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Axial variation in the cambium anatomy of *Schizolobium parahyba* var. *amazonicum*

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Abstract: *Schizolobium parahyba* var. *amazonicum* (paricá) is a promising forest species that has been planted in some states of the Amazon region in Brazil, to meet the demand of the plywood panel industry. The present work involves a study of the variations of the cambium and their impact on derivative tissues at different heights in the stem of *S. parahyba* var. *amazonicum*. Except for the tangential diameter of the fusiform initials (DFI) and the width of the xylem cell layer in differentiation (WXD), there was significant statistical variation between the evaluated axial positions for all anatomical parameters of the cambium. A strong positive correlation was noticed between the length of the fusiform initials (LFI) with ray height (RH) [$r=0.79$, degree of freedom (DF) = 7, $P<0.05$], vessel element length (VL) ($r=0.78$, DF = 7, $P<0.05$) and fiber length (FL) ($r=0.74$, DF = 7, $P<0.05$). The results of this study give quantitative support that the LFI is an important prognosis, not only for the VL and FL, but also for the rays, in hardwood species.

Keywords: axial variation, cambial initials, paricá wood, xylem differentiation

Introduction

Schizolobium parahyba var. *amazonicum* (Huber ex Ducke) Barneby is locally known as “paricá”. It is a woody species that belongs to the Fabaceae family (Barneby 1996; Lewis 2015) and naturally occurs in the amazon rainforest of Brazil, Peru, Bolivia and Venezuela (Carvalho and Viegas 2004). Paricá is the second most planted native species in the Amazon, 900.47 km^2 (IBÁ 2017). The species has been the focus of several research works, experimental or entrepreneurial. In the Amazon region, commercial plantations with the species in the region are recent (beginning in 1994 to 2001) and since then the research has been growing due to the demand of the plywood panel industry, for which the species is of proven use (Falesi and Galeão 2002; Marques et al. 2006).

The high variability of the wood properties is challenging for the wood industry to master how to efficiently process this raw material. The wood properties depend fundamentally on understanding the production and differentiation processes of the xylem cells (Whetten and Sederoff 1991). During the process of xylogenesis, characteristics of the xylem cells are partly determined by the dimension of the cambial initials and partly by the changes that occur during the cellular differentiation to constitute the xylem (Ridoutt and Sands 1993, 1994; Rathgeber et al. 2016).

Available literature indicates that there are very few studies that have evaluated the quantitative modifications in the cells of the cambium even though there is a relationship between the anatomy of the cambium and the wood. Those studies, however, have clearly demonstrated that there is variation, either in the dimension or quantity of cambial initials, in function of genetic and environmental factors and/or resulting from tree’s own development (Aref et al. 2014; Morel et al. 2015; De Vasconcellos et al. 2016; Marcati et al., 2016) and that these variations can influence the size and quantity of xylem cells (Ridoutt and Sands 1993; Larson 1994; Khan and Badruzzaman Siddiqui 2007; Patel et al. 2014).

While there is plenty of knowledge on the function and differentiation of primary growth meristems (apical and root meristems) based on studies in annual plants such as Arabidopsis (Ramos and Regan 2018), histological studies of the cambium for understanding wood structure and ecological responses of plants, mainly on tropical species, are still scarce (Callado et al. 2014; De Vasconcellos et al.

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2016). In the Amazon rain forest, which comprises around 14 003 species, nearly 6727 of which are trees (Cardoso et al. 2017), this process is even less understood given the high biodiversity of this region.

The present work involves a study of the variations of the cambium and their impact on derivative tissues at different heights in the stem of *S. parahyba* var. *amazonicum*.

Materials and methods

Three *S. parahyba* var. *amazonicum* trees were selected for the experiment. The trees were 21 years old coming from a enrichment planting in logging gaps, located in the county of Dom Eliseu, southeast mesoregion of the state of Pará, Brazil (4°30′48″S and 47°39′36″W). The original vegetation was denominated as submontane dense forest (IBGE 2004). The average temperature in the region is 25.4°C with an annual precipitation of 1755.1–2160.0 mm. The months of highest water deficiency are from August to October (150.2–266.8 mm), highest rainfall from February to March (750.1–1200 mm) and lowest rainfall from July to September (63.7–200 mm) (Monteiro 2013; Pismel et al. 2016). The average altitude in the study area is 320 m above sea level (masl) and the most common soil type found in the site is yellow Oxisol (Veloso et al. 1991; Sudam 1993; Embrapa 2006).

The experimental site underwent selective logging in 1995, in an area of 158 ha, which created the clearings, 108.0 ha of which served as treatment to conduct enrichment planting with “paricá” seeds in the same year (detailed in Schwartz et al. 2017).

The sample collection was made on March 17, 2016, during the growing period, i.e. the period of highest precipitation and best soil water availability (Monteiro 2013; Pismel et al. 2016). Stem samples containing recently formed cambium, xylem and phloem were collected from three individuals of *S. parahyba* var. *amazonicum*, free from bifurcations or apparent deformities. Samples were extracted from living trees at breast height using an increment borer (Pressler borer). Tree height was 15.2 m, 18.5 m and 21 m, with an average commercial height of 18.2 m (±2.9). The commercial height was considered as the length measured from the base of the tree until the first significant insertion of branches (Santos et al. 2001). The average tree diameter at breast height (DBH) was 40.6 cm (±12.3). The sampling was done in three levels of the commercial height, the base, middle and top (axial variation) of every individual (Table 1).

