

Anatomical features of increment zones in different tree species in the State of São Paulo, Brazil

Características anatômicas das zonas de incremento do lenho de diferentes espécies arbóreas do Estado de São Paulo, Brasil

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RESUMO: Amostras de madeira de 41 espécies arbóreas provenientes de 7 diferentes locais (Cerrado e Mata Atlântica) do Estado de São Paulo foram analisadas macro e microscopicamente quanto à ocorrência de zonas de incremento. Distintas zonas de incremento foram observadas em *Bombax grandiflorum* Cav., *Chorisia speciosa* (A. St. -Hil.) Dawson, *Ocotea puberula* (Rich.) Nees, *Ocotea porosa* (Ness & Mart. Ex Ness) L. Barroso, *Copaifera langsdorffii* Desf., *Hymenaea courbaril* L., *Schizolobium parahyba* (Vell.) Blake, *Centrolobium tomentosum* Guill. Ex. Benth. e *Alchornea sidifolia* Müll. Arg. As características anatômicas das zonas de incremento das 9 espécies foram descritas. De modo geral, as zonas de incremento foram demarcadas por fibras radialmente comprimidas de parede espessa ou parede delgada e lenho tardio. No entanto, em algumas espécies as bandas de parênquima marginal também demarcaram os limites das zonas de incremento. Espécies arbóreas com anéis porosos ou semi-porosos não foram encontradas entre as 41 espécies analisadas. Zonas de incremento distintas foram determinadas em todas as espécies classificadas como decíduas sendo também comumente encontradas nas semidecíduas.

PALAVRAS-CHAVE: Zonas de incremento; Anatomia da madeira; Anéis de crescimento; Dendrocronologia

ABSTRACT: Wood samples of 41 tree species from 7 different sites (Savanna and Atlantic forest) in the State of São Paulo were analysed macro- and microscopically for occurrence of increment zones. Distinct increment zones were found in *Bombax grandiflorum* Cav., *Chorisia speciosa* (A. St. -Hil.) Dawson, *Ocotea puberula* (Rich.) Nees, *Ocotea porosa* (Ness & Mart. Ex Ness) L. Barroso, *Copaifera langsdorffii* Desf., *Hymenaea courbaril* L., *Schizolobium parahyba* (Vell.) Blake, *Centrolobium tomentosum* Guill. Ex. Benth. and *Alchornea sidifolia* Müll. Arg.. The anatomical features of increment zones of those 9 species are described. In most cases, increment zones were marked by thick-walled and radially flattened latewood versus thin-walled early wood fibres. However, marginal parenchyma bands were found to mark the boundaries, too. Tree species with a ring-porous or semi-ring-porous structure could not be found within the 41 trees species investigated. Distinct increment zones could be found in all leaf-fall categories. The occurrence of distinct increment zones seems to be more common in deciduous and semi-deciduous tree species.

KEYWORDS: Increment zones, Wood anatomy, Tree-ring, Dendrochronology

INTRODUCTION

Tree ring research on tropical species nowadays is a known field of research. However, the knowledge about the existence of annual tree rings in tropical trees, which was already found at the beginning of the last century, was ignored by

many scientists for a long time (Worbes 1989). During the last two to three decades different researchers doubtlessly demonstrated the existence of annual tree rings in many different tree species throughout the tropics (Détienne, 1989; Fujii et al., 1999; Gourlay, 1995; Jacoby, 1989; Nobuchi et

al., 1995; Vetter e Botosso, 1989; Tomazello Filho e Cardoso, 1999; Tomazello Filho et al., 2000; Worbes, 1989 e 1999; Maria, 2002).

However, it is also well known that tree ring analysis in the tropics is more difficult than in the temperate climate zones or in the boreal climate zone. From different investigations it is known that species with distinct increment zones can be found directly beside species with scarcely distinct or indistinct increment zones (Worbes 1999). According to Mariaux (1995), every tropical tree species has its own growth rhythm and reacts different to seasonal variations. The high variability of sites concerning climatic, edaphic and mechanic site factors and the complex anatomical structure of tropical woods are also reasons for the varying distinctness of increment zones.

The periodicity of increment zones in tropical trees, which does not have to be annual (Alvim 1964; Wagenführ, 1989; Worbes e Junk, 1989), also makes tree ring analysis more difficult. The occurrence of distinct increment zones in tropical

trees is the first prerequisite for tree ring analysis. However, knowledge about the periodicity of the increment zones is absolutely essential. Different methods to proof the annual periodicity of increment zones are described in Worbes (1995); Roig (2000) and Botosso e Tomazello Filho (2001).

In the present study, were investigated 41 tree species of different forests in the state of São Paulo. Aim of the investigation was to examine the wood anatomy in order to find tree species with distinct increment zones.

MATERIALS AND METHODS

Forthy-one tree species belonging to 22 families were sampled in different forest reserves and forest plantations in the State of São Paulo, Brazil. The locations of the different areas under investigation are shown in Figure 1. All species are native in the State of São Paulo and grow either in the forest formations Savanna (Cerrado) or Atlantic forest (Mata Atlântica).

