ORIGINAL ARTICLE



Growth dynamics of *Centrolobium robustum* (Vell.) Mart. ex Benth. (Leguminosae-Papilionoideae) in the Atlantic Forest

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Abstract Knowledge about growth rhythm and longevity of tropical trees is essential to understand life strategies of native species, and consequently, of forest remnants. This study aims to investigate the growth dynamics of Centrolobium robustum, a representative species from Atlantic Forest. For this purpose, radial growth was examined through tree rings and cambium analysis, from macroscopical, anatomical, and ultrastructural perspectives. The apical and radial stem growth was evaluated through leaf and cambium phenology, respectively. Leaf and cambium behaviors were associated with environmental seasonality. The results showed that the period of cell production and cambial development occurred in association with leaf expansion and during the wet, warm, and long-day season. Seasonality of cambial and leaf phenology in response to the environment determined the annual formation of tree rings, and it allowed to evaluate C. robustum growth rates and longevity. Species seasonality also responded to

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abnormal climatic events during the study period, which shows its sensitivity to environmental changes and represents a factor to be considered in the forest management programs.

Keywords Cambial activity · Phenology · Tropical Forest · Wood production

Introduction

Periodicity of radial growth in tropical trees has been of increasing interest to researchers from several scientific fields. Although initial interest focused on economic management and timber exploitation, current investigations mainly focus on ecological, climatic, and conservation issues (e.g., Worbes 1995, 2002; Callado et al. 2001, 2004; Estrada et al. 2008; Rozendaal and Zuidema 2011; Zuidema et al. 2013; Vlam et al. 2014; Venegas-González et al. 2015).

Phenological behavior is an integrated response of plant growth and reproduction to environmental conditions and involves genetic and evolutionary issues (Kozlowski and Pallardy 1997; Savidge 2001; Groover and Robischon 2006; Elo et al. 2009; Gricar 2012; Rossi et al. 2013). In plants, apical meristems are responsible for height growth, while lateral meristems are responsible for radial growth (Kozlowski and Pallardy 1997; Evert 2013). Thus, investigations into leaf production in association with cambial divisions provide information about plant phenology.

Studies of radial growth rhythm are useful for interpreting dendrochronological data and determining the age of trees and the factors that regulate their growth (Marcati et al. 2008). Variations in abiotic and biotic factors are recorded in tree rings and may provide information about

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past environmental conditions (Gonçalves 2007; Callado 2010). In tropical species, periodic radial growth may be associated with periods of drought (Worbes 1989; Verheyden et al. 2004; Costa et al. 2013; Brandes et al. 2015), flooding (Worbes1989, 1999; Callado et al. 2001), photoperiod (Borchert 1999; Callado et al. 2001, 2004), stem apical phenology (Borchert 1999; Callado et al. 2001, 2004), stem (Fahn 1995; Callado et al. 2013), and endogenous rhythms (Fahn 1995; Callado et al. 2001). Recent revision papers about cambial activity in South America found that most of the studied species exhibit periodicity of annual growth mainly influenced by rainfall seasonality (Callado et al. 2013, 2014).

Previous studies of the genus *Centrolobium* found climatic influence on the periodicity of annual radial growth of *C. microchaete* (Mart. ex Benth.) H. C. Lima and *C. tomentosum* Guill. ex Benth from dry forests (Tomazello Filho et al. 2004; Lisi et al. 2008; López and Villalba 2010), but the growth behavior of species of *Centrolobium* in Ombrophylus Dense Forest is unknown. Thus, we investigated stem growth dynamics of *C. robustum* (Vell.) Mart. ex Benth through leaf and cambial phenology aiming to answer the following questions: (1) Does species show growth periodicity in humid forest (Ombrophylus Dense Forest)? (2) Are cambial and leaf phenological rhythms related? (3) How do environmental factors influence tree growth? (4) Is there a relationship between tree age and stem growth?

