ORIGINAL ARTICLE

Anatomical and tree rings differences in two provenances of *Cordia trichotoma* (Vell.) Arráb. ex Steud. (Boraginaceae)

Diferenças anatômicas e nos anéis de crescimento em árvores de duas procedências de *Cordia trichotoma* (Vell.) Arráb. ex Steud. (Boraginaceae)

Eduardo Luiz Longui[1] , Caroline Caum[2] , Mario Tomazello-Filho[3] , Claudio Sergio Lisi[4] ,
Fidel Alejandro Roig[5,6] , Carmen Regina Marcati[2]

[1]Centro de Inovação Tecnológica, Instituto de Pesquisas Ambientais, São Paulo, SP, Brasil

[2]Departamento de Ciência Florestal, Faculdade de Ciências Agronômicas, Universidade Estadual Paulista – UNESP, Botucatu, SP, Brasil

[3]Departamento de Ciências Florestais, Escola Superior de Agricultura "Luiz de Queiroz", Universidade de São Paulo – USP, Piracicaba, SP, Brasil

[4]Departamento de Biologia, Centro de Ciências Biológicas e da Saúde, Universidade Federal de Sergipe, São Cristóvão, SE, Brasil

[5]Laboratorio de Dendrocronología e Historia Ambiental, Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales – IANIGLA (CONICET-Universidad Nacional de Cuyo), Mendoza, Argentina

[6]Hémera Centro de Observación de la Tierra, Escuela de Ingeniería Forestal, Facultad de Ciencias, Universidad Mayor, Huechuraba, Santiago, Chile

Abstract

The parental effect on wood anatomy and growth rings of *Cordia trichotoma* trees was studied. Tree seeds of two provenances (Cerrado and Atlantic Forest biomes) were collected in 1986. Seedlings were planted, and after 25 years, twelve wood disks were collected from six trees from each provenance. Anatomical features and growth rings were analyzed according to standard techniques. Qualitative anatomy of wood indicated similarities between the two provenances, except for the presence of geniculate vessels found in woods from the Cerrado. However, the greatest differences in wood anatomy were quantitative. Provenances from Cerrado had wood with shorter vessel and fibers elements, less fiber lumen, less parenchyma per mm^2, and more vessels per group than did provenances from the Atlantic Forest. Cross dating among the radial growth ring series was performed through visual and statistical procedures. The relationships between tree rings and meteorological records were performed through Pearson's correlation, and through dendro-climatic analysis that identified the end summer precipitation as the major factor affecting tree growth at inter annual timescale. The standard chronologies of tree-ring width series showed similarity between Cerrado and Atlantic Forest provenances, but with small differences in the juvenile period of live of trees. The rains that decreased between April and June associated with the gradual decrease in temperature may have reduced the cambial activity and caused the formation of tree rings with small differences between the two provenances. The results of this study are relevant for climate adaptive forestry: they emphasize the importance of heritability in the plasticity of certain features of wood anatomy related to the environmental conditions in which they grow, while the growth rate and its year-by-year variability show small differences.

Keywords: Heritability; Louro-pardo; Rainfall; Temperature; Wood features.

Resumo

O efeito parental na anatomia da madeira e nos anéis de crescimento de árvores de *Cordia trichotoma* foi estudado. Sementes de árvores de duas procedências (biomas Cerrado e Mata Atlântica) foram coletadas em 1986. Mudas foram plantadas e após 25 anos foram cortados doze discos de madeira de seis árvores de cada procedência. Características anatômicas e dos anéis de crescimento foram analisados de acordo com técnicas padrão. A anatomia qualitativa da madeira indicou semelhanças entre as duas procedências, exceto pela presença de vasos geniculados encontrados em madeiras do Cerrado. No entanto, as maiores diferenças na anatomia da madeira foram quantitativas. As procedentes do Cerrado apresentaram madeira com elementos de vasos e fibras mais curtos, fibras com menor lume, menor porcentagem de parênquima por mm^2 e mais vasos por grupo do que as procedentes da Mata Atlântica. A datação cruzada entre as séries de anéis de crescimento radial foi realizada por meio de procedimentos visuais e estatísticos. As relações entre os anéis das árvores e os registros meteorológicos foram realizadas por meio da correlação de Pearson, e por análise dendroclimática foi identificada a precipitação do final do verão como o principal fator que afeta o crescimento das árvores na escala de tempo interanual. As cronologias padrão das séries de larguras de anéis das árvores mostraram similaridade entre as procedências do Cerrado e da Mata Atlântica, mas com pequenas diferenças no período juvenil de vida das árvores. As chuvas que diminuíram entre abril e junho associadas à diminuição gradativa da temperatura podem ter reduzido a atividade cambial e ocasionado a formação de anéis das árvores com pequenas diferenças entre as duas procedências. Os resultados deste estudo são relevantes para a silvicultura adaptativa ao clima, e enfatizam a importância da herdabilidade na plasticidade de certas características da anatomia da madeira relacionadas às condições ambientais em que crescem, e a taxa de crescimento e sua variabilidade ano a ano também mostram pequenas diferenças.

