

SEASONAL VARIATION IN WOOD FORMATION OF *CEDRELA FISSILIS* (MELIACEAE)

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SUMMARY

Cambial activity and periodicity of secondary xylem formation in *Cedrela fissilis*, a semi-ring-porous species, were studied. Wood samples were collected periodically from 1996 to 2000. The phenology was related to climate data of the region. The cambium has one active and one dormant period per year. The active period coincides with the wet season when trees leaf-out. The dormant period coincides with the dry season when trees lose their leaves. Growth rings are marked by parenchyma bands that begin to be formed, together with the small latewood vessels, just before the cambium becomes dormant at the beginning of the dry season. These bands are added to when the cambium reactivates in the wet season. At this time, the large earlywood vessels of the growth rings are also formed. As these bands consist of both terminal and initial parenchyma, we suggest the general term marginal bands be used to describe them. The growth layers vary in width among and within the trees.

Key words: *Cedrela fissilis*, cambial activity, secondary xylem, xylem differentiation, marginal parenchyma.

INTRODUCTION

Studies on growth periodicity in the xylem of tropical and subtropical species in Brazil have shown that rainfall variation defines the periodicity of xylem formation (Worbes 1985, 1989; Botosso & Vetter 1991; Luchi 1998). According to Worbes (1995), one dry season per year, with two or three months of monthly rainfall below 60 mm, leads to the development of one growth increment (ring) per year, whereas two dry seasons per year produce two increments.

Studies on the periodicity of xylem formation provide data on age and factors related to the control of tree growth. Such data are useful for dendrochronological studies and for the prediction of timber and biomass yield and for the study of forest dynamics (Jacoby 1989; Kozłowski *et al.* 1991; Eckstein *et al.* 1995; Priya & Bhat 1999).

Cedrela fissilis forms distinct growth increments of wood and is classified as a semi-ring-porous wood (Mainieri *et al.* 1983; Détienne & Jacquet 1983). The studies about wood periodicity in *Cedrela* have already demonstrated that its growth increments are

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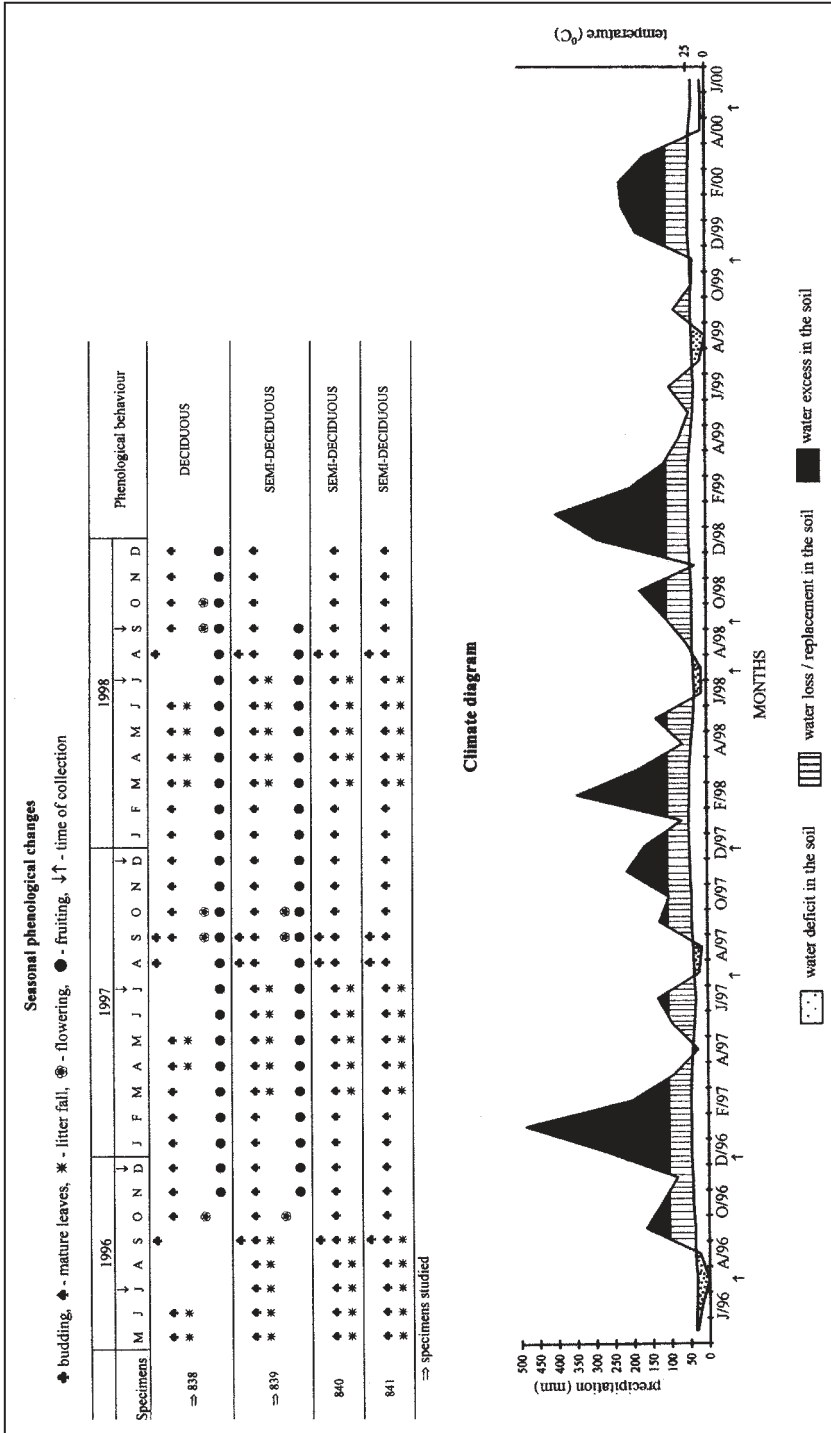