Sampled cores were fixed in a mixture of 2.5% glutaraldehyde, 4.0% formaldehyde and 0.05 M sodium cacodylate buffer at pH 7.2 (Da Cunha et al. 2000), dehydrated in an ascending alcohol series (Johansen 1940) and embedded in Historesin® (Leica Biosystems, Wetzlar, Germany) (Feder and O’Brien 1968). After embedding, the samples were sectioned on a rotating microtome Leica RM2245 (Leica Biosystems, Wetzlar, Germany) in transverse and tangential planes, with thickness varying from 3 to 5 μm along the cambium zone. Histological sections with 10 μm of thickness were also obtained from the same samples in the tangential longitudinal plane of the xylem, which was already differentiated, near the cambial zone. The histological sections in the tangential longitudinal plane of the cambial zone and xylem were used for counting and measuring the rays. Fibers and vessel elements were measured from macerated material in accordance with a method proposed by Franklin (1945).

Table 1: Diameter measurements at each evaluated tree height.

Levels of the commercial height	Diameter (cm)		
	Tree 1	Tree 2	Tree 3
Top	21.3	19.7	38.8
Middle	29.3	31.5	47.7
Base	34.4	35.6	54.7

Bright-field and fluorescence microscopy were used to verify the active and dormancy status of cambium. For the bright-field microscopy analysis of the cambium, the histological sections were stained with O-toluidine blue 0.05% (O’Brien et al. 1964) and analyzed in an Olympus BX 41 light microscope (Olympus, Tokyo, Japan). The Auramine fluorochrome-O was used to detect the presence of lignin. The fluorescence images were captured in a laser scanning confocal microscope LSM 780 with a transmitted light-PMT system and software Zen 2010 (Carl Zeiss, Oberkochen, Germany) using an objective EC Plan-Neofluar 10x/0.3 M27, detector ChS1, beam splitter MBS 488 nm with 0.2% of laser, with a blue excitation filter (470–490 nm) and a yellow emission filter (515–565 nm) (Barros and Miguens 1998).

The important characteristics of cambium were evaluated according to De Vasconcellos et al. (2016), and the parameters were: NCC, number of cellular layers in the cambial zone; WC, width of cambial zone (μm); RDF, radial diameter of fusiform cells (μm); WXD, width of cellular layers of xylem in differentiation (μm); LFI, length of the fusiform initials (μm); DFI, tangential diameter of the fusiform initials (μm); HCR, height of cambial rays (μm); HCRc, height of cambial rays (number of cells); WCR, width of cambial rays (μm) and WCRc, width of cambial rays (number of cells). The anatomical characterization of the wood followed the guidance of the International Association of Wood Anatomists (IAWA) Committee (1989), and the parameters were: VL, length of vessel elements (μm); FL, fiber length (μm); RH, ray height (μm); RHc, ray height (number of cells); RW, ray width (μm) and RWc, ray width (number of cells). A total of 25 counts and measurements were carried out for each of the anatomical parameters of cambium and wood that were made using the software Image-Pro Express 6.0 (Media Cybernetics, Rockville, MD, USA).

The data were grouped by sampled tree height and statistically analyzed aiming to identify the significant variations in cambial cells among the evaluated heights. The data were adjusted to a generalized linear model (GLM). The continuous anatomical variables of the cambium were adjusted to GLM assuming a Gaussian distribution (in cases where the data were normally distributed by the Shapiro-Wilk test at 5% of significance for normality) or gamma distribution (in cases where the data were not normally distributed by the Shapiro-Wilk test). For the anatomical parameters where discrete values were found, the GLM was adjusted using the Poisson distribution. All GLMs were submitted to residual analysis as a way to evaluate the adequacy of error distribution. Contrast analysis was then undertaken to test pairwise differences (Crawley 2013). From the average values obtained at the different heights of each tree, Pearson’s correlation and linear regression analysis was performed between the quantitative anatomical characteristics of cambium and xylem. All statistical tests were run at a 5% significance level using the software R, version 3.0.1 (R Development Core Team 2013).

Results and discussion

Anatomical axial variation in the cambium of *S. parahyba* var. *amazonicum*

Schizolobium parahyba var. *amazonicum* cambium showed NCC of 5–23 layers of fusiform initial cells, WC of 41–201 μm of length and large WXD, with thin-walled vessels still in the process of cellular expansion, which are adjacent to the cambial zone and were 226–817 μm of width (Table 2, Figure 1a–b). The fusiform initials were not stratified, elongated, with an LFI of 265–831 μm, DFI of 15–36 μm (Figure 1b) and RDF of 4–16 μm (Table 2). The cambial rays were also not stratified, with an average HCR of 137–782 μm and HCRc of 7–43 cells, and the average WCR was 24–98 μm disposed in a series of three (29%), four (7%) or five (7%) cells (Table 2, Figure 1b).

The cambial histology of the evaluated individuals showed characteristics of cambial activity, evident from the presence of many anticlinal divisions in the ray and fusiform initials (Figure 2a), and additionally by the presence of a large region of xylem cells in differentiation (Figures 1a and 2b). Fluorescence microscopy revealed that the cambial activity was present along the whole tree height; this could be proved by the existence of a gradient of lignification of the walls of xylem cell in differentiation, such as vessels and associated

Table 2: Quantitative anatomical parameters (mean and standard deviation) of the cambium structure of *S. parahyba* var. *amazonicum*.