Palavras-chave: Herdabilidade; Louro-pardo; Precipitação; Temperatura; Características da madeira.

INTRODUCTION

Wood anatomy is influenced by genetic, environmental and geographical factors (Klaassen, 1999), as well as allometry of plants (Rosell & Olson, 2014; Rosell et al., 2017). Although climate has been considered the main driver of wood variability in terms of total seasonal growth (Pratt et al., 2007; Zanne et al., 2010; Pfautsch, 2016; Hacke et al., 2017), heritability of silvicultural characteristics and wood properties cannot be overlooked (Cornelius, 1994; Matisons et al., 2021). Determining whether plasticity of response in wood anatomy or properties is functionally adaptive is of particular interest to both ecologists and evolutionists. Plants can adjust their phenotypes to maintain their physiological processes and functions in variable habitats (Sultan, 2000), and one of the ways in which plants do this is by adjustments in their wood anatomy.

In general, wood vessel diameter and length, vessel density, wall thickness, as well as length, height, width and density of rays have been reported as features with high phenotypic plasticity (Baas et al., 1983; Carlquist & Hoekman, 1985; Alves & Angyalossy-Alfonso, 2000, 2002; Marcati et al., 2001; Luchi, 2004; Luchi et al., 2005; Denardi & Marchiori, 2005; Barros et al., 2006). However, ecotypes might be the factor underlying the variability of all these features owing to climatic and environmental heterogeneity in their natural range. For instance, in *Myracrodruon urundeuva*, vessel diameter and density were linked to high genetic heritability (Tung et al., 2010). In relation to these evidences, the suitability of different provenances to grow under the same conditions should be tested, so that the provenance trials provide an optimal basis for comparing the performance of different origins under similar site conditions (Eilmann et al., 2014).

Although wood anatomy features vary, depending on environmental conditions, as cited before, the ability of an organism to express plasticity in a given trait is mediated by genetics (Nicotra et al., 2010), and the responses are a result of the relationship between parental and offspring environments (Sultan, 2000). As such, we argue that trees of the same species, but from different populations and genotypes, will express differences in their wood anatomy and in their absolute growth under similar environmental conditions.

In addition to anatomical features, it is expected that tree ring widths may vary in relation to genotype and environment, since seasonality affects annual cycles of cambial activity

(Schweingruber, 1996; Coradin, 2000; Marcati, 2000; Worbes, 2002; Marcati et al., 2006; Prislan et al., 2016). Climatic seasonality was pointed out as a determining factor in the cycles of reproduction / dormancy of the cambial tissue, which is also linked to the anatomical demarcation in the wood of seasonal growth. In the tropics, for instance, the presence of visible growth rings was demonstrated and mainly related to seasonal cycles of rain and drought (Worbes, 1989; Lisi et al., 2008; Soliz-Gamboa et al., 2011; Schöngart et al., 2017). Prislan et al. (2016) reported the same characteristic for the Mediterranean sub tropics. The distinction of tree rings is based on the anatomical variation of wood tissues derived from the cambium (Coradin, 2000), and their inter-annual variability is a reflection of environmental influence on physiological processes (Fritts, 1976; Tomazello-Filho et al., 2001; García-Cervigón et al., 2017). Thus, tree rings are a good source to investigate paleo-environmental conditions over long periods of time and with annual resolution (Buckley et al., 1995; Pumijumnong et al., 1995; Stahle et al., 1999; Enquist & Leffler, 2001; Speer, 2010).

Therefore, our goal was to evaluate the effect of genotype on wood anatomy and growth rings in 25-year-old *Cordia trichotoma* trees by comparing tree provenances from two biomes where the species occurs: Cerrado and Atlantic Forest. We hypothesized that both wood anatomical traits and growth ring variability are influenced by the origin of the plant material. Results of this study are relevant for climate adaptive forestry, and might indicate the importance of provenance in wood quality.

MATERIAL AND METHODS

Studied species

Cordia trichotoma (Vell.) Arráb. ex Steud. (Boraginaceae) is a representative tree species of the Neotropics with a wide geographic distribution in Brazil, including Amazonia, Caatinga, Cerrado, Atlantic Forest, Northeastern Argentina, Eastern Paraguay and Southern Bolivia (Reitz et al., 1988; Carvalho, 2003; Stapf, 2017). It is a semi-deciduous to deciduous species, considered to be a secondary initial, with a pioneer tendency and common in secondary vegetation (Carvalho, 2003). It is a highly appreciated timber species (Lorenzi, 1998; Mantovani et al., 2001; Carvalho, 2003), and a tree recommended for use as plantings for the enrichment of degraded forests (Montagnini et al., 1997; Lorenzi, 1998). The well-demarcated growth rings of *C. trichotoma* wood (Amano, 2002), associated with the deciduous characteristic (Carvalho, 2003), are indicative of an annual climatic factor acting in the secondary phenology (wood production) of this species, which allowed us to carry out the dendro-ecological analysis, as proposed in this article.

