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Does climate change alter the nutrient trends of *Cedrela fissilis* Vell. trees in the southern Brazilian Amazon?

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Abstract

Background The increase in the frequency and intensity of droughts is pointed out as one of the main factors altering biogeochemical cycles in the Amazon basin. An eco-nutritional approach using X-ray fluorescence micro-analysis (μ XRF) is proposed to verify the long- and short-term effects of droughts on the growth and xylem nutrient concentrations of *Cedrela fissilis* Vell.

Methods Fourteen radii were selected from a tree-ring width chronology and X-rayed by Itrax Multiscanner. Profiles of ring width, wood density, and concentrations of aluminum (Al), phosphorus (P), sulfur (S), calcium (Ca), potassium (K), manganese (Mn), iron (Fe) and strontium (Sr) together with Al/Ca, Ca/Mn, K/Ca, Sr/Ca and Mn/S ratios were constructed and correlated with precipitation, temperature, the difference between precipitation and potential evapotranspiration (P-PET) and standardized precipitation–evapotranspiration index (SPEI).

Results During dry years, *C. fissilis* showed narrower, less dense rings, lower Al, P, S and Ca, and higher K and Fe concentrations (the opposite was found in wet years). Ring width decreased (together with Al, P, S, K, Ca, Mn, Fe, Sr, Al/Ca, K/Ca and Sr/Ca) and wood density increased (together with Ca/Mn and Mn/S), which was associated with an increase in evapotranspiration and temperature over time, mainly since 1990. *Cedrela fissilis* showed a tendency to increase its capacity for resistance, and a recovery and resilience in growth over time associated with responses in Al, Ca, P and S. However, it showed a risk in the capacity for recovery of the pre-drought density values, associated with unsatisfactory responses in Al, Ca, K, Fe and P.

Conclusions This study is the first attempt to analyze tree-ring nutritional evidences of *C. fissilis* trees to climate sensitivity and resilience to drought, based on long-term data from seasonal moist tropical forests of the Amazon. Our data suggested that *C. fissilis* is undergoing alterations in the concentration, use and redistribution of nutrients associated with increasing wood density and decreasing growth over time, due to the increase of drought frequency in the southern Amazon.

Keywords Dendrochemistry, μ XRF, Drought, Tropical tree, Eco-chemical indicator, Resilience, Resistance, Recovery

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Introduction

Drought in the Amazon region affects the growth and nutritional status of trees, conditioning the ecological processes by pushing the forest to critical physiological thresholds. The observations in the last decades and the forecasts for the coming years show the dangerous tipping point of recovery that the Amazon region can reach (Lovejoy and Nobre 2018) as a consequence (among others) of the increases in the frequency of droughts and floods (Phillips et al. 2009; Marengo et al. 2016; Marengo and Espinoza 2016), large-scale deforestation (Lejeune et al. 2015; Boers et al. 2017; Exbrayat et al. 2017; Marengo et al. 2018), and forest fires (Marengo and Espinoza 2016; Aragão et al. 2018; Marengo et al. 2018). These agents of Amazon forest alteration can have important implications for hydrological cycle variation (e.g., evapotranspiration, heat flux and water yield and discharge) (Fu and Li 2004; Li and Fu 2004; Marengo 2009; Coe et al. 2016; Smith et al. 2023), forest ecosystem dynamics (e.g., tree mortality) (Aleixo et al. 2019; Fauset et al. 2019; Locosselli et al. 2020) and biogeochemical cycling (e.g., carbon sink and nutrient imbalances) (Brienen et al. 2015; Buscardo et al. 2016; Grace 2016).

The major factors underlying patterns in biogeochemical cycles in ecosystems, including Amazon forests, are represented by climate, species composition, soil fertility, and successional status (Vitousek and Sanford 1986). Disturbances in these factors generate an imbalance in the stocks, allocation and flows of nutrients (McGrath et al. 2001; Quesada et al. 2012; Buscardo et al. 2016; Malhi et al. 2021). Over recent decades, biogeochemistry studies in the Amazon region have focused on the carbon cycle (Brienen et al. 2015; Araújo et al. 2016; Gloor 2016; Grace 2016; Higuchi et al. 2016; Covey et al. 2021; Pinagé et al. 2023). The undisturbed Amazon forest acts as a substantial carbon sink that offsets carbon dioxide (CO₂) emissions from fossil fuel combustion and land use change in the region (Brienen et al. 2015; Phillips et al. 2017). The increase in the frequency of droughts and the associated occurrence of fires and mortality of species, mainly in the central and southern Amazon region (Phillips et al. 2016; Lovejoy and Nobre 2018), aggravated the natural carbon loss (Espírito-Santo et al. 2014), turning the basin into a strong source of CO₂ (Covey et al. 2021; Malhi et al. 2021). The interactions among other biogeochemical cycles, such as those of nitrogen (Figueiredo et al. 2019) and phosphorus (Fleischer et al. 2019), have also gained relevance due to their modulating role in the carbon cycle. The co-limitation by nitrogen (not deficient) and phosphorus (deficient in 90% of the Amazonian soils, Sanchez et al. 1982) is an important constraint to plant productivity (biomass) and CO₂ fertilization

responses of Amazon forest (Buscardo et al. 2016; Malhi et al. 2021; Cunha et al. 2022).

Other essential minerals for plant productivity, such as calcium, potassium, magnesium and sulfur (and their non-essential analog minerals, such as strontium) (Burger and Lichtscheidl 2019) are highly stocked by the canopy (Jordan et al. 1980; Jordan 1985), although they are poorly available in the most common Amazonian soils (75% classified as Ultisols and Oxisols) (Sanchez et al. 1982) due to the low cation exchange capacity of the soils (Sanchez et al. 1982; Cuevas and Medina 1986; Vitousek and Sanford 1986; Laurance et al. 1999; Moreira et al. 2006; Buscardo et al. 2016). These soils are deep, well-drained with mostly favorable physical properties, but they present low fertility characterized by the predominance of iron and aluminum oxides (also manganese oxides in less drained areas) (Moreira et al. 2006; Mesquita et al. 2011; De Souza et al. 2018) and kaolinite clay minerals, low organic matter content and low pH values (acid soil, pH < 5.5) (Sanchez et al. 1982; Buscardo et al. 2016; Souza et al. 2018). The low fertility of these soils is also due to parent material (predominantly sedimentary rocks), heavy rainfall (promotes leaching), and high temperatures that result in rapid decomposition of organic matter (De Souza et al. 2018). Furthermore, under a regime of climate change (longer and more intense dry seasons) (Phillips et al. 2016), it is expected that in soils with high clay content, such as Ultisols and Oxisols, forests will suffer significant losses of biomass, specifically, increased vulnerability and substantial decline in late-successional tree abundance (Levine et al. 2016).

Tree vulnerability to drought varies according to the functional diversity of the species in the stand (Grossiord 2020), its role in forest dynamics (Esquivel-Muelbert et al. 2019) and its adaptive capacity to the local environment (Aguirre-Gutiérrez et al. 2020), which translates into a heterogeneous response of the species throughout the Amazon (Malhi et al. 2021). Ecohydrological theories of tree responses to drought (Anderegg et al. 2018; Wang et al. 2020; Wu et al. 2020) are consistent with xylematic responses suggesting that more resilient hydraulic architecture (e.g., greater embolism resistance of their water-transporting xylem) is less likely to succumb to drought (Lachenbruch and Mcculloh 2014; Rowland et al. 2015; Islam et al. 2018; Janssen et al. 2019; Powers et al. 2020). Furthermore, trade-offs between growth and wood density are expected, where, for example, species with a strong growth response to water availability averaged a low wood density, which may facilitate stem water storage (Mendivelso et al. 2013, 2014; Camarero et al. 2020). Other defense mechanisms of plants against drought are possible if there is an optimal balance in nutrient supply (Gessler et al. 2017; Hevia et al. 2019). However, in

the event that the availability of soil nutrients is very low, the stock and reabsorption of nutrients in the xylem and phloem reservoirs will be low, altering the morphology of the plant (e.g., decreased growth and productivity, vessel size adjustments, trade-offs between sapwood area with leaf and root area) and physiology (e.g., decreased production of proline and enzyme synthesis) to withstand drought stress (St. Clair et al. 2008; Kreuzwieser and Gessler 2010; Gessler et al. 2017; Etienne et al. 2018; Salazar-Tortosa et al. 2018; Hevia et al. 2019; Durgante et al. 2023).

Regarding the vulnerability of *Cedrela fissilis*, the long-lived pioneer species (Peña-Claros et al. 2008) showed greater growth recovery, resilience and resistance to drought compared to other *Cedrela* species in the Peruvian Tropical Andean cloud forest (Rodríguez-Ramírez et al. 2022), providing xeric adaptation (Scholz et al. 2013). This characteristic may reinforce the idea of the species' ability to grow in marginal sites with suboptimal soil conditions and marked water deficit (e.g., seasonally dry forests) (Pereira et al. 2018), consistent with its wide distribution in Neotropical forests (Pennington and Muellner 2010; Barstow 2018; Siqueira et al. 2019). However, the species also shows poor hydraulic adjustment, which may suggest a higher risk of cavitation and/or embolism if the frequency or intensity of drought increases (Rodríguez-Ramírez et al. 2022). The hydraulic vulnerability of trees is also strongly influenced by maximum temperature and evapotranspiration (Rodríguez-Ramírez et al. 2022). Furthermore, in a population of *C. fissilis* in the southern Amazon forest, it was observed that warmer conditions during the wet season negatively affected xylem sulfur concentrations (Ortega Rodriguez et al. 2023a), nutrients that induce plant tolerance against high-temperature stress (Ihsan et al. 2019). However, to our knowledge, the degree of vulnerability to nutritional imbalances (modification of use and allocation of nutrients) associated with drought-induced *Cedrela* growth responses is unknown (see Villagra et al. 2013).