Anatomical parameters of the cambium	Average values/standard deviation
NCC – Number of cellular layers in the cambial zone	14 ± 3
WC – Width of cambial zone (μm)	116 ± 23
RDF – Radial diameter of the fusiform initials (μm)	8 ± 1
WXD – Width of cellular layers of xylem in differentiation (μm)	435 ± 93
LFI – Fusiform initials length (μm)	539 ± 71
DFI – Tangential diameter of the fusiform initials (μm)	25 ± 1
HCR – Height of cambial rays (μm)	352 ± 63
HCRc – Height of cambial rays (number of cells)	21 ± 3
WCR – Width of cambial rays (μm)	55 ± 14
WCRc – Width of cambial rays (number of cells)	4 ± 0.5

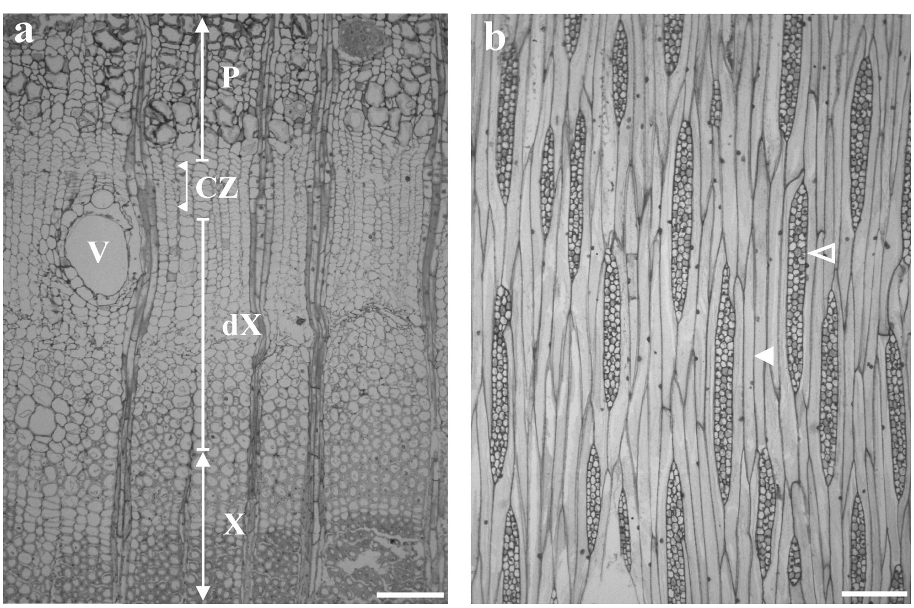

Figure 1: Cross section and and longitudinal tangential section of the cambium from stem of *S. parahyba* var. *amazonicum*.
(a) Stem transverse section with xylem and phloem recently differentiated, evidencing the cambial zone (CZ) and centrifugally differentiating xylem (dX) with vessel elements being the first structures to undergo differentiation (V). (b) Tangential longitudinal section of the cambium evidencing fusiform initials (full arrow) and cambial rays (empty arrow). Phloem (P) and differentiated secondary xylem (X). Scale bar: (a–b) 150 μm.

parenchyma cells, which were adjacent to the cambial zone, and were observed in the cambium histology (base to top) (Figure 2c–d).

Cambial activity has been demonstrated to be mainly affected by the rainy season in tropical forests (Die et al. 2012; Pumijumnong and Buajan 2013; Patel et al. 2014). According to Callado et al. (2013), the rain seasonality is the main trigger of cambial activity in woody species from the tropics and subtropics of South America.

Anatomical characteristics that indicate cambial activity in the month in the studied species, a large number of immature xylem cells differentiating and a cambial zone with cambial initials in intense division were also described by Marcati el al. (2008) for the active cambium of the same

