Dendrochronological potential of four neotropical dry-forest tree species: Climate-growth correlations in northeast Brazil

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ABSTRACT

Tropical dry forests (TDF) are highly important tropical forest ecosystems. Yet, these forests are highly threatened, usually neglected and only poorly studied. Understanding the long-term influences of environmental conditions on tree growth in these forests is crucial to understand the functioning, carbon dynamics and potential responses to future climate change of these forests. Dendrochronology can be used as a tool to provide these insights but has only scantly been applied in (dry) tropical forests. Here we evaluate the dendrochronological potential of four Caatinga neotropical dry forest tree species – *Aspidosperma pyrifolium*, *Ziziphus joazeiro*, *Tabebuia aurea*, and *Libidibia ferrea* – collected in two locations in northeastern Brazil (Sergipe state). We provide an anatomical characterization of the ring boundaries for the four species and investigate correlations of their growth with local and regional climatic variables. All four species form annual rings and show high intercorrelation (up to 0.806) and sensitivity (up to 0.565). Growth of all species correlated with local precipitation as well as with sea-surface temperatures in the tropical Atlantic and/or tropical Pacific oceans. We also show teleconnections between growth and the El Niño South Oscillation. The strong dependence of tree on precipitation is worrisome, considering that climate change scenarios forecast increased drought conditions in the Caatinga dry forest. Including more species and expanding dendrochronological studies to more areas would greatly improve our understanding of tree growth and functioning in TDFs. This type of knowledge is essential to assist the conservation, management and restoration of these critical tropical ecosystems.

1. Introduction

While covering only 7% of the global terrestrial surface, tropical forests are key parts of the global carbon cycle, accounting for about 50% of primary productivity and 30% of global carbon drainage (Pan et al., 2011). Among tropical forests, tropical dry forests (TDF) are highly important – representing as much as 42% of all tropical forest ecosystems (Murphy and Lugo, 1986) – but are usually neglected and poorly studied (Dexter et al., 2018). These forests are also among the most vulnerable to anthropic pressures, on the one hand because approximately one-third of the world's population lives in them and depends directly on their resources (Albuquerque et al., 2012; Banda-R et al., 2016), on the other because these forests are highly vulnerable to climatic changes (Pennington et al., 2018). TDFs are also one of the main drivers of inter-annual variation in simulation studies of tropical forest carbon sink (Poulter et al., 2014), while being poorly represented in these models (Sitch et al., 2003). Studies aimed at understanding the long-term influences of environmental conditions on tree growth (Brienen et al., 2010b) would greatly benefit our understanding of TDFs functioning and carbon dynamics.

Dendrochronology, the analysis of tree rings, can be used to reconstruct long-term growth variability of tropical tree species (Brienen et al., 2016), and assess the correlations of growth with local climate (Vlam et al., 2014), teleconnections with sea-surface temperatures (Brienen et al., 2010a; Patskoski et al., 2015), as well as with global climatic phenomena such as the El Nino Southern Oscilation (ENSO, Schongart et al., 2006). Additionally, and in combination with other analyses, such as cambial wounding, xylogenesis, modelling and stable isotopes, tree rings have been applied in the tropics to evaluate periodic tree growth cycles (Trouet et al., 2012; Mendivelso et al., 2016b), to simulate carbon allocation trade-offs in trees (Schippers et al., 2015), assess growth and physiological changes due to elevated atmospheric CO_2 levels (van der Sleen et al., 2014), as an aid for forest management (Schöngart, 2008; Groenendijk et al., 2017) and to understand growth

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adaptations to extreme dry conditions (Mendivelso et al., 2013, 2016b; Wagner et al., 2016). Although being increasingly applied in tropical regions (Brienen et al., 2016; Schöngart et al., 2017), and being an important tool to understand long-term environmental change effects on tropical forest growth, physiology and dynamics (Zuidema et al., 2013, 2018), dendrochronological studies in TDFs are still scarce (Mendivelso et al., 2016a; Brienen et al., 2016), especially in the neotropics.

In tropical dry regions, rainfall is scarce and seasonal and temperature are high most of the year (Bullock, 1995). Intra-annual variation in ring-width of tropical species is often related to local climatic conditions, as well as with global-scale climatic events such as the El Niño Southern Oscillation (Schongart et al., 2006; Pagotto et al., 2015). The limiting climatic conditions for tree growth in TDFs are registered in the inter-annual variation of ring width and dendrochronological studies have been efficient and accurate in analyzing correlations between tree growth and environmental conditions (Jiménez, 2011; Roig et al., 2009). These studies were made in TDFs from Africa (Therrell et al., 2007; Trouet et al., 2012; Tolera et al., 2013; Gebrekirstos et al., 2014), Asia (Vlam et al., 2014; Rahman et al., 2017), South America (Brienen et al., 2009, 2010a; Lebrija-Trejos et al., 2011; López and Villalba, 2016; Mendivelso et al., 2016a, 2016b). Although some studies exist in Brazilian tropical dry forests (Pagotto et al., 2015; Nogueira et al., 2017; Pereira et al., 2018), only a small number of species have been analyzed and it is paramount to increase this number considering the importance of these forests (Albuquerque et al., 2012).

Here we present an evaluation of the dendrochronological potential of four Caatinga dry forest tree species from two locations in northeastern Brazil (Sergipe state). For this purpose, we performed an anatomical characterization of the wood and ring boundaries for these species and assessed the relations of their growth with local and regional climatic variables. Specifically, we addressed the following questions: (i) what are the anatomical characteristics of the tree-ring boundaries for the four studied species? (ii) is tree growth correlated with precipitation from local meteorological stations? (iii) Is tree growth correlated with sea surface temperatures of the Atlantic and with the El Nino Southern Oscillation?

We addressed these questions using four species, from four different botanical families, which vary in leaf phenology and growth strategies. We described the anatomical structures that delimit annual rings in these species. Measured and synchronized radial growth series, and computed relationships of growth with local (precipitation), and large-scale (sea surface temperatures, and ENSO index) environmental variables. Finally, we compare our results with other tropical (dry) forest studies and discuss possible future climate change effects on these forests.

2. Material and methods

2.1. Study area

We sampled trees in two sites located in the Caatinga tropical dry forest in the northeast of Brazil, in the state of Sergipe. The Caatinga is Brazil´s most important dry forest. It covers a large geographic area (~850.000 Km^2), encompassing most of Northeastern Brazil, harbors a variety of vegetation types (Moro et al., 2016), and is home to ~4500 plant species, of which 812 are endemic (Siqueira Filho et al., 2012). Site 1 was the conservation unit Grota do Angico Natural Monument (9°39′ S, 37°40′W), a 2183 ha conservation area located on the margins of the São Francisco River in the municipalities of Canindé do São Francisco and Poço Redondo, about 200 km from the state capital Aracaju (Fig. 1) (Ferraz et al., 2013; Silva et al., 2013; SEMARH et al., 2016). Site 2 was located in the São Pedro farm (10°02′S, 37°25′W), in the municipality of Porto da Folha. This site consists of a TDF remnant with preserved shrubby–arboreal vegetation (Oliveira et al., 2013) (Fig. 1). Both municipalities have a registered high degree of

deforestation (Cintra et al., 1990; Bomfim et al., 2002; Jungles et al., 2011; SEMARH et al., 2016), and have suffered many severe drought events in the past (Jungles et al., 2011; Santos et al., 2014a, 2014b).

