Original Research Article

Drought and climate change incidence on hotspot *Cedrela* forests from the Mata Atlântica biome in southeastern Brazil

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ABSTRACT

The Atlantic Forest is a Neotropical biome encompassing mainly Brazil's coastline and parts of Paraguay, Uruguay, and Argentina, but today surviving largely in small degraded patches and protected areas. Being a region under threat of extinction of its biological components, little is known about how climate change could influence the biodiversity, dynamics, and stability of this ecosystem. Here, we analyze the response of tree-growth dynamics to regional climate variability and drought, both in temporal and spatial scale. For this purpose, five *Cedrela* spp forest sites located in the biogeographic region 'Serra do Mar' (AFSM) in southeastern Brazil was considered. This region contains the best-preserved secondary forests of the Atlantic Forest biome, a fact that represents a natural laboratory to ascertain the environmental influence on the tree development through large spatial scales. Correlation and regression analysis were used to explore the relationship between growth and rainfall, air temperature, and a drought index. Results indicate that 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 during the warm-rainy season is the main determining factor influencing tree-growth dynamics. This implies that the same environmental factor (rainfall) affect differentially the growth of *Cedrela* sites depending on the sector in the gradient in which they are. We found that the population located at the highest-altitude site experienced a growth decline in recent decades linked to increases of winter regional warming, being more sensitivity to long periods of drought (6–10 years). In summary, the seasonal response of cambium activity in AFSM trees to rainfall varies across a climatic gradient. These results are crucial to understand how the present and future global change may differentially impact on tree population dynamics of montane Neotropical forests.

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1. Introduction

The Atlantic Forest biome, or Mata Atlântica, is one of the largest areas of tropical ecosystems and biodiversity in the World (Myers et al., 2000). It is distributed in Brazil almost as a continuous strip in the Atlantic coastal plains although discreetly extend inland to encompass the foothills, the slopes and the highlands of Serra do Mar. Fragments of this forest are also found in Paraguay and the NE of Argentina (Rodrigues et al., 2009). The Atlantic Forest is considered a threatened biome due to the devastation that suffered during centuries by human occupation (pastures, crops and higher urban growth) and intensive exploration of its resources (mainly timbers) (Dean, 1996). Currently the Atlantic Forest is highly fragmented and it is reduced to less than 16% of its original area (Ribeiro et al., 2009). For these reasons the Atlantic Forest was declared as a Biosphere Reserve by UNESCO and has received the status of conservation hotspot (Myers et al., 2000).

Southeastern Brazil contains about 60% of the Brazilian sector of the Atlantic Forest (Rodrigues et al., 2009), and within this area, the São Paulo state shows the highest level of fragmentation and deforestation of this biome. Here, the Atlantic Forest is mostly concentrated in the coastal region, commonly named Serra do Mar (hereafter Atlantic Forest of Serra do Mar, AFSM; Colombo and Joly, 2010). The AFSM is characterized by a climatic gradient, ranging from 0 to 2000 m above sea level (m a.s.l.), involving changes in floristic composition and structure of the tree communities (Lacerda, 2001).

The AFSM represents the best-preserved identity of the Atlantic Forest biome, holding 36.5% of its original vegetation (Rodrigues et al., 2009). This includes populations of *Cedrela odorata* L. and *Cedrela fissilis* Vell., two Meliaceae trees considered among the most appreciated woods for their quality and aesthetics since the times of European colonization in South America (Dean, 1996). For this reason, they have been extensively exploited and today they are in a state of vulnerability and placed as target species in the red book of the Brazilian flora (Martinelli and Moraes, 2013). Both species have a similar crown and stem shape, wood anatomy, phenology, and autoecology (Muellner et al., 2010; Tomazello Filho et al., 2000).

Once a global warming has increased in the order of 0.07 °C per decade since 1900 (Jones and Moberg, 2003), and models predict an intensification during the 21st century (Pachauri et al., 2014), an increasingly frequency of warm nights and floods is expected in southeastern Brazil (Marengo et al., 2009), where AFSM occurs. This has been alerted as a worrying situation that compromises the plant diversity and sustainability of the Atlantic Forest (Colombo and Joly, 2010). Although many efforts have been made to identify how the ongoing global change affects the dynamics of different tropical tree species (e.g. Gea-Izquierdo and Cañellas, 2014; Mendivelso et al., 2014; Venegas-González et al., 2018; Allen et al., 2015), scarce is the knowledge about the effect of this global climate phenomenon on the Atlantic Forest.

The analysis of growth dynamics in environmental gradients is relevant to understand more in detail the synecology and resilience of forests. Since precipitation and air temperature may vary along a region, that change may finally be reflected in the growth of trees, giving the opportunity to identify the influence of stress factors along environmental gradients (e.g. Camarero and Gutiérrez, 2004, Lara et al., 2005). In this sense, environmental gradients can serve as potential natural laboratories to infer forest responses to global warming and climate change (Jump et al., 2009). However, the climatic response and drought sensitivity of Atlantic Forest along climatic gradients have been poorly documented up to now, a situation that can be reversed if we document what would be the reaction of these forests in face of climate change intensification. In this sense, the dendrochronology (the analysis of annual tree rings) allows us to evaluate forest growth and their association with climate variability and change at different spatial and temporal scales (Fritts, 1976). Previous dendrochronological studies in *Cedrela fissilis* and *Cedrela odorata* forests from the Neotropics showed that seasonal rhythms of radial growth are particularly influenced by rainfall amount at the end of the previous growing year (Brienen and Zuidema, 2005; Dünisch, 2005; Dunisch et al., 2003; Worbes, 1999). However, none of these studies considered a dendroecological vision under a biogeographic approach, considering the wide distribution of the genus. In the subtropical forests of Serra do Mar, moreover, the role of rainfall in annual xylem development of *Cedrela* spp. is poorly known, particularly under the influence of major droughts.

To partially solve the uncertainty of how long-term droughts and precipitation/temperature changes affects tree growth of Atlantic Forest remnants, we explored climate signals in *Cedrela* spp. tree rings at spatial and temporal scales along an environmental gradient. Based on the principles that tree rings can respond with differential intensity to climate variability (Fritts, 1976; Schweingruber, 1996) across environmental gradients (Jump et al., 2009), we first hypothesized that this phenomenon influence the ecology of the *Cedrela* forests in existing climatic gradients of Southeastern Brazil. Considering the divergences proven by different patterns of drought-growth responses in others Neotropical tree species, mainly in their long-term sensitivity (Mendivelso et al., 2014), we hypothesized that severe drought events linearly affects growth, even with delay effects in subsequent years of the event. Considering the ecological evidences of negative impacts by recent climate change on forest ecosystems in the World (Bonan, 2008; Walther et al., 2002), and the inverse relationship between climatic variables and elevation (Jump et al., 2009), we expect a negative growth resilience to rising global temperatures, mainly in sites located at higher altitudes, where trees are probably more adapted to lower temperatures.

2. Material and methods

2.1. Study sites and selected species

Five sites from southeastern Brazil containing populations of *Cedrela odorata* and *C. fissilis* were selected for this study (see Table 1). All sites are located in the center of the biogeographic subregion of the Atlantic Forest, the AFSM (22°-24°S), and all cases are represented by a secondary forest phytophysiognomy, recovering from past exploitations (Fig. 1). The subregion,

Table 1
Characteristics of the study areas.

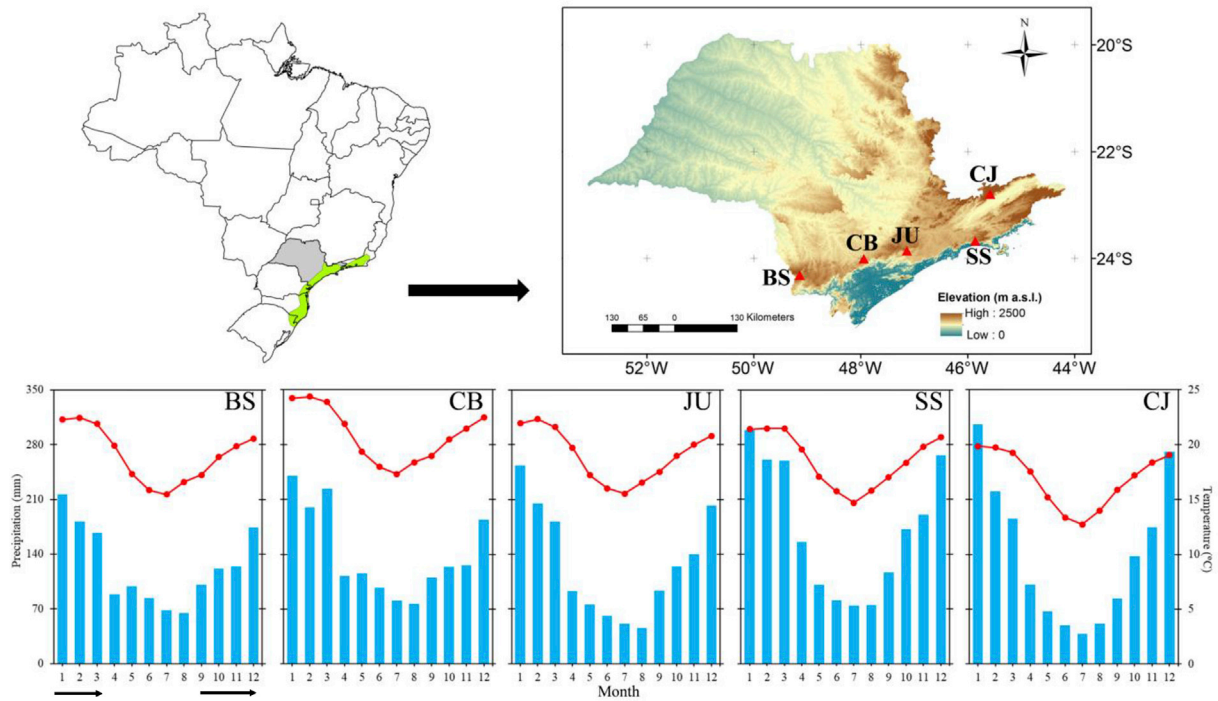| Site (code)	Forest type	Species	Altitude (m)	Annual mean temperature (°C)	Annual total precipitation (mm)
Campos de Jordão (CJ)	Public	*C. fissilis*	1600	17.3	1700
São Sebastião (SS)	Public	*C. odorata*	175	20.3	2050
Juquitiba (JU)	Private	*C. fissilis*	680	19.4	1600
Carlos Botelho (CB)	Public	*C. odorata*	750	21.2	1690
Bom Sucesso de Itararé (BS)	Private	*C. odorata*	900	19.2	1490