Provenances of the seeds and planting area

In 1985, seeds of *C. trichotoma* from open-pollinated plants were collected in two natural populations/provenances located in the municipalities of Bauru and Piracicaba, both belonging to the state of São Paulo, Brazil. Seeds were sown in 1986 in a single experimental forest plot at the Luiz Antônio Experimental Station (21°40'S, 47°49'W; 550 m a.s.l.), located in the municipality of Luiz Antônio, which belongs to the Forest Institute of the state of São Paulo (Figure 1). Climate in the cultivation area is tropical (Cwa, according to Köppen) with a dry winter and an average annual rainfall of 1280 mm (Gurgel-Garrido et al., 1997; Freitas et al., 2008). Little variation in temperature and precipitation was observed when comparing the three municipalities, corresponding to the seed collections (Bauru and Piracicaba) and plantation (Luiz Antônio) areas, respectively (Figure 2A-C). The historical data of temperature and precipitation were provided by INMET (National Institute for Meteorology) from a climate station located at São Simão municipality, 18 km away from the wood collection site. In Luiz Antônio, a rainy season with high temperatures (October to March) is followed by a dry period with mild temperatures (April to September).
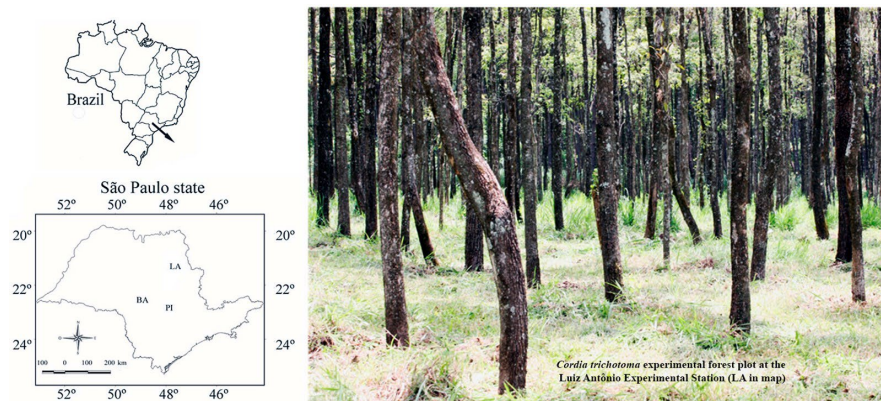
Figure 1. Location of the planting area: Luiz Antonio (LA) and areas of seed origin, Bauru (BA) and Piracicaba (PI).

Climatic analysis of Luiz Antônio showed high oscillations in the accumulated monthly precipitation. A higher average rainfall volume took place from January to March (620 mm/month), and lower average rainfall took place from July to September (123 mm/month). The temperature varied less throughout the year (19 to 25 °C). The region was characterized by a rainy season with high temperatures from October to March and a dry period with mild temperatures from April to September. Correspondingly, decreasing precipitation and temperature in autumn and winter characterized the region (Figure 2C).
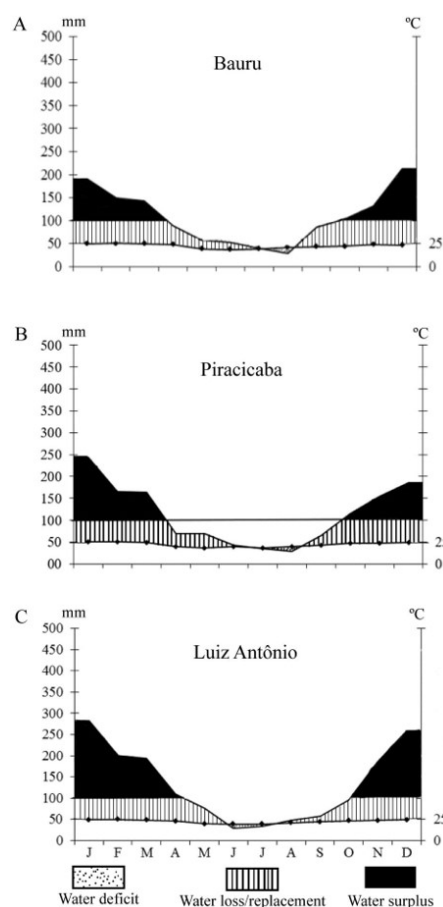
Figure 2. Climate diagrams according to Walter & Lieth (1960). Mean monthly precipitation, water deficit and surplus, water loss/replacement and mean temperature at Bauru municipality (1975-1985, Brasil, 2020)) (A), Piracicaba municipality (1980-2018, Universidade de São Paulo, 2020) (B), and Luiz Antônio municipality (2005-2015) (Instituto Nacional de Meteorologia, 2017) (C).