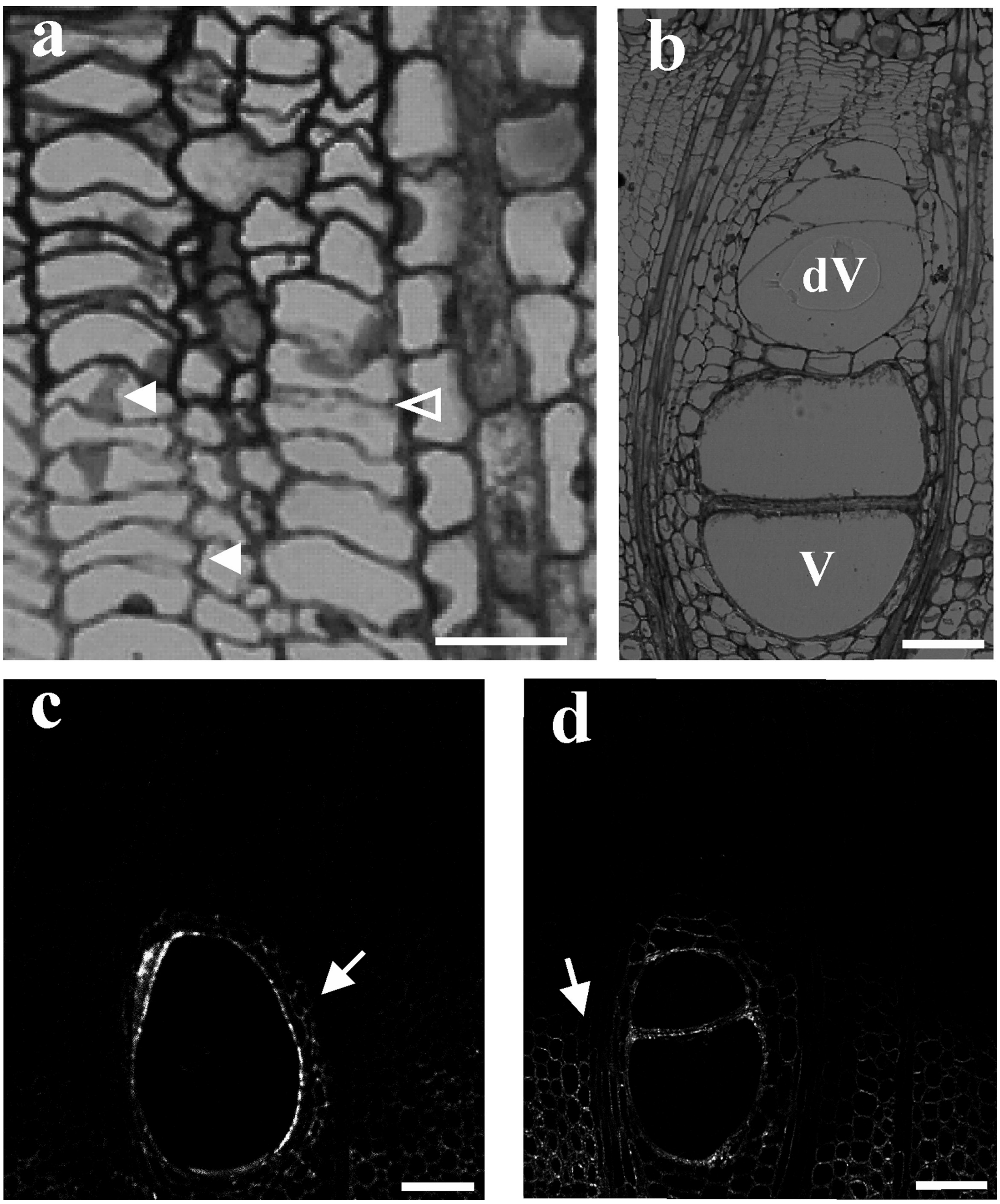

Figure 2: Characteristics of cambial activity in *S. parahyba* var. *amazonicum* in the month of collection.
(a) Cambial zone showing fusiform initials in anticlinal division (full arrow) and in periclinal division (empty arrow). (b) Secondary xylem next to the cambial zone, evidencing the formation of a group of vessels in differentiation (Dv) and vessels multiple of two already differentiated (V). (c–d) Gradient of lignification of the cell walls of the xylem in differentiation (adjacent to the cambial zone) stained with Auramine O (arrow), implying cambial activity in different axial positions of the stem of *S. parahyba* var. *amazonicum*. (c) 100% of commercial height; (d) 0% of commercial height (base). Scale bar: (a) 30 μm, (b–d) 100 μm.

species, *S. parahyba*, in a semi-deciduous seasonal forest in the state of São Paulo. In the county of Dom Eliseu, March is the month of highest precipitation (750–1200 mm) (Monteiro 2013; Pismel et al. 2016), which, according to Marcati et al. (2008), leads to the cambium activity for this species that arises in a period of the year with a higher precipitation index and high soil water content.

The Auramine O fluorophore highlighted a gradient of cell wall lignification in the secondary xylem undergoing differentiation, mainly by vessels. General results of cambial activity and xylem structure in *Arabidopsis* have shown that the vessel elements mature very quickly after being produced in the cambial zone (Chaffey et al. 2002). This characteristic of vessel maturation is consistent with the development of this cell in angiosperm trees such as *Eucalyptus* (Ridoutt and Sands 1994), *Populus* (Murakami et al. 1999) and *Moringa oleifera* (Patel et al. 2014).

Figures 3–5 illustrate the effect of the axial variation on the quantitative anatomical parameters evaluated in the cambium of *S. parahyba* var. *amazonicum*. The average values for the following parameters are: NCC ($P = 0.03758$); WC ($P < 0.0001$); RDF ($P < 0.0001$); LFI ($P < 0.0001$); HCR ($P < 0.0001$); HCRc ($P < 0.0001$); WCR ($P < 0.0001$); WCRc ($P < 0.0001$), all showed significant statistical variation between the evaluated axial positions; however, the analysis showed no significant effect for the average values of WXD ($P = 0.3069$) and DFI ($P = 0.1132$).

At the base, the NCC, WC and RDF presented higher average values compared to the top (Figures 3a,b,e and 4a–b), supporting the results found by Ridoutt and Sands (1994). Deslauriers et al. (2009) observed that the increase in the stem diameter of *Populus* spp. occurred along with the increase in the number of cells in the cambial zone. Die et al. (2012) state that the age difference among individuals of *Tectona grandis* led to significant differences in the width of the cambial zone in those trees. For *S. parahyba* var. *amazonicum*, the age inequality can be responsible for the differences seen in the cambium histology along the tree stems, older at the base and young at the top.