Fig. 1. Location of *Cedrela* spp. sites (red triangles) in São Paulo State, Brazil (right map; from east to west: CJ, SS, JU, CB, BS). São Paulo state is shown in gray in the left map, while that AFSM distribution is shown in green (figure adapted from Ribeiro et al., 2009). The climate diagram of each site is shown below (1 = January, 2 = February, etc.). Arrows indicate the theoretical growth period of this species between September to March (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

with a north-south orientation, included the following sites for analysis: Campos de Jordão (State Park - CJ), São Sebastião (State Park - SS), Juquitiba (private forest - JU), Carlos Botelho (State Park - CB), and Bom Sucesso de Itararé (private forest - BS) (see Table 1 for supplementary details). The AFSM is climatically characterized, according to Köppen's classification, as Cf (humid subtropical) with a hot/rainy summer (December to February) and a cold/dry winter (June to August) (Alvares et al., 2013). This region has a mean annual rainfall of 1700 ± 210 mm and a mean annual temperature of 19.5 ± 1.5 °C, with the hottest and coldest months of 22.4 ± 1.2 °C (February) and 15.4 ± 1.2 °C (July), respectively.

The vegetation of the AFSM is defined as Ombrophilous Dense Forest (Dos Santos et al., 1998; Guilherme et al., 2004). At these species-rich forest environments, tree canopy may reach 50 m tall, while the dense understory is composed of ferns, shrubs, palms, vines, and epiphytes (bromeliads and orchids) (IBGE, 2004). This dense cover structure is related to the highest thermo-pluviometric regime that characterizes the coastal region, where precipitation is roughly distributed throughout the year, but only decreasing in the winter months where also lower temperatures decrease evapotranspiration rates (Veloso et al., 1991). However, the occurrence of complex and non-linear gradients suggests the importance of several other abiotic features in the spatial distribution and abundance of tree species in the Atlantic Ombrophilous Dense Forest in the state of São Paulo (Scudeller et al., 2001).

Cedrela odorata and *C. fissilis*, commonly called cedro, are Neotropical tree species linked to stages of primary and secondary forest succession (Muellner et al., 2010). Both species reaches its northern natural distribution on Central America (*C. fissilis*) and Mexico (*C. odorata*), being the northern Argentina their southern limit. An important ecological role of these species is to conform the secondary stages of vegetation succession (Santos and Takaki, 2005). *Cedrela fissilis* and *C. odorata* are deciduous trees that are selectively hygrophyte, shadow tolerant in seedling and juvenile stages (Muellner et al., 2010), and heliophyte when adult. Tall trees up to 40 m in height may be found. In the AFSM, *Cedrela odorata* and *C. fissilis* behave as

late secondary species (Lacerda, 2001). Tree-rings of *Cedrela* spp. are well distinct and demarcated by a thin row of marginal parenchyma and a semi ring porosity with notoriously larger vessels placed at the beginning of the earlywood (Tomazello Filho et al., 2000). The cambium reactivates its cell division in coincidence with the rainy season and the tree leaf-out. In fall, the cambium enters in dormancy when the period of less precipitation begins, also causing leaf fall (Callado et al., 2013; Marcati et al., 2006). Andreacci et al. (2017) indicate that radial growth of *Cedrela* spp. trees at the AFSM occurs mainly from November to March (spring to fall).

2.2. Sampling design

At each site, 12—36 trees per site along a transect (1000 m approximately) were sampled, totaling 122 trees (~30 cm DBH) for the five sites (see Table 2). Two-three wood cores per tree were sampled from the main stems at 1.3 m above ground level (DBH, diameter at breast height) using increment borers. The samplings were made on different dates, i.e. CJ and BS were sampled in November 2006, JU and SS were sampled in March—April 2016, and CB was sampled in November 2015. We did not find the two species simultaneously in the same sites. Considering that *Cedrela* spp. is considered a tree of rare occurrence in AFSM (Muellner et al., 2010), the high biodiversity of plants in these forests (150—170 species per hectare, Dos Santos et al., 1998; Guilherme et al., 2004), and its historical situation of logging (Dean, 1996), make difficult to find remaining *Cedrela* spp. populations with enough number of trees close to each other for dendrochronological studies. Previous dendrochronological reports with *Cedrela* spp. have been based on the use of log cross-sections, taking advantage of adjacent logging concessions (e.g. Dunisch et al., 2003; Brienen and Zuidema, 2005; Granato-Souza et al., 2018). The use of large cross-sections allows an easier identification of the growth rings and the possibility of integrating a greater number of measured radii, avoiding local distortions of the ring widths and an easier detection of false or local missing rings. However, national laws do not currently allow timber exploration in the AFSM region, forcing the use of Pressler increment borers in obtaining wood samples. Wood cores were glued on wooden holders, and the cross-sections were polished with sandpapers with a gradient between 80 and 800 grains mm^{-2} until the anatomical features related to the ring boundaries were clearly identified (Stokes and Smiles, 1996).

2.3. Building tree-ring chronologies

Polished wood samples were scanned at 2400-dpi resolution with a reference scale, and tree-ring widths were measured using the ImageJ software (Rasband, 1997). The cross-dating quality was checked with the software COFECHA (Holmes et al., 1986), which calculates correlation coefficients between individual tree-ring series as a way to identify absent or false rings. This software identifies tree-growth patterns that can be synchronized between the samples of the same tree and between trees, allowing the building of a master series of tree-ring widths dated in the exact year of their formation (Grissino-Mayer, 2001).

To build site chronologies, we first removed the long-term growth trends potentially related to non-climatic fluctuations (tree ontogeny and forest natural dynamics) by a cubic spline with a 50% frequency response cutoff equal to 67% of the series length of ring-width measurements, preserving as much as possible both high- and low-frequency climatic signals in tree rings. We used the residual chronologies since the temporal autocorrelation related to the previous year growth was removed. This procedure was performed using the ARSTAN computer program (Holmes et al., 1986). The chronologies were characterized using the classic statistic parameters in dendrochronology (Fritts, 1976), i.e., average and standard deviation of tree-ring width, series mean sensitivity (MS), series intercorrelation (Rbt), the first-order autocorrelation of tree-ring series (AR1) and expressed population signal (EPS) of residual chronologies. EPS represents the chronology that has been infinitely replicated and is sensitive to both variations in the series intercorrelation and sample size. Although the ≥0.85 threshold has been considered for non-tropical tree species (Wigley et al., 1984), we employed a ≥0.80 threshold that is accepted in tropical

Table 2
Characteristics of studied trees and descriptive statistics of the chronologies (see methodology for site code definitions).

Site (code)	Trees[a]	DBH	RW±SD[b]	TS[c]	Age	MS[d]	Rbt[e]	AR1[f]
CJ	12/10	32.9 ± 8.3	2.07 ± 1.40a	1900—2005	77 ± 20	0.51	0.47	0.43
SS	20/18	33.5 ± 4.3	4.05 ± 1.40d	1960—2014	39 ± 12	0.47	0.47	0.48
JU	26/23	22.4 ± 2.9	2.35 ± 1.56b	1955—2015	45 ± 15	0.52	0.48	0.49
CB	28/20	23.1 ± 1.4	2.16 ± 1.62b	1949—2014	51 ± 13	0.54	0.40	0.49
BS1	20/17	30.6 ± 2.7	2.40 ± 1.77b	1935—2005	64 ± 28	0.60	0.57	0.44
BS2	10/10	37.6 ± 13.5	3.25 ± 2.30c	1936—2003	58 ± 29	0.62	0.64	0.40
BS3	6/4	63.5 ± 4.1	3.59 ± 2.12c	1932—2005	93 ± 15	0.48	0.33	0.54
Regional BS	35/27	34.1 ± 8.1	2.65 ± 1.93c	1927—2005	61 ± 29	0.60	0.57	0.42

[a] Numbers of sampled trees (trees used for the chronology).
[b] Chronology time span considering at least three trees.
[c] Mean ring width ± standard deviation (mm), different letters indicate significant difference according to Kruskal-Wallis test ($P < 0.05$).
[d] Mean sensitivity of tree-ring series.
[e] Mean correlation coefficient between all the tree-ring series.
[f] First-order autocorrelation of tree-ring series.

tree-ring chronologies (Mendivelso et al., 2014). We evaluated the growth stabilization by calculating the basal area increment according to the following equation:

$$BAI = \pi(r2t - r2t - 1)$$

where r_t and r_{t-1} correspond to tree radius at DBH calculated at both the end and beginning of the annual increment in year t, respectively (Biondi and Qeadan, 2008). BAI chronology is usually used to represent the time in which a tree reaches its mature phase of growth (Jump et al., 2006).

2.4. Climate data

There are few climate records in the AFSM region of São Paulo state. Therefore, and centered on the study sites, we obtained monthly climate data (mean temperature and accumulated precipitation) for the 0.5×0.5 grid from the Climate Research Unit dataset, University of East Anglia, version 4.00, using the KNMI-Climate Explorer webpage (http://climexp.knmi.nl/). Climate data were obtained for the period 1901−2014 (Fig S1). The gridded areas used for comparison with our tree-ring chronologies are: CJ (22.5−23.0S, 45.5−46.0W), SS (23.5−24.0S, 45.5−46.0W), JU (23.5−24.0S, 47.0−47.5W), CB (24.0−24.5S, 47.5−48.0W), and BS (24.0−24.5S, 48.5−49.0W).