The climate of the region is hot and semi-arid, the rains concentrated between April and July, and a dry season from August to December (Fig. 1; Köppen, 1948). In the January–March quarter, heavy rains can occur but are usually concentrated over a few days and small areas (Bernardes, 1999). We used precipitation data from two local weather stations close to our study sites: the first located ~15 km from site 1, in the Poço Redondo municipality, and the second ~13 km from site 2 in Porto da Folha (Fig. 1). It is important to ensure the quality of the meteorological data being used (Clark and Clark, 2011). We found that total annual precipitation correlates between the two stations as well as with interpolated regional precipitation and sea surface temperature data (more details in Appendix Fig. 1), suggesting data are consistent and of good quality. Total annual precipitation ranged from 380 to 760 mm for site 1 and from 300 to 700 mm for site 2 (in in both cases for the period 1964–2015). The average annual air temperature varied between 18 and 25 °C (over the period 2010–2015), and the annual evapotranspiration is greater than the annual precipitation in both sites (Fig. 1). The soils in site 1 consisted of luvisols and neosolslithols (cf. Santos, 2013), while in site 2, litholic, eutrophic, and bruno-non-calcic regosols predominate.

2.2. Selected species

Four species were selected for this research based on local floristic collections (Ferraz et al., 2013; Oliveira et al., 2013): *Libidibia ferrea* (Mart. ex Tul.) L. P. Queiroz (Fabaceae), *Tabebuia aurea* (Silva Manso) Benth. & Hook. F. S. ex. Moore (Bignoniaceae), *Ziziphus joazeiro* Mart. (Rhamnaceae), and *Aspidosperma pyrifolium* Mart. (Apocynaceae). These species are heliophytes, pioneers (*A. pyrifolium, Z. joazeiro*) or initial secondary species (*T. aurea; L. ferrea*), and they present differential leaf-fall behavior: one is deciduous (*A. pyrifolium*), two are semi-deciduous (*T. aurea; L. ferrea*) and one perennial (*Z. joazeiro*). All species have a high ecological and economic relevance for the region (Gandolfi et al., 1995; Silva and Coelho, 2007; Carvalho et al., 2012; Andrade et al., 2015). and are found in both sites. Their importance, different leaf-fall behavior and ecological strategies implies these species form interesting case studies to understand growth dynamics in Caatinga dry forests.

2.3. Dendroecological analyses

Sample collection was done in a stratified random design, in which we selected individuals of various sizes (diameter at breast height < 10 cm) randomly along two parallel transects of 200 m in length, located 50 m away from each other. Using a gasoline-powered motor drill (Stihl BT 45), we took two 12 mm radial samples from bark to pith from six individuals of each species at both study sites, totaling 48 trees. Some radial samples were discarded due to damage during the collection procedure. The radial samples were packed in paper bags, dried at air temperature, glued onto wood supports, and polished with increasingly finer sandpaper (grit from 80 to 1500) to allow for a good visualization of ring boundaries under a stereomicroscopy (Orvis and Grissino-Mayer, 2002; Gärtner et al., 2015).

To describe the wood anatomy and growth ring boundaries for each species, we collected additional samples using the same borer (Fichtler et al., 2010). Wood anatomical descriptions aids in the identification of true ring boundaries from confounding structures such as variations in wood density and sizes of vessel elements, and axial parenchyma variations (Locosselli et al., 2013; Bräuning et al., 2016). We used the methodologies of Brown (1919) and Johansen (1940) for the anatomical analyses, as well as the standards established by IAWA (Wheeler et al., 1989).

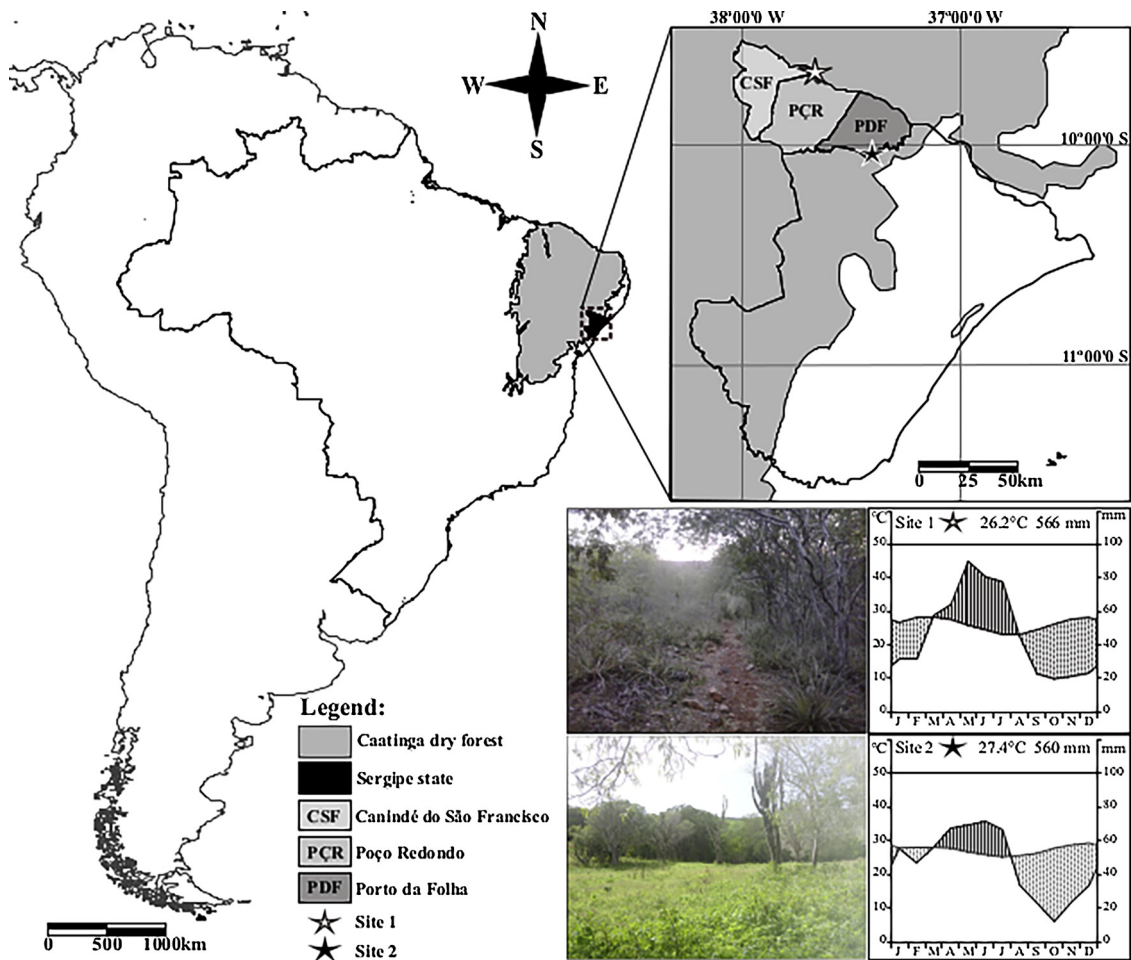To measure tree rings, we first observed and demarcated growth