The cambial RH was longer at the base and lower at the top of the tree, while the width was shorter at the base and longer at the top (Figures 3g–j and 5a–b). In the scientific literature, an increase has been reported regarding the length of cambial rays and WCR associated with growth in diameter, as well as with the detachment from the tree canopy (Ghouse and Hashmi 1981; Iqbal and Ghouse 1987; Ajmal and Iqbal 1992; Ridoutt and Sands 1993; Myskow and Zagórska-Marek 2004). Herein, for *S. parahyba* var. *amazonicum* in the top cambium, the anticlinal divisions of the ray initials were more frequent when compared to the base of the stem, which might have contributed to wider cambial ray at the top.

The fusiform initials from the tree cambium generally demonstrate the length of inferior values at the top when compared to the base of the stems and branches (Bailey 1923; Iqbal and Ghouse 1987); this tendency also seems to occur in *S. parahyba* var. *amazonicum*. The authors Philipson et al. (1971) and Ridoutt and Sands (1993) explain that the longitudinal variations observed in the LFI can be related to many factors, such as dimensional changes, which take place in fusiform cells due to age differences in the formation of the cambium (recently formed next to the branches and older at the base and treetop); furthermore, it can also be related to an increase in stem diameter. The same authors have also mentioned that the variation in the dimension of cambial cells due to the frequency of anticlinal pseudo-transverse division, the extension of the elongation of new cambial initials and even the preferential loss of shorter fusiform initials that maturate or are converted in ray initials are all possible responses for the axial variation, base – top, of the LFI from the cambium of the trees.

Effects of the variations in the cambium on the anatomical structure of the wood

Some anatomical parameters of the cambium show a significant effect on the characteristics of wood cells. The HCR (μm), $r = 0.71$, $P = 0.0310$, and number of cells, $r = 0.79$, $P = 0.0113$, were positively correlated with RHc. For *S. parahyba* var. *amazonicum*, the increase in the average value for cambial rays led to an increase in the wood RH; in this case, the HCR, in number of cells, was the most efficient parameter to predict the variation in the RH, explaining 62% of the observed variation (Figure 6).

The variations in size observed in the rays of *S. parahyba* var. *amazonicum* are mainly associated with anticlinal and transversal cellular division of the ray initials, as well as with the union, both vertical and lateral, of contiguous cambial rays (Lev-Yadun and Aloni 1991; Lev-Yadun and Aloni 1995).

Among the evaluated anatomical parameters, the LFI was the parameter that most demonstrated significant statistical correlations with the maximum number of wood anatomical variables (Table 3).

There was a strong crescent linear tendency between the LFI and RH. The LFI from the cambium was responsible for 85% of the variation noticed in the RHc of wood (Figure 7c); there was an improvement of about 23% compared to the functional relation seen between the HCRc and the RHc of wood (Figure 6).