The predominant vegetation in Bauru municipality, one of the seed collection areas, corresponds to Cerrado biome (Cavassan et al., 2006), which is characterized by soils that are acidic, sandy, deep and well drained with lower water retention capacity and high levels of soluble aluminum (Haridasan, 2000; Franco, 2002). The predominant vegetation in Piracicaba municipality, the other seed collection area, corresponds to the Atlantic Forest biome, with clayey soils (Rodrigues, 1999). The test to identify the nature of the woods and their growth according to their origin consisted in a randomized block design with 22 open pollinated progenies, with five trees per plot or row and six blocks. The spacing used among trees was 3 m x 3 m (1,111 trees ha^{-1}, 9 m^2 per plant) with two external border rows of the same species. For practicality and in order to standardize studied trees, collections were carried out in the same block.

Sampling and anatomical analysis

In 2011, after the harvesting of *Cordia trichotoma* trees from the Forest Institute of the state of São Paulo, we obtained 3 cm thick disks at breast height from 25-year-old trees with similar height, six from each provenance (Cerrado and Atlantic Forest, respectively). For wood anatomy, we removed wood blocks (1 cm^3) from two portions of the disk: (i) heartwood, in the transition of sapwood, used only for observation of organic and inorganic inclusions and (ii) sapwood, closest to the bark, for qualitative and quantitative anatomical analysis.

We softened the samples in boiling water mixed with glycerin (4:1) and cut 15 µm thick sections on a sliding microtome (Johansen, 1940). We bleached the transverse, tangential and radial sections with sodium hypochlorite (50%), washed in 1% acetic water, and double-stained with safranin and astra blue (1:9) (Bukatsch, 1972; Roeser, 1972). After staining, we dehydrated the sections in a graded series of alcohol concentration (30, 50, 70, 90, 95 and 100%), fixed the dye with butyl acetate, and mounted the slides permanently with Entellan®.

We prepared macerations according to Franklin (1945, modified by Kraus & Arduin, 1997), stained with safranin (1%) in ethanol (50%) (Berlyn & Miksche, 1976), and mounted the slides in a solution of water and glycerin (1:1). We followed the IAWA list (International Association of Wood Anatomists, 1989) for terminology. We measured vessel element length, vessel diameter, vessel density, inter-vessel pit diameter, vessel-ray pits, vessel grouping, fiber length, fiber diameter, fiber lumen diameter, fiber wall thickness, ray height, ray frequency and area of axial parenchyma. We obtained all anatomical measurements by using the facilities of a light microscope equipped with a digital camera and a computer with image analyzer software (Axiovision®).

We initially undertook descriptive statistical analysis to obtain the means and standard deviations used to test differences between groups. The "*t*-test sample size" was used to confirm that the number of measurements was enough to achieve statistical power for the test (0.75–0.90). Subsequently, the *t*-test was used for variables with normal distribution to determine which anatomical features varied significantly between samples from the two provenances. When the variables did not present normal distribution of data, data were square root-transformed.

Growth ring analysis

The cross sections of disks were polished with sandpaper (from 100 to 1200 grit). The ring boundaries observed on the Olympus SZX7 stereomicroscope were marked with a pencil (Figure 3). Then, the cross sections of the disks were scanned with a HP Scanjet 4470c (1200 dpi - with a scale), using HP Precision Scan Pro 3.1 software. The measurement of the width of growth rings was achieved using Image-Pro Plus, and data were exported with Microsoft Office Excel®. The growth rings of a total of 60 stem radii from 12 trees (5 radii each) were studied to be synchronized and after the quality control by COFECHA 6.06p software (Holmes, 1983), 22 ring width measured series from 11 trees were used for chronology and climate correlation.

After cross-dating, chronologies were prepared using the ARSTAN 44xp software (Holmes et al., 1986), in order to remove the growth trends contained in rings width series

applying a 65 smoothing spline detrending function. The inter-correlation and mean sensitivity values are presented to validate synchronicity and the sensitivity of trees to climate. To evaluate the impact of climate on tree-rings' widths, Pearson's correlation coefficients between both standard chronologies and averaged data of mean monthly temperature and total monthly precipitation were determined.

Figure 3. Transversal sections of *Cordia trichotoma* wood, where some growth rings (arrows) are pointed out as an example, for both wood disc and strip respectively.

