et al., 2010; Flores, 2018).

Cedrela fissilis can be classified as a longer-lived pioneer species, mainly due to its high light demand, height, longevity and denser wood (Corlett, 1995; Lima et al., 2009), although not without controversy (e.g. Gris et al., 2012; Konig Brun et al., 2017). It is characterized by its deciduousness, a morphological adaptation that is tied to the origin of the genus *Cedrela* at forests with seasonal climate (Muellner et al., 2010).

In this context, the aim of this study was to assess the responses of *C. fissilis* radial growth to climate in the South Central region of the state of Paraná, Brazil. We aimed to answer the following questions: i) How does climate influence *C. fissilis* tree growth in this region? ii) Which climatic variables are the best annual growth predictors for this species in this region? In this way, our central hypotheses were that: radial growth of *C. fissilis* shows a relevant sensitivity to changes in the local climate and temperature is a limiting factor for radial growth in the South Central region of the state of Paraná, Brazil.

2. MATERIAL AND METHODS

2.1. Survey area

The study was carried out in the municipality of Pinhão (PR) in area belonging to COPEL - Companhia Paranaense de Energia (the electric company of the state of Paraná), coordinates 26° 00' 23" S 51° 40' 06" W, located in the Terceiro Planalto Paranaense (Paraná's Third Plateau). The climate is classified as Cfb, with well-distributed rainfall, mild summers and occurrence of frost (Figure 1) (Miranda, 2009; Alvares et al., 2013). The average annual precipitation for the region in the surveyed period is 1,745 mm. The average temperature of the coldest month is below 14 °C and the average temperature in the hottest month does not reach 23 °C (KNMI, 2017; Brasil, 2017).

The local altitude is quite variable, with a gradient of 700 to 1,250 m.a.l.s. It has a hilly relief, with steep slopes (Miranda, 2009). Geologically, the region is part of the São Bento geological group (Grupo São Bento), and the predominant formation is the Serra Geral Formation, which resulted in acid and base rocks, usually basalt intercalated with sedimentary materials (Frank et al., 2009; Chahud & Petri, 2010; Lima, 2012). Local soils are predominantly Latosols, Nitisols and Cambisols (Miranda, 2009).

Vegetation is characterized as Ombrophilous Mixed Forest, although some characteristics of semideciduous seasonal forests occur in lower terrains (Miranda, 2009).



Figure 1. Climate diagram for study area, in the Ombrophilous Mixed Forest, Pinhão, Paraná, Brazil. Each bar represents the cumulative monthly precipitation (Jan: January; Feb: February etc) from 1945 to 2015 (data source: Brasil, 2017). Solid line represents the average temperature, dashed line represents maximum temperature (Max. temperature) and dotted line represents minimum temperature (Min. temperature), from 1901 to 2014 (data source: KNMI, 2017).

2.2. Data collection

In April 2016, wood samples from 11 (eleven) *Cedrela fissilis* Vell. (Meliaceae) adult individuals (according to tree size and presence of reproductive structures) were collected through a non-destructive method – 2 to 3 diametrically opposite increment cores per tree using a 5 cm increment borer at 1.3 m above ground level (DBH) (Fritts, 1976; Elling et al., 2009). Trees with a diameter greater than or equal to 40 cm were selected (Figure 2), with similar site conditions in a secondary forest formation with an approximate area of 60 ha.

Samples were dried at room temperature and set on wooden holders for the surface polishing process of their cross sections, using successively finer grit sizes (80-1,000 grits/cm²). Tree-ring delimitation was made using a stereo microscope, and samples were



Figure 2. Adult *Cedrela fissilis* tree in the Ombrophilous Mixed Forest, in study site (a) and macroscopic image of the annual rings of *Cedrela fissilis* showing typical tree rings with conspicuous marginal parenchyma bands and larger earlywood vessels (arrows) (b). Scale bar = 1 cm.

subsequently digitized (1200 dpi resolution) using an *HP Scanjet G4050* scanner. An image processing software was used to measure the tree-ring width.

To assess the climatic response of radial growth of these trees, historical precipitation data from the Jangada do Sul weather station (Copel) were used, which covered a period from 1945 to 2015. Historical temperature data comes from the *KNMI Climate Explorer* database and covers the period from 1901 to 2014 (KNMI, 2017). Air relative humidity data were obtained from the *National Oceanic & Atmospheric Administration NOAA/ESRL Physical Sciences Division* database (Kalnay et al., 1996) for the 1948 to 2015 period.