Here, we use dendrochemistry (Hietz et al. 2015) for an eco-nutritional approach. The inter-annual concentrations of nutrients in tree-rings of *Cedrela fissilis* Vell. (Meliaceae) of the southern Amazon region were used to assess how climate trends and droughts alter long- and short-term tree growth changes. We hypothesize that climate change and the increase in the frequency and intensity of extreme droughts alter long-term nutrient balances, affecting long-term growth patterns (Hevia et al. 2019). Specifically, we compared tree ring widths, wood density and nutrient concentrations in a drought-prone region of Amazonian forests (Agudelo et al. 2019). Our objectives were: (i) to assess long-term wood nutrient concentrations in *C. fissilis*; (ii) to investigate the

relationships among wood traits (tree-ring width, wood density and nutrient concentrations) and climate inter-annual variability and trends; (iii) to investigate the effects of extreme drought, and the long- and short-term nutrient imbalances. Investigating the role of nutrient changes in the wood of trees from moist forest exposed to marked seasonality in water availability will improve our understanding of how tropical species will react to climate change and whether these forests and their productivity will be vulnerable to drought damage.

Methods

Study area

We sampled trees of *C. fissilis* in the Forest Management Unit (FMU) No. 12 (harvest plan 2019, area 2455.7 ha) of Jamari National Forest (JNF) under permanent forest management conducted by the logging firm AMATA. JNF is located in the southern Amazon basin, in the state of Rondônia (09°15'00" S and 63°02'05" W; MMA 2005). The area is classified as a moist forest with a well-defined dry season from June to August (with less than 50 mm of rain per month) and a wet season from September to May. The potential evapotranspiration exceeds precipitation from April to October. The average annual rainfall in this region is 2438 mm and the annual average temperature is 26 °C (Additional file 1: Fig. S1).

The soil is classified as Oxisol (Additional file 1: Fig. S1a) (Soil Survey Staff 2022), deep (1 to 2 m) to very deep (>2 m) (MMA 2005), with a water retention capacity between 50% and 80% (Fengler et al. 2022). The soil has high acidity (pH<4) and Al exchange ($H+Al < 150 \text{ mmolc dm}^{-3}$), and low natural fertility with a predominance of low base saturation (<10%), cation exchange capacity (<150 mmolc dm^{-3}), Mg (<1 mmolc dm^{-3}), Ca (<2 mmolc dm^{-3}), K (<0.8 mmolc dm^{-3}) and P (<8 mg dm^{-3}) and soil organic matter (<40 g kg^{-1}) (Fengler et al. 2022).

Sampling and preparation

We selected 29 trees of *C. fissilis* felled and stored at log yards between April and May of 2019. Dominant trees >30 cm diameter at breast height (DBH) were collected in a random sampling design. Wood discs of each tree were cut at the top level of the first log (6 m) (Granato-Souza et al. 2018). Four radial samples (10 cm width and 5 cm thickness) from each disc were cut, air dried and polished gradually with sandpaper (from 80 to 600 grains inch^{-2}) for cross-dating and annual ring width (RW) measurement. Furthermore, a thin radial Sect. (2 cm width and 1.7 mm thickness) was cut transversely for each radial sample to analyze the ring wood density (RD, X-ray densitometry) and element content (micro X-ray fluorescence, μXRF).

Annual ring width measurements

Radial samples were cross-dated using skeleton plots and visual dating under the microscope (Stokes and Smiley 1996). Each cross section was scanned at 1200 dpi resolution with an Epson Expression 10000XL scanner, and the RW was measured with a resolution of 0.01 mm using CDendro and Coorecorder[®] software (Cybis Electronic 2013). The “Schulman Shift” convention (Schulman 1956) was not applied to the dating of the JNF series, which means that the tree growth of the period 2017/2018 was assigned to the calendar year 2018.

Wood density data collection

Thin radial sections from 29 trees were kept under constant temperature and humidity (20 °C and 60%, respectively) for 48 h in an atmosphere at 12% moisture content (Tomazello-Filho et al. 2008; Quintilhan et al. 2021). Wooden laths were then scanned, and X-rayed using an X-ray densitometry chamber (Faxitron MX20-DC12, Faxitron X-ray, Illinois, USA) with facilities at the Wood Anatomy and Tree-ring Laboratory, University of Sao Paulo, Brazil. X-ray images were then analyzed with WINDENDRO Density 2017a[®] software (Regent Instruments Inc., Quebec, Canada) to obtain the density profile with 15 µm intervals expressed in g cm⁻³.

Chemical data collection

The same thin radial sections of 14 trees used for density analyses were kept under controlled conditions (20 °C temperature and 50% humidity) and X-ray fluorescence micro-analyzed (µXRF) in an ItraxMultiscanner (Cox Analytical Systems, Mölndal, Sweden) at the laboratory of DendrOlavide, Universidad Pablo de Olavide (Seville, Spain).

Itrax was operated at 30 kV and 50 mA with a Cu-tube, and samples were exposed to the X-ray beam for 40 s at each measurement point in the radial direction (20-µm step size). Count rates of fluorescent photons of elements and a radiographic grayscale image at each measurement point of each sample were obtained. Peaks in the µXRF spectrum were assigned to specific elements using Q-spec software (Cox Analytical Systems, Mölndal, Sweden), producing relative concentrations (counts of fluorescent photons per second, cps) (Croudace et al. 2006) of those elements detected within the wood structure for every analyzed point. Radiographic images were synchronized with previously constructed ring width chronologies to corroborate the identification of the growth ring boundaries. Consequently, the element-specific count rates were assigned for each annual ring and the average annual time series for each radial section were produced using WinDendro[™] (Regent Instruments Inc., Quebec, Canada).

In this study, we selected: (i) aluminum (Al), which is an indicator of soil acidification (Göransson and Eldhuset 1991; Cutter and Guyette 1993); (ii) phosphorus (P), an structural component of plant compounds and associated with the formation of younger xylem cells (Peterson and Anderson 1990); (iii) sulfur (S), essential to define the cellular architecture and play a role in the detoxification of potential toxic metals (Fairchild et al. 2009; Yadav 2010); (iv) potassium (K), involved in the cambial activity related to cell expansion (Fromm 2010); (v) calcium (Ca), involved in the cambial activity related to cell differentiation (Lautner and Fromm 2010); (vi) manganese (Mn), enzymatic function involved in amino acid and lignin synthesis (Pittman 2005) but important growth-limiting factor in acid soils (Kogelmann and Sharpe 2006) and competitive elements of Ca, K, P and Fe at the xylem cation exchange sites (McClenahan et al. 1989; Peterson and Anderson 1990); (vii) iron (Fe), essential for plant growth (meristematic cell division) and chlorophyll synthesis, although highly reactive and toxic under acid ambient conditions (Morrissey and Guerinot 2009); and (viii) strontium (Sr), despite not being an essential element, plants store it in the cell wall, because it behaves identically to Ca in many biogeochemical processes (Drouet and Herbauts 2008; Tagami and Uchida 2017; Burger and Lichtscheidl 2019). We also evaluated the ratios of aluminum to calcium (Al/Ca) (Kuang et al. 2008) and calcium to manganese (Ca/Mn) (Kogelmann and Sharpe 2006), reliable indicators of soil acidification; potassium to calcium (K/Ca), which is an indicator of cambial activity (Fromm 2010); strontium to calcium (Sr/Ca), associated with wood density (Silkin and Ekimova 2012) and manganese to sulfur (Mn/S), potential indicator of plant toxicity and stress associated to soil acidification (Neves et al. 2017).

Building tree-ring series

Cross-dating of the RW and RD series was evaluated using the COFECHA program (Holmes 1983) by comparing the consistency of the different ring width series using Pearson correlations at 30-year intervals. The annual nature of the tree rings and the robustness of the aligned mean series were verified and confirmed using radiocarbon “bomb-peak” dating (Santos et al. 2021). Fourteen radii, which presented the best correlation statistics with the mean site series of width and density, were selected to construct the chemical (Al, P, S, K, Ca Mn, Fe and Sr) chronologies.

Raw series were standardized and detrended to obtain comparable ring-width, -density and -chemical series of each tree and remove the age-, size-related trend and non-climatic signals using the ARSTAN program (Cook and Krusic 2005). A horizontal line function through the

mean was initially applied only for the chemical series as an alternative for normalizing values. Then, ring-width, ring-density, and ring-chemical series were detrended by fitting a 30-year cubic spline function through the tree-ring series of each measured radius to retain high-frequency variability. We used a spline function, where the frequency response is 0.50 at a wavelength of 0.67 multiplied by the length of the series in years. Then, the ring data were divided by the fitted lines to obtain the standardized ring indices. All the wood trait chronologies were evaluated using dendrochronological statistics, including the mean correlation among all-time series (Rbar; Cook and Pederson 2011), the first-order autocorrelation (AC), the mean sensitivity (MS), and the Expressed Population Signal (EPS; Wigley et al. 1984).

Climate data set

Monthly precipitation and temperature data were obtained from (ANA, National Water Agency, Brazil; <https://dadosabertos.ana.gov.br/>) and INPE (National Institute of Space Research, Brazil; <http://bancodedados.cptec.inpe.br/tabelaestacoes/faces/consultawmo.jsp>). A regional mean precipitation (1975–2018) and temperature (1957–2018) series from five and six local meteorological stations, respectively, were created (Additional file 1: Table S1). The HOM and MET programs from Dendrochronology program library (DPL, Holmes 1994) were used to estimate missing data and calculate the regional time series. As a metric that expresses drought intensity, we used the difference between precipitation (P) and evapotranspiration (PET) (1975–2018) and the standardized precipitation evapotranspiration index (SPEI) (1950–2018). The PET and SPEI were calculated using the *SPEI* package (Vicente-Serrano et al. 2010) in R (R Core Team 2021).

Data analyses

To describe significant increasing or decreasing trends in raw series of RW, RD and *z*-scores of elements (i.e., the mean was subtracted from each value and divided by the standard deviation), we applied a linear regression *t* test for the period 1940–2018. To explore common long-term variance and associations among raw and detrended series of wood traits (RW, RD, elements and ratios), we applied principal component analysis (PCA) of the correlation matrix and Pearson's correlation.

