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Long- and short-term impacts of climate and dry-season on wood traits of *Cedrela fissilis* Vell. in southern Brazilian Amazon

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ABSTRACT

During the last two decades the tropical Amazon forests have been impacted by frequent and severe droughts. However, little is known about the impacts of these extreme events on wood traits. In this study, we quantified long- and short-term impacts on growth and wood density response and resilience strategies under extreme droughts, analyzing the wood trait trends and correlations with climate variables (temperature, precipitation, and the SPEI drought index). Then, we simulated tree-ring formation and its responses to soil moisture using the process-based VS-Lite growth model. Our results showed how climate anomalies and dry spells increased since 1990s in the southern Amazon region and have affected the growth and wood density of *C. fisillis*. Ring width, latewood width and minimum wood density experienced the highest sensitivity to drought. *C. fissilis* showed wider (narrower) and more (less) dense rings during wetter (drier) years, respectively, suggesting that the species undergoes functional plasticity in the formation of its wood in order to adapt to dry conditions. Changes in water limitations during the dry season modify growth thresholds and long-term resilience, leading to decrease growth and increase wood density, enhancing the vulnerability of *C. fissilis* to projected climate warming scenarios. The short-term resilience is evidenced more in wood density than in the ring width, indicating the species' ability to adapt to short drought periods. This study is a first attempt to evidence the characteristics of the annual growth rings of C. fissilis trees in relation to climate sensitivity and resilience to drought, based on long-term data from the seasonal moist tropical forest of the Amazon.

1. Introduction

The Amazon basin plays a crucial biogeochemical and hydrological role in the regional and global climate (Buscardo et al., 2016; Covey et al., 2021; Malhi et al., 2021; Nobre et al., 2016). The Amazon region is characterized by a huge spatiotemporal variation which is influenced by many factors on interannual and decadal time scales, such as the El Niño-Southern Oscillation, Pacific Interdecadal Oscillation, Atlantic Multidecadal Oscillation, meridional gradient across the tropical Atlantic Ocean, among others (Barichivich et al., 2018; Espinoza et al., 2019; Liebmann and Marengo, 2001; Marengo and Souza, 2018). Furthermore, the South American Monsoon System and the intertropical convergence zone (ITCZ) are the main mechanisms inducing seasonal precipitation regimes in most regions of the Amazon basin (Marengo et al., 2016), which variability depends mainly on the above-mentioned interannual, decadal and mutidecadal modes, but increasingly also by anthropogenic disturbances, mainly caused by deforestation and associated fires (Boers et al., 2017; Marengo et al., 2018; Staal et al., 2020). During recent decades, several studies have suggested that extreme hydroclimatic events induced by climate change have increased the structural and functional vulnerability of Amazonian tropical forests (Chai et al., 2021; Corlett, 2011; Marengo et al., 2009, 2011).

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Furthermore, agricultural conversion, illegal logging (Carvalho et al., 2019), fire (van Wees et al., 2021), deforestation of the river catchments (Costa et al., 2003), implementation of hydropower plants (Timpe and Kaplan, 2017), and illegal mining (Chambi-Legoas et al., 2021) have accelerated the forest loss affecting the carbon, energy and water cycles in the Amazon basin. Negative synergies between climate change, deforestation, and fire are inducing a tipping point for the Amazon system to flip to non-forest ecosystems in eastern, southern and central Amazonia (Lovejoy and Nobre, 2018).

The southern region of the Amazon basin is one of the most impacted by climatic extremes associated with longer duration of the dry seasons (Agudelo et al., 2019; Collini et al., 2008). The observed increasing duration of the dry season (about a month since the beginning of the 1970s) in this region is mainly caused by a later onset of the rainy season (Marengo et al., 2018). The presence of dry years in this region presents interannual time scales related to the occurrence of strong El Niño events in the tropical Pacific, or anomalously warm sea surface temperatures (SST) in the tropical Atlantic (Liebmann and Marengo, 2001; Marengo et al., 2008). Since 1990, lengthier dry seasons have been more frequent over the southern and eastern Amazon basin and model predictions suggest potential forest diebacks and a shift toward savanna vegetation to the east of the region (Chai et al., 2021; Poulter et al., 2010). The observed increase in mean temperature and longer dry seasons during the late 20th and early 21st century in the southern Amazon basin is evidenced by extreme drought events in 1981–1983, 1997–1998, 2004–2005, 2007, 2010, 2015–2016 (Caioni et al., 2020; Espinoza et al., 2019; Lovejoy and Nobre, 2018; Marengo et al., 2008; Ronchail et al., 2002; Williams et al., 2005), these forests being able to increase the vulnerability of forests by reducing their post-drought resilience after these climatic extremes (Allen et al., 2015; DeSoto et al., 2020).

These alterations in the hydroclimatic cycles may affect tree physiology, growth and mortality, which vary among different species and forest types (Aleixo et al., 2019; Brando et al., 2008; Gonçalves et al., 2021; Phillips et al., 2009; Schöngart et al., 2021; Smith et al., 2019; Zhou et al., 2013). The effects of climate trends on tropical forest productivity highlight the need to investigate the relevant wood traits providing tolerance to temporary water shortages (e.g., radial-growth plasticity, higher wood density, e.g., Brienen et al., 2016; Pompa--García and Camarero, 2020; Schöngart et al., 2017; Zuidema et al., 2013) and to assess how Amazonian forest can resist droughts and recover after them in relation to their long- and short-term tree seasonal responses (Mendivelso et al., 2014). Therefore, retrospective analysis based on tree-ring parameters (width, anatomy, wood density, $\delta^{18}O$ and $\delta^{13}C$ isotopes, carbohydrates or nutrients content) (Baker et al., 2016; Brienen et al., 2016; Cintra et al., 2019; Locosselli and Buckeridge, 2017) has the potential to provide insights of the impact of hydroclimatic extreme events and trends on tree growth, hydraulic conductivity and water and nutrient use efficiency in the Amazon basin on different time scales (Albiero-Júnior et al., 2019; Brienen et al., 2016; Granato-Souza et al., 2020; Humanes-Fuente et al., 2020; Schöngart et al., 2004). Although there are studies using tree-ring widths in tropical forests (Pompa-García and Camarero, 2020; Roig, 2000; Schöngart et al., 2017), other wood traits derived from vessel anatomical features (Islam et al., 2019, 2018; Quintilhan et al., 2021; Rodríguez-Ramírez et al., 2022), wood density (Gonçalves et al., 2021; Lisi et al., 2020; Tomazello-Filho et al., 2001; Worbes et al., 1995) or nutrient contents (Hietz et al., 2015; Ortega Rodriguez et al., 2022; Poussart et al., 2006), have been scarcely used in the tropics to analyze the impact of extreme hydroclimatic events and trends associated with climate change.

In non-flooded forests, negative impacts on tree growth related to extreme droughts have been reported in the eastern equatorial Amazon (Granato-Souza et al., 2020), western Amazon Andes (Humanes-Fuente et al., 2020) and southern Amazon (Lopez et al., 2017). The stress on trees caused by extreme or prolonged droughts may reduce the resilience of trees (Li et al., 2020; Rahman et al., 2019; Venegas-González et al., 2018) as a result of hydraulic failure (Rodriguez-Ramirez et al., 2020; Zanne et al., 2010) and/or carbon starvation (Bretfeld et al., 2018; Brienen et al., 2015; Corlett, 2016; Phillips et al., 2009). In some cases, individual trees are able to recover their pre-impact status (Folke et al., 2004), which produce physiological memory effects (Galiano et al., 2011). However, when the accumulated stress exceeds a physiological threshold which is reflected by radial growth, it may never return to its pre-stress condition (Sánchez-Salguero and Camarero, 2020), thereby causing decline and even mortality (Colangelo et al., 2018).

To understand the variability of short- and long-term growth response to severe droughts, we evaluated the post-drought resilience indices (*sensu* Lloret et al., 2011) in a moist tropical forest with a distinct dry season of the southern Amazon (Guan et al., 2015). To provide a mechanistic understanding of these growth responses to drought, we additionally used the Vaganov–Shashkin model of tree-ring formation, hereafter VS-Lite (Camarero et al., 2020a; Tolwinski-Ward et al., 2013; Vaganov et al., 2011). The VS-Lite model simulates the monthly growth responses to temperature and precipitation, which can help to understand the physiological responses thresholds of tropical tree species to climate warming and droughts (Vaganov et al., 2011). Nevertheless, in comparison to trees of Temperate, Boreal or Mediterranean forests (DeSoto et al., 2020; Gazol et al., 2018; Kunz et al., 2018; Sánchez-Salguero et al., 2018; Sun et al., 2020) drought resilience of tropical trees is still poorly understood (but see: Camarero et al., 2020; Islam et al., 2019; Rahman et al., 2019; Venegas-González et al., 2018).

Studies indicated that Neotropical trees have the ability to adjust their growth to water availability and this makes them more resilient to drier conditions (Camarero et al., 2020; Mendivelso et al., 2014; Rodríguez-Ramírez et al., 2022). However, it is unknown how tropical trees change their short-term responses in ring width and density and long-term resilience when these are influenced by drier conditions and how this plasticity affects radial growth in tropical species. Here, we combined VS-lite mechanistic models with resilience indices derived from wood traits on *Cedrela fissilis* Vell. (Meliaceae) of a natural forest in the southern Brazilian Amazon to assess how climate trends and increase in extreme drought events may endanger future tropical forests. We aimed to (1) investigate the relationships between climate, drought and wood traits (ring-, early- and late-wood widths and wood density) of *C. fissilis* of a drought-prone region of Amazonian forests, (2) analyze changes in growth responses across time using the VS-lite model, and (3) quantify resilience strategies of growth and wood density under climate extremes. We hypothesize that increasingly longer dry seasons would lead to lower ring width and higher wood density and consequently a reduction/increase in resilience for ring-width/wood density.