To analyze the relationship between tree growth and drought stress, we used monthly values of the Standardized Precipitation-Evapotranspiration Index (SPEI) calculated up to 12 months of cumulative time lag (Vicente-Serrano et al., 2010). The SPEI considers the effect of temperature on the evapotranspiration rate, with negative and positive SPEI values reflecting dry and wet conditions, respectively. The SPEI was calculated for the same 0.5×0.5 grid per site, and it was obtained from KNMI-Climate Explorer webpage.

2.5. Statistical analyses

Correlation functions were constructed between the residual tree-ring index chronologies of *Cedrela* sites from AFSM, and monthly values of precipitation, temperature, and SPEI index, during a common period (Blasing et al., 1984). Correlations were performed for the period between November of the previous growth year to March of the current growth year, since a tree-ring formation in the Southern Hemisphere is considered to be influenced by climate conditions that occur in shared summer months for two consecutive years. For this reason, we followed Schulmann's convention to establish the calendar year of a tree-ring formation for the Southern Hemisphere (Schulmann, 1956). Also, we performed the dendroclimatic analysis by season (fall: March to May; winter: June to August; spring: September to November; summer: December to February). We used the package bootRes for dendroclimatic analysis (Zang and Biondi, 2013) in R (R core Team, 2017), and significance was assumed at $P = 0.05$. We use 45 years as a common period between climate and tree-ring chronologies (1960−2005).

To analyze the growth resilience to drought periods, we built a regional SPEI chronology (calculated 1-months) for the area 22.5−24.5S, 45.5−49.0W, using the same database described before. Consecutive years with below average values (negative) SPEI is considered a dry period (Mendivelso et al., 2014). Later, we compared the standardized mean growth series per tree (average of the standard tree-ring series) before, during and after a drought period through a Kruskal-Wallis non-parametric H-test (95% confidence level).

To evaluate the influence of regional warming on tree rings, we performed a piecewise regression analysis of mean temperature at each chronology site. This approach allows to observe significant changes in temporal trends showing the break year. Piecewise regression models were made using the *segmented* package (Muggeo, 2008) in R (R core Team, 2017). Subsequently, linear regression analyses were performed between ring width and most significant seasonal temperature resulted from multiple regression analysis. This method detected which seasonal climatic variables are more related to the ring width variability. Predictor variables were selected by stepwise iterative construction of the regression model, allowing to an automatic selection of independent variables already included in the model and rejection of any variable that does not produce a *T-student* significant at the 0.90 level (Di Rienzo et al., 2001). We used the Variation Inflation Factor (VIF) to evaluate the multicollinearity that exists among the predictor variables, with VIF values close to 1, indicating a low or null multicollinearity, whereas VIF values > 10 indicate a certain collinearity between predictors (O'brien, 2007). All regression models were made by Infostat software (Di Rienzo et al., 2001).

3. Results

3.1. Spatial patterns of climate variation

The climate at the five analyzed sites is influenced by both altitude and latitude, as suggested in Fig. 1. CJ and BS have the lowest mean temperature and lowest accumulated rainfall H, respectively, while SS and CB are the rainiest and hottest sites, respectively (temperature: H = 377.9, $p < 0.001$, precipitation: H = 157.5, $p < 0.001$) (Table 1, Fig. 2). The highest correlation was detected in the temperature-altitude relationship ($R^2 = 0.62$ and $r = -0.79$, $p = 0.11$), indicating temperature decreases as one moves upwards from seacoast to highlands in the sites where populations of *Cedrela* spp. occurs
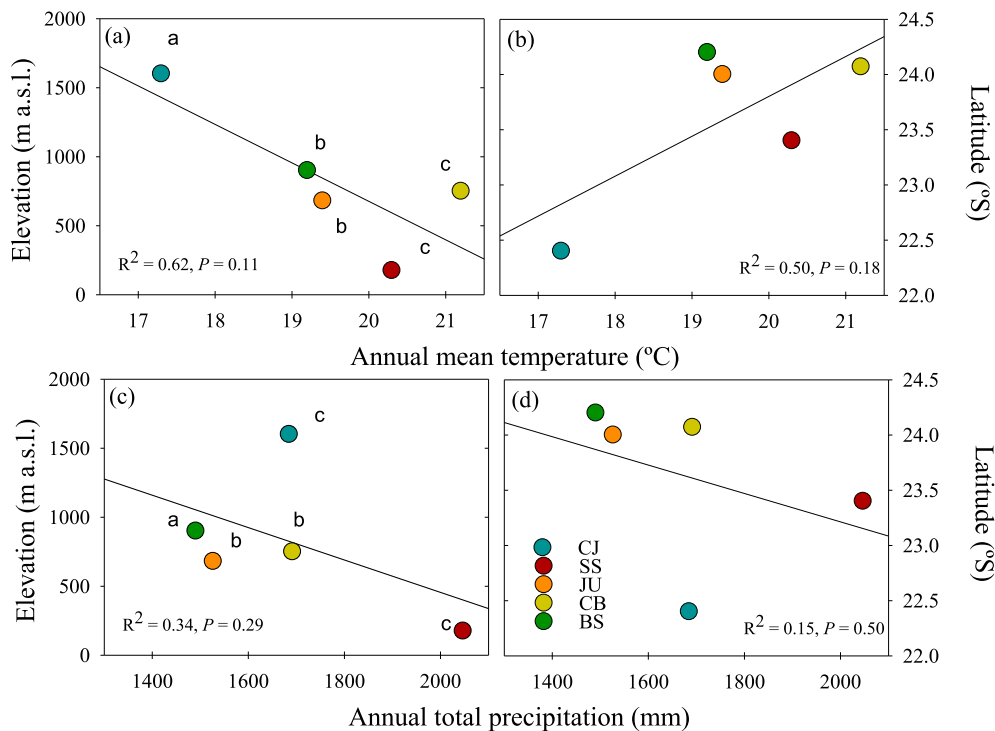
Fig. 2. Relationship between (a,b) annual mean temperature (°C) and (c,d) annual total precipitation (mm), with ground elevation (m a.s.l.) and latitude (°S) for the five study areas. Different letters indicate significant differences ($p < 0.05$) in annual mean temperature and annual total precipitation among sites for graphics a and c, respectively.

(Fig. 2a). Recognized as altitudinal lapse rate, the slope of this linear regression shows an average decrease (from lowest to highest altitude) in elevation of 279 m per Celsius degree (°C). As defined in this study, the CJ is the highest and coldest site, SS is the lowest and rainiest site, CB is the hottest site, and BS is the driest and southern site. JU shows an intermediate behavior.

3.2. Chronology characteristics and growth-climate relationship

Table 2 shows a summary of sites attributes and the statistics considered to evaluate the quality of the obtained *Cedrela* spp. chronologies. The average tree-ring width of all trees was 2.6 ± 1.5 mm, being the highest and lowest values found in SS and CJ, respectively (Table 2). The BAI of CJ, BS, and JU reached the mature phase (growth stabilization) by 1950s, 1970s, and 1980s, respectively (Fig. S2). Whereas *Cedrela* trees from SS site still does not reach this phase. In the CB site, we did not observe clearly stabilization in the growth.

All five chronologies show a high (>0.47) mean sensitivity (MS), corresponding the highest values to the southern stands (CB and BS). Overall, intercorrelation between series (Rbt) was high in all sites ($r > 0.47$), except in CB where Rbt was 0.40 but equally significant ($p < 0.01$). BS3 site showed lowest values of Rbt and MS from Bom Sucesso de Itararé. For this reason, this site was not considered in the construction of the BS regional chronology. Tree-ring chronologies obtained from SS, JU and CB covered a shorter time period compared to BS and CJ (Fig. 3). Four chronologies (CJ, JU, CB, BS) seem to show a temporal stability, good quality and a strong common signal for all the chronologies during the past 50 years, approximately, with EPS values above the defined threshold after 1960. SS has EPS values are below the referenced threshold of 0.80 in the early part of the chronology period, mainly due to the low number of series included in this period.