Fig. 1. Phenological characteristics of the experimental trees and meteorological data of the study site. (Adapted from Walter *et al.* 1975).

annual (Détienne & Mariaux 1977; Boninsegna *et al.* 1989; Mattos *et al.* 1999; Tomazello *et al.* 2000; Botosso *et al.* 2000). In addition to the semi-ring porosity, *C. fissilis* wood shows bands of axial parenchyma delimiting the growth increments (Mainieri *et al.* 1983; Détienne & Jacquet 1983). The axial parenchyma bands in *Cedrela* have been referred to as marginal bands by Mainieri *et al.* (1983) and Mainieri and Chimelo (1989). However, some authors have characterized them as initial: Détienne (1989) and Botosso *et al.* (2000) for the wood of *C. odorata*; Boninsegna *et al.* (1989) and Tomazello *et al.* (2000) for the wood of *C. fissilis*. Others have designated them terminal: Détienne *et al.* (1982) and Détienne and Jacquet (1983) for different species of *Cedrela*. In order to clarify this contradiction, this study analyzed the formation of growth rings in the wood of *C. fissilis*, and correlated the periodicity of wood formation with the phenology of the species and climate data.

MATERIALS AND METHODS

Study site and experimental sample collection of periderm, phloem, cambium, and xylem stem samples of *Cedrela fissilis* Vell. (Meliaceae) were collected from a semi-deciduous seasonal sub-tropical forest located at Botucatu, São Paulo State, Brazil. The site is on the campus of the School of Agronomic Sciences, São Paulo State University (UNESP) (20° 50' 00"–22° 47' 30" S and 48° 26' 15"–48° 22' 30" W). Local topography is irregular, ranging from 464 to 775 m elevation and with several types of soil from fertile clays of basaltic origin to nutrient-poor acidic sands (Engel & Parrota 2001).

Four trees were selected for the phenological characteristics, of which two were used for the wood and cambial activity study (SPFw 838 and SPFw 839; Table 1). The other two trees showed abnormal wood formation and were therefore exclusively used for phenological study.

Phenologic data (budding, mature leaves, leaf fall, flowering, and fruiting) were collected monthly during the vegetative period, and every two weeks during the reproductive period, in 1996, 1997 and 1998 (Fig. 1). Climate data (average temperature and precipitation) from 1996 to 2000 were obtained from the Weather Station of the School of Agronomic Sciences, São Paulo State University (UNESP), Botucatu. The mean annual precipitation for 1996–2000 was 1436 mm and the mean annual air temperature was 20.2°C. December, January and February were the warmest months (21.5°C), and June and July were the coolest (15.8°C) (Fig. 1).

Table 1. Data for the four trees of *Cedrela fissilis* used in this study.

Number of the tree (SPFw)	DBH* (cm)	Height (m)
838	30	11
839	55	20
840	35	17
841	35	16

*) DBH = diameter at breast height (1.3 m)

Light microscopy of cambium and wood samples

For the cambial activity study, we collected eight samples per tree. Initial samples were collected in July and December (dry and wet seasons) of 1996 and 1997. Analysis of the material revealed the need for additional collection dates, so we collected additional material in July and September of 1998, November of 1999, and March of 2000. For each collection date, new samples were taken from the same trees. Although eight samples were made per tree, no stresses were observed in the trees nor abnormal wood in the samples. The stem wounds of each tree were completely closed in about 17 months.