Fig. 1. Location of the two study sites within the Caatinga tropical forest (grey area), and three municipalities in Sergipe state, northeast Brazil. Site 1 (light star) is located in the Grota do Angico Natural Monument, and site 2 (dark star) is a tropical dry forest remnant located in a farm in the southwest of the Porto da Folha municipality. Pictures to illustrate both sites and climate diagrams of the meteorological stations nearest to each are also provided (cf. Walter and Lieth, 1960): grey lines show monthly mean temperature averages, black lines the precipitation averages, dotted area (when the precipitation curve < temperature curve) indicates the dry season, while vertical lines (precipitation > temperature) the rainy season.

layers under a Motic® stereomicroscope (10x to 40x amplification). Next, we scanned samples at 1200 dpi resolution (HP PSC 1510) in ".tif" format and measured ring widths using the ImagePro-plus software (version 4.5.0.29 for Windows), with an accuracy of 0.02 mm. We first visually crossdated ring-width series in Microsoft Excel (using graphics and Pearson correlations) and subsequently performed a statistical quality control of this crossdating using COFECHA software (Holmes, 1983) to resolve possible marking errors. Chronologies were constructed for each species x location combinations using the software ARSTAN (Cook, 1985; Cook and Kairiukstis, 1990). We double-detrended our series, with a linear regression followed by cubic splines with a cut-off filter of 65% (cf. Cook and Kairiukstis, 1990; Hughes et al., 2011) and used the standard versions of each chronology for climatic-growth comparisons.

To explore the relationship between growth and local climate, we computed Pearson´s correlations between the chronologies and precipitation data from the nearest meteorological stations for each site. We used total annual precipitation as well monthly precipitation averages over the period January of the previous year to December of the current year. We included the months in the year previous to the growth season to account for possible lagged effect of precipitation on growth (Pagotto et al., 2015). The short duration (only ten years) of the temperature records, did not allow us to include temperature in these analyses. Tree growth is often found to correlate strongly to combinations of months (i.e., seasonal averages) rather than monthly or yearly

values (Brienen and Zuidema, 2005). To identify the combination of months in which growth rings responded significantly to precipitation, we applied multiple regression models combined with generalized linear models (GLM) between growth and monthly precipitation data (cf. Hughes et al., 2011). Multiple regression models and GLMs are randomized analyses that help us to understand growth ring patterns (Li et al., 2014; Ciapała and Adamski, 2015), contribute to the evaluation of the relation between chronology and species-related climate factors, and have been widely used in dendrochronological research worldwide (Fritts, 1976; Cook and Kairiukstis, 1990; Hughes, 2002; Hughes et al., 2011; Locosselli et al., 2013).

Next, we explored the relationship of growth with global climatic patterns. We first produced maps of correlations between the chronologies and global sea surface temperature (SST) reconstructions using the KNMI Climate Explorer (Trouet and Van Oldenborgh, 2013) to identify which regions of the ocean have an effect on local tree growth. We used the Optimum Interpolation Sea Surface Temperature 0.25° reconstructions from the National Center for Environmental Information (Reynolds and Smith, 1994). These correlations were performed per month, but using running-means of 4 months for the SST data to account for autocorrelation in the data and lags in growth responses (Land et al., 2017).

To corroborate the results of these maps, we performed Pearson´s correlations between the chronologies and two often used indices of large-scale climatic variables (Pagotto et al., 2015; Pucha-Cofrep et al.,

2015; Schöngart et al., 2017): sea-surface temperatures of the South Tropical Atlantic (TSSA) and the El Niño Southern Oscillation (ENSO). The TSSA comprises of sea-surface temperatures of the South Tropical Atlantic in the area between 0°–20°S and 10°E-30°W (data source: http://www.esrl.noaa.gov/psd/data/correlation/TSSA.data; see annex Table 4). For the ENSO we used the Ocean Niño Index (ONI), which consists of ocean temperature anomalies in the Pacific between 5°N-5°S and 120°-170°W (http://www.cpc.noaa.gov/products/analysis_monitoring/ensostuff/ONI_change.shtml; annex Table S5). Similar to the analysis with local climate, we performed correlations of growth with monthly values and annual averages. We also applied the multiple regression and GLMs approach to decipher important periods of influence of these variables on growth.

All climate-growth analyses were computed using Pearson´s correlations (r; significance level of 95%) (Hughes et al., 2011), over the period of 1965–2015, using R 3.2.1 software (R Core Team, 2015). Multiple regressions and GLM were performed using the Past software 3.14 (Hammer et al., 2001).

3. Results

Growth rings of *A. pyrifolium* and *L. ferrea* were visible under a magnifying glass at 10x amplification, while *T. aurea* and *Z. joazeiro* rings were visible only with the help of a stereomicroscope (Fig. 2). *A. pyrifolium* had growth rings delimited by a thin line of marginal parenchyma, thick-walled latewood fibers, and differences in vessel diameters: larger vessels in earlywood and smaller in latewood (Fig. 2a and b). *Z. joazeiro* had growth rings delimited by a thin marginal parenchyma and thick-walled fibers that separated the of growth ring boundaries from apotracheal axial parenchyma bands typical of this species (Fig. 2c and d). *T. aurea* had semi-porous rings and the boundaries of rings were demarcated by a line of marginal parenchyma, followed by a fibrous zone with variable width (Fig. 2e and f). The boundaries of the *L. ferrea* rings presented a marginal parenchyma line and thick-walled fibers in the latewood (Fig. 2g and h).

False rings were observed in all species, consisting mostly of wood color variations, fibrous zones, and confluent aliform axial parenchyma (Fig. 2). *A. pyrifolium* presented numerous false rings, characterized by a narrow group of cells forming irregular and discontinuous layers, which were different from the marginal parenchyma boundaries of actual ring boundaries in color and wood density variation (Fig. 2a and b). *Z. joazeiro* had false rings that were recognizable by the variation in wood density and color (Fig. 2c and d). On the other hand, *T. aurea* and *L. ferrea* showed false rings associated with the structure of the confluence of aliform parenchyma, which again were visually distinct from the marginal parenchyma line that delimited its growth layers (Fig. 2e to h).