Materials and methods

Species, sampling, and site

Centrolobium robustum is an important representative in remnants of Atlantic Forest and has a restricted distribution, being found only in southeastern Brazil (Lima 1985; Carvalho 2003). This species is often recommended for reforestation, urban landscaping, and its wood can be used in the manufacture of luxury furniture and building construction (Inoue et al. 1984; Carvalho 2003).

The study was conducted at Reserva Biológica do Tinguá, in Nova Iguaçu, Rio de Janeiro State, Brazil ($22^{\circ} 28'$ – $22^{\circ} 39'$ S and $43^{\circ} 13'$ – $43^{\circ} 34'$ W), a well-preserved remnants of Atlantic Forest. Observations were made in 2004–2005, 2005–2006, 2009–2010, and 2010–2011, for a total of four years of study (Table 1). Twelve straightboled, emergent, adult trees of *C. robustum* with heights exceeding 30 m were selected for dendrochronological investigation. Ten of the trees were selected for apical phenological investigation due to their integrity and canopy visibility. The number of trees used for cambial investigation varied over the study years: in 2004–2005, five trees were selected; in 2009–2010, five more trees were observed for phenological investigation; in 2010-2011, two of these ten trees were monitored for ultrastructural analysis. Rainfall and temperature data from Nova Iguacu were obtained from SOMAR Meteorologia. Photoperiod data were obtained from the Observatório Nacional do Rio de Janeiro. A water balance diagram was constructed following the recommendations of Walter et al. (1975). The photoperiod at the study site varied annually such that the days were 2:47 h longer in December than in June. The mean temperature at the study site is 23.4 °C and the mean annual rainfall is 1551 mm. The dry season occurs from May to September and the wet season occurs from October to April. During the study period (2004-2011), the mean annual rainfall was 1345 mm; however, 2009-2010 showed abnormal rains, with an annual rainfall of about 2000 mm (Fig. 1).

Leaf phenology

Leaf phenology was monitored monthly for three years (Table 1). For determining phenophases (mature leaves, senescent leaves, leaf abscission, and leaf flushing), the Fourniers intensity index was used, in which the phenophases were scored from 0 to 4, corresponding to 0, 1–25, 26–50, 51–75, or 76–100 % of leaves (Fournier 1974; Bencke CSC and Morellato LPC 2002). These indexes were also used to estimate the total percentage of leaves on the tree canopy, regardless of their phenophase. The indexes of leaf flushing, senescent leaves, and leaf abscission synchrony of the ten trees were calculated using the equation of Augspurger (1983) for each study year.

Cambial phenology

Stem samples containing cambium and recently formed xylem and phloem were collected in a non-destructive method using a saw, chisel, and hammer at a height of 1.30 m above the ground (diameter at breast height - DBH). Samples were collected quarterly for the three years of the study (Table 1).

Light and electron microscopy were used to identify the growth and dormancy periods using the morphology of the cambium and xylem and phloem cells. The presence of callose in sieve tubes and the full lignification of xylem cells were used as proxy for dormancy, while the observation of cell divisions and lignin gradation indicated cambial activity. For bright-field and fluorescence microscopy analysis (Table 1), the samples were fixed in formalin-acetic acid-50 % ethanol or CRAF III (Sass 1958), dehydrated in an ascending alcohol series (Johansen 1940) and embedded in plastic resin (Historesin[®]). Samples were sectioned with a rotary microtome at a thickness of 2–5 µm

Years of study	Leaf phenology	Cambial activity				Microscopy techniques
	Months	Winter (DS)	Spring (WS)	Summer (WS)	Autumn (DS)	
2004-2005	Jul–Jun	July	Oct	Feb	May	Bright-field; fluorescence
2005-2006	Jul–Jun	_	_	_	_	_
2009-2010	Jul–Jun	Aug	Nov	Feb	May	Bright-field; fluorescence
2010-2011	_	Aug	Nov	Feb	May	Bright-field; transmission electron

Table 1 Periods, years, and months in which leaf and cambial phenology were monitored, and how microscopy techniques were used during each period