Samples 5 cm wide, 5 cm high and of variable depth, depending on bark thickness, were collected from the stem 1.30 m above the ground (breast height) using a chisel, hacksaw, and drill. The samples were immediately fixed in CRAF III (Berlyn & Miksche 1976) and remained in the fixative for about one month.

Cambial activity was analyzed macro- and microscopically for the different collection dates. For macroscopic analysis of the xylem, smooth surfaces were prepared using a sliding microtome. The surfaces were examined under a stereomicroscope, and ring width was measured.

For microscopic analysis of the cambial zone, 5 mm cubes containing inner areas of the phloem, cambium, and outer areas of the xylem, were embedded in plastic resin (Historesin[®]), according to Bennet (1976) and Mazzoni-Viveiros (1994). Sections of 5–10 μm were cut using a rotary microtome. The sections were stained with toluidine blue, in acetate buffer, pH 4.7, producing a metachromatic stain (O'Brien *et al.* 1964; O'Brien & McCully 1981).

We also prepared 1.5 cm cubes for microscopic analyses of the xylem. These samples were softened in boiling water and glycerin (4 : 1) (Ferreirinha 1958). Transverse, radial and tangential sections 15–20 μm thick were cut with a sliding microtome. The sections were cleared with sodium hypochlorite (50%) and stained with safranin (1%) in ethanol (50%), astra blue and basic fuchsin (aqueous, 1%), and astra blue and chrysoidine (aqueous, 1%) (Johansen 1940; Sass 1951; Gerlach 1984). Vessel diameters were divided into two separate categories (earlywood and latewood), and 30 vessels in each category were measured.

RESULTS

Phenology

The trees exhibited synchronous phenophases of leaf fall, corresponding to the beginning of the dry season, and budding and mature leaves coinciding with the beginning of the wet season (Fig. 1). Leaf fall occurred from March to September. Three trees had mature leaves throughout the observation period, indicating a semi-deciduous behavior, and one tree (SPFw 838) showed a deciduous behavior with complete leaf loss from June to August (Fig. 1).

Characteristics of the cambial zone and the wood

The active cambium was identified by the presence of mitotic figures and phragmoplasts (Fig. 2). When the cambium is active, it forms a large number of immature xylem cells (Fig. 3, 11 & 12). Naturally, the xylem tissue differentiates centrifugally (Fig. 3).