Maximum tree ages varied between species from 23 to 51 years and the chronologies contained between 11 and 12 radii. Visual synchronization of rings series and statistical crossdating showed that the individuals of each species showed similar growth variation. The species showed inter-correlations varying between 0.720 and 0.806, a mean sensitivity between 0.383 and 0.565 (Table 1). During sampling some samples lost the bark or did not present the pith, but we were able to synchronized all of them with the remainder of the samples.

We found strong positive correlations between chronologies of the four species in both sites and total annual precipitation (r between 0.69-0.87; Fig. 3). Additionally, precipitation between 2006–2015 decreased gradually in the two sites, and there was a very dry period in 2012/2013 leading to a decrease in rainfalls in subsequent years (Fig. 3). The chronologies of the four species at both sites reflected these rainfall declines (Fig. 3). Growth correlated positively with monthly precipitation values for all species and sites, with most significant correlations found for months between January and July, the months around the rainy season (Appendix Table 2), while negative correlations with rainfall in the months of the previous year were also found. We used

multiple linear regressions and GLMs to identify periods of significant relationship between chronologies and rainfall. We found that for all but one species, rainfall during all months from December of the previous year until July of the current year had an effect on growth. The exception was *L. ferrea*, for which this period comprised only the months January–July, not including December of the previous year (Fig. 5 and Table 2).

The correlation maps between the chronologies and the global sea surface temperatures (SST) running means, show that growth of most species correlates with the South Tropical Atlantic or Equatorial-South Tropical Pacific SSTs, and for some species with both (Fig. 4 and Appendix Fig. 2). For all species, correlations were observed for several four-month periods between December and August (results not shown), and the strongest correlations (higher r-values) were found in the period coinciding with the rainy season in the region (April-July, Fig. 1) for *A. pyrifolium*, *Z. joazeiro* and *L. ferrea*, while for *T. aurea* this was the case between January and April (Fig. 4).

Even though the two sites are part of the same morphoclimatic domain (Fig. 1), the effects of TSSA on growth differed between the sites (Fig. 5). In site 1, negative correlations were found between growth and TSSA in the current year for *A. pyrifolium* (in the month November) *Z. joazeiro* (May-June and December) and *L. ferrea* (April-July and December; Fig. 5 and Appendix Fig. 2 and Table 2). A positive correlation was also found between TSSA in the previous year for two species: *A. pyrifolium* (for the month November), and *T. aurea* (May-September and November). In site 2 we found negative correlations between growth and TSSA only for *A. pyrifolium* in November of the current year, while no correlations were found with previous-year TSSAs (Fig. 5 and Appendix Table 2). Using multiple linear regressions and GLMs to identify periods of significant relationships, we found that for *Z. joazeiro* and *L. ferrea* from site 1, the combined TSSA during the rainy season months (April-July) had a negative effect on growth (Fig. 4b and d and Appendix Table 5).

Finally, we found no correlations between growth of any of the four species in the two sites and monthly or annually averaged Ocean Niño Index (ONI). We only found a significant El Niño effect using a complementary approach in which we ran correlations on a subset of years considered "moderate", "severe", or "very severe" El Niño and La Ninã events over the last 50 years (L'Heureux et al., 2013). Using multiple linear regressions and GLMs on this subset of years, we found negative relationships between previous-year ONI in the months January, February, and March and the growth of *Z. joazeiro* of site 1 and *T. aurea* of site 2 (Fig. 4b and 4c and Appendix Fig. 3 and Table 6).

4. Discussion

In this study we described the tree-ring structures of four species from the Caatinga – a neotropical dry forest – and evaluated how environmental conditions influence their inter-annual growth variation in two sites. We show that the four species form annual rings, and that their growth variation correlates with local precipitation and surface temperatures of the South Atlantic. These results confirm the potential of these species for dendroecological studies in these tropical dry forests (TDFs).

The four species showed different types of ring boundaries (Fichtler et al., 2010), which coincided with descriptions from other studies on species level – for *Tabebuia aurea* (Pace et al., 2015) and *Libidibia ferrea* (Lisi et al., 2008) – or genus and family levels – for *Aspydosperma pyrifolium* (Woodson, 1951; Gutiérrez and Ramos, 2013) and *Ziziphus joazeiro* (Giménez and Moglia, 2003). The anatomical characterization of the growth ring boundaries improves their correct identification during measurements, decreasing measurement errors caused by false rings which are a common feature in tropical species. This type of care increases the accuracy of measurements, and contributed to the construction of reliable chronologies (Fritts, 1976; Cook and Kairiukstis, 1990; Hughes et al., 2011).
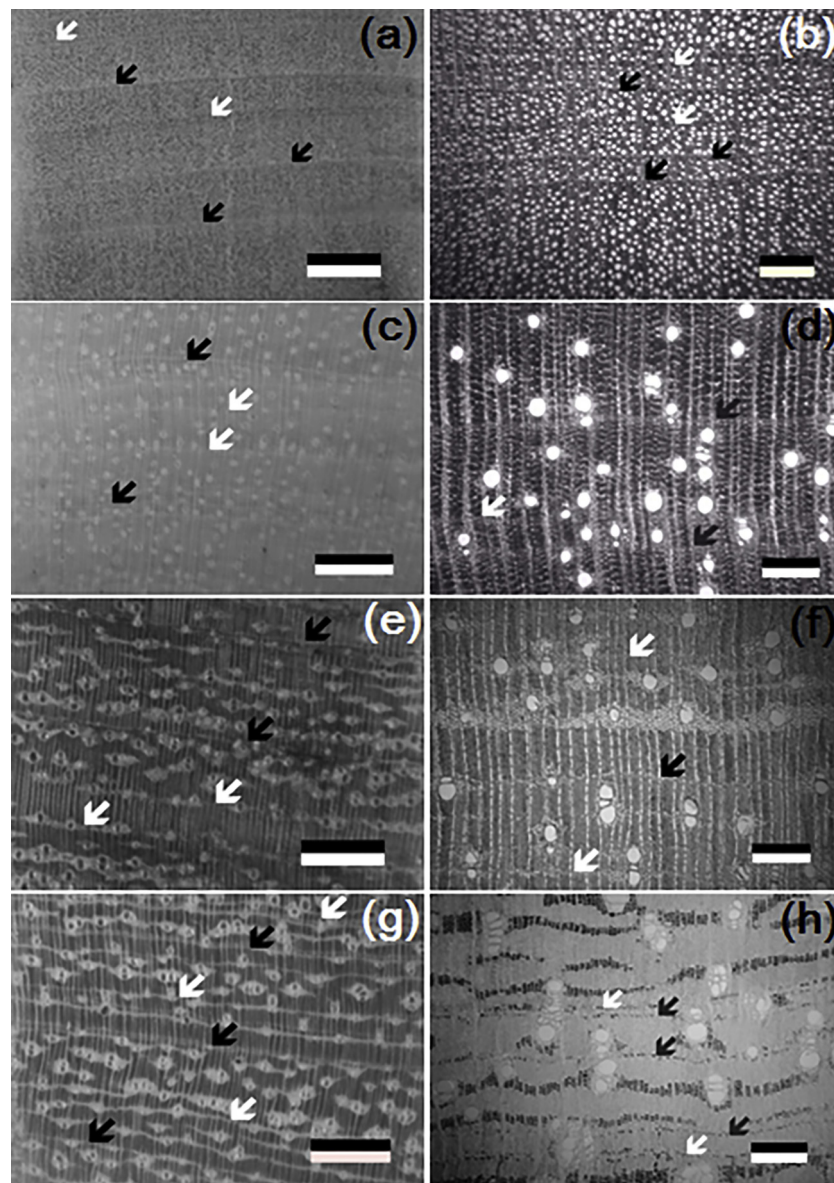
Fig. 2. Macroscopic and microscopic transversal images of the wood of the four species studied. True ring boundaries (dark arrows) and false rings (white arrows) are indicated. Species: *A. pyrifolium*, (**a**) and (**b**); *Z. joazeiro*, (**c**) and (**d**); *T. aurea,* (**e**) and (**f**); *L. ferrea,* (**g**) and (**h**). Scale bars: 1 mm in (**a**), (**c**), (**e**), (**g**), and 400 μm in (**b**), (**d**), (**f**) and (**h**).