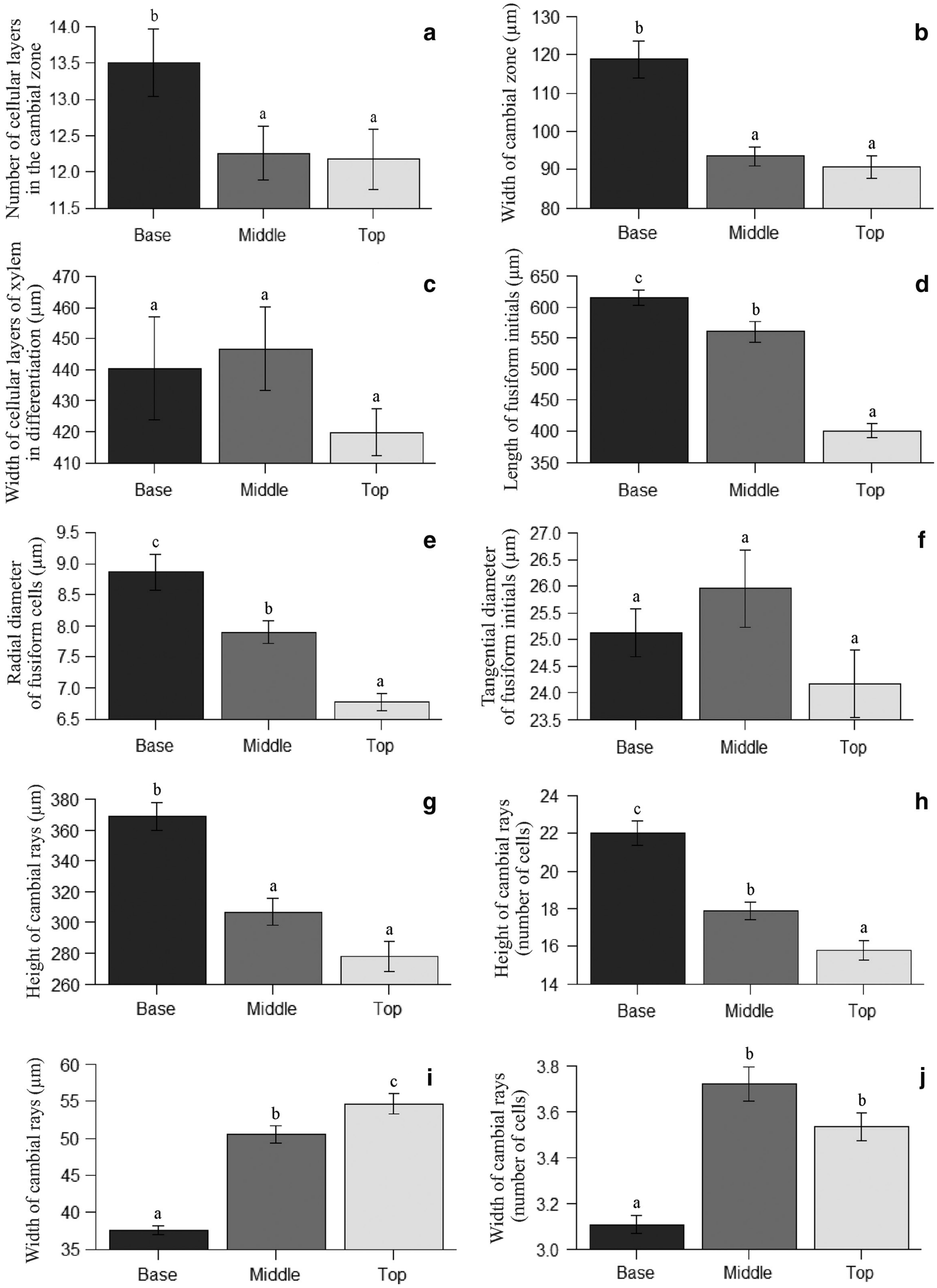

Figure 3: Averages of the quantitative anatomical parameters of the cambium between axial positions in *S. parahyba* var. *amazonicum*. Different letters show statistical differences ($P < 0.05$). (a) Number of cellular layers in the cambial zone, (b) width of cambial zone (μm), (c) width of cellular layers of xylem in differentiation (μm), (d) length of the fusiform initials (μm), (e) radial diameter of fusiform cells (μm), (f) tangential diameter of the fusiform initials (μm), (g) height of cambial rays (μm), (h) height of cambial rays (number of cells), (i) width of cambial rays (μm), (j) width of cambial rays (number of cells).

Fusiform initials can produce ray initials, either by the divisions of their ends or sides (Wilczek et al. 2011), or by segmentation or septation of a total fusiform initial or even by a part of it (Srivastava 1963; Rao 1988; Wilczek et al. 2011). For *S. parahyba* var. *amazonicum*, the LFI had a strong positive correlation with the HCR in

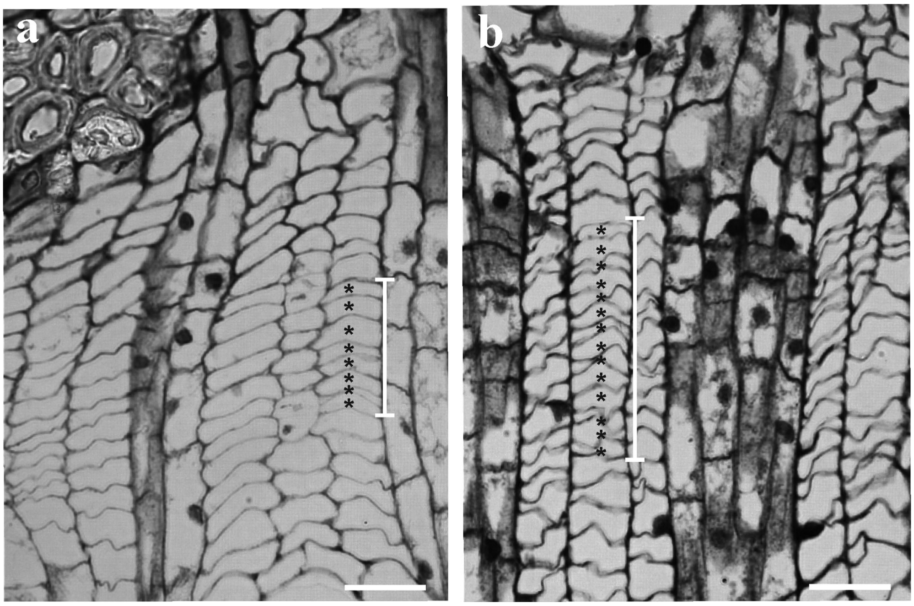

Figure 4: Cross section of the cambial zone of *S. parahyba* var. *amazonicum* showing the axial variation in the number of cell layers and the width of the cambial zone (μm).
(a) Top – note the smaller width of the cambial zone. (b) Base – greater number of layers and width of cambial zone. Asterisks differentiate fusiform cells in the cambial zone from the cells of secondary xylem and phloem in differentiation, already in an expansion process. Scale bar: 30 μm.

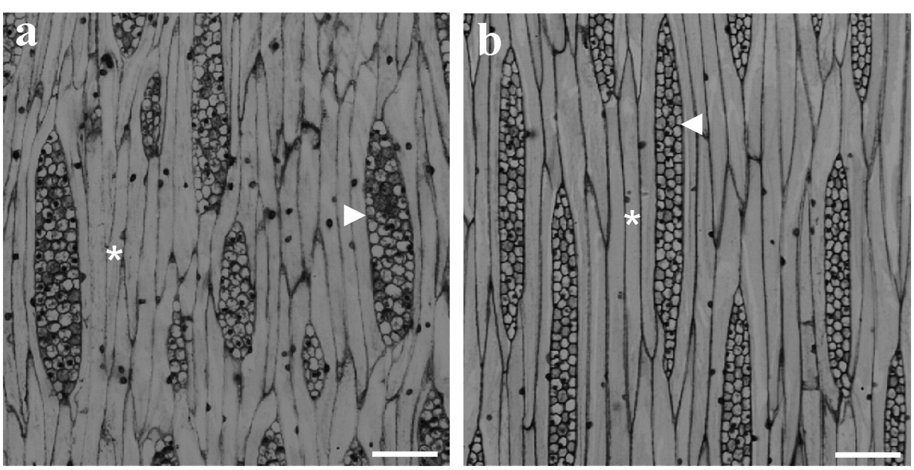

Figure 5: Longitudinal tangential section of the cambial zone of *S. parahyba* var. *amazonicum* showing axial variation in fusiform initials and rays.
(a) Top – fusiform initials are shorter, and cambial rays are shorter and wider. (b) Base – greater length in fusiform initials, and cambial rays are longer and narrower. Asterisks differentiate fusiform initials from cambial rays. Scale bar: 100 μm.