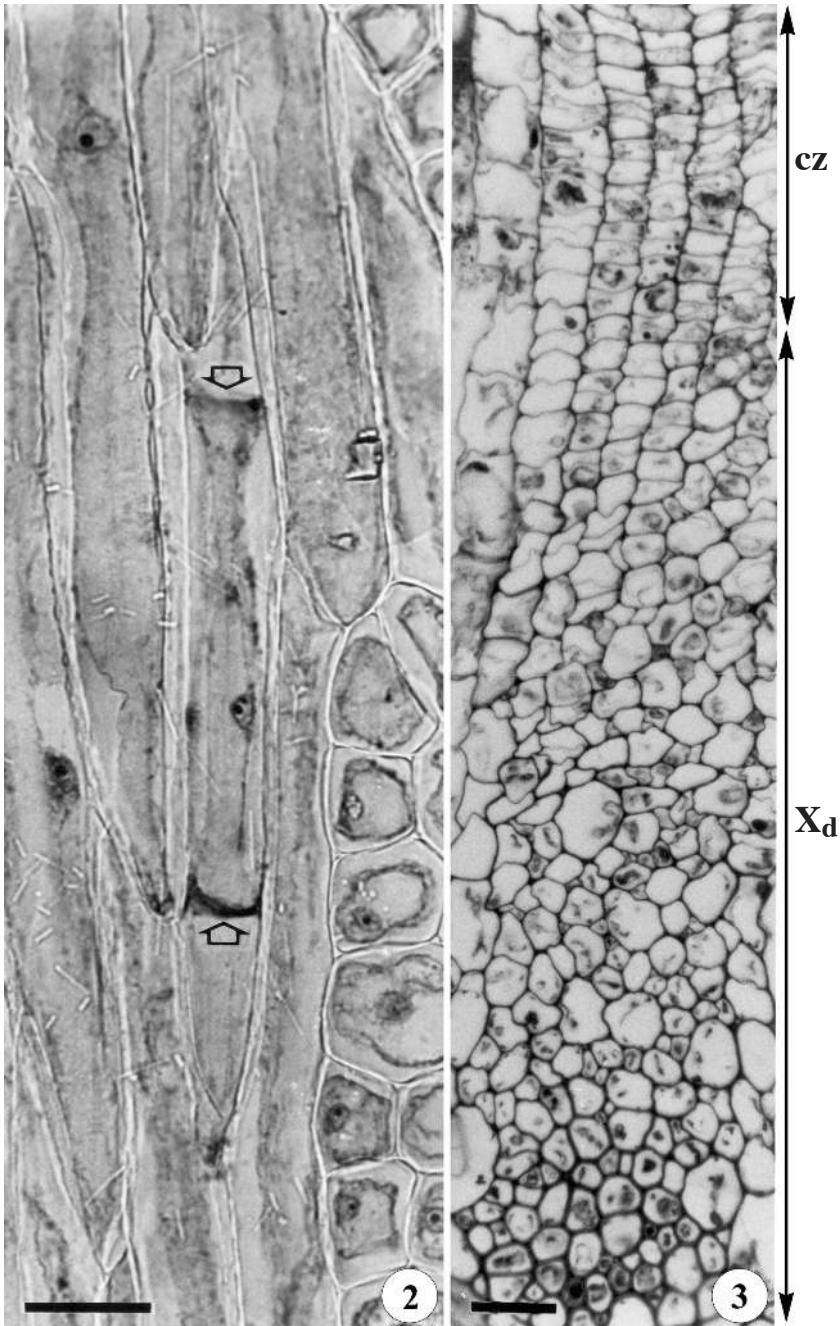


Fig. 2 & 3. – 2: Phragmoplast in periclinally dividing fusiform cell (arrows). – 3: Centrifugally differentiating xylem (X_d) in November 1999 collection. – cz: cambial zone. — Scale bars: 12 μm in Fig. 2; 30 μm in Fig. 3.