We calculated Pearson correlation coefficients for the common periods 1975–2018 for local precipitation and P-PET and 1960–2018 for temperature and SPEI to quantify associations between wood traits and climate data. These correlations were calculated monthly from September of the previous year to August of the current year, which included the period of wood formation

of *C. fissilis* close to the study region from prior September/October to current April/May, indicating a period of cambial dormancy from current June to August (period of leaf exchange) (Dünisch et al. 2003; Lobão 2011; Baker et al. 2017). We also calculated seasonal correlations considering the beginning of the rainy season (before September to November), middle of the rainy season (before December to current February), end of the rainy season (current March to May) and dry season (current June to August).

To compare the growth responses (RW and RD) and the chemical traces in tree-rings during dry and wet years, we used one-way ANOVA. The ten driest (1983, 1997, 2005, 2006, 2007, 2010, 2011, 2012, 2014, 2015) and wettest (1976, 1977, 1978, 1979, 1986, 1989, 1990, 2001, 2013, 2018) years were selected for the period 1975–2018 according to the ranking of normalized values of the P-PET (12 months, prior September to current September). The selected dry years are in accordance with the extreme drought events registered in the southern Amazon basin (Espinoza et al. 2019). To quantify the response of growth and the stability of element concentrations to extreme droughts during recent decades, we calculated the indices of resistance (Rt), recovery (Rc), resilience (Rs) and relative resilience ($rRs = Rs - Rt$) (Lloret et al. 2011). They were calculated using detrended data of wood traits (RW, RD, elements and ratios) instead of raw data to remove age and size effects and potential bias due to the eccentric growth of tropical species. The Rt index quantifies the difference between growth/chemical trace during the dry year and the preceding years, whereas the Rc index accounts for the growth/chemical trace reaction following the drought period. The Rs index quantifies the difference in growth/chemical traces before and after the dry year. Finally, the rRs index is the difference between Rs and Rt (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). Since extreme drought events in the Amazon region can last more than 1 year, the value of the pointer years was calculated through the average of the successive dry years. We selected the extreme drought events of 1981–1983, 1997–1998, 2005–2007, 2010–2011, and 2014–2015, which affected large areas of the southern Amazon basin (Ronchail et al. 2002; Williams et al. 2005; Marengo et al. 2008; Lovejoy and Nobre 2018; Espinoza et al. 2019; Caioni et al. 2020). Comparisons between wood trait responses during extreme droughts were assessed by one-way ANOVA and the increasing or decreasing trends of these responses over the years were evaluated by a linear regression *t* test.

Results

Growth and nutrient series and their associations

The descriptive statistics of all standardized chronologies are shown in Table 1. The RW and RD chronologies were based on 69% and 52% of all sampled *C. fissilis* trees, respectively. They showed a significant mean correlation among the series ($R_{\text{bar}}=0.31$ and 0.29 , respectively) and presented an EPS that was statistically reliable for the period 1901–2018 ($\text{EPS}>0.85$). The chemical chronologies presented a significant mean correlation among the series based on 54% (Al, $R_{\text{bar}}=0.21$), 45% (P, $R_{\text{bar}}=0.23$), 63% (S, $R_{\text{bar}}=0.30$), 45% (K, $R_{\text{bar}}=0.58$), 36% (Ca, $R_{\text{bar}}=0.26$), 54% (Mn, $R_{\text{bar}}=0.30$), 45% (Fe, $R_{\text{bar}}=0.25$), 45% (Sr, $R_{\text{bar}}=0.35$), 36% (Al/Ca, $R_{\text{bar}}=0.28$), 36% (Ca/Mn, $R_{\text{bar}}=0.33$), 54% (K/Ca, $R_{\text{bar}}=0.25$), 45% (Sr/Ca, $R_{\text{bar}}=0.32$) and 45% (Mn/S, $R_{\text{bar}}=0.44$) of all trees selected for chemical analysis. Only the K and Mn/S chronologies presented an $\text{EPS}>0.85$ for the period 1901–2018.

The correlation between raw data of *C. fissilis* tree-ring parameters showed a significant positive and negative association of almost all the elements with the RW (Al, S, K, Ca, Mn and Sr; positive loading in PC1) and RD (Al, S, K, Ca, Mn, Sr, Al/Ca, K/Ca, Sr/Ca; negative loading in PC1), respectively. The raw data of Ca/Mn and Mn/S ratios (negative loading in PC1) showed a significant negative association with RW and all other chemical

series but a positive association with RD (Fig. 1A, B). The first principal component for raw data explained 57% of the total variance, and the second axis explained an additional 12% (Fig. 1A). After detrending, a significant positive correlation between RW and RD was observed (positive loading in PC2). Significant positive correlations were maintained between K (negative loading in PC2) and Ca and K/Ca; Al/Ca (positive loading in PC1) and Al; P (positive loading in PC1) and Al/Ca, K/Ca and Sr/Ca; and Sr/Ca (positive loading in PC1) and Sr, Al/Ca and K/Ca. Significant negative correlations were maintained between Ca/Mn (negative loading in PC1) and P, Al/Ca, K/Ca and Sr/Ca (Fig. 1C, D). The first principal component for detrended data explained 18% of the total variance and 12% the second one (Fig. 1C).

Long- and short-term patterns of growth and nutrients

Raw data of RW together with z -scores of all elements (Al, P, S, K, Ca, Mn, Fe and Sr) and the molar ratios Al/Ca, K/Ca and Sr/Ca, while RD together with the molar ratios Ca/Mn and Mn/S showed similar long-term trends (Fig. 2). According to the fitted linear regression model, the RW (and Al, P, S, K, Ca, Mn, Fe, Sr, Al/Ca, K/Ca and Sr/Ca) decreased, while the RD (and Ca/Mn and Mn/S) increased between 1940 and 2018. The long-term trends of tree-ring parameters are not affected

Table 1 Tree population features and statistical characteristics of *Cedrela fissilis* tree-ring chronologies

Location	Sampling	Chemical analysis	DBH (cm)	H (m)	Age at 6 m (years)	SG (g cm^{-3})
Jamari National Forest	29 trees/116 radii	11 trees/14 radii	73.70 \pm 2.80	15.30 \pm 0.50	83.0 \pm 6.0	0.40 \pm 0.07
Statistics	No. trees/No. radii	Value	Rbar	AC	MS	EPS
RW (mm)	20/62	2.33 \pm 1.19	0.31	0.52	0.40	0.93
RD (g cm^{-3})	15/40	0.49 \pm 0.05	0.29	0.56	0.07	0.91
Al (cps)	6/7	20.40 \pm 2.65	0.21	0.47	0.06	0.65
P (cps)	5/6	1.43 \pm 0.26	0.23	0.52	0.49	0.66
S (cps)	7/7	31.59 \pm 7.22	0.30	0.63	0.08	0.76
K (cps)	5/5	289.70 \pm 190.00	0.58	0.88	0.06	0.87
Ca (cps)	4/5	6664.14 \pm 1907.59	0.26	0.53	0.10	0.65
Mn (cps)	6/6	279.00 \pm 27.70	0.30	0.63	0.02	0.72
Fe (cps)	5/5	417.34 \pm 94.95	0.25	0.56	0.11	0.62
Sr (cps)	5/6	48.51 \pm 5.88	0.35	0.50	0.06	0.76
Al/Ca	4/5	0.23 \pm 0.03	0.28	0.57	0.10	0.66
Ca/Mn	4/4	3.42 \pm 0.58	0.33	0.63	0.09	0.66
K/Ca	6/6	0.32 \pm 0.06	0.25	0.72	0.09	0.66
Sr/Ca	5/6	0.55 \pm 0.07	0.32	0.52	0.10	0.74
Mn/S	5/7	1.02 \pm 0.17	0.44	0.7	0.10	0.85

H tree height, SG specific gravity, RW ring width, RD ring density, Al relative tree-ring concentrations of aluminum, P phosphorus, S sulfur, K potassium, Ca calcium, Mn manganese, Fe iron and Sr strontium, DBH diameter at breast height, Rbar mean correlation among all series, AC first-order autocorrelation for raw tree-ring series, MS mean sensitivity, EPS expressed population signal, period 1901–2018, cps counts per second