DS Dry season, WS wet season

along the radial longitudinal and transversal planes. Histological sections were stained with toluidine blue O (Feder and O'Brien 1968) and with the fluorophores Auramine O. for lignin, and Aniline Blue, for callose (Barros and Miguens 1998; Ruzin 1999). Analyses with bright-field microscopy were performed on an Olympus BX 41 light microscope and images were taken with a O Color R3 video camera using Image-Pro Express 6.0 software. Fluorescence microscopy images were obtained using an Olympus BX 50 microscope equipped with a Cool Snap-PRO video camera and Image-Pro Plus 4.0 software. The fluorescence of the Auramine O fluorophore was observed with the blue excitation filter (470-490 nm) and yellow emission filter (515–565 nm) (Barros and Miguens 1998), and the Aniline Blue fluorochrome was observed with ultraviolet excitation filter (330-365 nm) and blue emission filter (455-480 nm) (Ruzin 1999).

For analysis under transmission electron microscopy, samples were fixed in solution of 2.5 % glutaraldehyde, 4.0 % formaldehyde, and 0.05 M sodium cacodylate buffer at pH 7.2 (Da Cunha et al. 2000). Subsequently, the samples were washed in the same buffer, post-fixed in a solution of 1 % osmium tetroxide, buffered with 0.05 M sodium cacodylate at room temperature, dehydrated in acetone, and embedded in epoxy resin (Epon 812 Polybed[®], Warrington, USA) (Luft 1961). Some samples were washed and post-fixed with potassium permanganate at a concentration of 0.05 mg/mL (Mérida et al. 1981). Ultra-thin sections of 70-80 nm were collected on 300-mesh copper grids, contrasted with 5 % uranyl acetate and lead citrate (Reynolds 1963). Images were obtained using a Zeiss TEM-900, transmission electron microscope (Oberkochen, Germany) under 80 kV.

Dendrochronology

For tree ring analysis, two to four samples were obtained from each tree in a non-destructive method using a Pressler probe at DBH. All the study trees had samples that reached the pith. Samples were fixed on a timber holder, kept at room temperature until complete dehydration, and then polished on the transverse face (Stokes and Smiley 1968) with successive sandpapers (grit size $36-600 \text{ cm}^{-2}$). Tree ring boundaries were marked under a Coleman XTB/3AT stereomicroscope and each sample was scanned at 600 dpi using an HP Photosmart C4680 flatbed scanner. Tree rings were measured on the obtained images using Image-Pro Plus 4.5 software. Measurements of tree ring series within the same tree were crossdated (Stokes and Smiley 1968) using visual and statistical techniques with COFECHA software (Holmes 1983; Grissino-Mayer 2001). For removing the low-frequency trend of the series (Grissino-Mayer 2001), we used different spline curves. We tested spline lengths from 1 to 40 years in order to determine the spline rigidity that led to the highest interseries correlations (Brienen and Zuidema 2005). Tree age was estimated through tree rings counting, and their annual growth rates were determined from the tree ring width mean. The correlation between the estimated age and stem diameter at DBH was tested using Spearman's test (Zar 1999).

Results

Leaf phenology

The studied species exhibited deciduous behavior at the study site. All trees showed high phenological synchrony in the first 2 years of the study and lower synchrony in the third study year (Table 2). Leaf senescence was detected during the dry and cold periods, followed by leaf abscission at the end of this period. Leaf flushing occurred during the onset of the rainy season (Fig. 1). However, in the third year of the study (2009-2010), we observed the anticipation of leaf senescence. This phenophase began in the middle of the rainy season (January) in 50 % of the monitored trees. In the late rainy season (March), 80 % of the trees showed leaf senescence (Fig. 1). From those late trees, 60 % had leaf fall and immediate leaf flushing (March and April). In the other remaining trees, the senescence period lasted until the beginning of the dry season (Fig. 1).