3.3. Growth–climate spatial relationships

Overall, ring-width chronologies showed stronger correlations with precipitation than with temperature; however, the significant months vary among sites (Fig. 4). Monthly precipitation before the current year of growth (dry season) was positively associated with tree-ring chronologies of SS (May, $r = 0.34$, $p < 0.05$) and BS (from April to June, $r \sim 0.37$, $p < 0.01$), while precipitation at the beginning of the growing season was positively linked to radial growth in CJ (October, $r = 0.31$, $p < 0.05$), SS (September, $r = 0.31$, $p < 0.05$), and JU (October, $r = 0.48$, $p < 0.01$) sites. In contrast, February precipitation (at the core of the rainy season) during the current year of growth was positively associated with the ring-width chronology at the
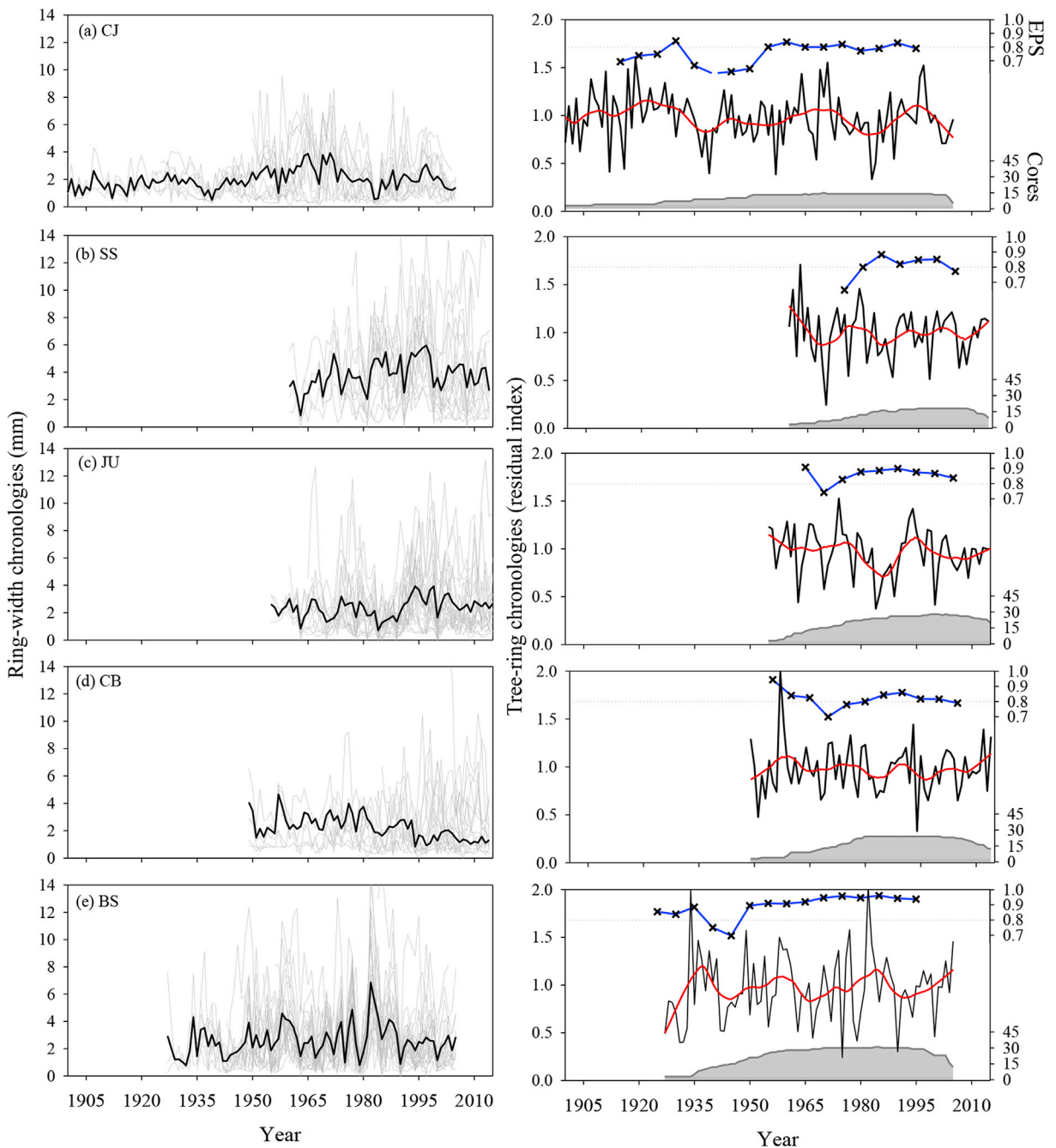
Fig. 3. Ring-width and tree-ring residual chronologies of the five studied sites. The left column indicates raw ring-width data in mm (gray lines are series and the black line is the average). Right column represents the residual chronologies (black line) with a superimposed smooth 15-year spline curve (red line). EPS statistic (blue line) computed in 20-year windows with an overlap 15 years; the 0.80 thresholds is shown by a dotted line. Number of cores sampled for each year is indicated by a gray area. (a) Campos de Jordão (CJ), (b) São Sebastião (SS), (c) Juquitibá (JU), (d) Carlos Botelho (CB), (e) Bom Sucesso Itararé (BS). (For interpretation of the references to colour in this figure legend, the reader should refer to the Web version of this article.)

highest site (CJ, r = 0.40, $p < 0.01$). For temperature, dendroclimatic results showed significant correlations only at CJ and BS sites during dry and cold months (June and July), being positive for CJ site (r ~ −0.32, $p < 0.05$) and negative for BS site (r ~ 0.35, $p < 0.05$). When we analyzed the seasonal links to growth, we observed that fall precipitation (from March to May) was positively associated with tree-ring chronologies at SS and BS sites, while summer precipitation (from December to February) was strongly correlated with tree growth of CJ and JU (all correlations with r > 0.40, $p < 0.01$). Cedrela trees of CB site did not show significant results.
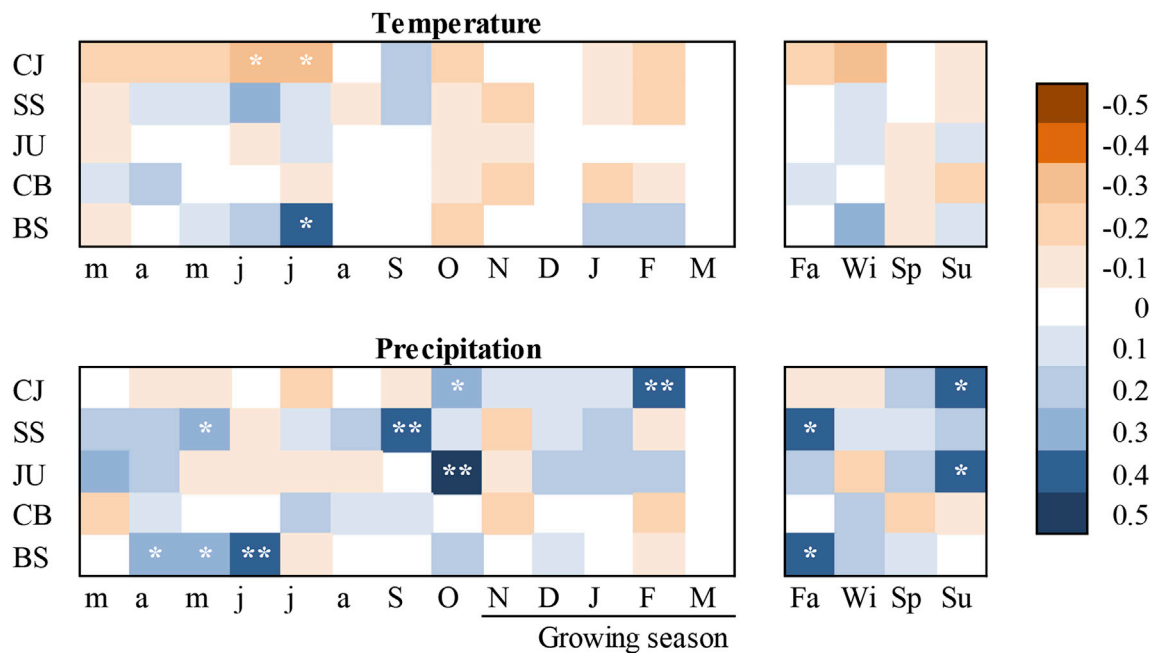
Fig. 4. Climate-growth relationship between *Cedrela* residual chronologies and precipitation and temperature, for the common period 1960−2005. See site acronyms in Table 1. Significance level at *0.05 ($r = 0.29$) and **0.01 ($r = 0.38$). Uppercase letters indicate current growing season. Fa: Fall, Wi: winter, Sp: spring, Su: summer.

3.4. Growth−drought spatial relationships

The correlation between the SPEI index and tree-ring residual chronologies is shown in Fig. 5, A high variability in the growth-drought dependence was found at scale 1-month, since chronologies were strongly sensitive to SPEI-1 in different months (CJ: February, $r = 0.50$; SS: May and September, $r = 0.40$; JU: October, $r = 0.46$; BS: June, $r = 0.43$ (all with $p < 0.01$); and CB: July, $r = 0.25$ ($p \sim 0.05$). In CJ and JU, the highest correlation was observed in SPEI-1. In contrast to SPEI-3, the signal is significantly stronger during September and June to SS ($r = 0.45$, $p < 0.01$) and BS ($r = 0.58$, $p < 0.01$), respectively, indicating that favorable moisture conditions of this and two previous months influence positively the tree growth in those sites. The lagged SPEI values until 12-month showed highly significant correlations in CJ, SS and BS sites ($r \sim 0.40$, $p < 0.01$) in summer, spring and winter, respectively (Fig. 5).

Using the highest correlations between tree-ring chronologies and the SPEI drought index (calculated at different month scales), we observed the difference in the climatic sensitivity of the population (CJ) at the higher altitude in relation to the other sites, a fact that seems to be associated with the climatic gradient that is evident during winter and summer (Fig. 6). CJ site receives less rainfall during end-fall/beginning-winter (May to July), which would negatively influence the tree-ring sensitivity to July SPEI 3-month and September SPEI 6-month (Fig. 6a,c). Moreover, the site at higher altitude, characterized by mild temperatures during summer, showed significant correlations between the ring width chronology and February SPEI 3-month and SPEI 6-month during the current year of growth (Fig. 6 b,d).

3.5. Effect of drought periods on tree-ring width

The chronology of SPEI calculated at 1-month scale showed three drought periods after 1950: (i) 1959−1971, (ii) 1984−1993, and (iii) 2001−2006 (Fig. 7). For the first dry period (13 years), we did not observe a significant influence on growth, while for the second (10 years) and third (6 years) dry periods, a significant difference in tree growth was observed (Table 3). Those differences were found mainly in the highest site (CJ), where lower values of tree-ring indices occurred in contrast to wet periods (before and after of dry period) (1984−1993: $H = 7.03$, $p = 0.029$; 2001−2006: H = 5.22, $p = 0.021$). However, we also found a significant difference in the CB site for the wet period 1994−2000, which showed lower growth than during dry periods (1994−2000: $H = 6.51$, $p = 0.038$).