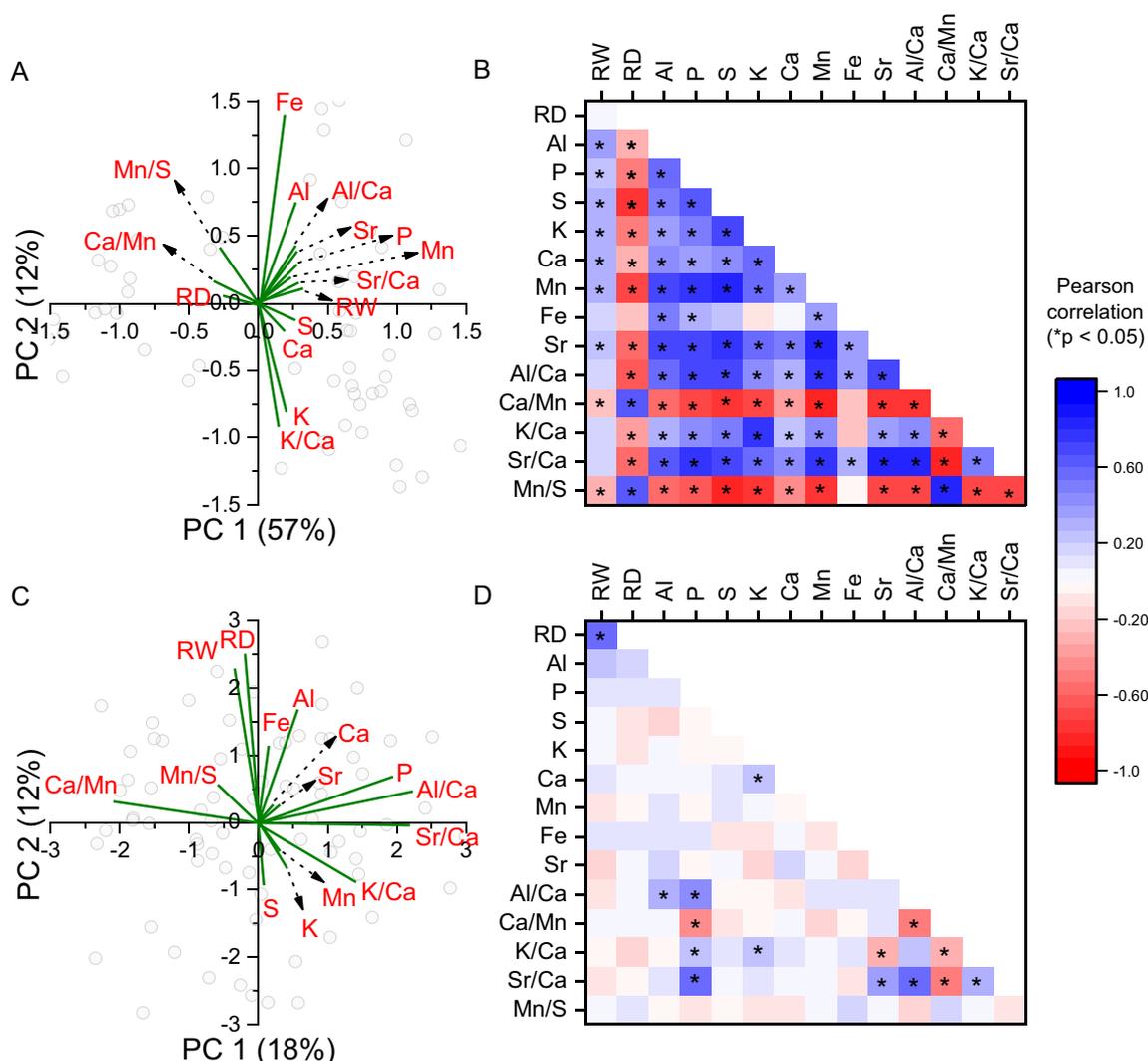


Fig. 1 a, c Principal component analysis of years (dots) and b, d Pearson’s correlation of raw (a, b) and standardized (c, d) tree-ring parameters of *Cedrela fissilis*. Raw data (tree-ring in mm, tree-ring density in g cm^{-3} , and z-scores of elements) and residual index of tree-ring width (RW), wood density (RD) together with series of aluminum (Al), phosphorus (P), Sulfur (S), potassium (K), calcium (Ca), manganese (Mn), iron (Fe), strontium (Sr), aluminum to calcium (Al/Ca), calcium to manganese (Ca/Mn), potassium to calcium (K/Ca), strontium to calcium (Sr/Ca) and manganese to sulfur (Mn/S) are projected in a reduced dimension space defined by principal components PC1 (x axes) and PC2 (y axes). The PCA and correlation were computed over the 1940–2018 period

by the sapwood–heartwood transition zone (2002 ± 6), although the Fe trend goes from increasing until 1984 and then decreasing until 2018, with a change occurring before the early to heartwood transition zone.

Normalized P-PET showed an increase during the dry years of the recent decades, mainly from 2000 onward (Fig. 3). A significant ($p < 0.05$) decrease in the tree-ring width and wood density together with the concentrations of Al, S and Ca was observed in the dry years compared with the wet years. In dry years, the concentrations of P also decreased, and those of K and Fe increased (significant, $p < 0.1$) compared with the values

in wet years (Fig. 3). The Mn, Sr and Al/Ca, Ca/Mn, K/Ca, Sr/Ca and Mn/S ratios did not show significant differences between dry and wet years (Fig. 3, Additional file 1: Fig. S2).

Climate–growth–nutrient relationships

The correlation between *C. fissilis* tree-ring parameters and precipitation showed that the local rainy season positively affected tree growth and density (RW, $r = 0.29$; RD, $r = 0.29$), particularly in March. The rainy season also positively affected the element concentrations of Al (in September, $r = 0.31$), S (in October,

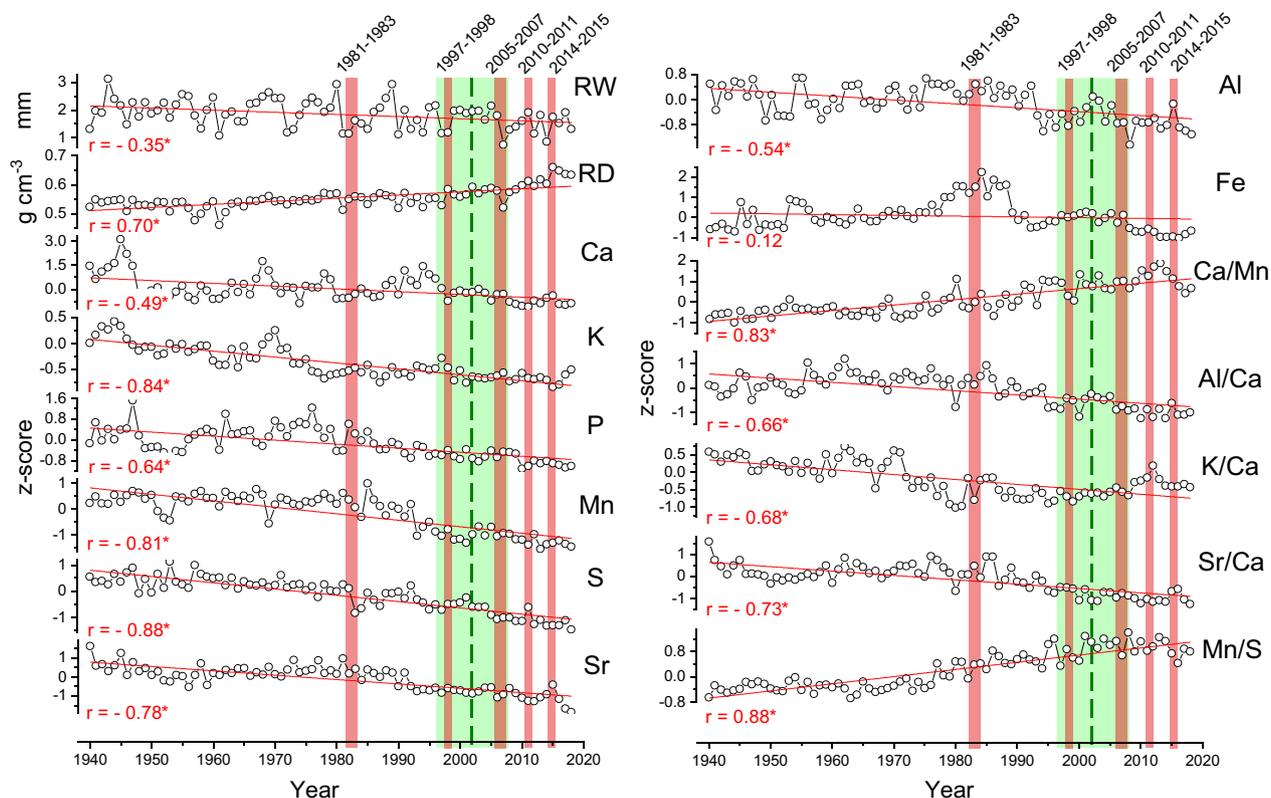


Fig. 2 Annual values and fitted (red lines) long-term trends of ring width (RW), wood density (RD), z-scores of element concentration and molar ratios of *C. fissilis* trees. Z-scores of aluminum (Al), phosphorus (P), sulfur (S), potassium (K), calcium (Ca), manganese (Mn), iron (Fe), strontium (Sr) and molar ratios of aluminum to calcium (Al/Ca), calcium to manganese (Ca/Mn), potassium to calcium (K/Ca), strontium to calcium (Sr/Ca) and manganese to sulfur (Mn/S). Vertical light red boxes represent extreme drought events registered in the southern Amazon basin in 1981–1983, 1997–1998, 2005–2007, 2010–2011, and 2014–2015 (Espinoza et al. 2019). The vertical green dashed line and error interval indicate the average year of sapwood–heartwood transition (2002 ± 6)

$r=0.33$), Ca (in November, $r=0.44$) and Sr (in March, $r=0.34$). Concentrations of Al, P and S (particularly in July) presented positive correlations ($r>0.29$) with precipitation in the dry season (Fig. 4). Warmer temperatures during the rainy season (mainly between January and April) and the beginning of the dry season (mainly between June and July) negatively ($r<-0.28$) affected the P and S concentrations. Warmer months during the rainy season positively affected growth (RW in October, $r=0.28$), K concentration (in May, $r=0.27$) and Ca/Mn (in February, $r=0.37$). Warmer months during the

dry season positively affected Ca (in July, $r=0.26$) and Ca/Mn (in June, $r=0.26$).

The correlations between P-PET and tree-ring parameters showed that months of low evapotranspiration in the rainy season positively affected tree growth (RW in March, $r=0.30$) and concentrations of Al (in September, $r=0.31$), P (in January, $r=0.30$), S (in October, $r=0.31$), Ca (in November, $r=0.43$) and Sr (in March, $r=0.32$), and negatively affected K (between March and May, $r=-0.29$) and K/Ca (in March, $r=-0.47$) (Fig. 4). Low evapotranspiration in the dry season positively affected

(See figure on next page.)