RESULTS AND DISCUSSION

Growth ring boundaries were distinct and marked by narrow bands of axial parenchyma and semi-ring porosity (Figure 3 and 4A). The percentage of solitary vessels was 60% and multiple vessels were 40%. The vessel density reached 13 vessels per square millimeter, regularly filled with tyloses. Some vessels formed clusters (Figure 4A). Vessels had simple perforation plates, and lateral walls showed bordered inter-vessel pits in alternate pattern (Figure 4C). Vessel-ray pits were similar to inter-vessel ones. Fibers were thin- to thick-walled and had simple to minutely bordered pits in their walls. Axial parenchyma was arranged as paratracheal, lozenge-aliform, confluent, and diffuse (Figure 4A). Rays were 2-5-seriate (Figure 4B) with procumbent body ray cells and 2-4 rows of upright and/or square marginal cells; for fused rays, a mix of procumbent, upright and square cells was observed (Figure 4D). Starch grains were present in axial parenchyma and ray cells. Crystals were present in chambered axial parenchyma and ray cells (Figure 4D). The geniculate vessel was the qualitative variable that was observed only in woods from the Cerrado biome (Figure 4B). Quantitatively, significant differences between provenances were observed in vessel diameter, vessel grouping, fiber and fiber lumen diameter, and area of axial parenchyma (Table 1).
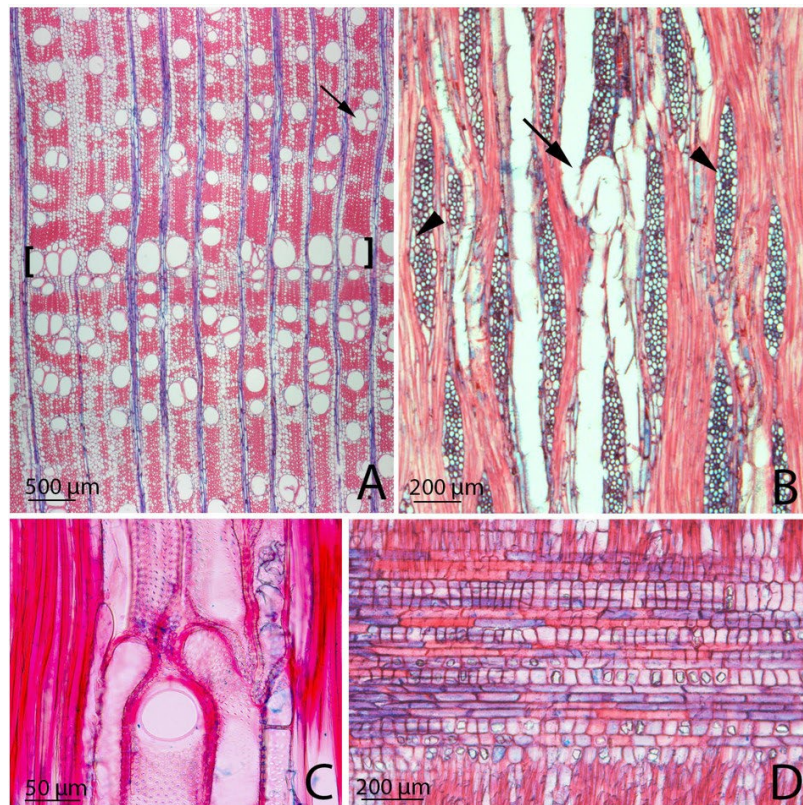
Figure 4. Wood anatomy features of *Cordia trichotoma*. A. Growth ring demarcated by a narrow band of axial parenchyma and larger vessels distributed at the beginning of the early wood (between brackets) in a wood transverse section of Atlantic Forest provenance. Note the vessels in clusters (arrow). B. Geniculate vessel in tangential longitudinal section of a wood from Cerrado provenance. Note the multiseriate rays and sheath cells (arrowheads). C. Simple perforation plate in radial section of a Cerrado provenance wood. Note the intervessel pits bordered and alternate (arrows). D. Crystals in ray cells and a mix of procumbent, upright and square ray cells of an Atlantic Forest provenance wood.

Table 1. Anatomical features of *Cordia trichotoma* for Cerrado and Atlantic Forest provenances.

Anatomical features	Provenance		F	p-value
	Cerrado	Atlantic Forest		
Vessel element length (µm)	327 ± 55	311 ± 55	0.47	0.510
Vessel diameter (µm)	115 ± 30 b	128 ± 46 a	10.49	0.009*
Vessel density (n°.mm^{-2})	14 ± 5	13 ± 6	0.09	0.769
Intervessel pit diameter (µm)	6 ± 0.6	6 ± 0.5	3.27	0.100
Vessel-ray pits (µm)	5 ± 0.5	5 ± 0.7	0.00	0.988
Vessel grouping	1.4 ± 0.1 a	1.2 ± 0.1 b	19.83	0.001*
Fiber length (µm)	1682 ± 337	1598 ± 329	0.74	0.408
Fiber diameter (µm)	21 ± 3 b	24 ± 3 a	8.04	0.018*
Fiber lumen diameter (µm)	8 ± 0.6 b	11 ± 0.5 a	8.91	0.014*
Fiber wall thickness (µm)	7 ± 1.9	7 ± 2.3	0.00	0.975
Ray height (µm)	671 ± 264	642 ± 302	0.12	0.734
Ray frequency (n°.mm^{-1})	4 ± 0.6	3 ± 0.6	4.87	0.052
Area of axial parenchyma (mm^2)	0.1979 ± 0.01 b	0.2971 ± 0.01 a	8.63	0.015*

Different letters (a or b) indicate statistical significance (p-value with *) by *t*-test.