3.6. Effect of temperature trends on chronologies

We observed a positive linear trend in both precipitation and temperature for the period 1901−2014 (both with $p < 0.001$) (Fig. S1). In this sense, a significant increase in annual mean temperature since 1990 for all the study sites was observed from
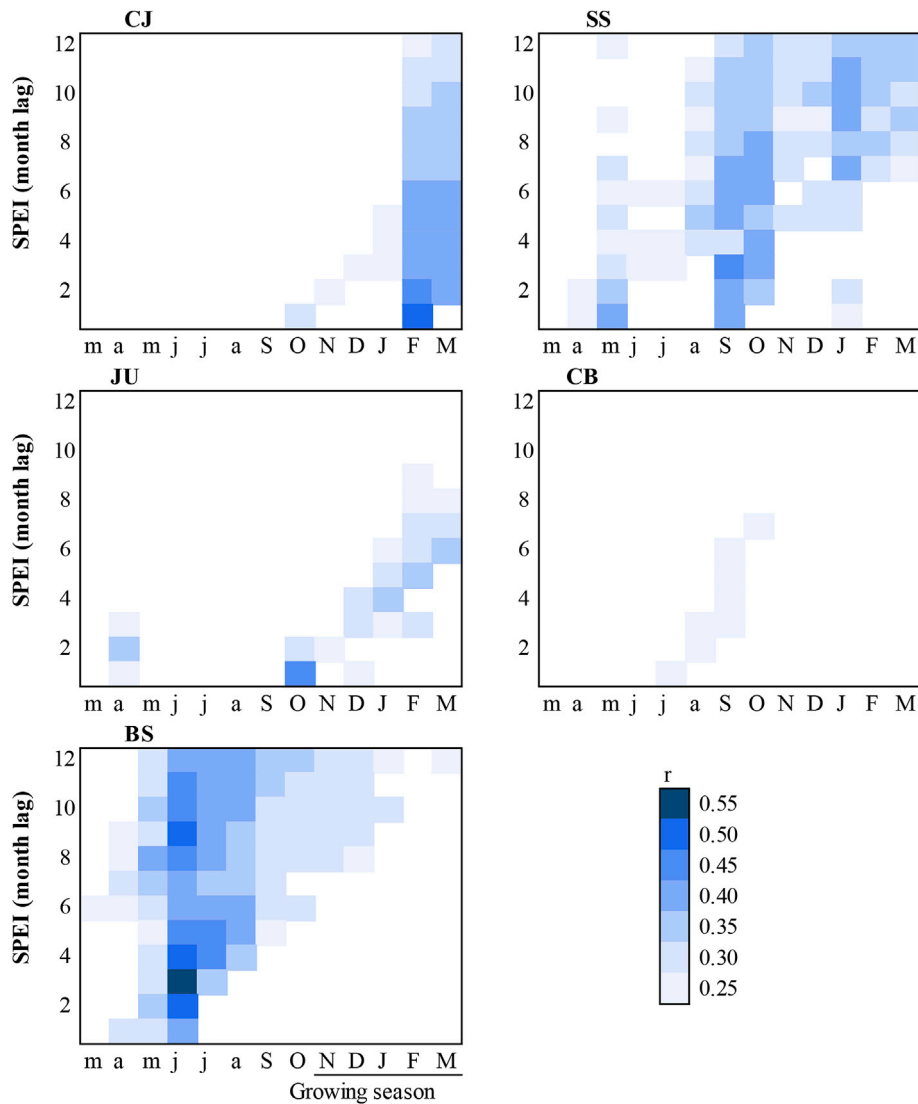
Fig. 5. The SPEI-growth relationship between residual *Cedrela* chronologies and SPEI drought index up to 12 months of cumulative time lag during the common period 1960−2005. See site acronyms in Table 1. Uppercase letters indicate current growing season. Only significant values ($p < 0.05$) are shown.

1950 to the present (Fig. 8a). The multiple linear regression analysis showed the temperature as the second predictor variable in all sites. Ring-width chronologies of CJ, JU, CB, and BS were negatively correlated with the mean temperature of winter, fall, summer, and spring, respectively ($p < 0.10$) (Table S1). However, we found a positive relationship between summer temperature and winter temperature in SS ($p < 0.05$). Analyzing those relationships, we found that significant trends of temperature from 1990 caused a significant decrease in the tree-ring growth only in the highest-altitude site (CJ) ($r = -0.56$, $p < 0.05$) during the dry and cold season (June to August). However, this rising temperature in winter had a positive effect on tree-ring growth of the southern tree population (BS) ($r = 0.63$, $p < 0.05$) (Fig. 8f). SS, JU, and CB do not show significant results (Fig. 8c, d, e).

4. Discussion

Considering the severity of recently droughts occurred in the São Paulo state (Coelho et al., 2016) and the global increase of air temperature detected in the tropics (Jones et al., 2007), the climate scenario is disturbing in relation to possible reactions of the biota. This justifies to analyze how trees can be affected by climatic extremes, particularly in the anthropized Atlantic Forest of Serra do Mar (AFSM). Our results showed a high sensitivity of the tree growth *Cedrela* spp populations to climate variability and droughts in AFSM. Therefore, we believe that these findings are essential to understand the tree growth dynamics in response to climate change, particularly in threatened tropical secondary forests such as the AFSM. In this sense,
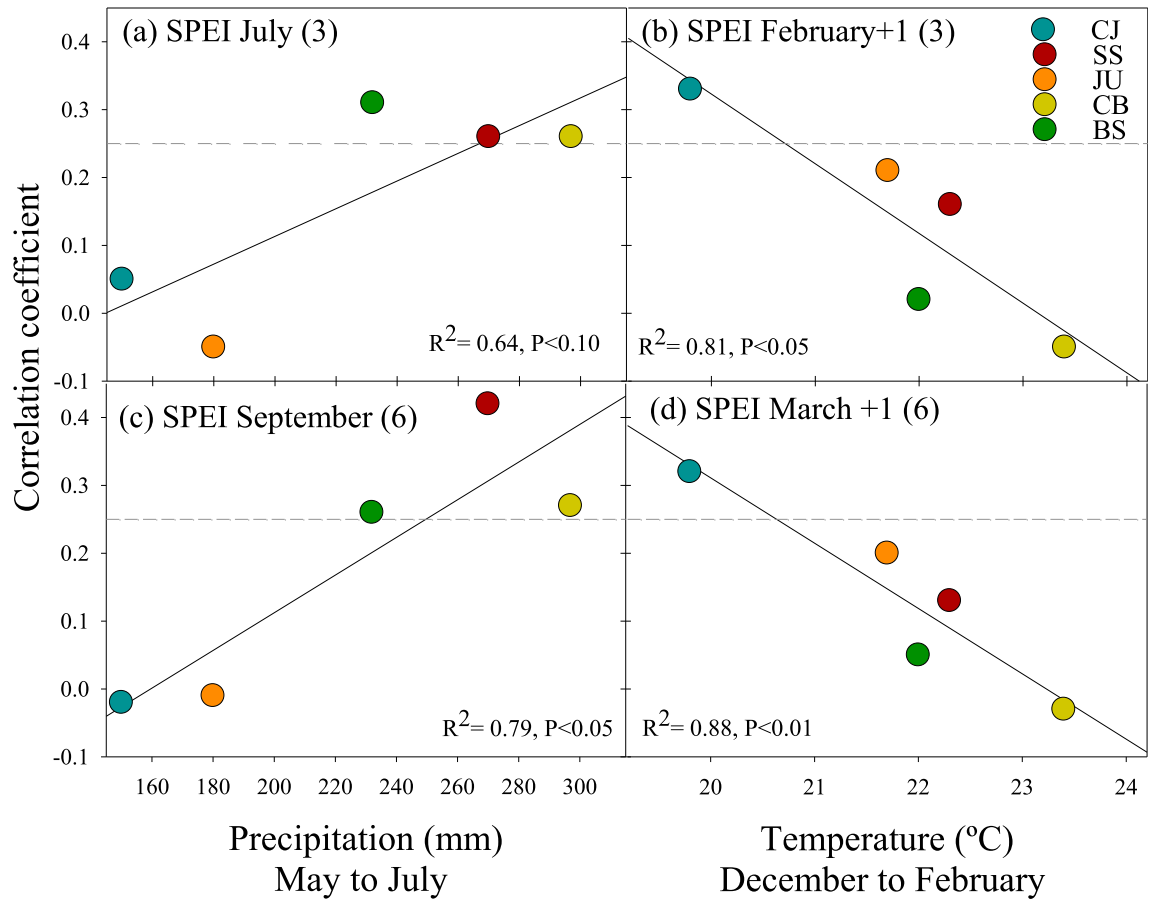
Fig. 6. Highest correlations between tree-ring chronologies and SPEI drought index calculated at different month scales against the climatic gradient of study sites (accumulated precipitation of May to July, and mean temperature of December to February). (a) July SPEI at 3-month scale, (b) February+1 SPEI at 3-month scale, (c) September SPEI at 6-month scale, (d) March SPEI at 6-month scale.
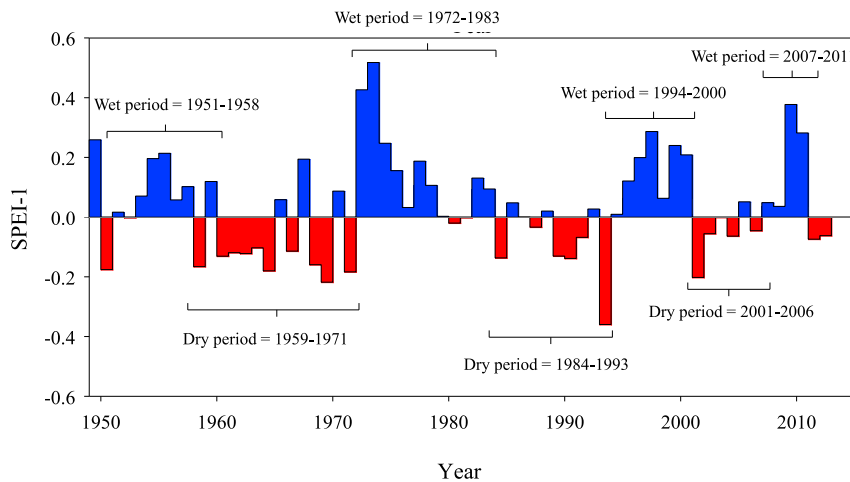

Fig. 7. Annual-SPEI chronology calculated at 1-month displacement scale, which allows to highlight the wet/dry periodicity during the second half of the 20th century.

Table 3
Comparison of mean tree-ring index (mean ± 1SE) before, during and after a drought period (see Fig. 7) at the five study sites.