Fig. 1 Mean monthly precipitation, temperature, and photoperiod from study period in association with phenological behavior and radial growth of Centrolobium robustum. a Photoperiod; b Climatic diagram (following the recommendations of Walter et al. 1975). Filled areas show the periods with water excess; hatched areas show periods with water deficit. c Time course of leaf phenology; d Periods of cambial activity and dormancy. Arrows indicate the periods when analyses were performed

Table 2 Indexes of synchronyof leaf phenological behavior	Indexes of synchrony						
among the studied	Years/Phenophase	Leaf flushing (%)	Senescent leaves (%)	Leaf abscission (%)			
Centroloblum robusium aces	2004–2005	100	91	95			
	2005-2006	86	94	81			
	2009-2010	71	79	66			

Cambial phenology

Variation in the number of cell layers and cell anatomy in the cambial zone revealed an annual period of cambial dormancy and, consequently, seasonality in cambial activity, in spite of abnormal leaf phenological behavior in 2009–2010.

The period of cambial dormancy was characterized by the reduction of cell layers in the cambial zone and by the thicker walls and wider lumens of these cells (Figs. 2, 3). Numerous minute vacuoles (Fig. 4), as well as nuclei in interphase, were observed in the cells of the cambium zone (Fig. 5). In addition, secondary xylem cells adjacent to the cambial zone had completely lignified walls (Fig. 6), corresponding to latewood produced at the end of the period of cambial activity (Fig. 7). In the phloem adjacent to the cambial zone, callose blocking the sieve plates of sieve tube elements was observed (Figs. 8, 9).

In the period of cambial activity, there was an increase in cells layers in the cambial zone (Figs. 10, 11). During this period, we observed several cell divisions in the cambial zone (Fig. 12) and pectin deposition in the middle lamella occurred irregularly (Fig. 13). The cells of the cambial zone had narrower and thinner walls (Fig. 14) compared to those observed during the dormancy period (Fig. 4). The Auramine O fluorophore highlighted a gradient of cell wall lignification in the secondary xylem adjacent to the cambial zone (Fig. 15). In the active periods, there was no callose deposition in the sieve plates of sieve tube elements near the cambial zone. Furthermore, narrow bands of parenchyma 3–4 cells wide were formed during these periods, characterizing the marginal parenchyma bands as initial in *C. robustum* wood.

We observed that new leaf production and cambial activity occurred in the same period, and they were influenced by environmental factors. The largest number of cell layers in the cambial zone was observed when the trees had a high percentage of mature leaves in the canopy, while cambial dormancy coincided with the period of senescence and leaf fall (Fig. 1). Moreover, the periods of both cambial and apical dormancy were observed in the dry, cold months with shorter days, whereas cambial and apical activity coincided with warmer, wetter months, when days were longer (Fig. 1). In 2009-2010, the most intense cambial activity period (November) coincided with a high percentage of mature leaves in the canopy. Cambial activity continued until the subsequent sampling in February, in spite of the anticipation of leaf senescence until January of 2010. We point out that although rain intensity was higher in 2009-2010, the wet season occurred during the same months in the three years of study (Fig. 1).

Dendrochronology

Cambial seasonality indicated the periodicity of wood production and demonstrated that tree ring formation follows an annual growth rhythm. According to this seasonal growth, the species showed distinct tree rings both macroand microscopically. Tree rings were marked by thickwalled and radially flattened fibers in latewood and narrow initial parenchyma bands (Fig. 7). Vessel elements of much reduced diameters were also identified in tree ring boundaries (Fig. 7).

The average intercorrelation among samples within the same tree was 0.55 and the intercorrelation among all tree samples was 0.24 (Table 3). The average radial growth rate was 2.56 (\pm 0.40) mm/year. The youngest tree was 62-year old, while the oldest was 121 years (Table 3). No relationship was found between age and stem diameter (r = 0.300, p = 0.343), since some young trees had greater diameters than older trees (Table 3).