2.3. Data analysis

Tree ring crossdating was performed using the COFECHA' software (Holmes, 1983) with a 30-year moving window and a 15-year overlap, allowing to check the cross-dating quality, which calculates correlation coefficients between individual tree-ring series as a way to identify absent or false rings (Venegas-González et al., 2018). The standardization of the radial time series, which was done in order to remove biological growth tendencies and to establish the chronologies, was performed by adjusting original tree ring measurements through the application of a cubic smoothing spline function with a 40% frequency cut-off using the ARSTAN° software (Cook & Holmes, 1986). The sample quality was verified based on Expressed Population Signal (EPS) and Rbar. EPS is a measure of the common signal present in a chronology compared to an infinitely replicated chronology and Rbar represents the average correlation coefficient between each series and tree-ring chronology (Wigley et al., 1984).

To assess climatic data, a Principal Component Analysis (PCA) with varimax orthogonal rotation was performed, which included the variables minimum temperature, average temperature, maximum temperature, monthly thermal amplitude (difference between monthly maximum and minimum temperatures), precipitation and air relative humidity. The Kaiser test was used for the determination of the number of significant components (Kaiser, 1958). Additionally, we tested the significance of the variables with PCA main components using the bootstrap randomization method (1000 randomizations). Generalized Linear Models (GLM) were adjusted using PCA components as predictors and chronology as a response variable, to verify the relationship between the components of the PCA and the chronology. Climatic and tree-ring data of the time period corresponding to the age of the youngest tree examined in this study were used to adjust the GLM. When necessary, we transformed the data. In this way, all climatic variables and trees were evaluated for the same period. The models were compared based on the Akaike Information Criterion (AIC) (Akaike, 1974). In addition, the scores of the PCA components were compared with tree-ring chronology using the Spearman correlation coefficient (rs).

Statistical analyzes were developed in the R software (R Development Core Team, 2017).

3. RESULTS

The ring-width chronology of *C. fissilis* covers the period from 1891 to 2014 (Table 1, Figure 2). Of the 11 trees and 24 time series initially sampled, it was possible to crossdate 9 trees and 15 time series. During the tree ring crossdating of *C. fissilis*, some samples did not result in satisfactory correlations with the master series and were excluded from the data set. Some characteristics that made identification more

Table 1. Descriptive dendrochronological statistics for the *Cedrela fissilis* tree-ring chronology in the Ombrophilous Mixed Forest, Paraná, Brazil. Numbers in parentheses mean the number of series or trees sampled. Master series represents the period covered by the wood samples. Series intercorrelation measures the association between series (Fritts, 1976) and critical correlation suggest the limit value for a crossdating with 30-year moving window and a 15-year overlap. Mean sensitivity is the average difference between successive ring index values. Mean sensitivity above 0.3 indicate the presence of considerable high-frequency variance (Fritts, 1976).

Description	Chronology
Master series	1891-2014
Number of series dated	15 (24)
Number of trees	9 (11)
Ages (years)	55-124
Average length of time series (years)	86.6
Series intercorrelation	0.313
Critical correlation (p < 0.01)	0.423
Mean sensitivity	0.535

difficult as: wood anatomical anomalies, inconspicuous rings and false or local missing rings.

Higher growth was observed in the early years of the chronology (1891-1918, Figure 3). However, only a few series make up the tree-ring chronology in this period, indicating that the higher growth may not be representative.

Three components were selected based on the analysis of the main components, explained 90.01% of data variability (total of explained variance after sum of eigenvalues \geq 90%, Figure 4, Table 2). Correlations (loadings) of the climatic variables with PCA components allowed the separation of data in sets of orthogonal latent variables: PCA1, formed mainly by the minimum, average and maximum temperatures, PCA2, formed basically by precipitation and air relative humidity, and PCA3, formed by monthly thermal amplitude.

The Generalized Linear Models indicated that the best predictor to describe the tree-ring chronology



Figure 3. The mean tree-ring width (dashed black line) and individual growth ring width (solid grey lines) (**a**); Rbar (dashed black line with circles) and Expressed Population Signal (EPS, solid black line with triangles) statistics (**b**) and the standard tree-ring chronology (solid black line) with number of series per year (grey area) (**c**) for *Cedrela fissilis* in the Ombrophilous Mixed Forest, Paraná, Brazil, for the reference period 1891–2014. The standard tree-ring chronology (tree-ring index) was built using a cubic smoothing spline function with a 40% frequency cut-off. Rbar represents the average correlation coefficient between each series and the chronology and EPS is a measure of the common signal present in a chronology compared to an infinitely replicated chronology.

includes, based on the Akaike Information Criterion, the first component of the PCA (PCA1), since it presents the lowest AIC value (Table 3).