micrometers ($r = 0.71$, $P = 0.029$) and in number of cells ($r = 0.75$, $P = 0.020$), indicating that the presence of longer fusiform initials contributes to increase in the HCR, which positively affects the height of the rays in the wood.

Ridoutt and Sands (1993) who studied *Eucalyptus globulus* observed that the initiation of new cambial rays occurs due to the apical and lateral segmentation of fusiform initials. Other authors, such as Patel et al. (2014), noticed that the LFI had a strong positive correlation ($r = 0.70$) with the HCR in species of *M. oleifera*. In their study, De Vasconcellos et al. (2016), evaluating the cambium structure of *Ceiba speciosa* in two different sites, one polluted and the other preserved, also saw differentiation of the fusiform initials into radials in both sites during the cambial activity period, but only in the polluted site during the dormancy period. Lev-Yadun and Aloni (1992) suggested that the initiation

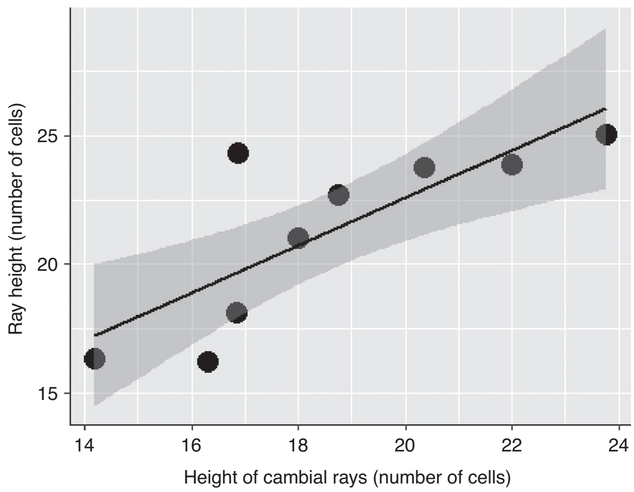

Figure 6: Functional relationship between ray height (average values) and the length of cambial rays (average values) in the axial positions of the stem of *S. parahyba* var. *amazonicum*. RH = 0.919 × HCR + 4.192, residual standard error = 2.296, R^2 = 0.623, DF = 7, F-statistic = 11.6, P-value = 0.0113.

Table 3: Pearson's correlation coefficient between the length of fusiform initials from the cambium and quantitative anatomical wood parameters.

Quantitative anatomical parameter	Length of fusiform initials from the cambium	
	r	Significance
Length of vessel elements (µm)	0.78	*
Fiber length (µm)	0.74	*
Ray height (µm)	0.79	*
Ray height (number of cells)	0.92	*
Ray width (µm)	−0.01	ns
Ray width (number of cells)	−0.18	ns

r, Pearson's correlation coefficient; *, significant; ns, not significant (P < 0.05). Adopted significance level of 5%.