Sites	Dry period (1959−1971)			Dry period (1984−1993)			Dry period (2001−2006)		
	Before	During	After	Before	During	After	Before	During	After
CJ	0.84 ± 0.08	1.02 ± 0.12	0.95 ± 0.07	0.95 ± 0.07	**0.78 ± 0.10**	1.13 ± 0.07	1.13 ± 0.07	**0.85 ± 0.07**	i/d
SS	i/d	0.86 ± 0.08	0.90 ± 0.09	0.90 ± 0.09	0.98 ± 0.08	1.11 ± 0.08	1.11 ± 0.08	0.87 ± 0.08	0.96 ± 0.09
JU	1.09 ± 0.07	0.97 ± 0.07	1.02 ± 0.06	0.92 ± 0.07	0.81 ± 0.02	1.05 ± 0.12	1.05 ± 0.12	0.93 ± 0.06	0.93 ± 0.07
CB	0.99 ± 0.20	0.96 ± 0.06	0.97 ± 0.06	0.97 ± 0.06	0.99 ± 0.08	**0.71 ± 0.07**	**0.71 ± 0.07**	1.04 ± 0.08	0.93 ± 0.06
BS	0.94 ± 0.10	0.94 ± 0.09	1.03 ± 0.17	1.13 ± 0.07	0.92 ± 0.09	0.89 ± 0.10	0.89 ± 0.08	1.08 ± 0.09	i/d

In bold is showing significantly differences among tree-ring indices for dry periods ($p < 0.05$). .i/d = insufficient data.

it should be noted that the Neotropical secondary forests play an important role in carbon storage, having a net carbon uptake eleven times the uptake rate of old-growth forests (Poorter et al., 2016).

Overall, tree-ring chronologies of *Cedrela* from AFSM show high inter-series correlations (r mean = 0.48), and mean expressed population signal >0.80, statistical elements that indicate a good performance of our tree-ring chronologies for dendroclimatic studies (Wigley et al., 1984). These correlations between trees were higher than any other attained in prior studies with *Cedrela* (e.g. $r < 0.28$ in Dunisch et al., 2003 and Paredes-Villanueva et al., 2016), but lower than observed by Brienen and Zuidema (2005) with $r = 0.57$. This variability in the correlation levels may be associated with the site characteristics themselves. CB site showed the lowest intercorrelation series, a fact that may be reflected in the weaker climatic (mainly precipitation) signal contained in this chronology (Table 2). The high values of the first-order autocorrelation of the tree-ring series justify the use of residual chronologies (Cook et al., 1990) for dendroclimatic analysis.

Cedrela fissilis and *C. odorata* have been over-exploited for the economic value of their highly qualified wood, which could explain the young age of the trees found in the analyzed sites. SS, JU, and CB produced the shorter chronologies (45 years approximately) in comparison to the CJ and BS sites that provided somewhat longer chronologies (70 years approximately). Although all sites suffered from logging, SS, JU, and CB sites were more affected probably by their easy access and transportation and lower distance from consumer centers, principally from Sao Paulo city where demand for timber increases largely since the 1950s (Dean, 1966). Besides, we must emphasize that forest under protected areas, such as the case of CJ, SS,
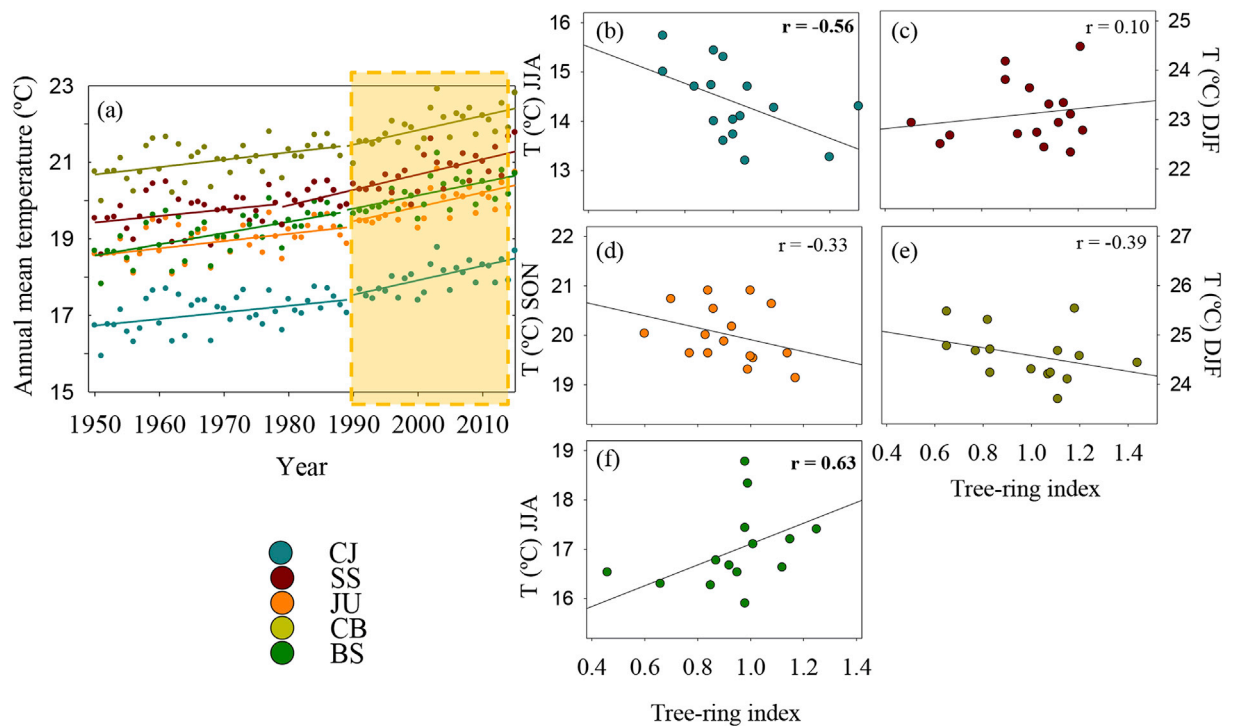

Fig. 8. (A) Annual mean temperature trends in the five sites for the period 1950−2014. Seasonal temperature is directly proportional to annual temperature (results not shown). Piecewise regression model identified different break years (p < 0.01) in all sites (CJ: 1990, SS: 1979, JU: 1989, CB: 1990 and BS: 1989). Orange rectangle represents the common period of significant increase in temperature for all sites (1990−2014). (b) to (f) shows the relationship between tree-ring residual chronologies and most significant mean seasonal temperature of multiple regression analysis (see Table S1), during the common period (1990−2005). In bold, significant correlations at 95% confidence level (For interpretation of the references to colors in this figure legend, the reader should refer to the Web version of this article).

and CB, the logging was disabled since 1941, 1977, and 1982, respectively. In addition, due to their vulnerable status and habitat preferences, *Cedrela* species were included in the list of priority species for conservation in 1981 (Paredes-Villanueva et al., 2016) and have been listed in Appendix III of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES, 2017).

4.1. Hypothesis 1: growth−climate relationship vs. climatic gradient

We found that tree-ring variability of our *Cedrela* chronologies from AFSM depends on water availability during certain months; therefore, any change in precipitation (which is directly related to soil water recharge), temperature (key controller in many physiological and chemical functions), and vapor pressure deficit (which controls transpiration rates) could differentially affect the growth performance at each site. Four sites (SS, JU, CB, and BS) showed favorable stimuli to rainfall during fall and winter months before the current year of growth (Figs. 4 and 5), in coincidence with others studies conducted in the Neotropics (Brienen and Zuidema, 2005; Dunisch et al., 2003). The rainfall during the dry season (fall and winter) would positively affect the moisture soil in spring, a season where cambial activity starts according to Andreacci et al. (2017). In addition, this interrelation would seem to be associated to the influence of the soil water supplement in the production of food reserves, which may be mobilized at the beginning of the next growth period playing an essential role in the physiological reactivation of meristematic tissues (Dunisch et al., 2003). In contrast to these results, highest and coldest site (CJ) did not show a significant influence of rainfall over xylem production at the times of the prior growing season, which seem to be more linked to winter rainfall contributions (May to July) (Fig. 6a,c). In addition, this site is subjected to the lowest mean temperature recorded in the regional gradient (Fig. 3), indicating a broad mechanism of adaptation or particular plasticity of *Cedrela* to different environmental conditions, affecting the phenology of cambium and foliage.

At CJ we found an interesting relationship of the tree growth sensitivity to summer rainfall during the current period of growth (Fig. 4), where maximum cambial activity occurs during the rainy season. This pattern has also been identified in other Brazilian tropical trees such as *Swietenia macrophylla* (Dunisch et al., 2003), *Amburana cearensis*, *Tachigali vasquezii* (Brienen and Zuidema, 2005), *Tectona grandis* (Venegas-González et al., 2016), and *Hymenaea courbaril* (Locosselli et al., 2013). Paredes-Villanueva et al. (2016) found a similar growth sensitivity to precipitation during the rainy season in three *Cedrela* spp. populations from Bolivia (*C. odorata*, *C. fissilis*, and *C. angustifolia*), indicating that radial growth is determined by the availability of soil water supply during the current year of growth. In the case of the CJ site, this association may be explained because this site is at the highest altitudinal position, where lower temperature during summer (Fig. 6b,d) would avoid an exacerbated evapotranspiration, maintaining a higher soil water availability than in the other analyzed sites.

4.2. Hypothesis 2: growth−drought relationship vs. climatic gradient

Tree-ring sensitivity to SPEI drought index confirm the tree growth dependence to favorable soil moisture conditions, being strongly significant for the site located at higher altitude (CJ) during the rainiest months, and during winter and spring (beginning of the growing season) for the others sites. However, SS, CB and JU also showed positive associations to precipitation ($p < 0.05$) during the rainy season (summer), but with low correlations (Fig. 5). This shows the hydric sensitivity of the *Cedrela* spp in these sites. All sites have high precipitation rates during December and January (~200 mm per month), this condition being able to exercise greater control over evapotranspiration. SS site showed the highest growth rate, a fact that could be explained by a larger rainfall amount (>2000 mm annual) and tree ages (Table 2). Other biogeographic studies claim that wet sites correspond to higher tree-ring widths in different forests, where stress by evapotranspiration would be reduced (e.g. Camarero et al., 2013; Lyu et al., 2017). Our results confirm the SPEI-growth relationship, indicating that wet forests respond to drought events during short periods of time (maximum SPEI/tree-ring correlation found), i.e. one to six-months, in comparison to dry forests (Vicente-Serrano et al., 2013).