All chronologies showed correlations with total annual precipitation, as well as with rainfall in the rainiest months (April–July) corroborating that growth of dry forest species Cambial activity of dry forest tree species depends directly on rain events, and trees enter a state of cambial dormancy during the dry season (Trouet et al., 2012; Callado et al., 2013; Mendivelso et al., 2016b; García-Cervigón et al., 2017). Therefore, changes in cambium activity get reflected in the growth ring boundaries, leading to well-delimited annual growth rings (Lebrija-Trejos et al., 2011; Paredes-Villanueva et al., 2013; Pagotto et al., 2015; Marcati et al., 2016). The strong responses of growth to rainfall suggests

Table 1
Characteristics of the chronologies for four species evaluated in the two study site (S1 and S2). Provided are: number of trees (and series in parenthesis) in the chronology; rbar: inter-tree correlation; sens: sensitivity; mean (and maximum) tree ages; Mean ø: mean (and maximum) tree diameter; Span: start and end of the chronology.

| Species	# trees (series)	rbar	sens	Mean age (max)	Mean ø (max)	Span
A. pyrifolium S1	6 (12)	0.797	0.554	25.3 (30)	12.6 (14.3)	1983-2015
A. pyrifolium S2	6 (12)	0.732	0.516	3.05 (40)	16.1 (21.7)	1975-2015
Z. joazeiro S1	6 (11)	0.72	0.383	17.1 (23)	13.9 (15.9)	1991-2015
Z. joazeiro S2	6 (12)	0.738	0.487	22.6 (29)	17.0 (21.0)	1986-2015
T. aurea S1	6 (11)	0.796	0.548	24.9 (34)	17.7 (28.7)	1980-2015
T. aurea S2	6 (12)	0.739	0.564	43.8 (51)	36.0 (41.1)	1965-2015
L. ferrea S1	6 (12)	0.806	0.459	18.3 (28)	14.6 (21.4)	1988-2015
L. ferrea S2	6 (12)	0.772	0.565	22.1 (24)	20.6 (33.6)	1983-2015
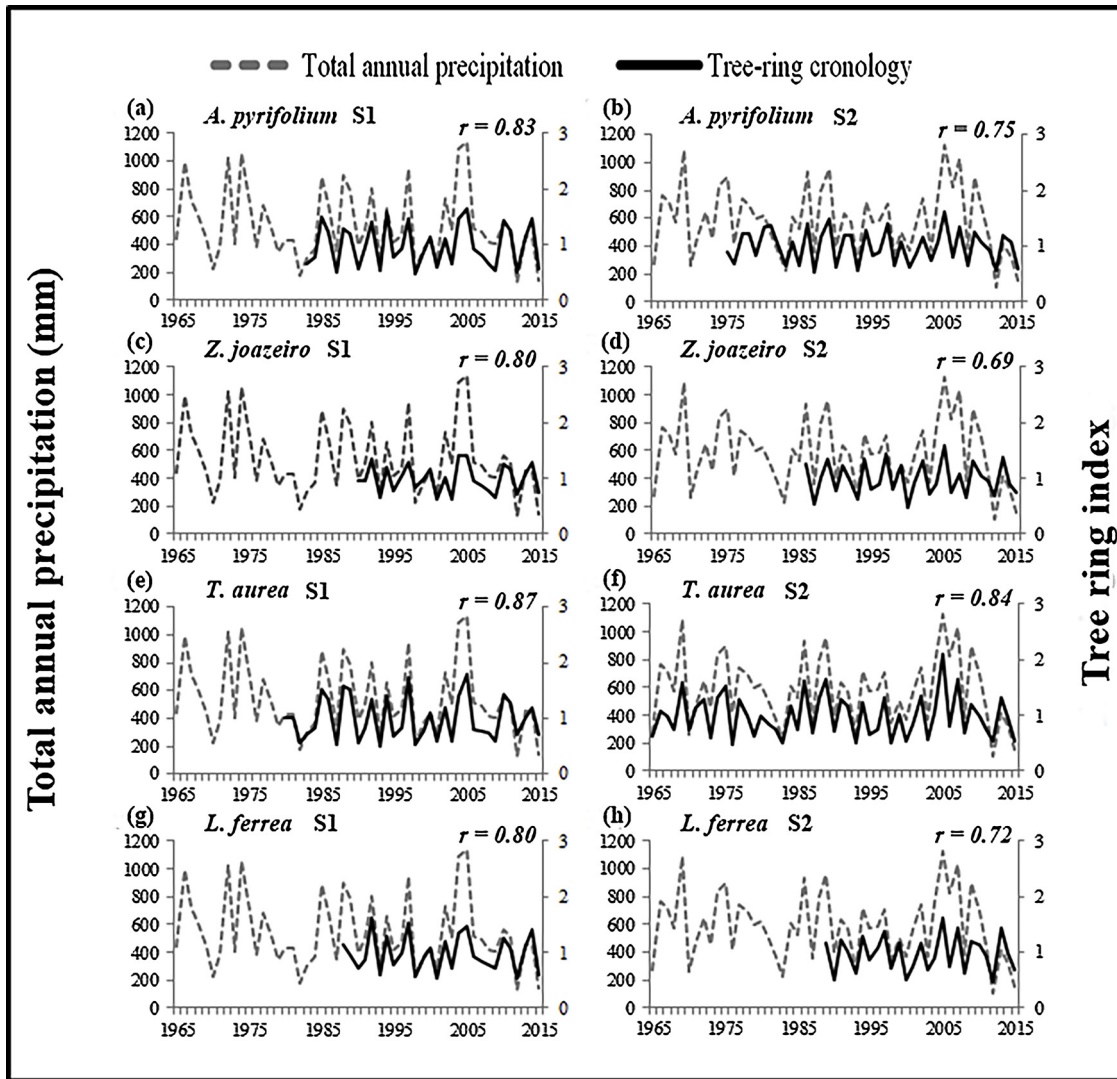
Fig. 3. Temporal relationship between standard chronologies and total annual precipitation for four species in two sites in Northeastern Brazil in the state Sergipe. Species are *Aspidosperma pyrifolium* **(a) (b),** *Ziziphus joazeiro* **(c) (d)**, *Tabebuia aurea* **(e) (f)**, and *Libidibia ferrea* **(g) (h)**. Wheather stations used are Poço Redondo for site 1 and Porto da Folha for site 2. Pearson´s correlations (*r*) given for the years 1965–2015.