2. Material and methods

2.1. Study area

The study area is located in the Jamari National Forest (JNF), located in the southern Amazon basin, at the northern limit of the state of Rondônia (09°00′00″ to 09°30′00″ S and 62°44′05″ to 63°16′54″ W; Ministério Do Meio Ambiente, 2005) (Fig. 1). JNF has 220,000 hectares with 43% of the area under permanent forest management conducted by private companies (Servicio Florestal Brasileiro, 2018). The area is located in the context of strong seasonal variability of the south america monsoon system (SAMS) (Marengo et al., 2012) and the intertropical convergence zone (ITCZ) (Ancapichún et al., 2021). The annual average temperature in this region is 26 °C, and the average annual rainfall is 2438 mm (Fig. 1a). The site is classified as a moist forest that experiences seasonality in water availability, with a dry season of approximately three months (Guan et al., 2015), from June to August with less than 50 mm of rain per month. The potential evapotranspiration exceeds precipitation from April to October. The wet period extends from September (t-1) to May with the highest rainfall amount between December and March (Fig. 1a). The soil is classified as Dystrophic

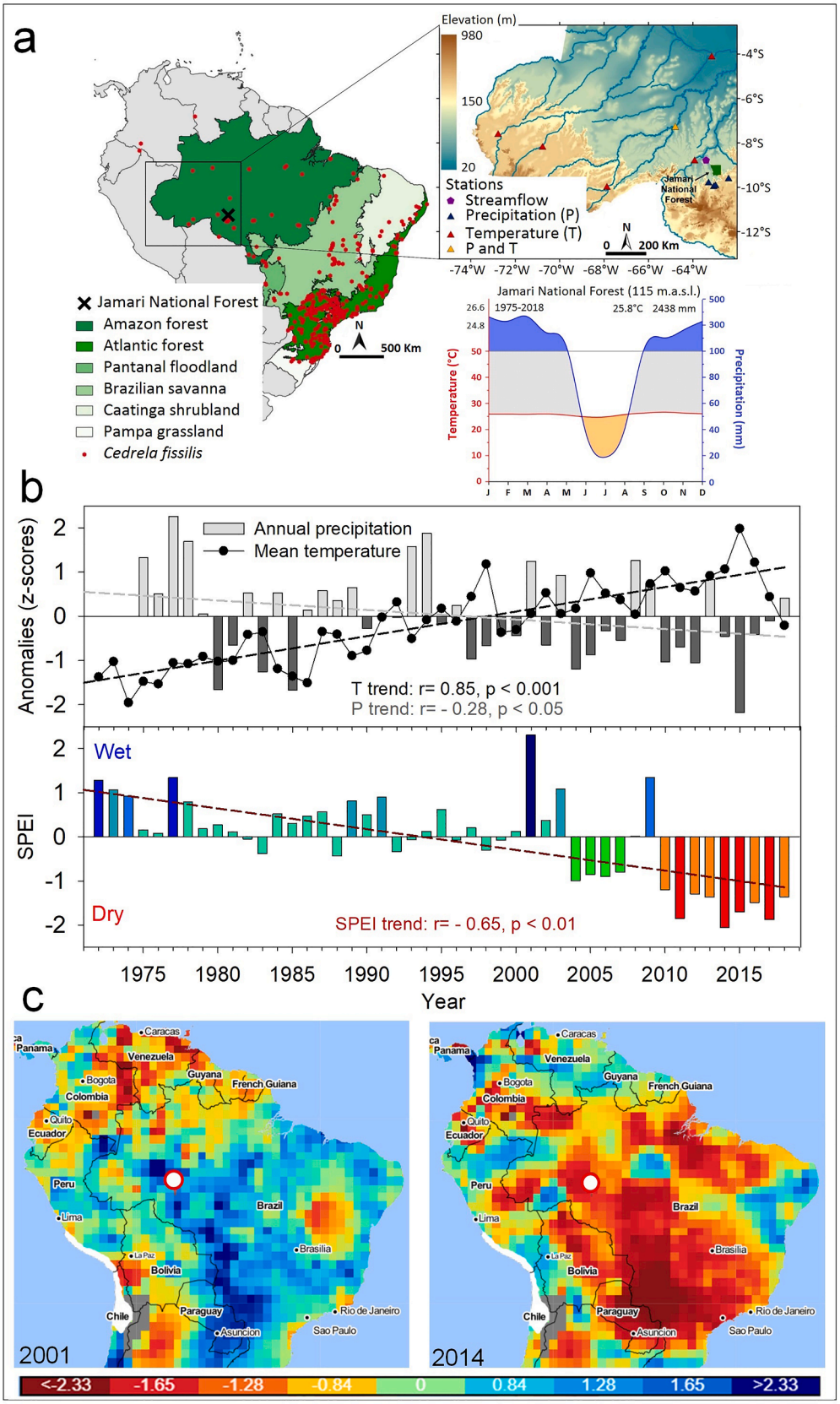

Fig. 1. a) Map showing the geographic distribution of *Cedrela fissilis* Vell (red points)(GBIF.org, 2021) and the location of the study area (cross). The inbox shows the location of the meteorological stations selected to build a regional precipitation and temperature series (color dots). Climate data were obtained from the Agência Nacional de Águas (ANA, National Water Agency) and the Instituto Nacional de Pesquisas Espaciais (INPE, National Institute of Space Research) (Table S1); the climate diagram was designed according to Walker & Lieth. b) Graphs showing the anomalies (standardized values) of total annual precipitation (P), mean annual temperature (T), the temporal Standardized Precipitation Evapotranspiration Index (SPEI 12-months scale). c) Spatial patterns of drought variability (SPEI maps) for a wet year (2001) and a dry year (2014) (Vicente-Serrano et al., 2010); the white circle indicates the location of the study area. The lower color scale shows the SPEI classes with red and blue colors corresponding to negative (dry conditions) and positive SPEI values (wet conditions), respectively. The maps and the time series show the 12-months SPEI calculated for September. SPEI maps were downloaded from SPEI Global Drought Monitor (https://spei.csic.es). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Yellow Latosol according to the Brazilian Soil Classification System (EMBRAPA, 2006).

2.2. The study species: cedrela fissilis vell

C. fissilis is a species of the family Meliaceae native to Central and South America (latitude: ±10º N to ±30º S; longitude: 37 to 83º W) and distributed from Costa Rica to Argentina (Siqueira et al., 2019). It is a vulnerable species according to the IUCN Red List. Overexploitation for timber, habitat conversion (Barstow, 2018) and climate change scenarios (Siqueira et al., 2019) are decreasing their overall population. The species is widespread in Brazil and occurs most densely in the southeastern and southern regions, but is uncommon (sparse stands) in the Amazon region (Fig. 1a; Barstow, 2018; Pennington and Muellner, 2010; Siqueira et al., 2019). *C. fissilis* occurs in regions where climatic conditions present temperatures between 13 and 26 °C, without long periods of low rainfall, but resist up to 6 months of hydrological deficit (Siqueira et al., 2019; Toledo et al., 2008). The species prefers well-drained, deep clay and loam soils with high water retention (Siqueira et al., 2019).

C. fissilis is a deciduous species (CNCFlora, 2012; Pennington and Muellner, 2010; Stefano et al., 2015) that sheds its leaves during the dry season and forming new leaves around the onset of the rainy season (Lobão, 2011). The species probably has a plasticity regulating phenological patterns which reflect the water status within the tree, in drier sites it shows a more pronounced leaf-fall behavior than in more humid sites (Borchert, 1999). The period of wood formation of *Cedrela* close to the study region is from September/October to April/May, with a earlywood formation from September to December and cambial dormancy from June to August (period of leaf exchange) (Baker et al., 2017; Brienen and Zuidema, 2005; Dünisch et al., 2003; Lobão, 2011). Ring structure is described as semi-ring-porous with large vessels embedded within the marginal parenchyma band formed during reactivation of the cambium, and fewer and narrower vessels distributed in the latewood formed later in the growing season (Dünisch et al., 2003; Marcati et al., 2006; Tomazello-Filho et al., 2000) (Figure S1).

2.3. Fieldwork and dendrochronological methods

Wood discs were cut at the top level of the first log (6 m) (Granato-Souza et al., 2018) from 29 living and dominant trees, which were felled and stored at log yards between April to May of 2019. Three to four radii (10 cm width and 5 cm thickness) from each disk were cut and polished with sandpaper (80–600 grain) until tree rings were clearly visible. Each tree-ring series was cross-dated using both skeleton plots and visual dating under the microscope (Stokes and Smiley, 1996). We compared and detected characteristic rings among radii of the same tree and then by matching the series from different trees (Fritts, 2001). Each cross-section was scanned at 1200 dpi resolution with Epson Expression 10000XL scanner and the annual ring-width (RW) series in the synchronized samples were measured with a resolution of 0.01 mm using CDendro and CooRecorder ® software (Cybis Electronic, 2013). The "Schulman Shift" (Schulman, 1956) was not applied to the dating of the JNF series. This means that the tree growth of the period 2017/2018 was assigned to the calendar year 2018.

For each radial sample a thin radial-section (2 cm width and 2 mm thick) was cut transversely for wood density analysis. Wooden laths were kept under constant temperature and humidity (20 °C and 60%, respectively) for 48 h in an atmosphere at 12% moisture content (Quintilhan et al., 2021; Tomazello-Filho et al., 2008). The samples were then scanned with a calibration scale of cellulose acetate using an X-ray densitometry chamber (Faxitron MX20-DC12, Faxitron X-Ray, Illinois, USA). The digital X-Ray images of cross-section samples were analyzed with WINDENDRO Density 2017a® software (Regent Instruments Inc.), obtaining the annual earlywood (EW) and latewood (LW) widths, and the density profiles (interval of 15 μm). We produced density time series of each radii from the whole ring (RD), earlywood (EWd), latewood (LWd), maximum (MXD) and minimum (MND) density values expressed in g cm^{-3}. The MND value was explained by the increase in the diameter and frequency of vessels and the presence of a marginal parenchyma at the beginning of the earlywood (Quintilhan et al., 2021). The position of the earlywood-latewood boundary (ELB) was defined as a floating threshold for each tree ring by the equation (Windendro® software, Regent Instruments Inc.):

$$ELB = \rho_{max} + \left(\frac{X}{100}\right)(\rho_{min} - \rho_{max}),$$

where X is the percentage of ring-specific minimum (ρ_{min}) related to maximum (ρ_{max}).