We observed that dry periods (6−10 years) caused a negative effect on tree growth mainly in the highest site (CJ), indicating that forests at these conditions could be more sensitive to drought, and with lower growth resilience during a post-drought period (Table 3). Therefore, this type of site in the gradient could be the most vulnerable to extreme drought episodes, risk that has been indicated at a global level (Allen et al., 2015). Deciduous tropical trees respond to drought altering their phenology by regulating their leafless times, improving the uptake water from deep soils sources, and increasing their resistance to cavitation or enhancing water storage in the stem and branches (Markesteijn et al., 2011). However, a leaf fall reaction to severe drought conditions would reduce transpiration rates, affecting tree growth processes (Wright and Cornejo, 1990) and exposing trees to risks of functional imbalances due to embolism (Choat et al., 2012).

4.3. Hypothesis 3: growth−global warming relationship vs. climatic gradient

The significant trends observed in both annual total precipitation and annual mean temperature in the transect of the AFSM indicate that although temperature rises, rainfall increases (Fig. S2), a fact that may explain why multi-annual droughts do not increase (Fig. 7). However, CJ (highest altitude) site was the only one in which a negative trend in tree growth was observed for the last decades, a fact that would be related to rising winter temperature (Fig. 8b). This relationship might be explained by an increase of soil water deficit coupled with rising temperatures during the dry season, a fact that would affect the cambial activity some months later (i.e. more evapotranspiration). Also, it is important to consider that the highest site

receives the least amount of rainfall during winter (Figs. 6a and 1S). Paredes-Villanueva et al. (2016) also found negative correlations between *Cedrela* spp. tree rings and dry season temperature. The increase in air temperature prior to the cambium activity start leads to greater evapotranspiration rates that reduce the water soil availability during the growth period in tropical tree species (López and Villalba, 2011).

However, we observed a positive trend linked to winter temperature in the southern site (Fig. 8f). This can be explained by the fact that warmer temperatures during the dry season are not a limiting factor to growth at this site, unlike the site located at higher altitudes, where the rains are greater (>80 mm) (Fig. 5). Therefore, we can argue that this regional rise in temperature has affected particularly those trees growing at the highest site (~1500 m a.s.l), where both water availability and soil fertility seems to impact more stronger tree growth and species distribution (Oliveira-Filho et al., 1998; Toledo et al., 2011). Overall, the highest site has shallow soil and lower fertility than the others study sites (Modenesi-Gauttieri and Hiruma, 2004), so a change in temperature may have implications in water dynamic storage and nutrient uptake of soils, affecting tree growth.

4.4. Implications and outlook

We concluded that growth-climate relationship of *Cedrela* forests varies across a climatic gradient in the hotspot Brazilian Atlantic forest at the biogeographic subregion Serra do Mar. We propose that the highest-altitude sites are more vulnerable to regional warming during winters (dry and cold season), being trees at these sites more sensitive to dry periods (6–10 years with negative SPEI). The recent drought produced in the region (2014–2015) has been described as the worst drought in the last 80 years, causing strong incidences in water shortage with serious consequences on water supplements to support huge human populations, agriculture and industrial activities (Coelho et al., 2016; Nobre et al., 2016). These droughts, if they persist, will have deleterious effects on forest populations located in highest sites of the gradient. However, this is still uncertain in AFSM, since an increase of rainfall extremes in the region is expected (Marengo et al., 2009). Our results verify the worse effect of future changes in climate and the hydrologic cycle on growth dynamic of Neotropical forests distributed in montane regions (Pounds et al., 1999), where different species are expected to experience displacements from their current occurrence due to warming effects (Moritz and Agudo, 2013). To our knowledge, the present study is the first report about relationships between tree rings and the SPEI index, calculated at different time-scales in southeastern Brazil. Therefore, these results highlight the importance of considering the SPEI dryness index in tropical dendroecological studies, allowing to better understand how trees react to drought both at long and short-time scales. It is, therefore, necessary to expand the network of *Cedrela* spp. chronologies to the whole Atlantic Forest, taking in advantage the wide geographic distribution of the species and their great climate sensitivity to detect climate change and variability processes.

Acknowledgments

Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.gecco.2018.e00408.

References

Allen, C.D., Breshears, D.D., McDowell, N.G., 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere 6, 1–55.

Alvares, C.A., Stape, J.L., Sentelhas, P.C., Goncalves, J.L.D., Sparovek, G., 2013. Koppen's climate classification map for Brazil. Meteorol. Zeitschrift 22, 711–728. https://doi.org/10.1127/0941-2948/2013/0507.

Andreacci, F., Botosso, P.C., Galvão, F., 2017. Vegetative phenology and growth of Cedrela fissilis in atlantic forest, southern Brazil. Floresta e Ambiente 24.

Blasing, T.J., Solomon, A.M., Duvick, D.N., 1984. Response functions revisited. Tree Ring Bul. 144, 1–15.

Biondi, F., Qeadan, F., 2008. A theory-driven approach to tree-ring standardization: defining the biological trend from expected basal area increment. Tree-Ring Res. 64, 81–96.

Bonan, G.B., 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. Science (80–.) (320), 1444–1449.

Brienen, R.J.W., Zuidema, P.A., 2005. Relating tree growth to rainfall in Bolivian rain forests: a test for six species using tree ring analysis. Oecologia 146, 1–12. https://doi.org/10.1007/s00442-005-0160-y.

Callado, C.H., Roig, F.A., Tomazello-Filho, M., Barros, C.F., 2013. Cambial growth periodicity studies of South American woody species–A review. IAWA J. 34, 213–230.

Camarero, J.J., Gutiérrez, E., 2004. Pace and pattern of recent treeline dynamics: response of ecotones to climatic variability in the Spanish Pyrenees. Climatic Change 63, 181–200.

Camarero, J.J., Manzanedo, R.D., Sanchez-Salguero, R., Navarro-Cerrillo, R.M., 2013. Growth response to climate and drought change along an aridity gradient in the southernmost Pinus nigra relict forests. Ann. For. Sci. 70, 769–780.

Choat, B., Jansen, S., Brodribb, T.J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S.J., Feild, T.S., Gleason, S.M., Hacke, U.G., 2012. Global convergence in the vulnerability of forests to drought. Nature 491, 752.

Coelho, C.A.S., Cardoso, D.H.F., Firpo, M.A.F., 2016. Precipitation diagnostics of an exceptionally dry event in São Paulo. Brazil. Theor. Appl. Climatol 125, 769–784.

CITES (Convention on International Trade in Endangered Species of Wild Flora and Fauna), 2017. Apéndices I, II, III. https://www.cites.org/esp/app/appendices.php. Accessed 15 February 2017.

Colombo, A.F., Joly, C.A., 2010. Brazilian Atlantic Forest lato sensu: the most ancient Brazilian forest, and a biodiversity hotspot, is highly threatened by climate change. Brazilian J. Biol. 70, 697–708.

Cook, E.R., Briffa, K., Shiyatov, S., Mazepa, V., 1990. Tree-ring standardization and growth-trend estimation. Methods dendrochronology Appl. Environ. Sci. 104–123.

Dean, W., 1996. A ferro e fogo: a história e a devastação da Mata Atlântica brasileira. Companhia das Letras.

Di Rienzo, J., Balzarini, M., Casanoves, F., González, L., Tablada, M., Robledo, C.W., 2001. InfoStat: Software Estadístico. Córdoba Univ. Nac, Córdoba.

Dos Santos, F.A.M., Pedroni, F., Alves, L.F., Sanchez, M., 1998. Structure and dynamics of tree species of the Atlantic Forest. An. Acad. Bras. Cienc.

Dünisch, O., 2005. Influence of the El-niño southern oscillation on cambial growth of Cedrela fissilis Vell. in tropical and subtropical Brazil. J. Appl. Bot. Food Qual. 79, 5–11.

Dunisch, O., Montoia, V.R., Bauch, J., 2003. Dendroecological investigations on Swietenia macrophylla king and Cedrela odorata L. (Meliaceae) in the central amazon. Trees Struct. Funct. 17, 244–250.

Fritts, H.C., 1976. Tree Rings and Climate. Elsevier.

Gea-Izquierdo, G., Cañellas, I., 2014. Local climate forces instability in long-term productivity of a Mediterranean oak along climatic gradients. Ecosystems 17, 228–241.

Grissino-Mayer, H.D., 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree-Ring Res. 57, 205–221.

Granato-Souza, D., Stahle, D.W., Barbosa, A.C., Feng, S., Torbenson, M.C.A., Pereira, G.A., Schöngart, J., Barbosa, J.P., Griffin, D., 2018. Tree rings and rainfall in the equatorial Amazon. Clim. Dynam. https://doi.org/10.1007/s00382-018-4227-y.

Guilherme, F.A.G., Morellato, L.P.C., Assis, M.A., 2004. Horizontal and vertical tree community structure in a lowland Atlantic Rain Forest, Southeastern Brazil. Braz. J. Bot. 27, 725–737.

Holmes, R.L., Adams, R.K., Fritts, H.C., Laboratory of Tree-Ring Research, U. of A, 1986. Tree-ring Chronologies of Western North America: California, Eastern Oregon and Northern Great Basin with Procedures Used in the Chronology Development Work Including Users Manuals for Computer Programs COFECHA and ARSTAN. The Univer. ed, Laboratory of Tree-Ring Research Archives, Tucson. https://doi.org/http://hdl.handle.net/10150/304672.

IBGE, 2004. o Mapa de Vegetação do Brasil. Inst. Bras. Geogr. e Estatística– IBGE.