Table 2
Results of the multiple regression analyses and GLM between the chronology (dependent variable) and historical monthly average precipitation, for each species and sites. Significant growth correlations with rainfall were found over the periods January to July (JAN-JUL) and with the month December (DEC). Shown are the GLM regression coefficient *b* (± standard error), standardized coefficient *β*, and p-values.

		Site 1			*Site 2*		
	Variables	*b*	*β*	GLM (p)	*b*	*β*	GLM (p)
A. pyrifolium	Intercept	0.4487 ± 0.0759			0.5121 ± 0.0758		
	JAN-JUL	0.0078 ± 0.0012	0.639	< 0.001	0.0068 ± 0.0011	0.529	< 0.001
	DEC	0.0029 ± 0.0011	0.267	< 0.001	0.0026 ± 0.0012	0.143	0.011
T. aurea	Intercept	0.4105 ± 0.0611			0.3046 ± 0.0675		
	JAN-JUL	0.0085 ± 0.001	0.703	< 0.001	0.0095 ± 0.001	0.682	< 0.001
	DEC	0.0035 ± 0.0009	0.300	< 0.001	0.0032 ± 0.0011	0.184	< 0.001
Z. joazeiro	Intercept	0.6493 ± 0.0602			0.5621 ± 0.086		
	JAN-JUL	0.005 ± 0.0009	0.585	< 0.001	0.0056 ± 0.0012	0.461	< 0.001
	DEC	0.0028 ± 0.0013	0.195	0.016	0.0031 ± 0.0013	0.187	0.011
L. ferrea	Intercept	0.5389 ± 0.073			0.5211 ± 0.095		
	JAN-JUL	0.0072 ± 0.001	0.652	< 0.001	0.007 ± 0.0013	0.532	< 0.01
	DEC	–	–	n.s.	–	–	n.s.

Respective coefficients of determination R^2: *A. pyrifolium* S1 = 0.71 (n = 33) and S2 = 0.58 (n = 41); *Z. joazeiro* S1 = 0.66 (n = 30) and S2 = 0.55 (n = 26); *T. aurea* S1 = 0.80 (n = 36) and S2 = 0.73 (n = 51); *L. ferrea* S1 = 0.65 (n = 28) and S2 = 0.53 (n = 27).
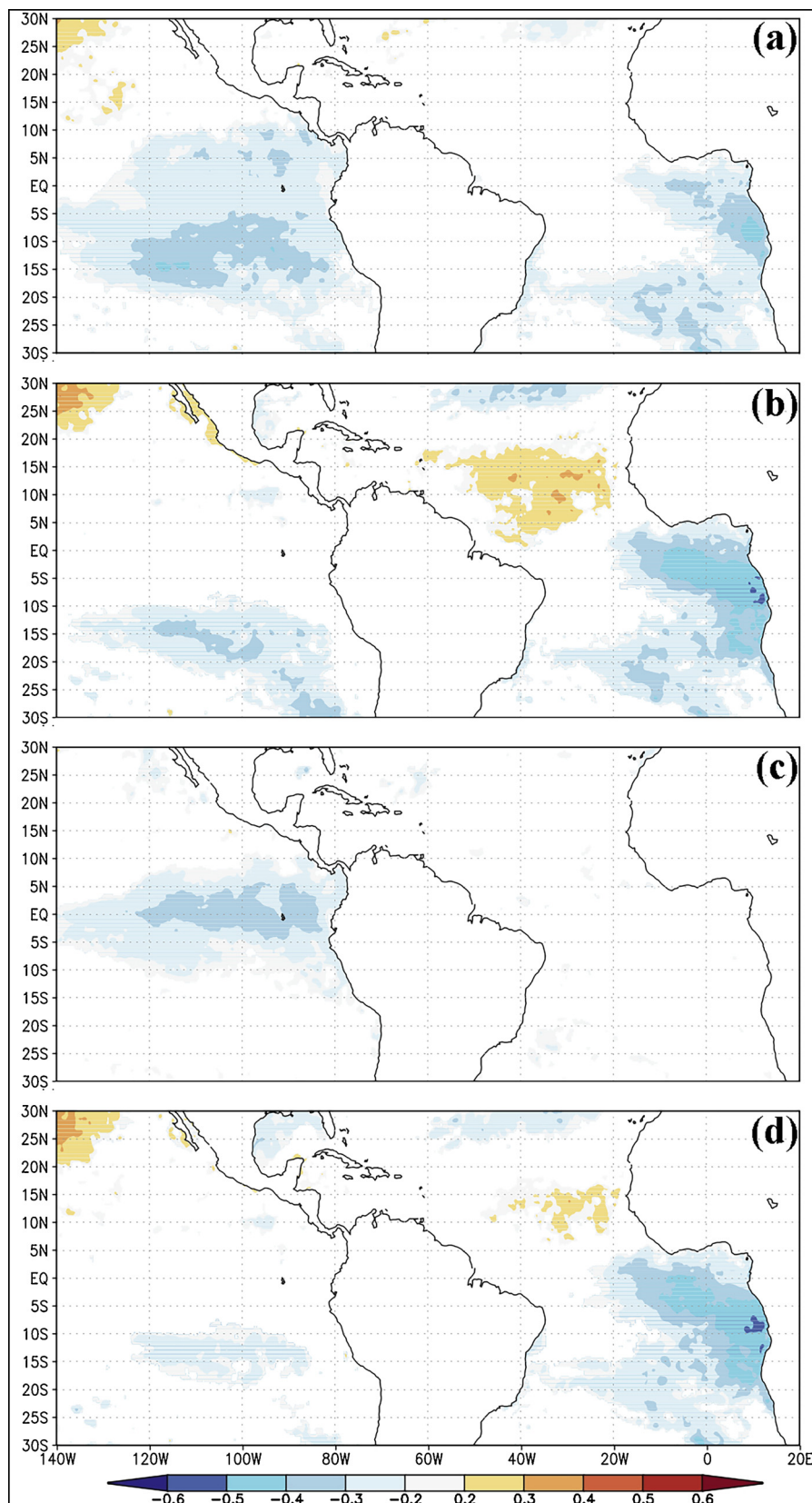
Fig. 4. Spatial correlations between ring-width index (RWI) chronologies of four Caatinga dry forest tree species and gridded sea-surface temperatures (SSTs) in the Atlantic and Pacific oceans. Gridded data from the Optimum Interpolation Sea Surface Temperature 0.25° reconstructions from the National Center for Environmental Information (Reynolds and Smith, 1994). Shown are the 4-month periods with the highest correlations for each species. Colors indicate Pearson´s correlation coefficients. Panels: **(a)** *Aspidosperma pyrifolium* site 1 RWI vs. April-July SSTs (for the years 1982–2015) **(b),** *Ziziphus joazeiro* site 1 RWI vs. SSTs (1990–2015) **(c)** *Tabebuia aurea* site 2 RWI vs. SSTs (1965–2015) **(d)** *Libidibia ferrea* site 1 RWI vs. SSTs (1988–2015). For details on the sites, see Fig. 1 and for maps of all species × sites Appendix Fig. 2.