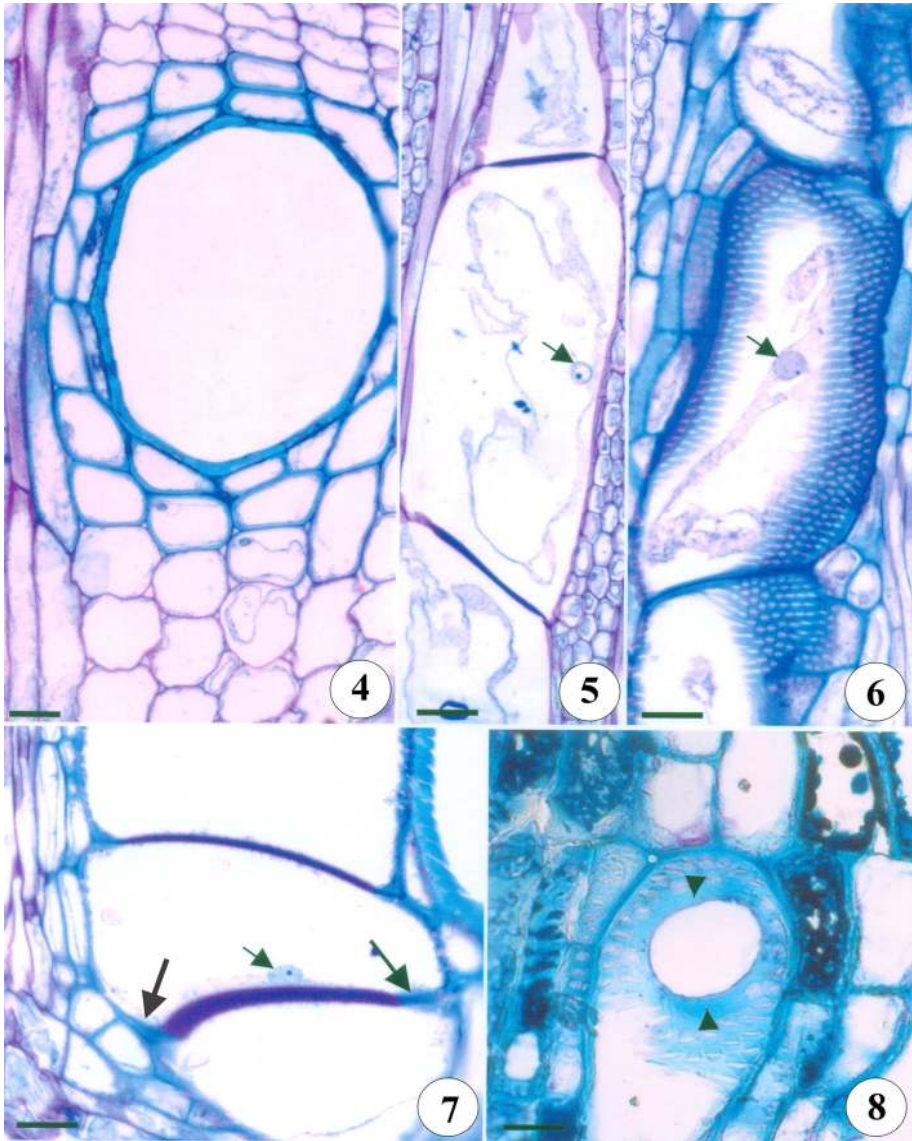


Fig. 4–8. – 4: Vessel and adjacent parenchyma cells with lignified secondary walls in blue, and cells with nonlignified primary walls in violet. – 5: Differentiating vessel element with primary walls. At the perforation sites (above and below) the primary wall is conspicuously thickened. Arrow points to nucleus. – 6: Vessel element with lignified secondary walls showing bordered pits in lateral walls. The protoplast, including nucleus (arrow), is still present. Adjacent parenchyma cells also have pitted, lignified secondary walls. – 7: Thickened primary wall at perforation site between vessel elements with secondary walls. Large arrows point to rim of future perforation plate, small arrow to nucleus. – 8: Portion of mature vessel element showing simple perforation plate. Arrowheads point to rim of the perforation plate. — Scale bars: 20 μm in Fig. 4 & 8; 50 μm in Fig. 5; 40 μm in Fig. 6; 30 μm in Fig. 7.

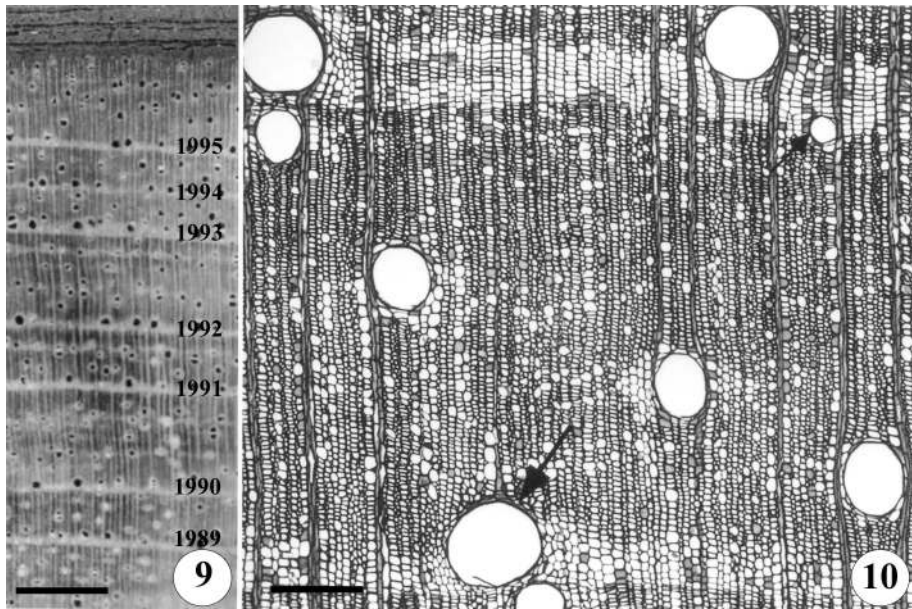


Fig. 9 & 10. Cross sections of SPFw 839, July 1996 collection. – 9: The marginal parenchyma bands delimiting six growth increments are indicated. – 10: Growth ring marked by banded parenchyma and large earlywood vessel (large arrow). Vessel diameter decreases gradually across the growth increment. Small arrow points to small terminal vessel in latewood. — Scale bars: 500 μm in Fig. 9; 250 μm in Fig. 10.

Vessel elements are the first cells to complete differentiation, along with adjacent parenchyma cells (Fig. 4). Figure 5 shows a differentiating vessel element, with nucleus and cytoplasm, prior to discernible secondary wall formation. Deposition of the secondary wall and formation of intervessel pits are near completion in the vessel element shown in Figure 6. The nucleus and cytoplasm can still be identified in this cell. The primary wall at the site of the future perforation is thicker than elsewhere and is apparent early in the differentiating vessel element (Fig. 5). It is clearly set off from the secondary wall, which forms the rim of the future perforation plate (Fig. 7). The vessel elements in *Cedrela* have simple perforation plates (Fig. 8).