Cross-dating of the tree-ring width and density series was evaluated using the COFECHA program (Holmes, 1983) by comparing the consistency of the different ring-width series with mean site series using Pearson correlations for 20-year intervals. To obtain comparable ring-width and density series of each tree and remove the age-, size-related trend and non-climatic signals, cross-dated raw series were standardized and detrended using the *dplR* library (Bunn et al., 2021) in the R statistical language (R Core Team, 2021). Each ring or density series was detrended fitting a 30-year spline through the ring-width and density series of each measured radius to retain high-frequency variability. We used a spline function where the frequency response is 0.5 at a wavelength of 0.67 multiplied by the length of the series in years. Then, the ring-width or density data were divided by the fitted lines to obtain standardized ring-width or density indices. We obtained standardized series for ring-width (RWi), earlywood width (EWi), latewood width (LWi), ring density (RDi), earlywood density (EWdi), latewood density (LWdi), maximum density (MXDi) and minimum density (MNDi). We did not remove the first-order autocorrelation of the standardized data to maintain the year-to-year growth variation, which could be meaningful to correctly assess the lagged effects of drought conditions in post-drought resilience of *C. fissilis* (see Sánchez-Salguero et al., 2018). The resulting mean chronologies of each wood trait were described by calculating dendrochronological statistics for the common period 1900–2018: the mean correlation between individuals (Rbt), the first-order autocorrelation (AC), the mean sensitivity (MS) of indexed series, and the Expressed Population Signal (EPS), which measures the statistical quality of the mean site chronology compared with a perfect infinitely replicated chronology (Wigley et al., 1984). The part of the chronologies that reached EPS values equal or higher to 0.85 was regarded reliable enough for calculating climate-growth correlations (Table 1).

2.4. Climate dataset

To obtain long and reliable climate data we created a regional mean precipitation (1975–2018) and temperature (1957–2018) series with data from five and six local meteorological stations, respectively (Fig. 1a, Table S1). Monthly precipitation and temperature data were obtained from Agência Nacional de Águas (ANA, National Water Agency) and instituto nacional de pesquisas espaciais (INPE, National Institute of Space Research). We used the HOM and MET programs from DPL version 1.05 (Krusic, 2006) to estimate missing data and calculate the regional time series. To estimate the effect of increasing drought intensity and duration on wood traits, we used the difference between precipitation (P) and potential evapotranspiration (PET) and the standardized precipitation evapotranspiration index (SPEI), which is calculated using precipitation and temperature data from the same homogeneous and spatially dense dataset of local observatories from CRU climate data (Vicente-Serrano et al., 2010). The SPEI varies from negative to positive values corresponding to dry and wet periods, respectively. The SPEI monthly values were calculated for the studied sites considering the period 1975–2018 and 1–24-month- long scales

Table 1
Site features and statistical characteristics of selected tree-ring series, ring width (RW), earlywood width (EW), latewood width (LW), tree-ring density (RD), earlywood density (EWd), latewood density (LWd), minimum tree-ring density (MND) and maximum tree-ring density (MXD) for the common period 1900–2018. SD is the standard deviation.

Location	DBH (cm)*	Tree height (m)		Age at 6 m (years)		SG (g cm^{-3})	
Jamari Nat. For.	73.7 ± 2.8	15.3 ± 0.5		83 ± 6		0.4 ± 0.07	
Dendrochronological Statistics	N° trees / N° radii	Value (mm or g cm-3)	Rbt	AC	MS	PC1 (%)	Time span (EPS > 0.85)
RW	22/72	2.26 ± 0.05	0.51	0.46	0.41	36.71	1900–2018
EW	16/50	1.19 ± 0.03	0.47	0.43	0.5	31.31	1900–2018
LW	13/40	1.06 ± 0.03	0.44	0.34	0.47	29.97	1950–2018
RD	14/45	0.54 ± 0.01	0.48	0.55	0.07	33.96	1915–2018
EWd	13/43	0.47 ± 0.01	0.43	0.37	0.11	29.52	1940–2018
LWd	13/38	0.62 ± 0.01	0.42	0.45	0.08	26.67	1910–2018
MND	13/25	0.33 ± 0.01	0.34	0.46	0.16	24.63	1965–2018
MXD	14/27	0.74 ± 0.01	0.42	0.42	0.09	44.22	1935–2018

* Abbreviations: DBH, diameter at breast height, DBH and tree height data obtained from forest inventories; SG, average wood basic specific gravity determined by hydrostatic balance method; Value, mm for RW, EW and LW, and g cm^{-3} for RD, EWd, LWd, MND and MXD; Rbt, mean between-trees correlation of indexed values; AC, first-order autocorrelation for raw tree-ring series; MS, mean sensitivity; PC1, variance accounted for by the first principal component; EPS, Expressed Population Signal.

since this is a multiscalar index. The SPEI accounts for the negative effect of warmer temperatures on water availability by statistically modeling cumulative water balances. Therefore, different SPEIs are obtained for different time scales representing the cumulative water balance over the previous months (Vicente-Serrano et al., 2010). The P-PET and SPEI is useful to identify time-dependent growth response to drought scales (see Pasho et al., 2011). The PET was calculated following the method propose by Thornthwaite (1948) and explained in Vicente-Serrano et al. (2010). The PET and SPEI values were calculated using the *SPEI* package (Vicente-Serrano et al., 2010) in R (R Core development team 2021).

To assess the significance of monotonic trends in climate time series (P, T, P-PET and SPEI, period 1975–2018) and raw chronologies (RW, EW, LW, RD, EWd, LWd, MXD, MND, period 1970–2018) we applied the non-parametric Mann-Kendall trend test (Kendall, 1948; Mann, 1945). In order to describe increasing or decreasing trends, the Mann-Kendall Z_{MK} value (positive or negative, respectively) was taken into consideration (Liang et al., 2010) (Tables S1 and S2).

2.5. Climate-wood traits association

To quantify climate-growth associations between wood traits (ring-, early- and late-wood widths and densities) and monthly climate data, we calculated bootstrapped Pearson correlation coefficients for the common period 1975–2018. Correlations were performed between September of the previous year to September of the current year, months that include the period of wood formation of *Cedrela*, broadly from September/October to April/May, and the period of cambial dormancy from June to August (period of leaf exchange) (Baker et al., 2017; Dünisch et al., 2003; Lobão, 2011). Correlation was also calculated for seasonal variables based on climate data (beginning of the rainy season: September to November; middle of rainy season: December to February; end of the rainy season: March to May; and dry season: June to August). Comparison among wood trait responses were assessed by one-way ANOVAs or Mann-Whitney tests. Lastly, we also calculated correlations between wood traits and SPEI obtained for 1- to 24-month long scales (see Pasho et al., 2011). The climate-growth relationships were calculated using the *treeclim* package (Zang and Biondi, 2015).

2.6. Growth response to extreme dry-seasons

The VS-Lite forward growth model was used to assess climate and drought impacts on tree growth. This model simulated annual standardized ring width (RWi) anomalies as a function of climate based on mean temperature and precipitation using the principle of limiting factors in dendrochronology (Fritts, 2001). For each annual ring, the VS-Lite simulates the growth response functions for temperature (gT) and soil moisture (gM) using two parameters (T1 and T2, M1 and M2, respectively) over the time window from prior to current growing season on this species (Lobão, 2011). This simplified version of Vaganov-Shashkin model simulates non-linear growth response to climate using a Bayesian framework that contains the above parameters: the minimum (T1) and optimal (T2) growth temperatures that showed low variation in tropical species (Camarero et al., 2020a), and the growth–soil moisture parameter, the minimum (M1) and optimal (M2) soil moisture (Tolwinski-Ward et al., 2013; S.E. 2011; Vaganov et al., 2006). The T1 and M1 determine when growth will occur, and the T2 and M2 determine when growth is no longer limited by temperature and soil moisture, respectively. The model also estimates the solar radiation (gE parameter) from the site latitude by considering no interannual variability. The median for each parameter was used to obtain the "calibrated" growth response parameters for the study site. We then related the simulated tree-ring chronologies to the observed tree-ring chronologies (RWi) from the observed tree-ring data (Tolwinski-Ward et al., 2013), allowing for estimation of all the above parameters. We used these parameters to simulate the ring width indices for the 1975–2018 period; then, we divided this calibration period into two subperiods to evaluate the temporal stability of the calibrated growth response functions (1975–1995, 1995–2018), withholding the second half for validation of the parameters estimated in the first half (Table 2). We assumed uniform priors for the growth function parameters, and independent, normally distributed errors for the ring width indices evaluated by 10,000 iterations using three parallel chains and a white Gaussian noise model error (see Tolwinski-Ward et al., 2013). To estimate monthly soil moisture from temperature and total precipitation, the VS-lite model uses the empirical leaky bucket model of hydrology (Huang et al., 1996). The specific parameters (e.g., runoff, root depth, growing season length, etc.) were taken from previous studies using a process-based models in tropical forests (Camarero et al., 2020a; Ditzer et al., 2000; Fauset et al., 2019). To compute annual RWi values, we

Table 2
Pearson correlation coefficients (r) calculated between ring-width index (RWi) and VS-lite ring width index for the period (1975–2018) and for the validation sub-periods 1975–1995 and 1996–2018. Pearson correlation values (r), are significant at the 0.05 level. Statistics of the Bayesian estimation of the growth response parameters (T1, T2, M1, and M2 for minimum and optimal temperature and soil moisture values, respectively) are presented.

	r	T1	T2	M1	M2
1975–2018	0.31	5.93	16.69	0.03	0.48
1975–1995	0.28	5.85	15.26	0.02	0.22
1996–2018	0.33	5.50	18.02	0.05	0.53

integrated the overall simulated growth rates (i.e., the point-wise minimum of monthly gT, gM and gE) over the time window from September of the year prior to growth to December of the year of tree-ring formation. This period was determined following previous dendroecological studies performed on Amazonian *Cedrela* forests (e.g., Dünisch, 2005; Lobão, 2011).