Fig. 3 Mean index residual chronologies of tree-ring width (RW), wood density (RD) and element concentration of aluminum (Al), phosphorus (P), sulfur (S), potassium (K), calcium (Ca), manganese (Mn), iron (Fe), and strontium (Sr) from *C. fissilis* trees from southern Amazon and the total annual difference between precipitation and potential evapotranspiration (P-PET, time-scales from prior September to current September). Vertical light red boxes represent extreme drought events registered in the southern Amazon basin in 1981–1983, 1997–1998, 2005–2007, 2010–2011, 2014–2015 (Espinoza et al. 2019). On the right is the boxplot of normalized parameters in dry and wet years; a significant difference (SD) between means is also presented ($p<0.05$)

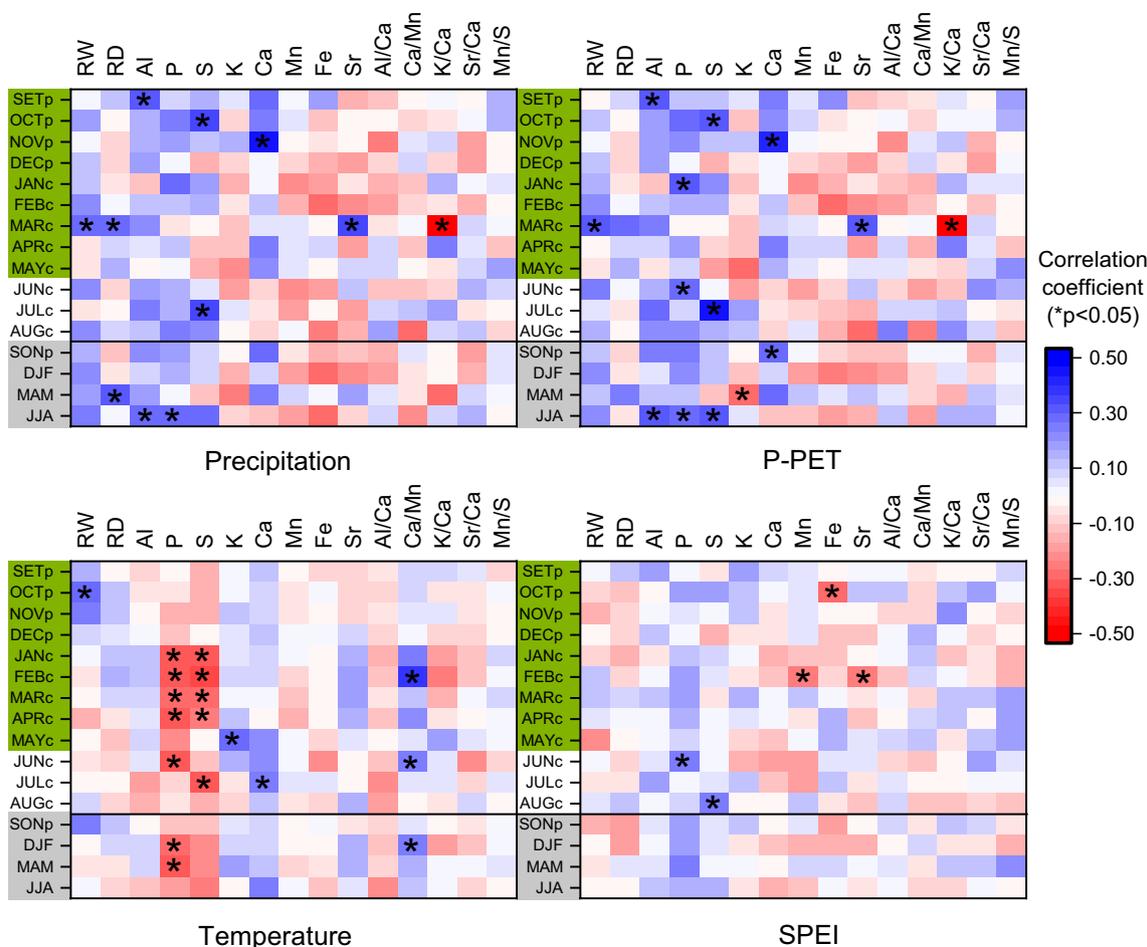


Fig. 4 Correlation values between mean index residual chronologies of tree-ring width (RW), wood density (RD), element concentrations of aluminum (Al), phosphorus (P), sulfur (S), potassium (K), calcium (Ca), manganese (Mn), iron (Fe) and strontium (Sr) and molar ratios of aluminum to calcium (Al/Ca), calcium to manganese (Ca/Mn), potassium to calcium (K/Ca), strontium to calcium (Sr/Ca) and manganese to sulfur (Mn/S) of *C. fissilis* trees with monthly and seasonal precipitation (period 1975–2018), temperature (period 1960–2018), the difference between precipitation and potential evapotranspiration (P-PET, period 1975–2018) and the standardized precipitation–evapotranspiration index (SPEI, period 1960–2018) from the southern Amazon. The green shading includes the rainy months for the study region and gray shading shows the seasonal correlations

Al, P and S ($r > 0.30$). Regarding the SPEI drought monitor, low evapotranspiration in the dry season positively affected P (in June, $r = 0.24$) and S (in August, $r = 0.26$). In contrast, low evapotranspiration in the rainy season negatively affected Mn, Sr (in February, $r = -0.24$) and Fe (in October, $r = -0.28$).

Drought–growth–nutrients resilience

Growth (RW) and wood density (RD) resistance for *C. fissilis* increased with time (from 1981–1983 to 2014–2015 droughts), and a similar increasing trend was observed for the resistance explained by the concentrations of Al, Ca, P, Ca/Mn and Mn/S, unlike S, K, Mn, Fe, Sr, Al/Ca, K/Ca, and Sr/Ca, which decreased (Fig. 5, Additional file 1: Figs. S3, S4). Growth and wood density resilience

increased with time, and similar increasing trends of resilience were observed for Al, S, Ca, Mn, Sr and Ca/Mn, unlike K, P, Fe, Al/Ca, K/Ca, Sr/Ca and Mn/S, which decreased. A significant positive correlation between resistance and resilience of growth and wood density to years of droughts was observed. Furthermore, the resilience explained by Sr concentration presented a significant positive correlation with the resilience of growth and wood density (Additional file 1: Fig. S5). A significant positive correlation was also observed between the resistance of Mn and Sr and the resilience of Al/Ca and K/Ca. A significant negative correlation was observed between Ca/Mn and Sr/Ca resistance and the resilience of Mn and Fe, Mn and Mn/S, and S and Sr/Ca (Additional file 1: Fig. S5). The highest growth and wood density resistance and

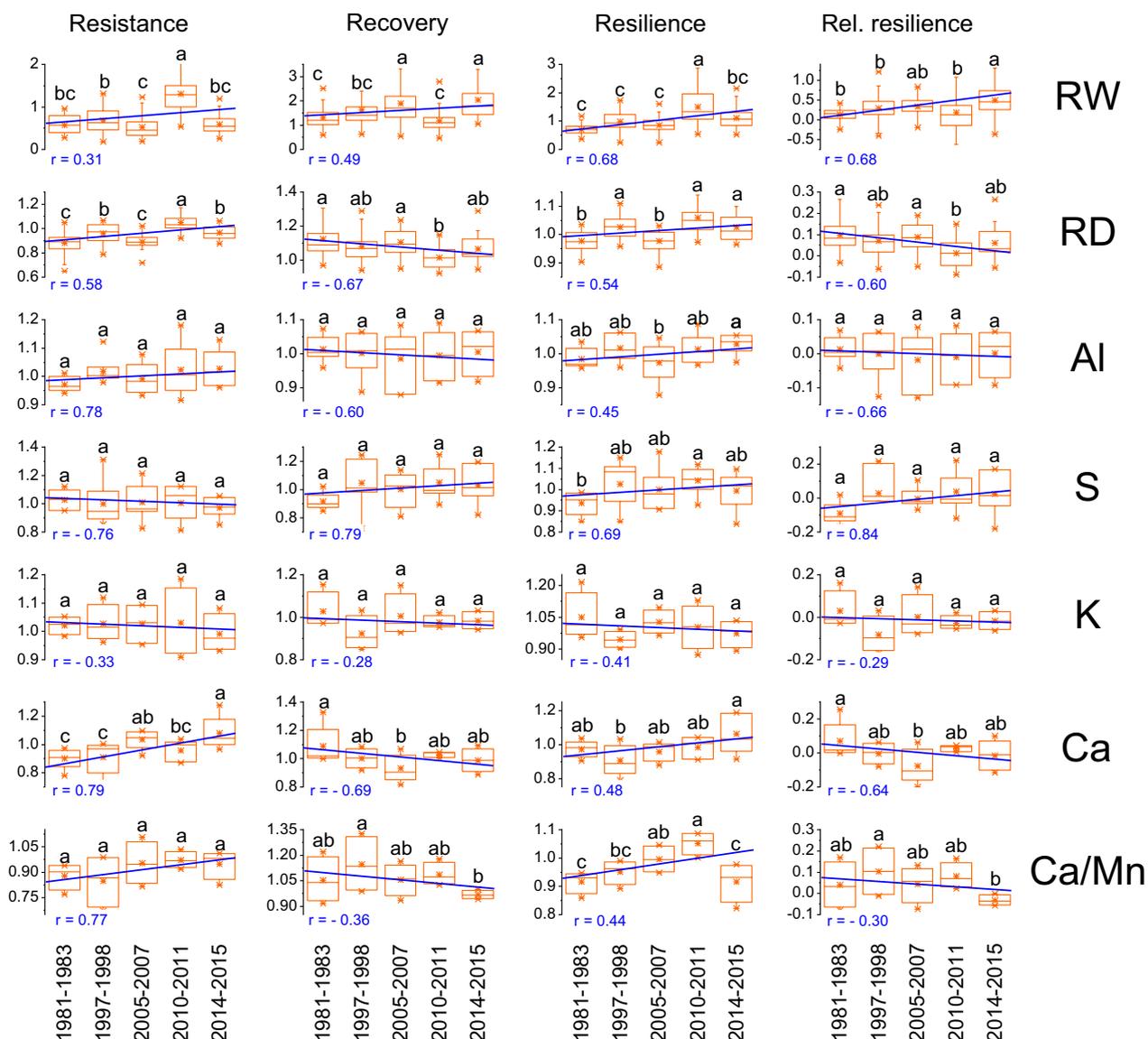


Fig. 5 Boxplots showing standardized ring width (RW), wood density (RD), concentrations of aluminum (Al), sulfur (S), potassium (K), calcium (Ca) and calcium to manganese ratio (Ca/Mn) stability during extreme droughts from *C. fissilis* trees from the southern Amazon. Different letters indicate significant differences ($p < 0.05$) between droughts. In the box plots, the boundary indicates the 25th percentile, a solid line within the box marks the median, an asterisk 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. Blue lines show the relations between tree-ring parameters and years of extreme droughts, and Pearson's correlation coefficient is presented at the bottom. Extreme drought events in 1981–1983, 1997–1998, 2005–2007, 2010–2011, and 2014–2015 in the southern Amazon basin were selected (Espinoza et al. 2019)

resilience (together with S- and Ca/Mn-resilience) were observed in the 2010–2011 drought. The lowest growth resistance was registered in the 2005–2007 drought, while the lowest wood density resistance and the lowest growth and wood density resilience (together with S- and Ca/Mn-resilience) were registered in the 1981–1983 drought (Fig. 5, Additional file 1: Figs. S3, S4).