In *Cedrela fissilis* the wood forms distinct growth increments (Fig. 9). Each ring includes a marginal parenchyma band with large-diameter vessels (mean 211 μm , range 107–326 μm) that characterize the earlywood (Fig. 9 & 10), and a zone of small- to medium-sized vessels characterizing the latewood (mean 146 μm ; range 64–198 μm) (Fig. 10). Vessel diameter decreases somewhat abruptly from early- to latewood, resulting in the semi-ring-porous condition (Fig. 9 & 10).

Growth rings within the same sample varied in width (Fig. 9). They were wider in specimen SPFw 838 than in specimen SPFw 839 (Table 2). The width of the marginal parenchyma band was also variable, ranging from 3–13 cells wide (Fig. 10). Occasional small latewood vessels occurred within the marginal parenchyma band (Fig. 10).

Table 2. Width of growth increments (mm) in the stems of *Cedrela fissilis*.

Tree	Years							
	90-91	91-92	92-93	93-94	94-95	95-96	96-97	97-98
SPFw 838	–	–	–	–	8	13	13	6
SPFw 839	3.5	2	3	2	1.5	6	4	–

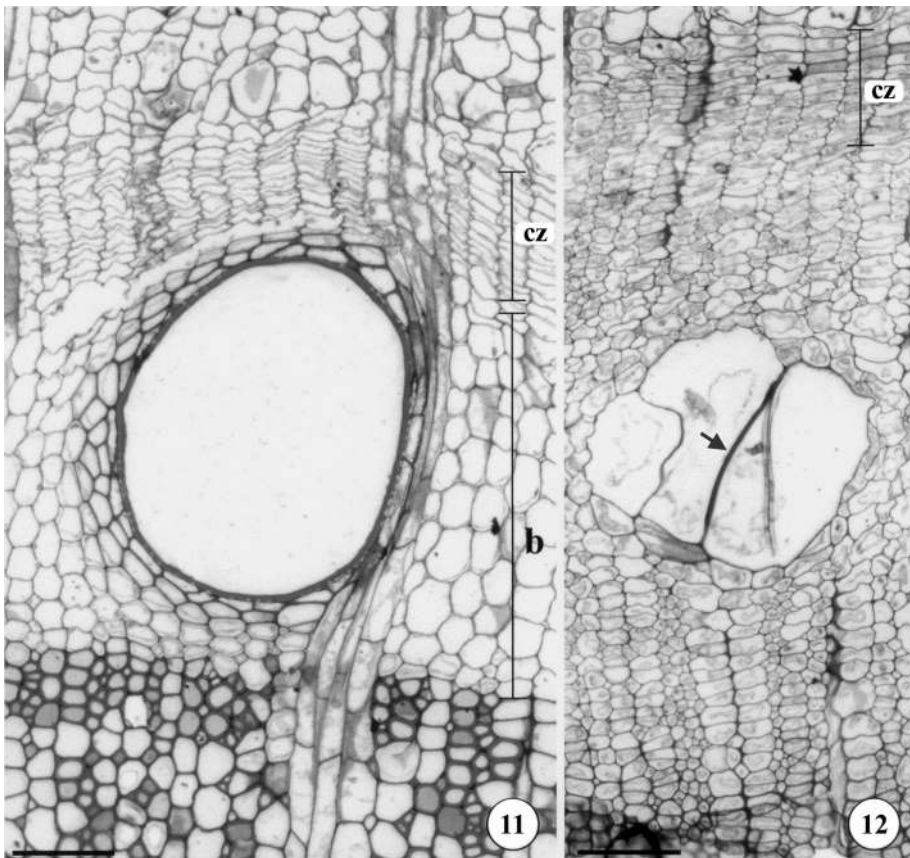


Fig. 11 & 12. Cross sections. – 11: SPFw 838, September 1998 collection. Banded parenchyma (b) with large earlywood vessel. The vessel and contiguous parenchyma cells have lignified secondary walls. – 12: SPFw 839, November 1999 collection. A large amount of immature xylem is present. The thickened primary wall of a perforation site (arrow) can be seen between two vessel elements of multiple vessels, in which secondary wall deposition had not begun. – cz: cambial zone. — Scale bars: 80 μ m.