To quantify the response of growth to extreme droughts during last decades, we calculated the indices proposed by Lloret et al. (2011): resistance (Rt), recovery (Rc), resilience (Rs) and relative resilience (rRs = Rs–Rt). They were calculated using detrended data of wood traits (RWi, EWi, LWi, RDi, EWdi, LWdi, MXDi, MNDi) instead of raw data in order to remove age and size effects as well as potential bias due to the eccentric growth of tropical species. The Rt index quantifies the difference between growth/density during the dry year and the preceding years (i.e. it quantifies the capacity of trees to buffer drought stress and continue growing during dry-year), whereas the Rc index accounts for the growth/density reaction following the drought period (i.e. it quantifies the difference in growth/density between the dry year and the subsequent period). The Rs index quantifies the difference in growth/-density before and after the dry year (i.e. it measures the capacity of trees to recover in terms of growth rates and wood density observed before the drought event). Lastly, the rRs index is the difference between Rs and Rt, i.e. the net balance between buffering (during) and recovering (after) an extreme drought (cf. Sánchez-Salguero et al., 2013). To quantify these indices, we defined a period of 3 years before and after drought occurrence according to the previously applied criterion (e.g., Gazol et al., 2017). To calculate the pointer years and the resilience indices, we used the *pointRes2.0* package (van der Maaten-Theunissen et al., 2021). One severe drought per decade were selected (e.g., 1981, 1997, 2007 and 2015) as those affecting large areas of the southern Amazon basin (Figs. 1 and S2; Caioni et al., 2020; Espinoza et al., 2019; Lovejoy and Nobre, 2018; Marengo et al., 2008; Ronchail et al., 2002; Williams et al., 2005). Despite the 2005 and 2010 extreme droughts are considered in other studies (e.g., Lewis et al., 2011), to analyze the temporal responses and trends in growth resilience we considered only the most extreme drought for each decade since 1980s, following pointer years' analysis (Gazol et al., 2018).

3. Results

3.1. Long-term climate trends

Negative significant trend in annual precipitations ($r = -0.28$, $Z_{MK} = -0.57, p < 0.05$) and positive significant trend in annual temperatures ($r = 0.85$, $Z_{MK} = 6.3$, $p < 0.05$) were observed since 1975 (Fig. 1b, Table S1). The SPEI showed a significant negative trend ($r = -0.65$, $Z_{MK} = -4.81, p < 0.05$) since 1975 and the most severe droughts in the study area occurred after 2010, while 2001 was the wettest year of the analyzed period (Fig. 1b, Table S1). Negative significant trend in P-PET ($Z_{MK} = -2.47$, $p < 0.05$) were also observed since 1975 (Table S1). In some years, the spatial patterns showed that when JNF recorded very dry or very wet periods, these were also recorded in the Brazilian southeast (ecoregions of Atlantic Forest, Pantanal Floodland and Brazilian Savannah), while an opposite pattern was registered in the Brazilian northeast (ecoregion of Caatinga Shrubland) (Figs. 1c, S2). According to dry-season precipitation, the most severe droughts (values exceeded at least 1.5 standard deviation from the observed mean precipitation) occurred in 1990s (1997–1998), 2000s (2005, 2007), and 2010s (2010, 2014–2016) (Fig. S2).

3.2. Growth and density patterns

C. fissilis trees showed a mean DBH of 73.7 (± 2.8) cm, height of 15.3 (± 0.5) m, age of 83 (± 6) years at 6 m from ground level, and average wood basic specific density of 0.4 (± 0.07) g cm^{-3}. The tree-rings presented an average width of 2.26 (± 0.05) mm with proportions of 52% and 48% of earlywood and latewood, respectively, and average minimum and maximum wood relative density of 0.54 (± 0.01), 0.33 (± 0.01) and 0.74 (± 0.01) g cm^{-3}, respectively (Table 1). Raw tree-ring width series (RW, EW and LW) showed a decreasing trend (average r= - 0.33, $p < 0.05$) since 1970s. For the same period, tree-ring density series (RD, EWd, LWd, MND and MXD) showed an increasing trend (Figs. 2 and S4, Table S2). The P-PET (from June to August) showed a strong association during dry spells since 1995 in relation to narrow and less dense rings (Fig. 2).

The chronologies of RW, EW and LW width were based on 72, 50 and 40 radii from 22, 16 and 13 trees, respectively, and showed a significant mean correlations (Rbt) among the series ($r = 0.51$, 0.47 and 0.44, $p < 0.01$; Rbar = 0.38, 0.28, 0.23, respectively). The RD, EWd, LWd and MXD series showed a significant mean correlation among the series ($r = 0.48$, 0.43, 0.42, 0.42, $p < 0.01$; Rbar = 0.25, 0.2, 0.21, 0.24, respectively). The chronology of MND presented a lower correlation among series ($r = 0.34$, $p < 0.01$; Rbar = 0.18). The RD series had the highest values of first-order autocorrelation (AC) followed by the of RW and MND series. The RW (1900–2018) chronology was the one with the longest period with the EPS above the 0.85 threshold, while the MND (1965–2018) chronology was during the shortest period (Table 1, Fig. S3).

Almost all tree-ring growth and density variables presented positive and significant correlations (Table S2). The highest correlation among the variables of growth, density and both was between RW-EW (0.9), RD-EWd (0.81), and EW-MXD (0.7) respectively (Table S2).

3.3. Relationships between seasonal climate, drought and wood traits

Wet conditions during the months between October and May improved growth (RW, EW, and LW; statistically evident for February and March) and MND (statistically evident for October, January and March) of the *C. fissilis* tree. Warmer conditions in the rainy season increased ring density (RD and EWd), and negatively affected tree ring growth (RW and EW) and MND, mainly at the end of the rainy season. Wetter March positively affected density (RD, EWd and MXD) (Figs. 3 and S5).

We found positive and significant correlations between growth and density tree-ring variables with SPEI drought index recorded at 1–24-month long scales, corresponding to short dry or wet periods (Figs. 4, S6 and S7). Significant drought-wood traits correlations were found for time scales varying from 1 to 24 months, especially in the wet period of the previous year (January to May) for RWi and LWi and during the previous year (January to December) and the middle of the wet period (January to February) of the current year for minimum density (MNDi). Significant drought-density traits correlations were also found for time scales varying from 1 to 12 months, mainly in the wet period of the previous year (January and February) for RDi, EWdi and MXDi, and at the beginning of the wet period of the current year (September) for RDi and EWdi. The weakest SPEI-wood traits associations were observed for EWi and LWdi (Figs. S6 and S7).

3.4. Forward growth modeling of tree growth responses

The VS-Lite model tracked the year-to-year growth variability of *C. fissilis* trees (Fig. 5). The highest growth limitations due to low soil moisture (gM) were observed in extreme drought years (1983, 1997–1998, 2005–2007, 2010–2011, 2015–2016). The model indicated no limitations by temperature (e.g., gT =1 for 1975–2018 period). The growth showed a lagged effect since it was limited by low soil moisture at the transition between the previous dry period and the beginning of the current wet period. Extremely dry years limited growth between two (August-September) to five (August-December) months. Growth limitations were also observed up to three years after (e.g., 2007) the drought year. The estimated soil moisture thresholds (M1, M2) for growth confirmed the increasing sensitivity of *C. fissilis* to more severe

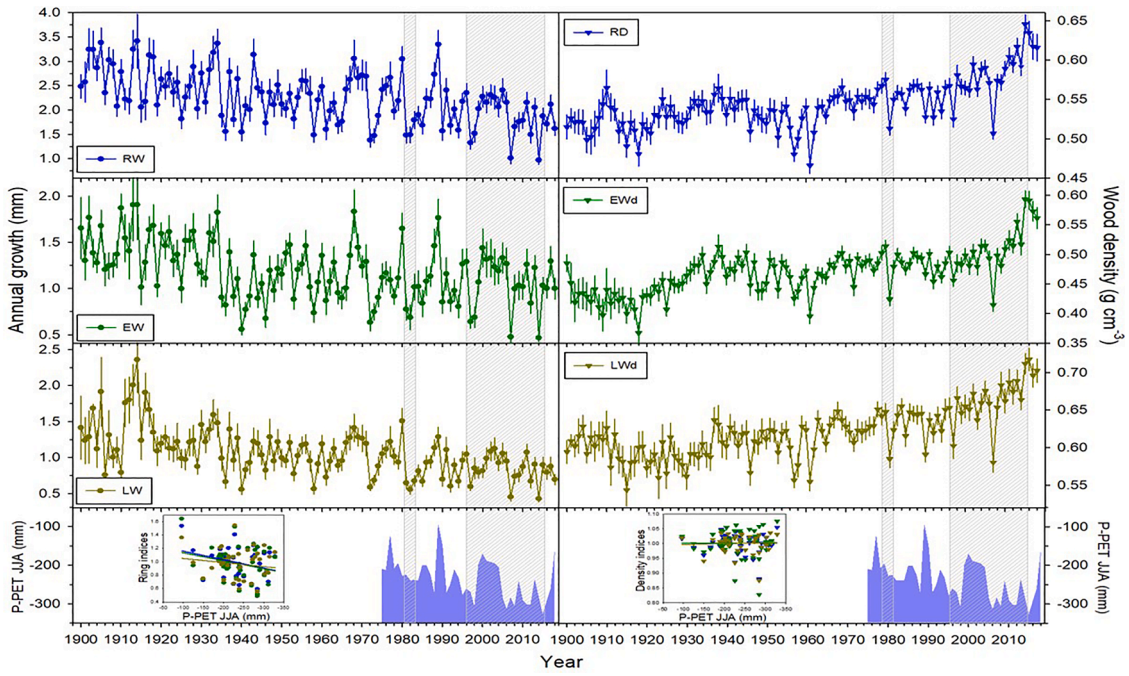

Fig. 2. Raw tree-ring series of tree-ring width (RW), earlywood width (EW), latewood width (LW), ring density (RD), earlywood density (EWd) and latewood density (LWd). Values are means and error bars are standard errors. The bottom plot shows the difference between precipitation (P) and potential evapotranspiration (PET) from June to August as a proxy of drought stress for specific years that are related to narrow and less dense rings (vertical gray boxes).