By comparing tree-ring chronology behavior with the PCA latent variables, several points of synchrony among series can be observed, where years with higher scores correspond to higher growth rates (Figure 5).



Figure 4. Diagram of ordination in the two first axes yielded by Principal Component Analysis varimax rotation) of climatic (with variables, "ThermAmplitude" given as vectors: = monthly relative thermal amplitude; "AirHumid" = humidity; "Precipitation" precipitation air = (rainfall); "MaxTemp" maximum temperature; = "AverageTemp" average temperature; = "MinTemp" = minimum temperature.

Table 2. Principal Component Analysis (with varimax rotation) statistics. Eigenvalues: quantify the amount of inertia in each component (Jombart et al., 2009); EV (%): explained variance; Variables: show the composition of the latent variables (PCA main components); Loadings: indicate the correlation of the variable with the main component (*95% probability level; **99% probability level, according to bootstrap randomization method).

Eigenv	alues	EV (%)	Variables	Loadings
PCA1 3.02			Minimum temperature	0.92*
	3.02	50.0	Maximum temperature	0.91*
			Average temperature	0.98*
PCA2 1.44	1 4 4	24.1	Precipitation	-0.85**
	1.44		Air relative humidity	-0.75**
PCA3	0.94	15.6	Monthly thermal amplitude	0.92*



Figure 5. Tree-ring chronology of *Cedrela fissilis* and latent variables scores constructed from a Principal Component Analysis for the reference period 1960–2014. Latent variables: PCA1 = component comprising the minimum, maximum and average temperatures; PCA2 = component comprising precipitation and air relative humidity; PCA3 = component comprising the monthly thermal amplitude. Solid black line represents the tree-ring chronology (tree-ring index), solid grey line represents PCA2 and dashed grey line represents PCA3.

Table 3. Models examining effects of latent variables chronology using the on tree-ring Akaike Information Criterium (AIC). Latent variables: PCA1 = component comprising the minimum, maximum and average temperatures; PCA2 = component comprising precipitation and air relative humidity; PCA3 = component comprising the monthly thermal amplitude. Df = degrees of freedom.

Models	Df	AIC
PCA1	1	-16.790
PCA2	1	-16.189
PCA3	1	-16.171
PCA1xPCA3	2	-14.975
PCA1xPCA2	2	-14.791
PCA2xPCA3	2	-14.217
PCA1xPCA2xPCA3	3	-13.005

The Spearman correlation between PCA1 and the tree-ring chronology for the period corresponding to the age of the youngest tree collected (1960-2014) was not significant (rs = 0.14; p = 31). However, correlation was significant for the 1960-1979 time period (rs = 0.65; p = 0.005). For the last time period (1980-2014), the correlation with PCA1 was not significant (rs = 0.05; p = 0.76). The other latent variables showed no correlation to the tree-ring chronology.

4. DISCUSSION

Our results showed that *C. fissilis* perform a relevant sensitivity to changes in the local climate, endorsing the possibility of using growth rings as proxies to detect disturbances in the climate scenario (Fan et al., 2009; Venegas-González et al. 2018). The mean sensitivity for the whole set of series is considered high (> 0.3) (Fritts, 1976). Although the time series intercorrelation did not reach critical correlation, this result indicates the high sensitivity of the species to record climate changes (Fritts, 1976).

The EPS, another important parameter to verify the quality of the chronology, reinforces the reliability of the data, especially after 1935, where its value is higher than 0.75. Although it is suggested by Wigley et al. (1984) that the EPS is adequate if higher than 0.85, this parameter can be adjusted depending on the ecological characteristics of the species analyzed (Piraino et al., 2015). Difficulties in crossdating process of *C. fissilis*, like wood anatomical anomalies, inconspicuous rings and false or local missing rings, were also found by other authors that studied this species (Andreacci et al., 2014; Paredes-Villanueva et al, 2016; López & Villalba 2016; Cusatis et al, 2013).