these species are vulnerable to the reduction in rainfall expected under climate change (IPCC, 2014). Growth rates of dry forest species are expected to decline in the next decades (Brienen et al., 2010a; Boakye et al., 2016; Hiltner et al., 2016), and understanding these changes is crucial for improved predictions of forests responses to climatic changes and their role in the global carbon cycle (Sitch et al., 2003; Poulter et al., 2014). Indeed, we found a gradual decrease in the growth rates during the last decade, concomitant with decreases in the rain volumes (Huang et al., 2011; Rivetti et al., 2014; Kwon et al., 2016; Bertrand et al., 2016). These results further illustrate the possible negative
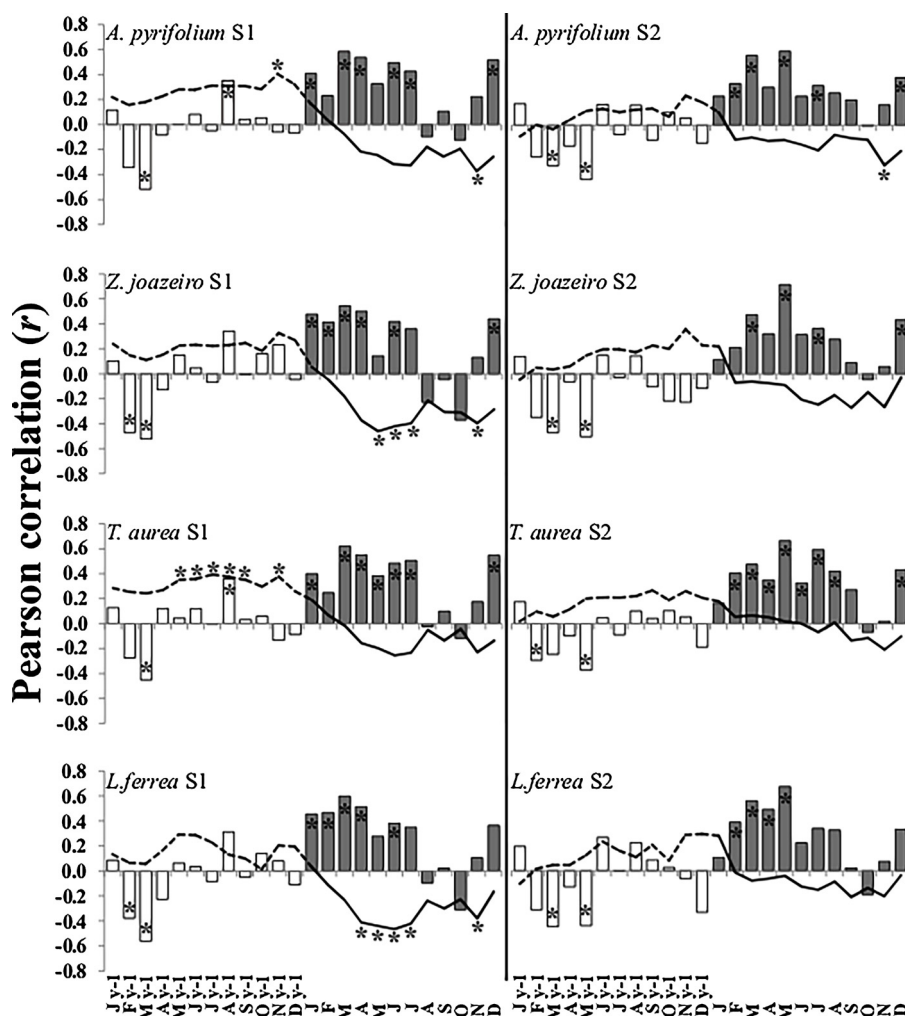
Fig. 5. Pearson´s correlations between ring-width chronologies and monthly precipitation (bars) and between chronologies and sea-surface temperatures in South Atlantic Ocean (lines) for four species from two Caatinga tropical dry-forest sites in Northeast Brazil. Grey bars and continuous lines indicate current-year correlations while white bars and dashed lines correlations with previous-year values. Significant correlations (p < 0.05) indicated with an * (inside the bars for precipitation).

impacts of global warming on the growth dynamics of TDF species (Brienen et al., 2010a; Santos et al., 2014a, 2014b). Our results high-light the importance of dendrochronology as a tool to evaluate climate-growth relations and understand the plasticity of TDFs tree species in the face of changing environmental conditions (Hughes et al., 2011; Baas et al., 2013; Bräuning et al., 2016).

Rainfall events in December of the previous year also affects growth of three of the species (*A. pyrifolium*, *Z. joazeiro*, and *T. aurea*) in both sites (results from the multiple regressions + GLM), indicating that these species may present fast cambial responses to irregular pre-cipitation events. Periodic growth reactions to such sporadic rainfall events has been observed in other species from similar environments (Marcati et al., 2006; Pumijumnong and Buajan, 2013; Wang et al., 2013; Marcati et al., 2016) and may contribute to the development of false growth rings observed for some of our species. Although sporadic and poorly distributed in space, the occurrence of rainfall events during the dry season is common in TDF in northeastern Brazil, (Bernardes, 1999). These events (known as *trovoadas*, or thunderstorms) are enough to stimulate foliar regrowth and, thus, to restart the production of biomass in tree species (Araújo, 2011; Albuquerque et al., 2012; Salgado et al., 2015), and thus explain the observed correlations be-tween tree growth and rainfall in the months outside the core of the rainy season. However, not all species showed the same response, suggesting diverging strategies in the xeromorphic adaptations of TDF species (Lima and Rodal, 2010). Using multiple regressions combined

with GLMs (Li et al., 2012; Ciapała and Adamski, 2015) in climate-growth analyses allows to distinguish the periods that are relevant to tree growth, and to better understand different growth responses or phenological adaptation to rainfall periodicity in these environments (Silva et al., 2003; Marcati et al., 2006; Callado et al., 2013; Marcati et al., 2016; Pagotto et al., 2015; Nogueira et al., 2017).