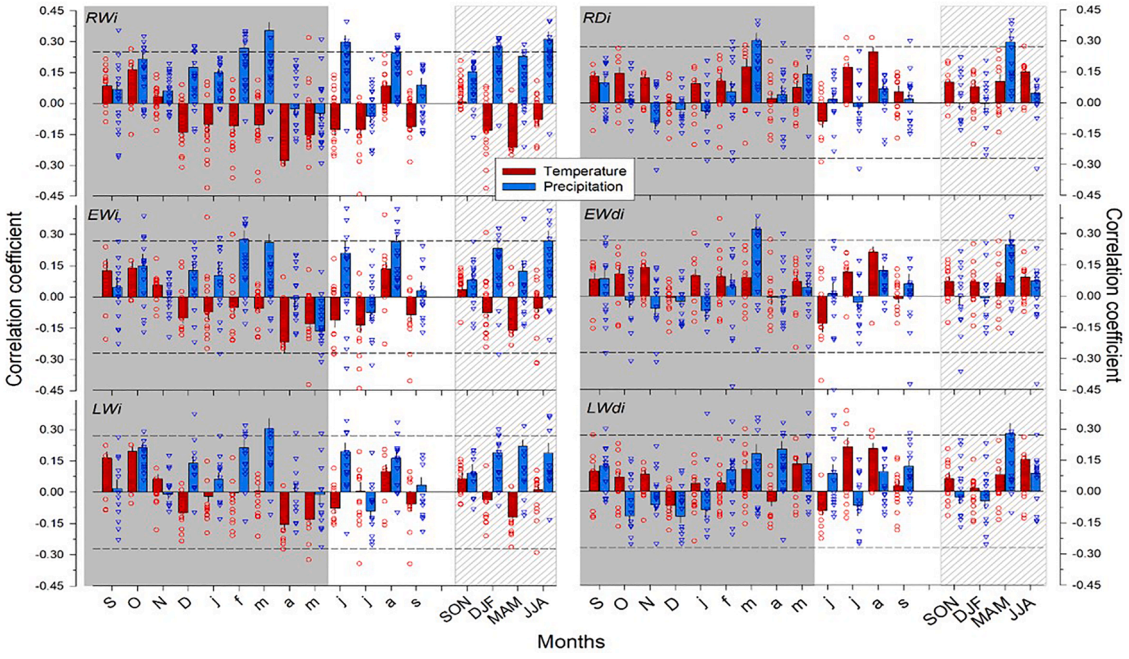

Fig. 3. Pearson's correlation coefficient (r) for the relationship among tree-ring width indices (RWi, EWi, LWi), density indices (RDi, EWdi, LWdi) and the climate variables (temperature and precipitation) for the common period 1975–2018. Each bar shows the mean correlation ± standard error. The individual tree correlations are also displayed (circles for temperature, triangles for precipitation). The analyzed temporal window spans from previous year (uppercase letters), previous growing season up to current growing season (lowercase letters). The gray vertical box includes the assumed growing period for current year and gray vertical area with line pattern shows seasonal responses. Dashed horizontal lines show the 0.05 significance level.

dry seasons (Table 2).

The growth response to soil moisture during extreme droughts dropped early and recovered latter in relation to the mean growth response. We found a shift during the last decades to longer dry-seasons with growth decrease (density increases) augmented length and water limitation during the growing season (Figs. 2 and 5).

3.5. Growth and density stability under extreme conditions

The growth resistance for *C. fissilis* (RW, EW, LW standardized and raw data) were higher in 1981 and 1997 droughts compared to the 2007 and 2015 droughts, while recovery values presented an opposite trend increasing with time (Figs. 6 and S8). The highest resilience indices for

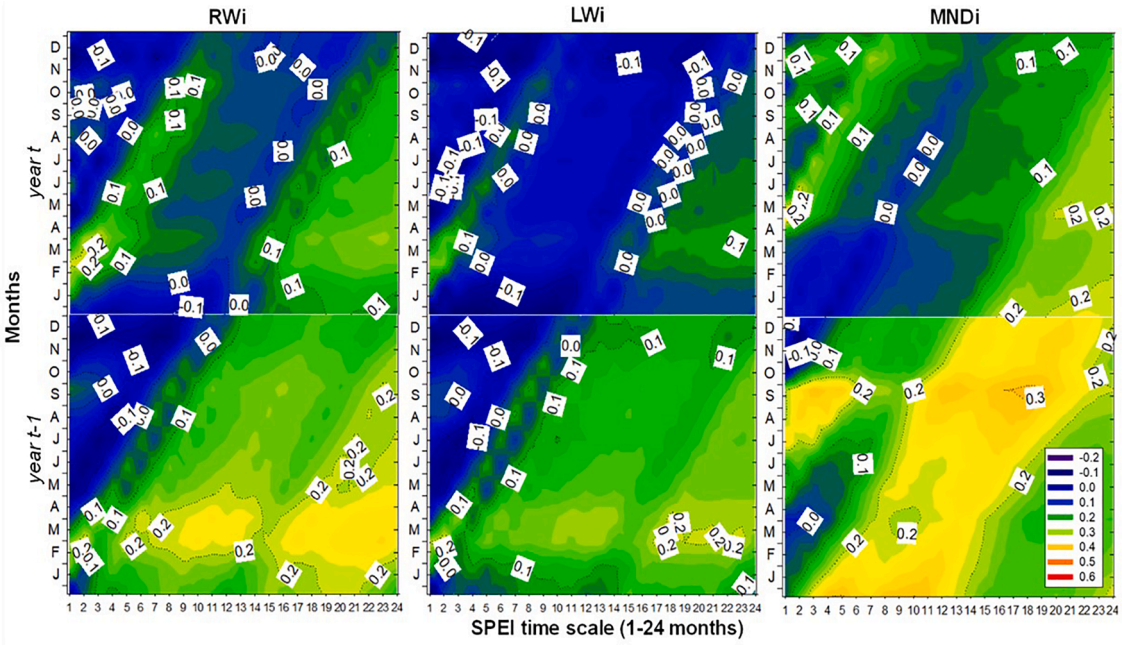

Fig. 4. Standardized ring width (RWi), latewood width (LWi) and minimum wood density (MDNi) responses of *Cedrela fissilis* to drought. The color scale shows the correlations (Pearson coefficients) calculated between standardized series and the SPEI drought index obtained for 1- to 24-month-long scales (x-axes). The correlations were calculated for the common and best-replicated period 1975–2018 and considering the months of the previous year (t-1) and the year of tree-ring formation (t). Correlation values above +0.20 and below −0.20 are significant at the $P < 0.05$ level. See Figs. S6 and S7 for more correlations.

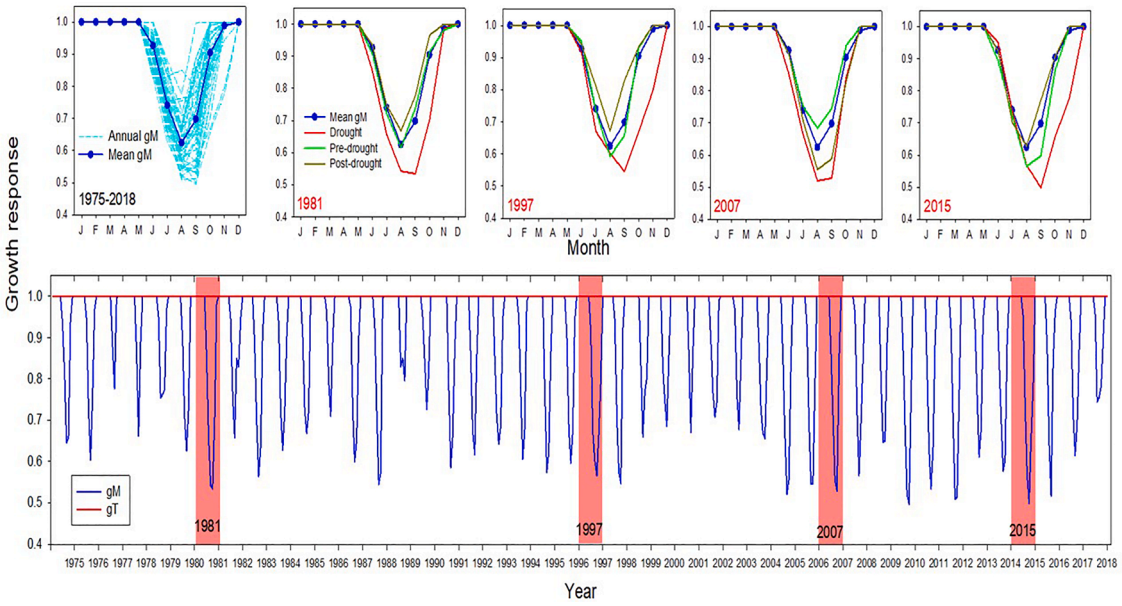

Fig. 5. Simulated monthly growth response curves for soil moisture using the VS-Lite model of tree growth and considering the period 1975–2018. Note that high and low *gM* values indicate more and less growth, respectively. Mean growth responses to soil moisture during the studied period (blue) and annual growth responses to soil moisture (cyan lines). The average (1975–2018) (Mean gM), before (Pre-drought), during (Drought) and after (Post-drought) growth responses. We selected the mean growth responses 3 years before (green color), during red color) and 3 years after (dark yellow color) the selected drought (see Fig. 2). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

growth were observed during 1997 (RW, EW, LW standardized and raw data) and 2015 (EWi and LWi) drought. Relative resilience indices for growth increased in the latest 2015 drought. The lowest recovery, resilience and relative resilience indices for growth were observed during the 1981 drought.