It was possible to synchronize 22 ring width series from 11 trees, totaling the analysis of 512 growth rings. Only one tree did not synchronize due to its eccentric pith and the presence

of reaction wood. No false rings were observed. Differences were found in the results of the COFECHA analysis according to genetic origin. The samples originating in Bauru (Cerrado) presented a significant intercorrelation 0.515 (higher than critical correlation of 0.5155) between trees, and the mean sensitivity was 0.332, while the samples originating in Piracicaba (Atlantic Forest) presented a significant intercorrelation 0.653 and the mean sensitivity 0.382. The ages of the trees reached 25 years corresponding to the period from planting in 1985 and the sampling in 2010. With that, two standard chronologies were determined by ARSTAN (Figure 5), one to the Bauru (Cerrado) genetic origin and other from Piracicaba (Atlantic Forest). The Pearson correlation between these two chronologies was 0.61 indicating similarity between them, possibly due to the trees having grown on the same site, but it was possible to observe that in the 1990s they showed some differences, probably due to the young phase of the trees.
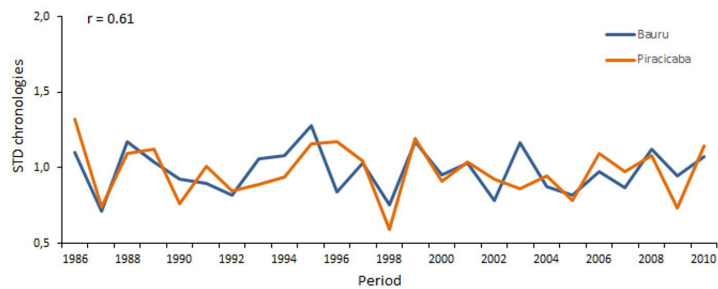
Figure 5. Standard chronologies from two provenances of Cordia trichotoma trees, Bauru (blue line) and Piracicaba (orange line).

Cordia trichotoma chronologies were related to regional precipitation and temperature from Luiz Antônio Climate Station, considering a comparison period of 25 years. Within the results above significance level of 0.39, however, the April (0.37 Pearson Cor.) precipitation from the period of March to June seems to have promoted the annual growth rings in trees of Bauru (Cerrado) genetic origin (see Figure 6A). Similarly, the March (0.32 Pearson Cor.) precipitation seems to have promoted this in trees of the Piracicaba (Atlantic Forest) genetic origin (Figure 6B). Temperature had negative results on plant growth in the Bauru (Cerrado) genetic origin; April and October (-0.35 Pearson Cor.) were the months that most influenced growth ring formation (Figure 6C). In the Piracicaba (Atlantic Forest) genetic origin, April (-0.26 Pearson Cor.) and November (-0.27 Pearson Cor.) were the months that most influenced the growth ring formation (Figure 6D).
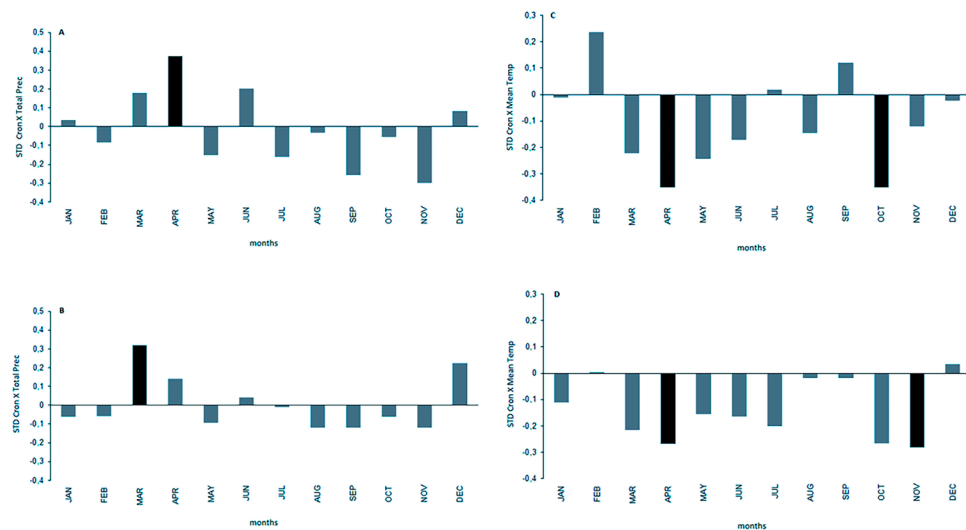
Figure 6. Relation between standard chronologies of *Cordia trichotoma* by Bauru (Cerrado) and Piracicaba (Atlantic Forest) provenance, and total monthly Precipitation (A, B) and monthly mean Temperature (C, D), respectively, which grew in the Luiz Antônio plantation. Significance level of 0.39.