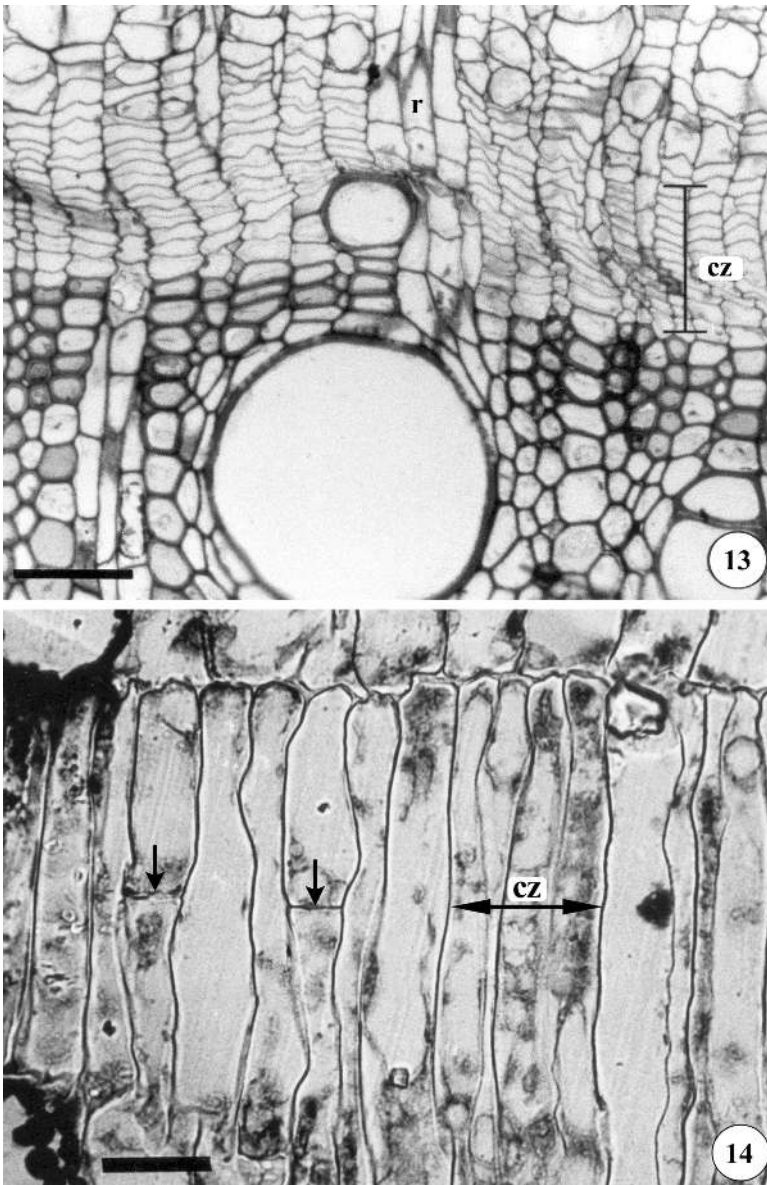


Fig. 13 & 14. Cross and radial sections of SPFw 839, respectively, March 2000 (Fig. 13) and July 1997 (Fig. 14) collections. In both collections the cambium was dormant. – 13: A small latewood vessel bordered laterally by immature parenchymatous elements. The larger vessel seen here is also a latewood vessel. – r: ray; cz: cambial zone. – 14: Transverse walls (arrows) can be seen between two immature strand parenchyma cells. In cross sections these cells would appear to belong to the cambial zone. These cells and the fusiform cells interspersed among them are precursors of marginal parenchyma cells. The actual cambial zone (cz) may consist of no more than the four radially narrow cells so labelled. — Scale bars: 80 μm in Fig. 13; 30 μm in Fig. 14.

Seasonal variation of cambial activity

In September, November and December, the cambial zone was twelve to eighteen cell layers wide. The presence of mitotic figures and phragmoplasts indicated that, during this period, the cambium was active (Fig. 2). In September 1998, approximately 30 days after budding, the trees produced mature leaves (Fig. 1). The production of mature leaves coincided with earlywood formation. At that time, the marginal parenchyma band consisted of approximately thirteen layers of immature cells, and the large earlywood vessels were already formed (Fig. 11). In December 1996 and 1997 and November 1999, the trees had mature leaves (Fig. 1). The cambium was active and consisted of thirteen (December) to eighteen (November) layers of cells (Fig. 12).