Regarding density stability (Figs. 7, S9 and S10), the highest resistance indices for *C. fissilis* densities (standardized and raw data) were observed during the 1997 drought and the lowest resistance during the 2007 drought, while recovery values presented an opposite trend (Fig. 7). The highest resilience and relative resilience values for density were observed in the 2014 (for RD, EWd, LWd, MND standardized and raw data) and 2007 (for RD, EWd, LWd, MND, MXD standardized and raw data) droughts, respectively. The lowest recovery and relative resilience indices for density were observed in the 1981 and 1997 droughts.

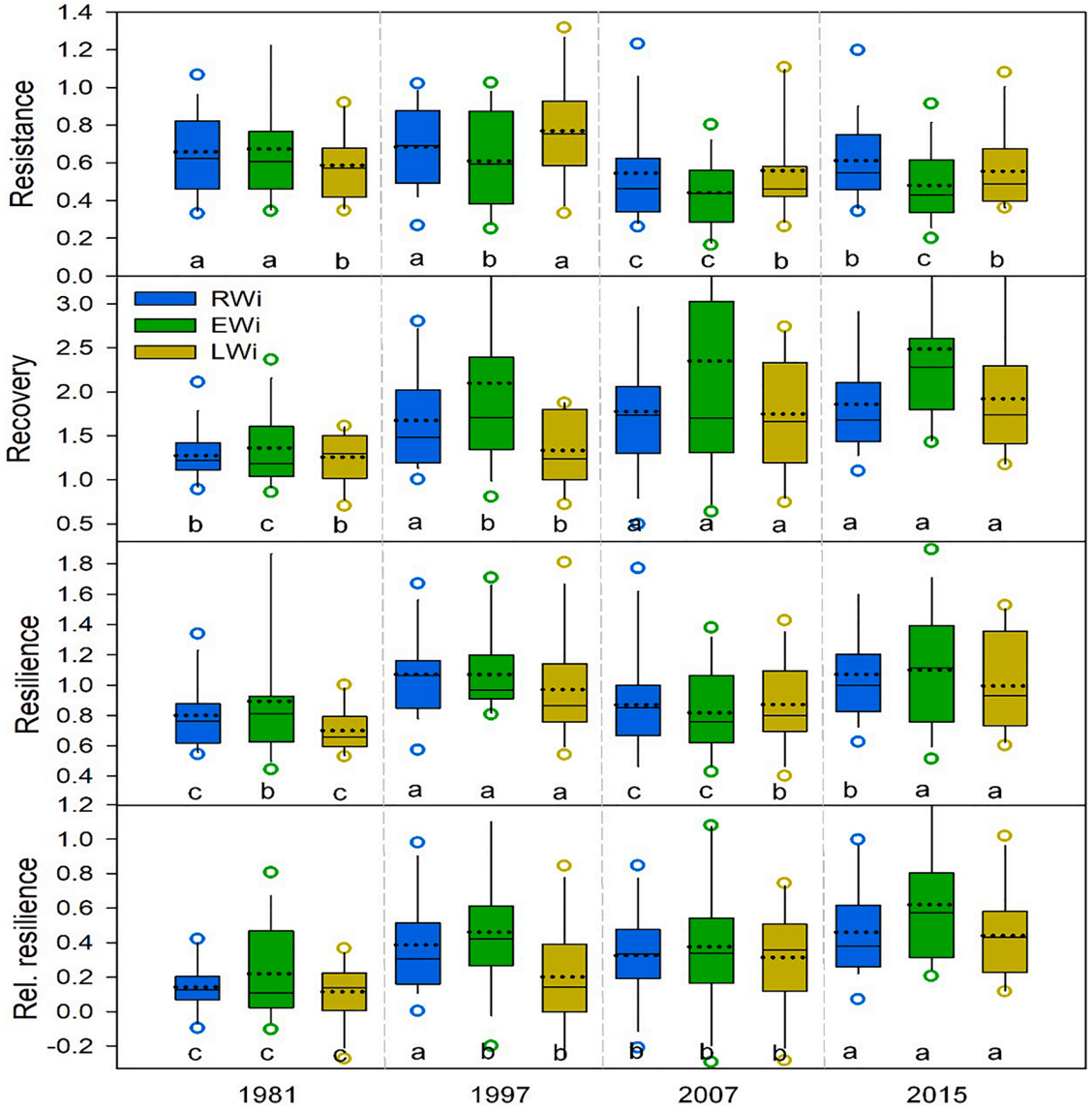

Fig. 6. Boxplots showing standardized ring, early and late-wood growth stability during the extreme years (see Figs. 1, 2 and 5). Different letters indicate significant differences ($P < 0.05$) between years. In the box plots, the boundary of the box indicates the 25th percentile, a black solid line within the box marks the median, a dotted black line within the box marks the mean, and the upper boundary of the box indicates the 75th percentile. Whiskers above and below the box indicate the 10th and 90th percentiles. Points above and below the whiskers indicate outliers outside the 10th and 90th percentiles.

4. Discussion

4.1. Climate variability and wood traits trends

Our main findings showed that the increasing drought conditions during the last decades have affected the growth and wood density responses of *C. fissilis*, influencing short-term resilience strategies (Figs. 1, 2). These results are consistent with findings of climatic studies (e.g. Espinoza et al., 2019; Marengo et al., 2018) which report declining rainfall during the dry season in the southern Amazon region and a delayed onset of the rainy season.

Changes in temperature and precipitation regimens have modified the amount of water available for trees in dry-seasonal moist tropical forest and consequently decelerating tree growth (Feeley et al., 2007). Dendrochronological wood traits of *C. fissilis* showed that the tree-ring widths (RW, EW, LW) have decreased since 1990s (Fig. 2). Negative impacts on tree growth in specific drought years have been described in other non-flooded Amazon forests for *C. fissilis* Vell. and *C. odorata* L. (Granato-Souza et al., 2018), *C. odorata* L., *C. nebulosa* T.D. Penn. & Daza, *Juglans neotropica* Diels (Humanes-Fuente et al., 2020) and *Centrolobium microchaete* (Mart. ex Benth.) H.C. Lima (Lopez et al., 2017). In a seasonally dry forest of Brazil (14.5° S and 44.2° W), tree-ring widths of *C. fissilis* decreased from 1994 to 2015 and the rainfall-tree-growth correlation was weaker and not significant in this period (Pereira et al., 2018), whereas in a Bolivian dry forest (16° S and 61.4° W) long-term chronologies of *C. microchaete, Acosmium cardenasii* H.S. Irwin & Arroyo, *Caesalpinia pluviosa* DC., *Aspidosperma tomentosum* Mart., *Zeyheria tuberculosa* (Vell.) Bureau, *Anadenanthera macrocarpa* (Benth.) Brenan and *Tabebuia impetiginosa* (Mart. ex DC.) Standl. showed a correlation between growth and SPEI, a variable that has declined since 1985 (Mendivelso et al., 2014). These results suggested that possible climate-growth teleconnections among Amazon and dry tropical forests (Figs. 1c, S2) are driven by large-scale climatic components such as SST in the tropical Pacific (El Niño-Southern Oscillation) and the Atlantic Ocean (Atlantic Multidecadal Oscillation), which also explain part of the extreme hydrological changes in these Neotropical ecosystems (Camarero et al., 2020; Espinoza et al., 2019; Granato-Souza et al., 2020; Lopez et al., 2017; Stahle et al., 2020).