Growth (similar to S, Mn, Sr) recovery and relative resilience increased with time, unlike wood density (similar to Al, K, Ca, P, Fe, Ca/Mn, Al/Ca, K/Ca, Sr/Ca and Mn/S) recovery and relative resilience which decreased (Fig. 5, Additional file 1: Figs. S3, S4). The recovery and relative resilience of growth and wood density presented significant negative correlations with the recovery and

the relative resilience explained by the P concentration and Sr concentration, respectively (Additional file 1: Fig. S5). A significant positive correlation was observed between the recovery of S and Mn and K and Sr/Ca and the relative resilience of S and Mn. A significant negative correlation was observed between recovery and the relative resilience of S and K/Ca, S and Sr/Ca, Mn and Al/Ca and Mn and K/Ca (Additional file 1: Fig. S5). The highest growth recovery and relative resilience were observed in the 2014–2015 drought, while the lowest growth recovery (together with Sr-recovery) and relative resilience (together with Sr-relative resilience) were observed in the 1981–1983 drought. The highest wood density recovery (together with Ca-, Al/Ca- and K/Ca-recovery) and relative resilience (together with Ca-, Al/Ca- and K/Ca-relative resilience) were observed in the 1981–1983 drought, while the lowest wood density recovery (together with K/Ca-recovery) and relative resilience (together with K/Ca-relative resilience) were observed in the 2010–2011 drought (Fig. 5, Additional file 1: Figs. S3, S4).

Discussion

Growth and nutrient changes

Significant long- and short-term growth and nutrient imbalances of *C. fissilis* were observed, linked to the increased frequency of dry years in recent decades (Figs. 2, 3, Additional file 1: Figs. S1, S2). The alterations in the soil water regime and nutrient bioavailability linked to hydroclimate trend alterations cause a reduction in the physiological responses of trees, inhibit photosynthesis and alter carbohydrate and amino acid metabolism (Gavrilescu 2021; Malhi et al. 2021). These physiological and metabolic alterations reduce tree productivity (in most cases) (Schlesinger et al. 2016) and produce a long-term trade-off between growth and wood density (Bergès et al. 2000; Bouriaud et al. 2004; Bontemps et al. 2013; Vannoppen et al. 2018), as was observed for *C. fissilis*, which presented density increases ($r=0.70$, $p<0.05$) and growth decreases ($r=-0.35$, $p<0.05$) since 1940 (Fig. 2, Ortega Rodriguez et al. 2023a).

The decrease in *C. fissilis* growth over time has been previously reported in trees from forests with marked climatic seasonality that suffer a historical increase in extreme drought (Feeley et al. 2007; Mendivelso et al. 2014, 2016; Islam et al. 2019). The severity of these droughts is related to an increase in the intensity of the dry season and a delay in the onset of the rainy season in the southern Amazon region (Marengo et al. 2018; Espinoza et al. 2019). This region also shows a significant negative trend in SPEI values ($r=-0.65$, $p<0.01$), P-PET values ($r=-0.39$, $p<0.05$), and precipitation ($r=-0.28$, $p<0.05$) and a significant positive trend in temperature since 1970 ($r=0.85$, $p<0.001$) (Additional file 1: Fig. S1),

which reinforces the idea of changes in the water regime in recent decades.

Regarding the wood density trends, *C. fissilis* is a deciduous long-lived pioneer species (Peña-Claros et al. 2008), and its radial wood density gradient is expected to increase in mature stages of development to generate stem stability (Nock et al. 2009). This explanation could satisfy the 5.62% gradual increase in wood density of *C. fissilis* trees in the JNF between 1940 and 1999 (Fig. 2). However, between 2000 and 2018 (sapwood region), the trend of wood density began to increase gradually by 14.11%, coinciding with the increase in the frequency of dry years. The sapwood region of *C. fissilis* presents lower wood density values due to the higher number of empty spaces (active vessels) through which water is transported (Mendivelso et al. 2013). However, positive associations between the increase of drought events and the wood density of the species have been observed in recent decades (Mendivelso et al. 2016; Ortega Rodriguez et al. 2023b). Another possible explanation for this positive wood density trend over time could be linked to atmospheric CO₂ increases (NOAA 2021); however, there is insufficient evidence that this relationship is cause and effect for all angiosperms (Yazaki et al. 2005; Arsić et al. 2021).

Contrary to our expectations, we did not observe an increase over time in the Ca xylem concentration trend (or analogous elements, such as Sr or Mn) despite the wood density (Ortega Rodriguez et al. 2022) or local temperature increase (Sánchez-Salguero et al. 2019). Even mobile elements such as P, K, and S were expected to increase in the sapwood and close to the bark of *C. fissilis* trees (Ortega Rodriguez et al. 2022) due to strong symplastic transport (through plasmodesmata) in cambial regions of active growth (Smith et al. 2014; Hietz et al. 2015). P, K, and S presented a decreasing trend in their concentrations associated with growth decrease in the pith to bark direction (Fig. 1A, B). Our results suggest that alterations in the local water regime directly influenced all nutrient concentrations in the xylem tissues, mainly since 1980 ($p<0.05$: Ca, $r=-0.49$; K, $r=-0.84$; P, $r=-0.64$; Mn, $r=-0.81$; S, $r=-0.88$; Sr, $r=-0.78$, Al, $r=-0.54$, and $p<0.10$: Fe, $r=-0.12$). When soil water reserves decline during prolonged drought, microbial activity is inhibited, and diffuse and mass flow uptake between roots and soil decreases; likewise, the total water potential gradient between root, xylem, and leaf cells results in lower nutrient concentrations in tree tissues (He and Dijkstra 2014; Schlesinger et al. 2016; Gessler et al. 2017; Gavrilescu 2021).

Regarding element ratios, drought may also modify cross-talk between nutrients (uptake and storage) and hence modify leaf demands with potential consequences

in storage organs (Etienne et al. 2018). The Ca/Mn increases and Al/Ca decreases over time suggesting a decrease in soil acidity and an increase in the effective rates of cation mobilization (e.g., Ca, Mg, Fe, Mn and Zn) (Kogelmann and Sharpe 2006; Kuang et al. 2008). Increases in temperature and droughts are associated with increased pH in arid soils (Jiao et al. 2016), and possibly in acid soils. This facilitates the acropetal mobility of cations through the xylem, which is fast in Ca and slow in Mn (Etienne et al. 2018) and Al (Shen and Ma 2001). However, with extreme droughts, a deficit in water plus nutrient (soil solution) flow is generated, which appears first in the new leaves, inducing their senescence and remobilizing the nutrients from the senescent organs to the reserve organs (Etienne et al. 2018). In this process, Ca (available above pH 6.5) is not affected as much as Mn (Etienne et al. 2018) and Al (both available below pH 5.5), so its proportion will be higher in the respective ratios of xylem tissues.

An increase in Mn/S was also observed with time. Although the improvement in soil pH (with increases in temperature and drought) suggests improvements in S-soil availability (Etienne et al. 2018), the water deficit caused by this same stress decreases the basipetal leaf-xylem S mobility and xylem storage (Ihsan et al. 2019). These cellular spaces left by S could be occupied by Mn when acropetal mobility occurs and could generate toxicity due to the decrease in water-soluble nonprotein thiols (-SH, functional group), which become defense mechanisms when cellular Mn concentrations increase (Neves et al. 2017). This has been studied in Mn phytotoxicity experiments, although neither the water deficit nor the temperature were controlled (Neves et al. 2017).

Contrary to what we expected, the K/Ca and Sr/Ca ratios presented an opposite trend to density over time (Fig. 2). According to Fromm (2010), in situations of a low K regime (frequent dry periods), the secondary cell walls begin their formation earlier (fibrillary phase), apparently forming a cell wall with greater volume; in contrast, the process of cell division and formation of the primary cell wall (amorphous phase) decreases. Furthermore, according to Silkin and Ekimova (2012), Ca distributed in the primary cell wall and the middle lamella is proportional to the cell cross-sectional area, while Sr uniformly distributed along the cell wall is proportional to the cell wall cross-sectional area. Thus, the historical increase in density was expected to imply an increase in the K/Ca and Sr/Ca ratios. However, it is possible that, similar to Mn and Al cations, K and Sr fluxes in the tree are also affected more than Ca under water deficit. Acropetal and basipetal mobility (both in the xylem and phloem) of K (Carvalho et al. 2005) imply their frequent distribution from older to younger tissues, and their re-translocation

to permanent organs. Furthermore, K and Ca reduce Sr uptake (Isermann 1981) in acropetal motility pathways (Feller et al. 2015). With water deficit, deficient Sr (Østmoen 2020) and K (Armstrong and Kirkby 1979) mobility occurs in the phloem, so its reallocation toward the xylem and the root will be less, while Ca is not affected.