Discussion

Well-defined phenological behavior may reflect the responses of plants to environmental periods that are favorable and unfavorable for growth (Lipschitz and Lev-Yadun 1986). The analysis of the growth rhythm of C. robustum corroborated the associations between leaf and cambial phenology and between plant phenological behavior and environmental variables. Leaf abscission and cambial dormancy of all trees occurred in the drier, cooler periods with shorter days, which allowed us to identify such periods as being unfavorable for C. robustum growth. In contrast, an increase in these variables characterized favorable periods, when all the trees showed apical and radial growth. Unfavorable environmental periods promoted leaf abscission, and consequently determined cambial dormancy in C. robustum. Similar to our findings, other studies in tropical environments have shown that leaf abscission and cambial dormancy are mainly associated with water deficit and short day length (Worbes 1995; Borchert 1999; Morellato et al. 2000; Borchert and Rivera 2001, 2005; Marcati et al. 2006; Bianchini et al. 2006; Callado et al. 2014; Costa et al. 2013.

Aloni (2007) links the production of dormancy callose to increase in cytokine levels relative to auxin levels, which are lower due to leaf abscission. In early growth recovery, the absence of callose plugs in sieve plates of sieve tube elements near the cambial zone is associated with leaf flushing. In *C. robustum*, the formation of callose plugs was observed only in the phloem-conducting cells near the dormant cambium. This callose can be attributed to the low percentage of leaves during this period, whereas its absence



Figs. 2–9 *Centrolobium robustum* during the period of cambial dormancy. **2–3** Cross and longitudinal radial sections, respectively, of the cambial zone (CZ) and adjacent newly formed xylem (X) and phloem (P). **4** Cross section of a fusiform cell in the cambial zone containing numerous vacuole formations (*dashed arrow*), observed under transmission electron microscopy. **5** Interphase nucleus found in a fusiform initial cell observed by transmission electron microscopy. **6** Cross section of secondary xylem with the cambial zone stained with Auramina O. The open arrow indicates the complete lignification in the xylem cell walls during this period. **7** Cross section of the wood showing the edge of a tree ring, the fibrous zone (FZ), the band of initial parenchyma (*white arrow*), and the vessel elements with very small diameters. **8–9** Cross section of phloem stained with Aniline Blue **8**. Note the presence of callose in the plates of the sieve tube elements near the cambial zone (*white arrows*). **9** Details of a plate riddled with callose deposition. **2–3**, **6** and **8–9** scale bar = 50 µm; **4** scale bar = 2 µm; **5** scale bar = 500 nm; **7** scale bar = 100 µm

during cambial activity can be explained by removing it after the beginning of ethylene production in response to high levels of auxin produced by buds (Aloni 2007). Assessment of tree rings found one living tree older than 120 years, revealing the potential longevity of *C. robustum* in remnants of Atlantic Forest. Based on tree ring analysis,



Figs. 10–15 *Centrolobium robustum* during cambial activity. 10–11 Radial and longitudinal sections of the cambial zone (CZ), respectively, and adjacent tissues in differentiation: xylem (X) and phloem (P). 12 Cross section of a fusiform cell in the cambial zone with newly formed periclinal walls. 13 Cross section of the cambial zone showing the middle lamella between initial cambial cells with irregular distribution of pectin (*dashed arrows*). 14 Initial cross section of fusiform cells in the cambial zone showing periclinal walls (*white arrow*) that are thinner than the anticlinal walls (*black arrow*). 15 Cross section of the secondary xylem near the cambial zone stained with Auramina O. The open arrow indicates the process of lignification of the cell walls. 10–11 and 15 *scale bar* = 50 µm; 12 *scale bar* = 1 µm; 13 *scale bar* = 2 µm; 14 *scale bar* = 8 µm

we also found no relationship between tree age and stem diameter of *C. robustum* in the Atlantic Forest. This lack of relationship was also observed in other studies, and there has been an indication that this relationship can vary according to growth site (Brienen and Zuidema 2006; Shimamoto et al. 2014; Costa et al. 2015). Nonetheless, studies on forest age structure are generally performed through evaluating tree diameter (Pires-O'Brien and O'Brien 1995; Sokpon and Biaou 2002). Therefore, we suggest that studies of tree age of different populations should be based on counting the annual tree rings, and that estimates based just on tree diameter should be avoided.