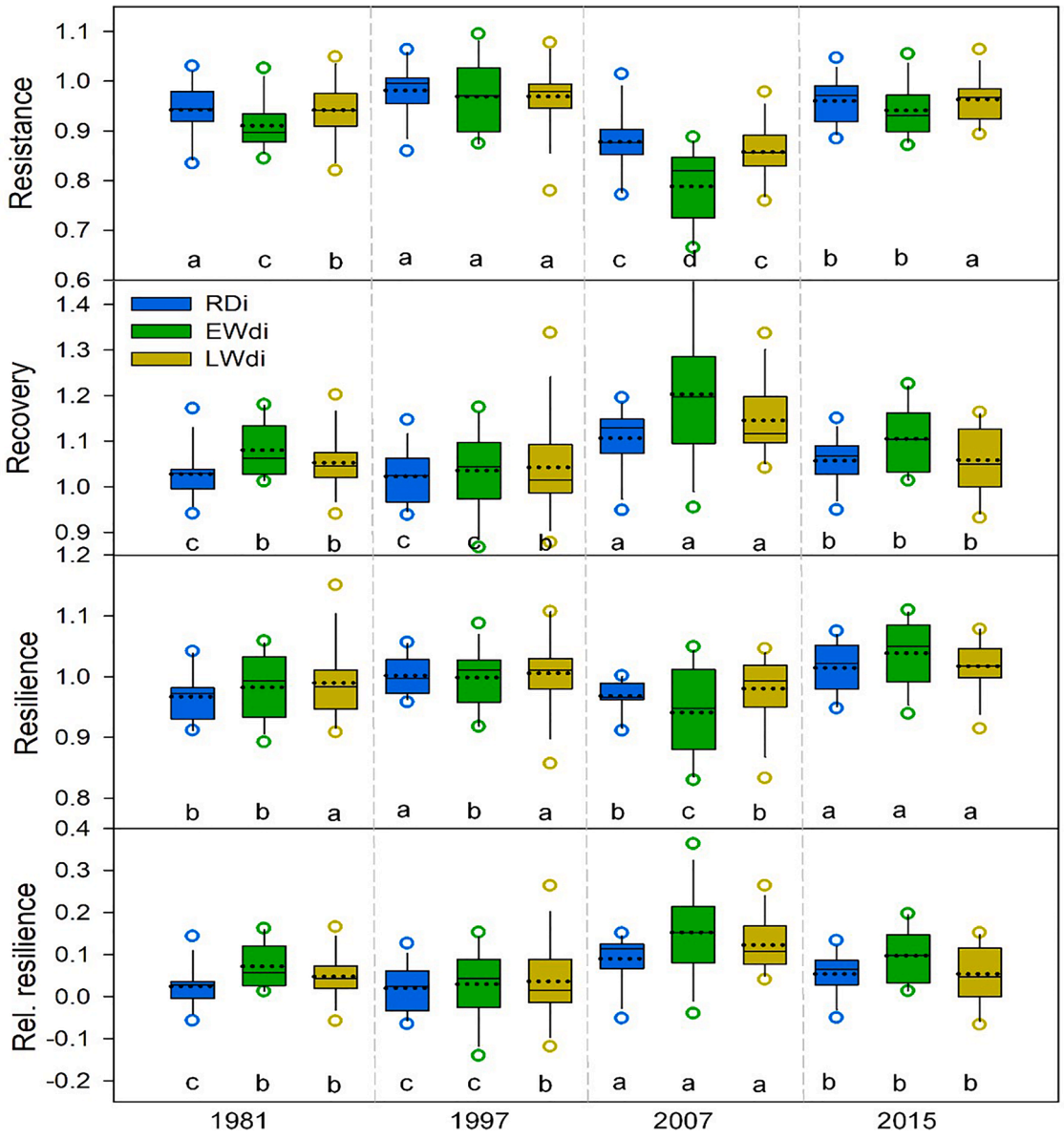

Fig. 7. Boxplots showing standardized ring, early and late-wood density stability during the extreme years (see Figs. 1, 2 and 5). Different letters indicate significant differences ($P < 0.05$) between years. In the box plots, the boundary of the box indicates the 25th percentile, a black solid line within the box marks the median, a dotted black line within the box marks the mean, and the upper boundary of the box indicates the 75th percentile. Whiskers above and below the box indicate the 10th and 90th percentiles. Points above and below the whiskers indicate outliers outside the 10th and 90th percentiles.

Wood density parameters integrated in the climate growth relationships and their long-term variation have been scarcely studied in the Amazon region (but see Gonçalves et al., 2021; Worbes et al., 1995). Our results showed that the long-term trends of wood density traits (RD, EWd, LWd, MND, MXD) increase since 1990s (Figs. 2 and S4). This increase is similar to that expressed by the concentration of CO_2 in the atmosphere (NOAA, 2021), and could be interpreted as a potential driver for the long-term trends. However, there is still controversy to affirm this hypothesis since some studies in angiosperms indicate that no substantial changes in wood density would occur under differential CO_2 levels (Arsić et al., 2021; Yazaki et al., 2005). We hypothesized that the experienced long-term trend in wood density might concurrently vary in an opposite direction to the observed trend in tree-ring width (Vannoppen et al., 2018). However, there is not much knowledge concerning the possible long-term density-climate trend relationships worldwide (Bontemps et al., 2013). In temperate and mediterranean forests, historical increases in growth and decreases in density have been reported in ring-porous species such as *Quercus petraea* Liebl. from 1811 to 1993 (Bergès et al., 2000), from 1970 to 2012 (Toïgo et al., 2015) and from 1970 to 2014 (Vannoppen et al., 2018), and diffuse-porous species such as *Fagus sylvatica* L. from 1900 to 2000 (Bontemps et al., 2013) and from 1990 to 2014 (Vannoppen et al., 2018). Climate change may induce a feedback on radial growth and wood density, affecting the carbon sequestration capacity of these forests, probably linked to these changes recorded in recent decades (Babst et al., 2014; Björklund et al., 2017; Brienen et al., 2020; Briffa et al., 2002). Complementary studies would help verify whether these growth and density trends are really associated with climate change or are simple an ontogenetic signal. Radial gradients in wood density of tropical pioneer trees usually have an age-dependent pattern, producing low-density wood in juvenile stages and higher-density wood towards mature stages of development, as a requirement for more efficient stability of stems (Nock et al., 2009).

4.2. Relationships between growth, density and climate

Our results showed that radial wood formation starts at the beginning of the rainy season in October of the previous year and is completed towards May of the current year, coinciding with the end of the rainy season (Figs 3 and S5). Previous studies in this region described that *Cedrela* present the highest monthly diameter increment in the period from September/October to December which corresponds to the period of earlywood, and completing the ring formation in April/May (Brienen and Zuidema, 2005; Dünisch et al., 2003; Lobão, 2011). The earlywood formation that comprises about 52% (Table 1) is characterized by marginal parenchyma (both, terminal and initial parenchyma; Marcati et al., 2006) in combination with large vessels (MND). The development of this tissue occurs between the end of the dry season and the beginning of the rainy season (September/October), along with or even before flushing new leaves (Lobão, 2011). *Cedrela* possibly use the non-structural carbohydrates (NSCs that prevent carbon starvation and aid hydraulic efficiency, Cintra et al., 2019; Dickman et al., 2018; Locosselli and Buckeridge, 2017; Plavcová and Jansen, 2015), minerals (e.g., Ca, K and S, related to the cell differentiation, expansion and architecture, respectively, Hevia et al., 2018; Ortega Rodriguez et al., 2021), and water for the mobilization at the initial stages of the growing season. The warmer condition at the end of the rainy season and excess of soil water, which occurs between April and May, induces a decrease in the cambial activity (RW, EW, LW), forming latewood fibers (LWd, MXD), to then start the period of dormancy (Figs. 3 and S5, Lobão, 2011) and storing organic compounds (e.g. hemicellulose and pectin, related to the strengthening cell wall structure and control of cell wall porosity, respectively, Locosselli and Buckeridge, 2017).

We found that *C. fissilis* forms large dense rings during wetter years, and narrow less dense during drier years, a variation also observed for the ring early- and latewood widths and their respective densities (Table S2). Similar strong relationship between larger *Cedrela* tree rings and wetter years were observed in previous works (Dünisch, 2005; Dünisch et al., 2003; Granato-Souza et al., 2018; Humanes-Fuente et al., 2020; Lisi et al., 2020; Lobão, 2011; Paredes-Villanueva et al., 2016; Pereira et al., 2018; Pereyra Espinoza et al., 2014; Villalba et al., 1992).

In contrast with our hypothesis, similar positive tree-ring width-density relationship in *C. fissilis* woods (Fig. 2) was observed in other tree species whose growth rings are delimited by marginal parenchyma and ring porosity, both in tropical (Quintilhan et al., 2021) and temperate forests (Bergès et al., 2000; Toïgo et al., 2015; Vannoppen et al., 2018). Furthermore, the close relationship between density, wet conditions (during the growth-dormancy transition) (Fig. 3) and (quantitative) wood anatomy variations in *C. fissilis* (areas with larger vessels that coincide with lower density values and vice-versa, Quintilhan et al., 2021), suggest that the variation in wood density is a good proxy of hydroclimatic oscillations and hydraulic adaptations to droughts in the southern Amazonian forests (Figs. 2, 3, 4). These results are in agreement with Mendivelso et al. (2013) who proposed that tree species with lower wood density have higher potential to store water in the sapwood and the capacity to tolerate better the incidence of drought stress, presenting more marked growth responsiveness to changes in precipitation or in water balance (Figs. 3 and 5). Wood density is related to the volume partitioning of wood relative to the proportion of vessels, axial parenchyma, fiber, and the thickness of the cell wall and the lumen of these components (Janssen et al., 2019; Ziemińska et al., 2013). Trade-offs between volumes of different tissues (and consequently wood density) are fundamental for biomechanics equilibrium, water transport efficiency and storage of water, nutrients, and carbohydrates (Gleason et al., 2016; Janssen et al., 2019; Pratt and Jacobsen, 2017). Studies on the relationships between wood fiber density, vessel bending strength, and xylem embolism are crucial to understanding drought resistance in tropical plant communities under future extreme climates (e.g., Anderegg and Meinzer, 2015; Janssen et al., 2019; Lachenbruch and Mccul-loh, 2014; Patiño et al., 2012).

Growth and density response to climate may also depend on other traits such as water and nutrient use efficiency (Hevia et al., 2019) or rooting depth (Kunert et al., 2010). Further research must include these other traits in combination with long-term monitoring of permanent plots (xylogenesis, dendrometers, in situ climate data). Nonetheless, to best of our knowledge, this study provides new links between key functional traits and responses to climate in Amazonian tropical forests with a dry season.

4.3. Growth and density vulnerability to droughts

Many dendroclimatic studies of *Cedrela* show that climate conditions before the actual growing season (in the transitional months from the previous rainy season to the beginning of the dry season) affect the ring width (e.g., Brienen and Zuidema, 2005; Dünisch et al., 2003; Pereyra Espinoza et al., 2014) and the ring density (Fig. 3). This suggests that ring formation at the begin of the growing season might depend on the storage of NSC at the end of the previous growing season, as suggested by stable isotope analyses (e.g., Cintra et al., 2019; Ohashi et al., 2009). Earlywood formation, characterized by marginal parenchyma and large vessels occur at the end of the dry season (August/September), together or even before flushing of the new leaves (Lobão, 2011). The relationship of the SPEI of the previous growing season and dry season also suggests this idea (Figs. 4, S6 and S7). Thus, *C. fisillis* cannot buffer accumulated negative effects of drought on a long-term scale that can last up to 24 months. The strong water shortage during the dry season and a delay of the onset of the rainy season (see Marengo and Souza, 2018), lead to the formation of smaller earlywood vessels and possibly larger marginal parenchyma bands to avoid failures and increase resilience in the hydraulic system. This would explain the observed increasing wood density during the last decades (Fig. 2).