Despite the different functional types (deciduous or evergreen), successional strategies (pioneer or secondary), and physiological, morphological, and anatomical adaptations of the four species, in general all species showed a homogeneous growth response to pre-cipitation. These results agree with other studies of tree growth re-sponses in dry forests (Gandolfi et al., 1995; Quesada et al., 2009; Silva et al., 2003; Silva and Coelho, 2007; Carvalho et al., 2012; Andrade et al., 2015) and suggest that tree growth is strongly driven by pre-cipitation in TDFs (Olson et al., 2001; Ceccon et al., 2006). However, some differences between the species and sites were found. In general, the chronologies of the species at site 2 presented lower correlations to rainfall variations, as well as, with variations in sea-surface tempera-tures. This site receives more rainfall than site 1 and is on the wetter edge of the dry forest (Fig. 1), which may explain the lower correlations and sensitivity to rainfall of the trees growing there. Also, growth of the evergreen species *Z. joazeiro* presented the weakest correlations with rainfall events (lowest *r*-values), suggesting this species is less depen-dent on rainfall variation and could have metabolic or radicular adaptations for the maintenance of growth even during dryer months.

On the other hand, growth of the three deciduous species showed the highest correlations with rainfall variability (especially for *T. aurea*), suggesting these species are possibly the most vulnerable to climate change (Brienen et al., 2010a, 2010b; Zuidema et al., 2012). Results on the climate sensitivity of tree species can be taken into account when choosing species for restauration projects that take future climatic scenarios into account.

Rainfall events in northeastern Brazilian are influenced by several atmospheric and oceanic factors, such as the sea-surface temperatures (SST) of the Atlantic ocean (Amorim et al., 2014) and the El Niño Southern Oscillation (Woodhouse, 1997; Rodrigues et al., 2011; Nobrega and Chagas, 2016). Oscillations in both the SSTs and ENSO modify the passage of the Intertropical Convergence Zone (ITCZ) over the region, which is the main driver of its intra-annual climate variation (Marengo et al., 2017). For instance, ITCZ shifts may cause disruptions to the region´s precipitation (Marengo et al., 2017; Martins et al., 2018) or intensify rainfall (Uvo et al., 1998; Hastenrath, 2006; Nóbrega et al., 2016; Martins et al., 2018). These fluctuations in SST and/or ENSO also affected growth of our study species, with large oceanic areas in the Atlantic and Pacific presented correlations between SSTs and growth variation. This effect was detected for several months but was strongest during the during the core of the wet season from April to July. Correlations with indices of temperature for specific oceanic areas (e.g., South Tropical Atlantic sea-surface temperatures (TSSA), or in the El Niño 3.4 region) did not always show the same results as the correlation maps but largely corroborated the findings and are in agreement with other studies (Pagotto et al., 2015). We will discuss the specific results below. Yet, we highly recommend using tools such as the KNMI Climate Explorer (www.climex.knmi.nl) (Trouet and Van Oldenborgh, 2013) to identify important oceanic regions prior to defining specific areas for analysis.

Growth variation of two species – *Z. joazeiro* and *L. ferrea* – were negatively corelated with TSSA in several of the months between April and November of the current year. In general, lower south-tropical Atlantic surface temperatures lead to higher precipitation in the region (Appendix Fig. 1; Nobrega and Chagas, 2016), explaining the negative correlations found. Numerous studies have confirmed the influence of the TSSA on the formation of growth layers (Woodhouse, 1997; Schongart et al., 2006; Patskoski et al., 2015), including in the TDFs of northeastern Brazil (Pagotto et al., 2015; Nogueira et al., 2017). However, growth also showed correlations with months in the previous year, including positive correlations (e.g., for *T. aurea*). These apparently conflicting results have been found in previous studies (Pagotto et al., 2015), and could be explained by different sensitivity and growth strategies of particular tree species to variations in the local hydrological regime, as described by Woodhouse (1997). The positive responses of growth to dry conditions in the previous year (positive correlations with TSSA) could also be due to lagged responses of leaf and flowering phenology (Barbosa et al., 1989; Silva et al., 2003; Andrade et al., 2015), representing a possible trade-off between reproduction and growth (Alfaro-Sánchez et al., 2017).

Although we found no direct significant correlations between the ENSO and growth, the KNMI Climate Explorer correlation maps suggest that sea-surface temperatures in the Equatorial Pacific near South America do influence tree growth variation in the Caatinga TDF. This area is under strong influence of ENSO events (Rodrigues et al., 2011). ENSO events modify rainfall and temperature in different places on the planet (Gergis and Fowler, 2009) and cause precipitation changes throughout Brazil (Bombardi et al., 2014). In northeastern Brazil, years under the influence of ENSO are characterized by severe drought, strengthened by the association of these events with dipole-positive (TSSA alterations), which mostly occur at the start of the rainy season in March, April, and May (MAM) (Nobrega and Chagas, 2016). Besides the MAM period, ENSO also influences precipitation in this region between September and February (SON–DJF), due to the shortening of the Pacific-South American circulation (PSA), thus also affecting

precipitation at the beginning of the rainy season (Rodrigues et al., 2011). Climate variation drives phenology of tree in TDFs, independent of the functional groups they occupy (Barbosa et al., 1989; Silva et al., 2003), explaining the effect of ENSO on TDF tree growth (Rigozo et al., 2004; Rodríguez et al., 2005; Fowler et al., 2007, 2012; Spannl et al., 2016; Chowdhury et al., 2016). The increases in ENSO frequency predicted for the future (IPCC, 2014), and the predicted increases in the drought period in northeast Brazil (Nobrega and Chagas, 2016) may generate deleterious effects for tree growth (Brienen et al., 2010a) and increase the vulnerability of tropical dry-forest tree species (Anadón et al., 2014).

In conclusion, we confirm the annual nature of tree-ring formation for four species from the Caatinga tropical dry forest in northeastern Brazil and show their potential for the development of chronologies. Inter-annual growth variation is strongly driven by seasonal rainfall and is also under the influence of Atlantic and Pacific sea-surface temperatures. We suggest further research should focus on increasing chronology length by including individuals with greater diameter and species with higher longevity. Evaluating the dendrochronological potential on more species would contribute to climate reconstructions of these dry regions Such approaches would be most fruitful if performed in large research networks to create extensive shared databases. Finally, three of the studied species occur over large geographical and environmental gradients, thus forming interesting case studies to understand plant functioning under changing climate (Sterck et al., 2014). This type of knowledge is essential to assist management, restoration and conservation actions bearing global climate change in mind.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.dendro.2018.10.011.

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