PCA main components evidenced the connections between climatic data. The climatic variables formed three main components, which can be seen as latent variables that express most of the information in the data (Wold et al., 1987). This pattern was expected, since it grouped variables correlated with each other. Minimum, average and maximum temperatures are, in essence, collinear, because they originate from the same meteorological variable. Precipitation and air relative humidity are also related to each other, considering that higher volumes of precipitation are related to a more humid atmosphere. Precipitation occurs mainly due to air relative humidity, which can be generated locally, by evapotranspiration or transported from other areas (Quadro et al., 2012). Finally, PCA3 comprises monthly thermal amplitude, the temperature variability - an important variable, since exhibited the role of temperature fluctuations (Folguera et al., 2009).

By graphically observing the behavior of chronology and temperatures, it is possible to distinguish a pattern where higher temperatures contribute to an improved tree growth. Other studies have found temperature as the main growth predictor of several species from Ombrophilous Forests in the South region of Brazil (eg Machado et al., 2010; Kanieski et al., 2012, 2013; Cusatis et al., 2013; Andreacci et al., 2014), where climate variations are related to the seasonality of the temperatures. The South region of Brazil is located almost entirely in the subtropics. Even though it does not have a dry season, the climate presents an important thermal oscillation throughout the year, with a stronger distinction between winter and summer (Rosemback et al., 2010). For this reason, secondary growth occurs mainly in spring and summer, with temperatures responsible for the cambium activate and xylem differentiation (Begum et al., 2013).

Cedrela is a genus of deciduous behavior occurring in Ombrophilous and Seasonal Forests, as well as in Brazilian Cerrado and Caatinga (Muellner et al., 2010; Flores, 2018). In regions where there are droughts, there is a clear seasonality of the growth determined by leaf abscission and cambial dormancy in the driest period (Costa et al., 2013). In regions where temperatures are seasonal, the cold period is decisive (Jeong et al., 2011). In addition, in mid-latitudes seasonal variations in temperature are associated with variations in the photoperiod, with longer days. The light regime is a critical component in determining the biomass production of photoautotrophic beings, which use light as their source of energy (Wahidin et al., 2013). Thus, it is possible that in tropical and subtropical areas, where precipitation is relatively well-distributed throughout the year, growth increase occurs all year long and temperature and photoperiod may promote a stimulus to cambial activity for some species (Santarosa et al., 2007; Shimamoto et al., 2016).

The adjusted model did not elect the component comprised of precipitation and air relative humidity

as a significant for the prediction of *C. fissilis* growth. The fact that there was no well-defined dry season probably contributed to the absence of large variations in air relative humidity and precipitation, not incurring in significant growth responses. Nevertheless, when inferring about growth responses to annual precipitation, there is a tendency that years with stronger rainfall and higher growth match, while fewer rainfall corresponds to a reduction in growth. It can be observed that even in places where precipitation is not seasonal - thus not generating significant responses in the growth prediction model - this climatic variable match with some of the points in the chronology. Increased cambial activity depends on tree water status during periods of high metabolic activity (Zweifel et al., 2006), which could justify the correlation between precipitation and temperature rates and the width of the rings.

Andreacci et al. (2014) evaluated climatic signs in C. fissilis tree rings also in Ombrophilous Forests and suggests that water supply and high temperatures in the growing season have consequences in tree-ring width. Bud break, flowering and cambial activity are events that entail cellular expansion, a process inhibited by the lack of water, even just a moderate one (Borchert, 1994). These events can be even more affected in deciduous species, since one of the basic requirements for metabolic activities is water availability, for the hydrolysis of macromolecules and enzymatic activities (Essiamah & Eschrich, 1986; Borchert et al., 2002). Zanon & Finger (2010), while studying the relationship between temperature and air relative humidity and the growth of Araucaria angustifolia, occurring in the same phytogeographic domain of C. fissilis in this study and having similar light needs in the early stages of life, also found larger increments associated with higher average monthly temperatures and periods with greater precipitation.

In regions where drought and rain periods occur regularly, the influence of precipitation can be seen more clearly. In the Amazon basin, Baker et al. (2017) explored possible variation factors in the periodicity tree-rings from *Cedrela* species and affirm that growth rates are probably influenced by the seasonality of the precipitations. In the same way, a research developed in a tropical dry forest in eastern Bolivia, showed that *C. fissilis* was sensitive to precipitation in almost all analyzed time scales, with leaf flushing and radial-increment rate related to a synchronous response to water availability (Mendivelso et al., 2016). In spite of the precipitation influence in tree growth is evident in areas with droughts, the effects may be different in gradients. Venegas-González et al. (2018), indicated that the precipitation affects differentially the growth of *Cedrela* depending on the sector in the gradient in which they are. In their study, tree growth performance is highly dependent to the dry season rainfall amounts in the most humid sector of the gradient, while sites settled in areas of lower summer temperatures, rainfall is the main determining factor.