During dry years (negative values of P-PET) of the period 1970–2018, *C. fissilis* showed narrower (RW) and less dense (RD) rings, lower Al, S, Ca ($p < 0.05$) and P ($p < 0.10$), and higher K ($p < 0.10$) concentrations (the opposite was found in wet years) (Figs. 1D, 3). The positive relationship between dry years and narrower rings has been previously reported for *Cedrela* species (Villalba et al. 1992; Dünisch et al. 2003; Dünisch 2005; Lobão 2011; Pereyra Espinoza et al. 2014; Paredes-Villanueva et al. 2016; Granato-Souza et al. 2018b, a; Pereira et al. 2018; Lisi et al. 2020; Humanes-Fuente et al. 2020; Rodríguez-Ramírez et al. 2022). The positive tree-ring width-wood density relationship of *C. fissilis* was also observed in other semiring porosity tree species in both tropical (Quintilhan et al. 2021) and temperate forests (Bergès et al. 2000; Toigo et al. 2015; Vannoppen et al. 2018). The ring early- and latewood widths and their respective densities in *C. fissilis* also presented positive relationships (Ortega Rodriguez et al. 2023b).

The positive relationship between the ring width and density of *C. fissilis* suggests that the species quickly stops or strongly limits its radial growth together with the cessation of the wood densification process as soon as a soil water deficit occurs (Bouriaud et al. 2004). This compromises the hydraulic safety (risk of cavitation or embolism) of *C. fissilis*, whose 52% of the ring width (earlywood) is formed mainly by the combination of large vessels and marginal parenchyma (Ortega Rodriguez et al. 2023b). In extremely dry situations, the species can buffer its vulnerability to cavitation by losing foliage (Mendivelso et al. 2016), developing vessels with smaller diameter size (Islam et al. 2019; Rodríguez-Ramírez et al. 2022) as a strategy to resist water flow, which reduces the amount of water lost through transpiration. However, as already observed by Rodríguez-Ramírez et al. (2022), this strategy may be compromised by the poor hydraulic adjustment of the species due to the predominance of large vessels.

In dry tropical tree taxa (such as *Cedrela*), only wood mass invested in fiber walls contributes to hydraulic security (Janssen et al. 2019). This invested mass in cell wall thickening can result in decreased cell division and enlargement (Bouriaud et al. 2004). Fiber wall thickening may help surrounding vessels resist partial implosion and prevent stretching or rupture of pit membranes and microfractures in vessel walls, thereby reducing the risk of embolism (Jacobsen et al. 2005). The thickening

of fiber walls and the decrease in cell division may be related to the higher K and lower Ca concentrations in dry years, respectively. K has been shown to be a mandatory factor for the cell wall thickening of xylem cells in trees (Wind et al. 2004; Fromm 2010). High levels of K favor the osmotic potential of the cambium, widening it and increasing the fiber and vessel size in the xylem (Fromm 2010). The vessel-associated radial (and possibly axial) parenchyma plays an important role in K recycling within the stem (Fromm 2010) and facilitates K flux through the plasma membrane H^+ -ATPase into the vessels (Arend et al. 2004). On the other hand, Ca is mainly deposited in the apoplast, where it binds to various cell wall sites, offering rigidity to developing cell walls in the course of xylem differentiation (Lautner and Fromm 2010). Ca deficiency in the xylem not only causes a decrease in cambium activation and cell differentiation (Follet-Gueye et al. 1998; Lautner and Fromm 2010) but also decreases lignification and the crosslinking of carboxyl groups within the pectin layer, decreasing the hardness and elasticity of the wood (Wimmer and Lucas 1997).

Narrow rings of dry years also showed lower concentrations of macronutrients, such as P and S, and Al, which is not considered an essential element. P plays a role in photosynthetic, respiratory, nutrient synthesis, and plant growth processes (Vance et al. 2003). In some Amazonian Ultisols and Oxisols, symbiotic activity between roots and mycorrhizae increases P availability by making more P available than is fixed by iron and aluminum oxides (Alexander 1989; Hu and Schmidhalter 2005; Quesada and Lloyd 2016). However, under dry soil conditions, mycorrhizal activity decreases, decreasing the P uptake of trees (Hu and Schmidhalter 2005). By decreasing the water flow and P, the meristematic activity decreases, interrupting the formation of young leaves and apical and cambial growth (Kurita et al. 2022). Low P availability can also alter the re-translocation of the element from the meristematic regions to the phloem and xylem parenchyma cells in the senesce period (Kurita et al. 2022).

S plays a role in plant growth, development processes and redox regulation, as it is a component of amino acids (e.g., methionine, cystine and cysteine) in proteins (Herschbach and Rennenberg 2001; Abrol and Ahmad 2003; Fairchild et al. 2009). It is also a component of metabolites (e.g., glutathione and phytochelatin), cofactors of modulating enzymes of effective defense mechanisms to encounter plant stress (Khan et al. 2014; Ihsan et al. 2019). Trees acquire the required S mainly through the uptake of sulfate by nonmycorrhizal and mycorrhizal roots and some amount from sulfur dioxide in the atmosphere by photosynthetically active tissues (stomata)

of mature leaves (Herschbach and Rennenberg 2001). Drought stress causes a decrease in S uptake by roots and its allocation to leaves (Herschbach and Rennenberg 2001; Abrol and Ahmad 2003). The leaf loss of *C. fissilis* as a strategy to overcome water stress (Mendivelso et al. 2016) decreases the leaf production of reduced S and simultaneously decreases its storage in the parenchyma cells of the phloem and xylem, as well as ray and pit cells (Herschbach and Rennenberg 2001).

Although Al is highly rhizotoxic and is a major stress factor to plants on acid tropical soils, many native trees are well-adapted to high Al conditions (Brunner and Sperisen 2013). Al-oxalate processed in root cells is converted to Al-citrate in the xylem and translocated to leaf cells for reconversion to Al-oxalate (Shen and Ma 2001). Al is mainly stored in the cell wall of the leaves and roots (Brunner and Sperisen 2013). The uptake of water and nutrients by plants under stress conditions (e.g., drought, high temperatures, salinity and nutrient deficiency) increases due to a greater root surface area induced by Al (Bojórquez-Quintal et al. 2017). Drought stress changes the porosity of the cell wall structure (reduce the space between cellulose, xyloglucan, pectin and structure protein) of roots and reduces the accumulation of Al and its effect on plants (Bojórquez-Quintal et al. 2017).

Climate–growth–nutrient relationships

Our results showed that the radial wood formation (RW, significant positive correlation in March) and wood density levels (RD, significant positive correlation between March and May) of *C. fissilis* starts at the beginning of the rainy season in September/October and is completed at the end of the rainy season in April/May, similar to other *Cedrela species* in the southern Amazon region (Dünisch et al. 2003; Brienen and Zuidema 2005; Lobão 2011). Furthermore, when *C. fissilis* begins to produce the marginal parenchyma between the end of the dry season and the beginning of the rainy season (Marcati et al. 2006), the initial promoter of root and shoot activity will be Al (mainly in September) (Ka et al. 2008; Bojórquez-Quintal et al. 2017), inducing the absorption of nutrients, such as P (Tomioka et al. 2005), Mg (Bose et al. 2013) K and Ca (Bojórquez-Quintal et al. 2014). Then, the formation of large vessels of the earlywood together with or even before the flushing of new leaves (Lobão 2011) will generate conductive pathways for the acropetal mobility of S, Ca and P (mainly in October, November and January, respectively) through the sap flux between the roots and the new leaves in the months of low evapotranspiration in the rainy season (McElrone et al. 2013). The phosphate and sulfate transport systems initiate coordinated operations for the physiological functioning of the tree

(Smith 2001), promoting the formation of young xylem cells (Peterson and Anderson 1990) and defining its cellular architecture (Fairchild et al. 2009), respectively. Furthermore, Ca stimulates cambial reactivation and cell division at the beginning of the growing season, between September and November (Lautner and Fromm 2010).

Low evapotranspiration in the rainy season will also positively affect Sr storage (mainly in March), a nonessential element analogous to Ca (Burger and Lichtscheidl 2019) while negatively affecting the xylem storage of Mn and Fe (mainly in February and October, respectively). Mn and Fe, elements with low mobility, are mainly used in the leaf for respiratory processes (Glavac et al. 1990; Morrissey and Guerinot 2009) and, as in the case of Mn, can increase their levels in the xylem sap immediately before and after leaf emergence (Glavac et al. 1990). The months of low evapotranspiration in the rainy season also negatively affect the K concentrations and K/Ca (mainly between March and May). This apparently happens, because under normal conditions of water availability, *C. fissilis* prioritizes cambial activity based on cell division and vessel enlargement (positive relationship with Ca) and not thickening of the cell wall (negative relationship with K) (Fromm 2010).

The rainfall and low evapotranspiration during the dry period (between June and August) also influenced the Al, P and S storage. This can reinforce the idea of the high stimulation for nutrient uptake of roots by Al (Bojórquez-Quintal et al. 2017), as well as the activity of P and S in the transport systems and nutrient redistribution in the tree (Smith 2001). Furthermore, this positive relationship of P and S concentrations with precipitation in the dry period suggests that when the demand for these nutrients decreases in the young leaves, P (Kurita et al. 2022) and S (Hartmann et al. 2000; Herschbach and Rennenberg 2001) are re-translocated (basipetal mobility) to xylem storage tissues (marginal parenchyma, Ortega Rodriguez et al. 2022) to be used in the following growing season when sap flux increases again.

Our study also reported a strong negative association between P and S records and temperature during the wet seasons (mainly between January and April) and during June and July of the dry season (Fig. 4). It is possible that with high temperatures, there is an increase in S translocation from the xylem to the growing parts of the shoot and discharge on the leaves to play a defense function against heat stress (Herschbach and Rennenberg 2001; Ihsan et al. 2019). S in its glutathione (GSH) form is triggered by heat and drought stress and, upon oxidation, maintains optimal biochemical and redox cellular functions within plant cells (Ihsan et al. 2019). Regarding P, the leaves and young shoots are its main sink (Kavka and Polle 2016), and its xylem concentration is more affected

than S by seasonal activity (Barrelet et al. 2006). During warmer temperatures, tree transpiration increases (Will et al. 2013), suggesting an acceleration in P plus water flux toward the tree apex (Kurita et al. 2022), decreasing xylem P storage. Under these conditions, the regulation of P transport will depend on the species adaptations of vascular structures (Raghothama 1999; Lin et al. 2014; Zavišić and Polle 2018).