Jones, P.D., Moberg, A., 2003. Hemispheric and large-scale surface air temperature variations: an extensive revision and an update to 2001. J. Clim. 16, 206–223.

Jones, P.D., Trenberth, K.E., Ambenje, P., Bojariu, R., Easterling, D., Klein, T., Parker, D., Renwick, J., Rusticucci, M., Soden, B., 2007. Observations: surface and atmospheric climate change. Climatic Change 235–336.

Jump, A.S., Hunt, J.M., Penuelas, J., 2006. Rapid climate change-related growth decline at the southern range edge of Fagus sylvatica. Global Change Biol. 12, 2163–2174.

Jump, A.S., Mátyás, C., Peñuelas, J., 2009. The altitude-for-latitude disparity in the range retractions of woody species. Trends Ecol. Evol. 24, 694–701.

Lacerda, M.S., 2001. Composição florística e estrutura da comunidade arbórea num gradiente altitudinal da Mata Atlântica.

Lara, A., Villalba, R., Wolodarsky-Franke, A., Aravena, J.C., Luckman, B.H., Cuq, E., 2005. Spatial and temporal variation in Nothofagus pumilio growth at tree line along its latitudinal range (35 40'–55 S) in the Chilean Andes. J. Biogeogr. 32, 879–893.

Locosselli, G.M., Buckeridge, M.S., Moreira, M.Z., Ceccantini, G., 2013. A multi-proxy dendroecological analysis of two tropical species (Hymenaea spp., Leguminosae) growing in a vegetation mosaic. Trees Struct. Funct. 27, 25–36. https://doi.org/10.1007/s00468-012-0764-x.

López, L., Villalba, R., 2011. Climate influences on the radial growth of centrolobium microchaete, a valuable timber species from the tropical dry forests in Bolivia. Biotropica 43, 41–49. https://doi.org/10.1111/j.1744-7429.2010.00653.x.

Lyu, L., Suvanto, S., Nöjd, P., Henttonen, H.M., Mäkinen, H., Qi-Bin, Z., 2017. Tree growth and its climate signal along latitudinal and altitudinal gradients: comparison of tree rings between Finland and the Tibetan Plateau. Biogeosciences 14, 3083.

Marcati, C.R., Angyalossy, V., Evert, R.F., 2006. Seasonal variation in wood formation of Cedrela fissilis (Meliaceae). IAWA J. 27, 199–211.

Marengo, J.A., Jones, R., Alves, L.M., Valverde, M.C., 2009. Future change of temperature and precipitation extremes in South America as derived from the PRECIS regional climate modeling system. Int. J. Climatol. 29, 2241–2255.

Markesteijn, L., Poorter, L., Bongers, F., Paz, H., Sack, L., 2011. Hydraulics and life history of tropical dry forest tree species: coordination of species' drought and shade tolerance. New Phytol. 191, 480–495.

Martinelli, G., Moraes, M.A., 2013. Livro vermelho da flora do Brasil.

Mendivelso, H.A., Camarero, J.J., Gutiérrez, E., Zuidema, P.A., 2014. Time-dependent effects of climate and drought on tree growth in a Neotropical dry forest: short-term tolerance vs. long-term sensitivity. Agric. For. Meteorol 188, 13–23.

Modenesi-Gauttieri, M.C., Hiruma, S.T., 2004. A expansão urbana no planalto de Campos do Jordão: diagnóstico geomorfológico para fins de planejamento. Rev. do Inst. Geologi (Helsinki) 25, 1–28.

Moritz, C., Agudo, R., 2013. The future of species under climate change: resilience or decline? Science 80 (341), 504–508.

Muellner, A.N., Pennington, T.D., Koecke, A.V., Renner, S.S., 2010. Biogeography of Cedrela (Meliaceae, sapindales) in central and south America. Am. J. Bot. 97, 511–518.

Muggeo, V.M.R., 2008. Segmented: an R package to fit regression models with broken-line relationships. R. News 8, 20–25.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858. https://doi.org/10.1038/35002501.

Nobre, C.A., Marengo, J.A., Seluchi, M.E., Cuartas, L.A., Alves, L.M., 2016. Some characteristics and impacts of the drought and water crisis in Southeastern Brazil during 2014 and 2015. J. Water Resour. Protect. 8, 252.

O'brien, R.M., 2007. A caution regarding rules of thumb for variance inflation factors. Qual. Quantum 41, 673–690.

Oliveira-Filho, A.T., Curi, N., Vilela, E.A., Carvalho, D.A., 1998. Effects of canopy gaps, topography, and soils on the distribution of woody species in a central Brazilian deciduous dry forest. Biotropica 30, 362–375.

Pachauri, R.K., Allen, M.R., Barros, V.R., Broome, J., Cramer, W., Christ, R., Church, J.A., Clarke, L., Dahe, Q., Dasgupta, P., 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.

Paredes-Villanueva, K., López, L., Cerrillo, R.M.N., 2016. Regional chronologies of Cedrelafissilis and Cedrela angustifolia in three forest types and their relation to climate. Trees (Berl.) 30, 1581–1593.

Poorter, L., Bongers, F., Aide, T.M., Zambrano, A.M.A., Balvanera, P., Becknell, J.M., Boukili, V., Brancalion, P.H.S., Broadbent, E.N., Chazdon, R.L., 2016. Biomass resilience of Neotropical secondary forests. Nature 530, 211–214.

Pounds, J.A., Fogden, M.P.L., Campbell, J.H., 1999. Biological response to climate change on a tropical mountain. Nature 398, 611.

R core Team, R, 2017. R Language Definition. Austria R Found. Stat. Comput., Vienna.

Rasband, W.S., 1997. Image J, US National Institutes of Health, Bethesda, Maryland, USA, vol. 2014.

Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J., Hirota, M.M., 2009. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. Biol. Conserv. 142, 1141–1153.

Rodrigues, R.R., Brancalion, P.H.S., Isernhagen, I., 2009. Pacto pela restauração da mata atlântica: referencial dos conceitos e ações de restauração florestal. Escola Superior de Agricultura" Luiz de Queiroz"/Instituto BioAtlântica.

Santos, D.L. dos, Takaki, M., 2005. Phenology of Cedrela fissilis vellozo (Meliaceae) in Itirapina, São Paulo state, Brazil. Acta Bot. Bras. 19, 625—632.

Schulman, E., 1956. Dendroclimatic Changes in Semiarid America. Dendroclimatic Chang. Semiarid Am.

Schweingruber, F.H., 1996. Tree Rings and Environment: Dendroecology. Paul Haupt AG Bern.

Scudeller, V.V., Martins, F.R., Shepherd, G.J., 2001. Distribution and abundance of arboreal species in the atlantic ombrophilous dense forest in Southeastern Brazil. Plant Ecol. 152, 185—199.

Stokes, M.A., Smiles, T., 1996. An Introduction to Tree-ring Dating. University of Arizona Press, Tucson.

Toledo, M., Poorter, L., Peña-Claros, M., Alarcón, A., Balcázar, J., Leaño, C., Licona, J.C., Llanque, O., Vroomans, V., Zuidema, P., 2011. Climate is a stronger driver of tree and forest growth rates than soil and disturbance. J. Ecol. 99, 254—264.

Tomazello Filho, M., Botosso, P.C., Lisi, C.S., Roig, F.A., 2000. Potencialidade da família Meliaceae para dendrocronologia em regiões tropicais e subtropicais. In: Dendrocronología en América Lat. la Univ. Nac. Cuyo, Mendoza, pp. 381—431.

Veloso, H.P., Rangel Filho, A.L.R., Lima, J.C.A., 1991. Classificação da vegetação brasileira, adaptada a um sistema universal. Ministério da Economia, Fazenda e Planejamento, Fundação Instituto Brasileiro de Geografia e Estatística, Diretoria de Geociências. Dep. Recur. Nat.

Venegas-González, A., Chagas, M.P., Anholetto Júnior, C.R., Alvares, C.A., Roig, F.A., Tomazello Filho, M., 2016. Sensitivity of tree ring growth to local and large-scale climate variability in a region of Southeastern Brazil. Theor. Appl. Climatol. 123. https://doi.org/10.1007/s00704-014-1351-4.

Venegas-González, A., Juñent, F.R., Gutiérrez, A.G., Tomazello Filho, M., 2018. Recent radial growth decline in response to increased drought conditions in the northernmost Nothofagus populations from South America. For. Ecol. Manage 409, 94—104.

Vicente-Serrano, S.M., Begueria, S., Lopez-Moreno, J.I., 2010. A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. J. Clim. 23, 1696—1718. https://doi.org/10.1175/2009jcli2909.1.

Vicente-Serrano, S.M., Gouveia, C., Camarero, J.J., Beguería, S., Trigo, R., López-Moreno, J.I., Azorín-Molina, C., Pasho, E., Lorenzo-Lacruz, J., Revuelto, J., 2013. Response of vegetation to drought time-scales across global land biomes. Proc. Natl. Acad. Sci. Unit. States Am. 110, 52—57.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. Nature 416, 389—395.

Wigley, T.M.L., Briffa, K.R., Jones, P.D., 1984. On the average value of correlated time-series, with applications in dendroclimatology and hydrometeorology. J. Clim. Appl. Meteorol. 23, 201—213. https://doi.org/10.1175/1520-0450(1984)023<0201:otavoc>2.0.co;2.

Worbes, M., 1999. Annual growth rings, rainfall-dependent growth and long-term growth patterns of tropical trees from the Caparo Forest Reserve in Venezuela. J. Ecol. 87, 391—403. https://doi.org/10.1046/j.1365-2745.1999.00361.x.

Wright, S.J., Cornejo, F.H., 1990. Seasonal drought and leaf fall in a tropical forest. Ecology 71, 1165—1175.

Zang, C., Biondi, F., 2013. Dehdroclimatic calibration in R: the bootRes package for response and correlation function analysis. Dendrochronologia 31, 68—74. https://doi.org/10.1016/j.dendro.2012.08.001.