The MNDi, RWi and LWi traits are the most sensitive to drought, to a lesser extent RDi, EWdi and MXDi and the least sensitive EWi and LWdi. This could mean that prolonged and extreme dry periods initially limit the formation (decrease mass and increase volume) of vessels and parenchyma (related to MNDi) of *C. fissilis*; both anatomical elements related to hydraulic efficiency and homeostatic storage and maintenance of NSC, respectively (Janssen et al., 2019).

Cedrela fissilis, a long-lived deciduous species with low sapwood density (Mendivelso et al., 2014), is more vulnerable to cavitation and, consequently embolism, than shade-tolerant and deciduous species with higher density of sapwood (Markesteijn et al., 2011; Méndez-Alonzo et al., 2012). Thus one response to resist this partial implosion of the vessels is to increase the density of the wood (Figs. 4, S6 and S7), specifically through the increased thickness of the cell wall of fibers (EWdi) or by increasing the number of thick-walled fibers (MXDi and LWi), or both (Figs. S6 and S7). Janssen et al. (2019), observed that in dry tropical tree taxa (like *Cedrela*) only wood mass invested in fiber walls contributes to hydraulic safety while wood mass invested in parenchyma does not. The thickening of the fiber walls can aid the bordering vessels to resist partial implosion, prevent stretching or rupture of the pit membranes and microfractures in the vessel walls, lowering the risk of embolism (Jacobsen et al., 2005). However, in extreme and prolonged dry conditions (more than 12 months), a process that may have increased in the last two decades (Fig. 2), stress could decrease the formation of MXD-LW fibers, generating a decrease in the amount of stored carbon necessary to form the next growth layer (Locosselli and Buckeridge, 2017). Thus, as the dry conditions continue in the following years, it is expected that the EW density would decline due to the generation of EW fibers with a thinner cell wall than normal, fibers which fail to give resistance to the further formation of irregular vessels, thus, making them prone to developing embolism (Anderegg and Meinzer, 2015; Janssen et al., 2019).

The evolutionary trade-off between xylem water transport efficiency and xylem hydraulic and mechanical safety of *C. fissilis* is a physiological regulation associated with the basic anatomical and biophysical

properties of wood (Anderegg and Meinzer, 2015; Janssen et al., 2019; Rodríguez-Ramírez et al., 2022). However, the trade-off hypothesis is not entirely clear, but seem crucial in understanding drought resistance in Amazon plant communities (Janssen et al., 2019). Thus, multi-proxy analysis of tree rings approaching structural (e.g., vessel diameter and frequency), physical (e.g., wood density) and (bio)chemical (e.g., stable $\delta^{18}O$ and $\delta^{13}C$ isotopes, and chemical elements) characteristics could be the next major advances to explain the trade-off hypothesis in these endangered forests.

4.4. Changes in climatic thresholds under extreme conditions leading wood traits adaptation

The exercise of climate response analysis using a forward growth model suggest that drier conditions have led to a more pronounced limitation of growth in *C. fissilis* because of a decline in soil water availability and increased evaporative demands (Rodríguez-Ramírez et al., 2022). We found a longer dry season limitation (gM < gT) and more extreme water limitations (lower peaks of gM) (Fig. 5). Increases in growth sensitivity to climate were previously observed in other neotropical tree species (e.g., Camarero et al., 2020; Mendivelso et al., 2014; Venegas-González et al., 2018), however longer and more intense dry seasons negatively impact the performance of *C. fissilis* by increasing the water loss through new leaves and affecting the vulnerability to drought (Fig. 5). Nevertheless, Lobão (2011) suggest that *C. fissilis* probably has a plasticity regulating phenological patterns which reflect the water status within the tree (Borchert, 1999). After the 1990s, M2 (the lowest percentage of soil moisture under which growth is not limited) was lower during the growing season, suggesting an increasing water deficit to growth due to the increasing evaporative demand as a consequence of the delayed onset of the rainy season (Marengo et al., 2018), thus experiencing more drought stress during late earlier growing season (Sánchez-Salguero and Camarero, 2020). This was particularly noticeable during the recent dry spells (Figs. 1, 5, S2 and Table 2).

C. fissilis, compared to other *cedrelas* from the Peruvian Tropical Andean Cloud Forests, showed greater growth recovery, resilience and resistance to drought in stands with low tree density, demonstrating that it can thrive in marginal sites with suboptimal soil conditions (Rodríguez-Ramírez et al., 2022). However, the specific vessels traits showed a poor hydraulic adjustment, which can be suggests increased risk of cavitation and/or embolism if drought conditions increase in frequency or intensity (Rodríguez-Ramírez et al., 2022). In this study, the recovery of growth (RW, EW, LW) during dry spells increased with time in *C. fissilis*, indicating a reduced ability of the species to grow during drought but faster adaptation to recover pre-drought growth following extreme events (Fig. 6). Instead, the drought tolerance of trees was negatively related to the severity of drought (Figs. 5 and 6) and related with carbon reserves, hydraulic conductivity and trade-off between physical (density) and biomechanical (carbon and nutrients)-water use efficiency (Janssen et al., 2019). The stability of growth resilience in *C. fissilis* is engaged by the increase in the frequency of longer and more extreme dry seasons (Figs 1 and 5). Since Rs < 1, this indicate a sustained negative impact of the drought on subsequent growth, i.e. a lagged effect of long-term drought stress (Gazol et al., 2020). For wood density traits, the differences between dry years are more evident in EWd and MND producing lower density (e.g., year of 2007; Figs. 2, S3 and S4) that decrease density resistance and increase recovery during extreme years, with relative stable long-term resilience (Figs. 7, S9 and S10). These changes in the trade-off between growth and wood density plasticity in response to punctual longer dry seasons could explain long-term trends in growth and density in response to increasing temperature and evapotranspiration (Figs. 1, 2 and S11) (Mendivelso et al., 2014; Rodríguez-Ramírez et al., 2022), which in turn are associated with the increase in the frequency of anomalies in the surface temperature of the Tropical Pacific (El Niño/La Niña) and the Tropical North Atlantic (Fig. S11; Espinoza et al., 2019; Marengo and Espinoza, 2016; Marengo and Souza, 2018). Furthermore, anthropogenic activities in the southern Amazon region, such as deforestation, can increase the impact of natural causes by lengthening the dry season (Agudelo et al., 2019; Caioni et al., 2020; Lejeune et al., 2015).

Our results agree with other studies that found variation in growth-related adaptations under extreme conditions (George et al., 2019; Hevia et al., 2020; Martínez-Vilalta et al., 2009; Rathgeber et al., 2019). We hypothesize that, *C. fissilis* cope punctually with drought by forming more drought-tolerant xylem (lower growth, larger vessels and lower density), that is, with a probably low vulnerability to embolism, or by probably adjusting their leaf production, but this adaptation does not seem to be sustainable on the long-term scale. This is also consistent with the results found for *C. fissilis* in the Peruvian Tropical Andean cloud forests (Rodríguez-Ramírez et al., 2022), and for other tropical species (Espinosa et al., 2018; García-Cervigón et al., 2021, 2017; Mendivelso et al., 2014, 2013). In particular, some wood traits may provide a better adaptive capacity to withstand drought stress by allowing more integrated adjustment of the hydraulic system (e.g. leaf area-to-sapwood area ratio) (Martínez-Vilalta et al., 2009; Mendivelso et al., 2013). Our results based on growth and density suggest that these features could operate in the Amazonian *C. fissilis* forests, although a legacy effect may create a negative impact on these mechanisms for years (Huang et al., 2018), but this idea should be tested.

To our knowledge, studies quantifying the long- and short-term responses of wood traits in tropical species in order to understand the mechanisms underlying vulnerability under longer dry seasons in Amazonian forests are scarce (but see Rodríguez-Ramírez et al., 2022). This approach allows identifying growth and density shifts to long-term warmer and drier conditions and, together with the use of a forward growth model and resilience indices, allows to understand growth reactions to drought. Our approach can be useful to improve the knowledge about resilience strategies in Neotropical forests and together with forest dynamic data (regeneration, reproduction, mortality rates, e.g., Ma et al., 2016) provide a new framework to forecast climate change effects in the tropics, thus implementing conservation and sustainable use of this tree species.

5. Conclusions

Our study shows evidence that there is a reduction in growth and an increase in wood density in populations of *C. fissilis* in southern Brazilian Amazonia from 1990 onwards. These trends could be associated with a decrease in water availability and more severe dry season in the region during the last decades. This hypothesis should be reinforced with future studies to verify how much of these trends respond to climatic incidence and how much to ontogenetic signals. Radial wood formation was strongly related to February-March precipitation, whereas wood densities showed positive response to March-May precipitation. *C. fissilis* showed wider and dense rings during wetter years, and narrower and less dense during drier years, which suggest that the species changes its wood functional traits as an adaptation to long-term drought trends. The forward growth model showed that changes in the seasonal timing of soil moisture are triggering the long-term growth decline. The presented results showed functional mechanisms of *C. fissilis* to control wood traits plasticity under short-term dry anomalies, whereas growth thresholds and long-term resilience suggest shifts in the growth and density sensitivity to trends in climate conditions and longer dry seasons, increasing the vulnerability to projected climate warming scenarios. This study is one of the first attempts to illuminate aspects of wood traits climate sensitivity and resilience to drought based on long-term annual data in Amazon dry seasonal moist forests.

Declaration of competing interest

All authors have no conflict of interest to declare. We also state that

all authorizations and ethical issues regarding this research were carried out in accordance with local laws and procedures. We greatly appreciate the opportunity of publishing our work in the journal *Agricultural and Forest Meteorology*.

Data availability

The data from this article will be incorporated into the ITRDB BRA015 (https://www.ncei.noaa.gov/access/paleo-search/study/37,447) as a complement to the chronologies already registered.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2023.109392.

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