Growth–nutrient resilience under extreme droughts

C. fissilis showed an increase in growth and wood density resistance and resilience over time (from 1981–1983 to 2014–2015 droughts) (Fig. 5) as a consequence of the delayed onset of the rainy season that increased the water deficit in the southern Amazon region (Marengo et al. 2018). The increase over time in the capacity of *C. fissilis* trees to absorb drought stress and continue growing during the dry years (resistance) was also associated with increases in resistance explained by the concentrations of Al, Ca, P, Ca/Mn and Mn/S and decreases in S, K, Mn, Fe, Sr, Al/Ca, K/Ca and Sr/Ca (Fig. 5, Additional file 1: Figs. S3, S4, S5). In the context of decreased soil acidity conditions (Ca/Mn increases and Al/Ca decreases), *C. fissilis* trees have an adaptation strategy improving their root system, potentiated by Al uptake, which facilitates the elongation of roots and proliferation of lateral roots both in the short and long term (Ghanati et al. 2005; Bojórquez-Quintal et al. 2017). The increases over time in the resistance associated with P and Ca uptake reinforce the idea of a cambial activity process prioritizing vascular regulation (Lautner and Fromm 2010) developing a greater number of smaller vessels (Rodríguez-Ramírez et al. 2022) and probably more elongated vessels (Scholz et al. 2013), which are necessary for the flow of phosphates that regulate carboxylation in photosynthesis (Raaimakers et al. 1995). Furthermore, the decreases over time in resistance associated with K uptake and K/Ca ratios reinforce the species' initial strategy of prioritizing the formation of many small vessels to the detriment of thickening its cell wall. On the other hand, elements related to the physiological activities of the leaf, such as S, which is involved in defense against heat stress (Ihsan et al. 2019), and Fe and Mn, which are involved in the respiration process (Glavac et al. 1990; Morrissey and Guerinot 2009), decrease over time. This may be associated with the leaf loss strategy of *C. fissilis* (Mendivelso et al. 2016).

Our results also showed that the recovery process in growth over time increases (associated with the recovery capacity explained by S, Mn and Sr) and the wood density decreases (associated with the recovery capacity explained by Al, K, Ca, P, Fe, Ca/Mn, Al/Ca, K/Ca, Sr/Ca, Mn/S). The increase over time in the capacity of trees

to recover in terms of growth rates and wood density observed before the drought event (resilience) was also associated with increases in resilience explained by Al, S, Ca, Mn, Sr and Ca/Mn and decreases in K, P, Fe, Al/Ca, K/Ca, Sr/Ca and Mn/S (Figs. 5, Additional file 1: Figs. S3, S4, S5). This suggests that for recovery processes over time, both growth and density, requires sources of S. As previously mentioned, S seems to be one of the essential elements in containing the stress caused by dry conditions (Ihsan et al. 2019), and its storage and re-translocation to the regions of meristematic activity will guarantee the resumption of physiological processes toward normal conditions (Herschbach and Rennenberg 2001; Fairchild et al. 2009; Ihsan et al. 2019). However, there is a risk that the species will not return to the density values prior to drought, which is associated with a deficit in the functions performed by key elements in promoting tree nutrition such as Al (Bojórquez-Quintal et al. 2017), cambial activity such as K and Ca (Fromm 2010) and xylem cell formation such as P (Peterson and Anderson 1990) and Fe (Morrissey and Guerinot 2009). This risk may be even more serious, because *C. fissilis* records the effects of drought stress up to 24 months after the extreme event, making the species demand accelerated compensation strategies between growth and wood density (Tao et al. 2022; Ortega Rodriguez et al. 2023b).

Conclusions

The eco-nutritional evidence obtained in this study showed that *C. fissilis* is undergoing alterations in the concentration, use and redistribution of nutrients associated with the wood density increase and growth decrease over time. This is due to the decrease in the water availability generated by the increase in the frequency of drought spells in the southern Amazon. Alterations in the concentration of nutrients in the xylem pointed to adaptations in (i) the roots due to a decrease in acidity of soil and water flow (e.g., Al, Ca/Mn and Al/Ca); (ii) cambial activity and vascular regulation as part of the ring-width and density trade-off (Ca, K, P, S, Sr, K/Ca and Sr/Ca); (iii) the formation, function and senescence of shoots and leaves as part of the first response to tree stress (S, Fe, Mn and Mn/S). The species presents a tendency to increase its capacity for resistance, recovery and resilience in growth over time, associated with responses in the capacity to use Al (growth promoter and root function), Ca, P (xylematic growth activators) and S (essential for the reduction of drought stress). However, there is a risk in the capacity for recovery of the normal pre-drought density values, associated with unsatisfactory responses in the capacity to use Al (promoter of tree nutrition), Ca, K (essential for cambial activity and cell wall structure), Fe and P (essential in the formation

and architecture of the xylem cells). This study is one of the first attempts to clarify aspects of climate sensitivity and drought resilience from a nutritional approach based on long-term annual data obtained by dendrochemical techniques in Amazon dry seasonal moist forests. Future works should relate the chemical traces in the xylem with the proportion of anatomical elements, hydraulic adjustments and vulnerability of the vessels to verify the nutritional demands related to the plasticity of anatomical wood traits of *C. fissilis*.

Abbreviations

AC	First-order autocorrelation
cps	Counts per second
DBH	Diameter at breast height
EPS	Expressed population signal
GSH	Glutathione
H	Tree height
JNF	Jamari National Forest
MS	Mean sensitivity
P-PET	Difference between precipitation and potential evapotranspiration
PCA	Principal component analysis
RW	Ring width
RD	Ring density
SG	Specific gravity
SPEI	Standardized precipitation–evapotranspiration index
μXRF	X-ray fluorescence micro-analysis

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13717-023-00472-7>.

Additional file 1: Fig. S1. **a** Map showing the location of Jamari National Forest, JNF (red triangle), *Cedrela fissilis* Vell. distribution (dark gray dots) and Amazon soil classification according to the Brazilian Soil Classification System (EMBRAPA 2006). Soils according to Soil taxonomy (Soil Survey Staff 2022): Ultisols (Argisols), Inceptisols (Cambisols), Entisols (Neosols, Gleysols), Oxisols (Latosols), Histosols (Organosols), Alfisols (Luvisols, Plinthosols), Spodosols (Spodosols). **b** Climate diagram of Walter and Lieth, based on regional meteorological and hydrological records from 1975 to 2018 (data source in Table S1), indicates dry months (solid orange area) and months with rainfall above 50 mm (solid blue areas). Green bars represent the estimated growing period of *C. fissilis*, which generally falls between September (previous year) and the end of May (current year) according to Lobão (2011). Phenology stages are represented by leaf icons based on *C. fissilis* data from Lobão (2011): open, gray filled and dark filled indicate periods of leaf fall, leaf flash and leaf fall/leaf flash (occurring simultaneously), respectively. **c** Anomalies (standardized values) of total annual precipitation, mean annual temperature, total annual difference between precipitation and potential evapotranspiration (P-PET) and total annual standardized precipitation evapotranspiration index (SPEI). **Fig. S2.** Mean index residual chronologies of molar ratios from *C. fissilis* trees from the southern Amazon and total annual difference between precipitation and potential evapotranspiration (P-PET, time-scales from prior September to current September). Vertical light red boxes represent extreme drought events registered in the southern Amazon basin in 1981–1983, 1997–1998, 2005–2007, 2010–2011, and 2014–2015 (Espinoza et al. 2019). On the right is the boxplot of normalized parameters in dry and wet years; a significant difference (SD) between means is also presented ($p < 0.05$). **Fig. S3.** Boxplots showing standardized ring width (RW), wood density (RD), concentrations of aluminum (Al), sulfur (S), potassium (K), calcium (Ca) and calcium to manganese ratio (Ca/Mn) stability during extreme droughts from *C. fissilis* trees from the southern Amazon. **Fig. S4.** Boxplots showing standardized ring width (RW), wood density (RD), concentrations

of aluminum (Al), sulfur (S), potassium (K), calcium (Ca) and calcium to manganese ratio (Ca/Mn) stability during extreme droughts from *C. fissilis* trees from the southern Amazon. **Fig. S5.** Pearson's correlation of stability of tree-ring parameters: width (RW), wood density (RD), elements (aluminum, Al; phosphorus, P; sulfur, S; potassium, K; calcium, Ca; manganese, Mn; iron, Fe; strontium, Sr) and ratios (aluminum to calcium, Al/Ca; calcium to manganese, Ca/Mn; potassium to calcium, K/Ca; strontium to calcium, Sr/Ca; manganese to sulfur, Mn/S) of *C. fissilis*. Statistical significance of Pearson's correlation: * $p < 0.05$. **Table S1.** Information from meteorological stations for collected precipitation (P, 1975–2018) and temperature (T, 1957–2018) data.

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Author contributions

Conceptualization: DROR, RSS, FAR, MTF. Methodology: DROR, RSS, AH. Resources: RSS, AH, MTF. Sample collection and preparation: DROR. Sample analysis: DROR, RSS, AH, FAR. Data analysis: DROR, RSS, AH. Writing: DROR, RSS, AH, FAR, RCB, MJF, JHS, MTF. Reviewing: DROR, RSS, AH, FAR, RCB, MJF, JHS, MTF. Editing: DROR, FAR, JHS. Supervision: RSS, AH, FAR, MTF.

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Availability of data and materials

The data from this article will be incorporated into the ITRDB BRA015 (<https://www.ncei.noaa.gov/access/paleo-search/study/37447>) as a complement to the chronologies already registered. Analysis data will be available on request. Supplementary material to this article can be found in Additional file 1.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential competing interests.

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