The anticipation of leaf senescence in 2009–2010 may have been influenced by the abnormal rainfall rates observed in this period in the state of Rio de Janeiro, which was attributed to the El Niño phenomenon (INPE 2009; Lopes et al. 2011). The Instituto Nacional de Pesquisas Espaciais report (INPE 2009) points out that 2009 was marked by abnormal rainfall in southeastern Brazil. The main weather systems responsible for these anomalies were

Trees	Interseries correlation	Spline curves	Number of rings	Mean radial increment (mm/year)	Stem diameter (cm)
1	0.585	25	62	2.82	46
2	0.580	5	68	2.59	56
3	0.554	10	62	3.20	54
4	0.176	3	121	2.33	71
5	0.600	5	103	2.36	73
6	0.483	5	86	2.07	54
7	0.553	10	71	2.19	76
8	0.690	5	62	3.25	64
9	0.289	20	78	2.14	44
10	0.799	3	74	2.32	41
11	0.698	5	70	2.83	45
12	0.612	5	87	2.68	64
All trees	0.240	3	-	2.56 (±040)	57 (±12.13)

Table 3 Results of cross-dating control by COFECHA (intercorrelation values between samples from same tree and spline rigidity used), number of rings, average radial increment, and stem diameter of the study trees

the Intertropical Convergence Zone, high temperatures and high humidity, and the South Atlantic Convergence Zone. These systems contributed to higher than average rains in the state of Rio de Janeiro (INPE 2009), which seems to have caused soil water accumulation and, consequently, abnormal leaf phenological behavior in C. robustum. Water saturation leads to soil hypoxia or anoxia because air spaces are filled with water, which reduces oxygen absorption by the roots (Kozlowski and Pallardy 1997; Larcher 2006; Salisbury 2012; Ashraf 2012). The shortage of oxygen in the roots inhibits ethylene synthesis in this organ (Jackson 1985), but stimulates its synthesis in leaves (Salisbury 2012). Ethylene accumulation in large amounts in leaves induces, among other things, their senescence and abscission (Jackson 1985; Morgan and Drew 1997; Larcher 2006; Salisbury 2012; Taiz and Zeiger 2013). Immediate leaf flushing after a period of abnormal rainfall was also observed by Borchert and Rivera (2001) in deciduous and brevi-deciduous species.

We point out that trees of *Cedrela odorata* L. developing in the same study site during the same period (Costa et al. 2013) exhibited the same periods of cambial activity and dormancy as *C. robustum*, but did not exhibit anticipation of leaf senescence in response to the abnormal rainfall of 2009–2010. The difference in phenological leaf response between these species may be associated with the restricted geographical distribution of *C. robustum* (Pirie et al. 2009) in relation to *C. odorata*. This last species has a widespread distribution and possesses a conservative growth rhythm, as discussed by Costa et al. (2013). Callado et al. (2001) also investigated cambial and leaf phenological behavior of four species in a swamp in the Atlantic Forest of the state of Rio de Janeiro. They reported that only *Tabebuia cassinoides* (Lam.) DC had an extra period of leaf shedding due to the El Niño event, and it was the species with the most restricted distribution among the species included in their study. Like *C. robustum*, differences in secondary xylem formation during the abnormal period were not observed for *T. cassinoides*.

In conclusion, results revealed that *C robustum* (Vell.) Mart. ex Benth exhibits annual stem growth periodicity in Ombrophylus Dense Forest. Cambial activity occurred when the canopy had mature leaves and the days were warmer, wetter, and longer. The annual growth periodicity permitted the investigation of tree rings in order to determine tree age and growth rates. We did not observe a relationship between tree age and stem diameter. Responses of species to stochastic climatic events demonstrate that species with restricted geographical distributions seem to be more susceptible to environmental changes.

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