The correlation of the PCA1 with the chronology was not significant, considering the entire period evaluated. However, the GLM demonstrated this trend, in which temperatures were the best growth predictors of *C. fissilis*. When separating in time periods, the correlation was significant until the year 1979, even with a smaller sample, in which the effects of the outliers may be larger (Goodwin & Leech, 2006). In the other periods, there was no significant correlation with this latent variable. The correlation between growth and temperatures in one period, followed by a lack of correspondence in the following years, may indicate some alteration in how tree growth was influenced by the climatic variables studied.

Observing the PCA1 scores, we can see an increase in temperatures from 1982, since this latent variable is composed by the mean, maximum and minimum temperatures. Being in a region with characteristics of seasonal temperatures and no drought, we could expect an increase in the growth of C. fissilis in response to local warming. Although the increase in temperatures did not lead a proportional increase in growth, it may have influenced the climatic response. Whereas no correlation was found from 1980, but there was correlation in the previous period, an indirect impact of temperature increase may have occurred, acting independently or in combination with another factors (Lindner et al., 2010; Bellard et al., 2012). This result could be related to the particularly sensitive of forests to climate change, because the long life-span of trees does not allow for rapid adaptation to environmental changes (Lindner et al., 2010).

Concerning to niche evolution of *Cedrela*, Koecke et al. (2013) demonstrated that temperature had an increasing impact on ecological diversification of the genus from the Miocene onwards, with recent speciation events may be related to divergence of climatic tolerances. The increase in temperature seems to be a major driver in promoting diversity on Tropical Rain Forests, apparently caused by in situ speciation (Jaramillo & Cárdenas, 2013). But what about longer-lived pioneer species, how do they react? Our results indicated that, from C. fissilis, changes in growth and in correlation with the temperature in response to local warming have occurred. The most negative impacts from a warmer climate are expected for slow-growing trees, and, the least negative for pioneer species, who gain a growth competitive advantage and moving into open habitats (Körner & Basler, 2010; Corlett & Westcott, 2013). Cheesman & Winter (2013) shown that increasing temperatures, especially at night, under well-watered conditions, promote an increase in biomass accumulation on pioneer tree species. On the other hand, C. fissilis is more suitably framed as a long-lived pioneer, because it has long life and dense wood, despite several characteristics that classify it as a pioneer (Corlett, 1995). As a whole, being a long-lived pioneer, C. fissilis did not grow proportionally to the increase in temperature but experienced a change in its growth pattern, suggesting sensitivity to climate changes.

Climatic factors such as temperature and precipitation are directly related to the physiological processes fundamental to plant growth (Reyer et al., 2012; Venegas-González et al., 2016). However, the relationship between these climatic elements and growth is not a direct one, since it is not possible to be sure if the resources will be available (Ribeiro et al., 2011). It is important to understand the factors controlling ring formation at smaller scales, since the variation of these factors between regions may cause trees in different regions to form rings at different times (Baker et al., 2017).

Understand the relative influence of specific climate parameters on tree growth and predict species' responses to climate changes is a major challenge in ecology (Wolkovich et al., 2012; Williams et al., 2013). Even if studying these relationships is challenging, with obtaining additional tree-ring chronologies from *C. fissilis*, it should be possible to make climate reconstructions covering the past 150 to 200 years (Pereira et al., 2018). This advance could improve our understanding of tree-rings as proxies for climate reconstructions, identifying past and future trends in climate changes (Fan et al., 2009; Liang et al., 2009).

5. CONCLUSION

Temperature is the main climatic variable that affects the radial growth of *Cedrela fissilis*. The seasonal behavior of this variable seems to be the main reason for its role as the best radial growth predictor of the species in the region. The fact that there is no well-defined dry season contributed to the non-occurrence of significant responses to air relative humidity and precipitation.

Our results indicated a change in the *C. fissilis* growth pattern after the year of 1980, a corresponding period to an increase in temperatures, suggest a sensitivity of the species to climate changes.

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CORRESPONDENCE TO

Amanda Koche Marcon

Universidade Federal do Paraná, Centro de Ciências Florestais e da Madeira, Av. Prefeito Lothário Meissner, 632, CEP 80210-170, Curitiba, PR, Brasil e-mail: amandakoche@gmail.com

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