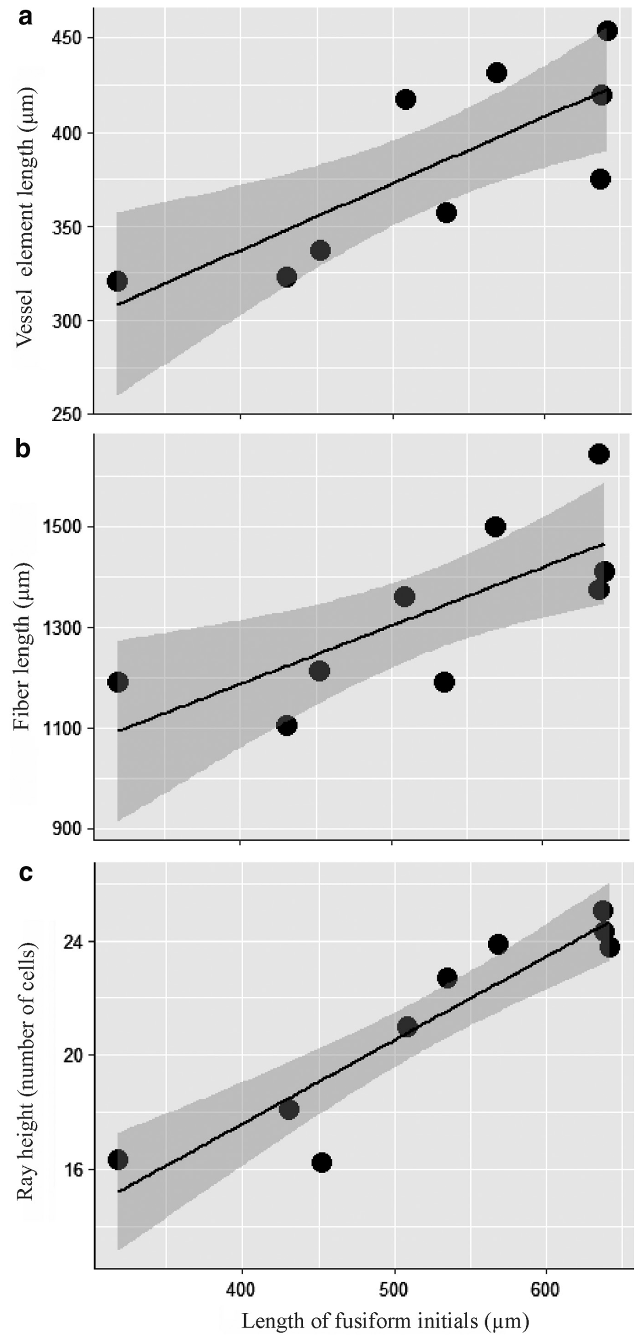

Figure 7: Functional relation between the length of fusiform initials (average values) and the length of vessel elements, fiber length and ray height (average values) in the axial positions of the stem of *S. parahyba var. amazonicum*.
(a) Length of vessel elements (VL = 0.353 × LFI + 195.9, residual standard error = 33.66, R^2 = 0.607, DF = 7, F-statistic = 10.83, P-value = 0.0133); (b) fiber length (FL = 1.155 × LFI + 725.7, residual standard error = 123.8, R^2 = 0.549, DF = 7, F-statistic = 8.52, P-value = 0.0219); (c) ray height (RH = 0.029 × LFI + 5.898, residual standard error = 1.425, R^2 = 0.855, DF = 7, F-statistic = 41.28, P-value = 0.00035) in the axial positions of the stem of *S. parahyba* var. *amazonicum*.

of rays is affected by the presence of ethylene. The rays drain the ethylene from the xylem to the periphery of the stem and thus the fusiform initials, which are not associated with the rays, are exposed to high levels of ethylene. This makes them more susceptible to reach maturity or to convert themselves into ray initials. Recently, Pramod et al. (2013) proved that the presence of high concentrations of ethylene led the fusiform initials to undergo extensive transformation into ray initials through transformative divisions and segmentation.

The LFI explained about 60% of the variation in the average values of length for vessel elements; there was a tendency of longer fusiform initials producing longer vessel elements as well (Figure 7a). There was a reduction of 27% in average values of fusiform initials (539 µm) in comparison to the average values of length for vessel elements (382 µm), indicating that vessel elements of *S. parahyba* var. *amazonicum* are always shorter than the fusiform initials of the cambium.

The LFI demonstrated a positive linear relation with FL, and was capable to explain 55% of the variation for these cells (Figure 7b). When comparing the averages of LFI (539 µm) and FL (1333 µm), there is an accentuated increase in the percentage of approximately 147%, showing that, differently from vessel elements, the FL of *S. parahyba* var. *amazonicum* is always greater than the LFI of the cambium.

The quantitative results observed supports the theory that the fusiform initials' variation in length has direct effects on the vessel elements' length (Kitin et al. 1999; Khan and Badruzzaman Siddiqui 2007; Patel et al. 2014) and on tree fibers (Bailey 1920; Ridoutt and Sands 1993, Ridoutt and Sands 1994; Khan and Badruzzaman Siddiqui 2007). The results also show that part of the variation in vessel elements' length and fibers depends on dimensional changes that occur during the cellular differentiation step of these cells. This justifies, for example, the VL and FL of *S. parahyba* var. *amazonicum* having lower and higher average values, respectively, compared to the LFI.

According to Kitin et al. (1999), the shorter VL already seen in relation to fusiform initials, as in *S. parahyba* var. *amazonicum*, can be related to a rearrangement of the extremities of the wall of these cells during differentiation, as the fusiform initials have hexagonal ends and the vessel elements have oblique and slightly transverse ends, or explained by the shortening of cambial initials that go through anticlinal divisions, which reduces its length, before it effectively concludes the cellular differentiation step. The opposite behavior observed for FL is an effect of an intrusive growing index, which is common among tree species with a non-stratified cambium, and of the extension of the cellular elongation that occurs in future fibers during cellular differentiation (Butterfield 1973; Ridoutt and Sands 1993, 1994).

Conclusion

The study on cambial tissues of *S. parahyba* var. *amazonicum* revealed that the cambium is composed of fusiform initials and non-stratified radial cells that demonstrated outstanding characteristics of activity in all evaluated axial positions (base to top).

The dimension and quantity of fusiform initials and ray initials from the cambium varied significantly in function of the tree height, reflecting the differences of the age of the cambium and of the stem diameter between the assessed heights. The variations observed in the cambium influenced the RHs, VL and FL in the wood. The results presented quantitatively demonstrate and support that the LFI is an important predictor, not only for the VLs and FL, but also for the rays, in hardwoods. The results demonstrated that the final VL and FL are determined by the variations in size that occurs during cellular differentiation.

Lastly, this is the first study conducted in a unique growth period that describes the cambium and its variations inside the tree and that quantitatively supports the understanding of the interactions of cells from the cambium of a commercial native species from the Brazilian Amazon. This demonstrates the potential to increase properties of wood in a planted forest, from the knowledge of the cambium anatomy of the species.

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