Anatomical features of our wood samples confirm previous descriptions for *Cordia trichotoma* wood (Amano, 2002) and other species of the same genus like *Cordia gerascanthus* from Mexico (Rebollar et al., 1994), *Cordia alliodora* from Colombia (Briceño et al., 2016) and Peru (Portal Cahuana et al., 2021), nine other *Cordia* species from Venezuela (Williams, 2003), and a *Cordia* fossil hardwood from Chile (Schöning & Bandel, 2004). Considering this background, the features described here seem to be diagnostic for the genus *Cordia*.

Geniculate vessels were the only qualitative wood anatomical features that were identified only in samples of the Cerrado biome. Geniculate vessels are those vessels that deviate from their axial orientation, forming an angle of 90° (Amano, 2002) and, as claimed by other authors (Mattos-Filho, 1971; Mattos Filho & Rizzini, 1978), this type of vessels seems to be related to seasonal dry environments. Despite the differences in precipitation and temperature that characterize the Cerrado and Atlantic Forest biomes, other physical factors may exacerbate the drought conditions in the Cerrado. While the Atlantic Forest is characterized by clayey soils with good water-holding capacity (Rodrigues, 1999), the Cerrado (Cavassan et al., 2006) presents acidic soils that are sandy, deep and well drained, with consequent lower water-holding capacity (Haridasan, 2000; Franco, 2002). This combination of factors (climate and soils) contributes to the two biomes having significant differences in the humidity conditions of the soils. Thus, we can assume that the presence of geniculate vessels in *C. trichotoma* wood from the Cerrado provenance may also be linked to an edaphic drought condition, since the soils have a lower water-holding capacity in relation to the soils of the Atlantic Forest.

Xeromorphic traits recorded in *C. trichotoma*, such as narrower vessel and fiber lumen, small amount of parenchyma per mm^2, and higher number of vessels per group were found in the Cerrado provenance trees. In classical studies, narrower vessels with higher grouping level were proposed to represent greater hydraulic safety, since this can reduce the embolism risk of the hydraulic system (Carlquist, 2001; Tyree & Zimmermann, 2002; Baas et al., 2004). The soils of Cerrado, as noted above, indicate more restrictive water conditions for plants compared to those from the Atlantic Forest. Therefore, the presence of narrower and geniculate vessels in the trees from Cerrado could indicate a useful inherited adaptive character to safeguard the hydraulic system of *C. trichotoma* under the most restrictive water conditions in this biome.

We found fibers with larger diameter and lumen in the woods from the Atlantic Forest provenance, with a higher water-holding capacity in soils. Fibers with larger diameters and lumen in more humid environments had already been reported in *Croton urucurana* and *Alnus japonica* (Luchi 2004, and Yamamoto et al., 1995, respectively). These results reinforce our hypothesis of the influence of seed origin (genetic influence) on the wood anatomical features found in *Cordia trichotoma*: since plants from the Cerrado provenance showed more xeromorphic wood features. Additionally, a larger area of axial parenchyma, most of which was associated with vessels, was found in the Atlantic Forest provenance where soil has a higher water retention capacity than the Cerrado provenance. The higher amount of paratracheal parenchyma seems to be an adaptation of the species for hydraulic efficiency. Since parenchyma cells contribute to hydraulic conductivity (Zheng & Martínez-Cabrera, 2013; Carlquist, 2015), helping to refill water in vessels (Secchi & Zwieniecki 2011; Morris et al., 2016), a higher area of paratracheal parenchyma in the Atlantic Forest provenance seems to be related to a greater hydraulic efficiency when compared to the Cerrado provenance.

Knowing the planting age and having access to discs contributed to the cross-dating process of *C. trichotoma*. Thus, the cross-dated tree rings series of the studied trees showed similarity in both the COFECHA control results and the chronologies; however, small differences were also found, especially in the juvenile period of the trees' life. The end of the period with more annual precipitation (between April and June) seems to have had an influence on growth. The fact that the number of tree rings corresponds to the period of growth of the plants prove that the rings of these plants are annual and false growth rings were not formed in *C. trichotoma*.