In March and July, the cambial zone was inactive. In March 2000, the cambial zone was eight to ten cell layers wide (Fig. 13). Adjacent to the cambial zone were one or two layers of immature fibers and axial parenchyma cells, and an occasional mature latewood vessel element bordered laterally by immature parenchymatous elements (Fig. 13). In July 1996, 1997 and 1998, one tree (SPFw 838) had total leaf fall and the other (SPFw 839) had partial leaf fall (Fig. 1). At these collection dates the cambial zone was dormant; no cell divisions were observed. As seen in transverse sections, about nine to fourteen layers of undifferentiated rectangular cells occurred between the fully differentiated xylem and phloem elements. However, when viewed in radial sections some of the cell layers nearer the fully mature xylem contained septate elements, that is, immature parenchyma strands. Portions of two such strands are shown in Figure 14. Interspersed among them were fusiform (nonseptate) parenchymatous elements.

DISCUSSION

Cedrela fissilis is semi-ring-porous and the rings are annual, as previously shown by D tienne and Mariaux (1977), Boninsegna *et al.* (1989), Mattos *et al.* (1999), Tomazello *et al.* (2000) and Botosso *et al.* (2000).

The width of the growth rings varied among and within the trees examined during this study. The widest rings occurred in the tree located at a more open site. Luchi (1998), studying *Hymenaea courbaril* (Leguminosae) in S o Paulo State, also correlated variation in width of growth increments to specimen age and site; younger specimens found at more open sites had wider rings. According to Kozlowski (1971), trees in open sites have larger crowns and such trees produce wider growth rings in the wood. As the trees become older, their crowns become larger, increasing the competition between them; the trees then form narrower growth rings in the wood (Farrar 1961).

Differentiation of the xylem was gradual and centrifugal. The first cells to mature were the earlywood vessel elements, undoubtedly a reflection of the importance to create early on a conduit for the conduction of water (Zimmermann 1983).

The pattern of vessel differentiation observed in *Cedrela* parallels that reported in other angiosperms (Esau & Hewitt 1940; Esau & Charvat 1978; Butterfield 1995). Briefly, thickening of the primary wall at the perforation sites occurs early in differentiation of the vessel element, before discernible secondary wall deposition has begun.

The end walls are thickest in the median portion and thinnest at the margins. Eventually, the margins are covered by secondary wall material, forming the rims of the perforation plates. Following secondary wall deposition, the cell undergoes autolysis, affecting the protoplast and parts of the wall not covered by lignified secondary wall layers. The latter include the pit membranes between vessels and the primary wall at the perforation plate between vessel elements. Senescence of the vessel element protoplast is a good example of programmed cell death (Groover *et al.* 1997; Fukuda *et al.* 1998; Groover & Jones 1999).

In this study, small-diameter latewood vessels, bordered laterally by two to three layers of immature parenchymatous elements, were formed at the end of the growing season. Quite clearly these parenchymatous elements, being associated spatially with latewood vessels, may be termed terminal parenchyma. After dormancy, with the renewal of cambial activity, additional layers of axial parenchyma were produced, adding to the width of the parenchyma band. These layers of parenchyma cells are spatially associated with the large earlywood vessels, and may be termed initial parenchyma. Consisting of both terminal and initial parenchyma, it is appropriate to refer to these parenchyma bands as marginal. The width of the marginal parenchyma bands was highly variable. The factors that determine this variability merit further study.

Large-diameter earlywood vessels and associated marginal parenchyma cells were found in the September 1998 collection, approximately 30 days after the development of new leaves, in the beginning of the wet season. This agrees with the findings of Villalba (1985) and Venugopal and Krishnamurthy (1987) who found that the large earlywood vessels were formed one month after bud break in the wet season for *Prosopis flexuosa* (Leguminosae) and *Tectona grandis* (Verbenaceae), respectively.

The results of this study agrees with Worbes' (1995) statement that an annual dry season that lasts from two to three months with rainfall below 60 mm, leads to the formation of visible growth increments in tropical tree species. Although São Paulo State is considered by Worbes (1995) as a wet region, we conclude, based on the climate diagram, that the region of Botucatu, São Paulo State, has an annual dry season with two to three months of rainfall below 60 mm.

In conclusion, semi-ring-porous *Cedrela fissilis* forms annual growth increments delimited by marginal parenchyma bands and large earlywood vessels. The marginal bands consist of parenchyma cells laid down at the end of one period of cambial activity and at the beginning of the next. The period of cambial dormancy correlates to the dry season and leaf fall. The period of cambial activity correlates to the wet season and the presence of mature leaves.

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