These results were similar to those for *Prosopis flexuosa* studied in a seasonal dry environment in Argentina (Giantomasi et al., 2015) and different from *Tectona grandis* from a seasonal dry environment in the central region of Brazil (Ugulino et al., 2014), which showed the occurrence of different types of false growth rings. For *Cordia alliodora* several authors (Brienen et al., 2009, 2016) described the annual tree-rings. Intra-annual density fluctuations have been reported in some rings due to the presence of fibrous areas (Portal Cahuana et al., 2021). Difficulty in dating the rings was also reported, especially due to the irregularity in width along the stem (Briceño et al., 2016). Furthermore, Tschinkel (1966) points out that in *C. alliodora* the rings close to the pit were not formed or were indistinct, which made it impossible to date the first life rings of some trees. In addition, eccentric growth made it difficult to identify the pattern of growth (Tschinkel, 1966). Differences in seasonal increment patterns of *C. alliodora* circumference were also shown by Hazlett (1989) and are related to tree age; seasonal rainfall distribution; reproductive phenology and, to a lesser degree, the seed source of a plantation.

The juvenile effect may have caused differences between the chronologies generated for two genetic origins during the 1990s (Figure 5), and this tendency decreased after 1998. During the period of greatest growth, an abrupt decrease in the chronologies (especially in the Piracicaba – Atlantic Forest - genetic origin) in 1998, evidencing a probable response to environmental conditions in this population. A similar growth response for that year has been reported by Callado & Guimarães (2010) in *Schizolobium parahyba* growing in the Atlantic Forest of Rio de Janeiro state in Southeastern Brazil, and by Lobão (2011) for *Cedrela* genus in the Amazon Forest of Acre state in Northern Brazil. Coincidentally, during 1997/98 a strong El Niño event was recorded (Rao et al., 2002). That event was considered one of the most intense for the last century in Southeastern Brazil, causing dramatic anomalies in rainfall distribution over the entire country. Thus, the sharp decline in radial growth of *C. trichotoma* during that year might be associated in response to the strong El Niño event.

As a common sign of climatic response, the standard chronologies showed that the precipitation of final rainfall period affected the tree ring formation (positive signal). Thus there were small differences between genetic origin materials, more sensitive in Bauru (Cerrado). The Bauru plants showed the more sensitivity to temperatures (negative signal). The relationships between tree growth with precipitation and temperature were also reported for other tropical tree species (Pumijumnong et al., 1995; Worbes, 1999; Enquist & Leffler, 2001; Brienen & Zuidema, 2005; Schöngart et al., 2006; Lisi et al., 2008; Soliz-Gamboa et al., 2011; Kose & Guner, 2012).

Détienne & Mariaux (1977) and Détienne (1989) reported that radial growth rate of some tropical species was reduced with the decrease of precipitation during the autumn/winter. Botosso & Vetter (1991) studied growth rhythms and monthly increment of tropical species from the Amazon Forest and verified that water stress during the low precipitation period caused a decrease or absence of radial growth. In Peru, the growth of *C. alliodora* in urban areas was not correlated with precipitation, while in Costa Rica the months of higher rainfall promoted a greater radial growth in that species (Hazlett, 1989). Several studies on tropical dendroclimatology indicate a positive response of radial growth at the beginning of the rainy season (Pumijumnong et al., 1995; Luchi, 1998; Worbes, 1999; Enquist & Leffler, 2001; Brienen & Zuidema, 2005; Schöngart et al., 2006; Lisi et al., 2008; Bhattacharyya & Shah, 2009; Oliveira et al., 2010; Rozendaal & Zuidema, 2011; Soliz-Gamboa et al., 2011; Kose & Guner, 2012). In the Atlantic Forest, some species also show a positive correlation with the previous year's precipitation, while others can even have a negative response to precipitation (Fontana et al., 2018). On the other hand, in *C. alliadora* no correlation with precipitation was found in Peru (Portal Cahuana et al., 2021).

The incidence of temperature was investigated by Devall et al. (1995) in different tree species from a tropical forest in Panama, including *Cordia alliodora*. They verified that growth was positively correlated with July and August temperatures, while in Peru it was positively correlated with the temperature of the early dry season (June) (Portal Cahuana et al., 2021). For *C. trichotoma* a negative relationship between growth and temperature was found. There

was a positive relation on the radial growth in subtropical but colder climate trees, as observed by Oliveira et al. (2010) and Zanon & Finger (2010) in *Araucaria angustifolia* in Southern Brazil.

CONCLUSION

Our results suggest that the differences in wood anatomical features between the two provenances of *C. trichotoma* are strongly related to the genetics of the mother plant and its ecological provenance. The presence of geniculate vessels, narrower vessels and higher vessel grouping in the wood from Cerrado provenance trees suggests strategies aimed at shaping structures with greater hydraulic safety when compared to trees of Atlantic Forest provenance. Differences in some anatomical features and between annual growth patterns were observed between the two provenances; with more sensibility to precipitation and temperature in the plants from the Cerrado (biome) provenance. This indicates that environmental influences interfere with the seasonal formation of the xylem, but does not prevent the expression of anatomical factors linked to the progeny (mother plant). Thus, where certain anatomical features define the technological qualities of wood, special attention is required whenever plant material of different seed origins is used.

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