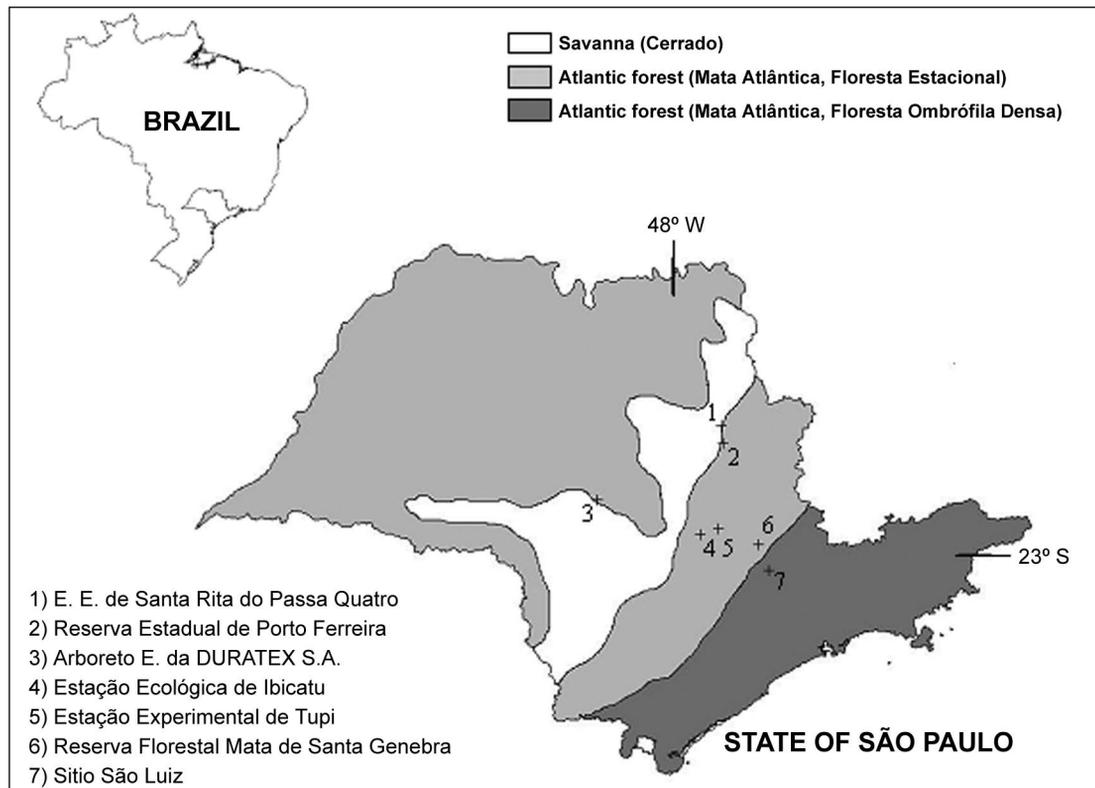


Figure 1 Map of location of the 7 research areas in the State of São Paulo, Brazil. (Rizzini et al. 1988, modified), the map also gives an idea about where the ecosystems Savanna and Atlantic forest occur. (Mapa da localização dos 7 locais de estudo no Estado de São Paulo, Brasil e indicação da localização dos ecossistemas cerrado e mata atlântica. (Rizzini et al. 1988, modificado)

The forest formation Cerrado, typical for the Brazilian interior, is the second largest ecoregion in Brazil, covering 21 % of the territory. It consists mainly of tree and scrub, but some grassland can also be found. As a result of a pronounced dry season a lot of species are drought-adapted. Adaptations to fire, which is an important ecological feature of the Cerrado, are also common (Rizzini et al., 1988; Oliveira and Marquis, 2002). The total plant diversity in this forest formation is estimated at 10000 species (Mittermeier et al., 1999). Taxonomists have classified approximately 700 species of trees and shrubs (Rizzini et al., 1988).

Beside the Amazonian rain forest, the Mata Atlântica is the second major rain forest block of Brazil, covering 13 % of the territory. Once it stretched from Rio Grande do Sul up to Rio Grande do Norte. In the northern parts of Brazil these forest covered only a narrow coastal strip of approximately 50 – 100 km in width. However, in the State of São Paulo as in other south eastern states, in some places it covered an area 500 – 600 km² inland. With an estimated 20000 plant species, biodiversity in this forest formation is extremely high (Mittermeier et al., 1999).

Samples were collected in the following forest reserves and plantations:

- 1) The Estação Experimental de Santa Rita do Passa Quatro (EESRP) is located in the municipality of Santa Rita do Passa Quatro (21°40' S, 47°30' W). The area has a size of 96,3 ha and consist of plantations. Average altitude is 715 m.
- 2) The Reserva Estadual de Porto Ferreira (REPF) is located in the municipality of Porto Ferreira (21°50' S, 47°28' W), and has an average altitude of 570 m. The area consists of 611,6 ha of natural forest.
- 3) The Arboreto Experimental of the Duratex S.A. (AED) is located in the municipality of Agudos (22°25' S, 48°50' W). Average altitude is 600 m, the area consists of plantations.
- 4) The Estação Ecológica de Ibicatu (EEI) is located in the municipality of Piracicaba (22°46' S, 47°43' W). The area has a size of 76,4 ha and consists of natural forest. Average altitude is 500 m.
- 5) The Estação Experimental de Tupi (EET) is located in the municipality of Piracicaba (22°43' S, 47°31' W), and has an average altitude of 515 m. The area has a size of 198 ha and consists of plantations and natural forest. All trees sampled in this area were planted.
- 6) The Reserva Florestal Mata de Santa Genebra

(MSG) is located in the municipality of Campinas (22°44' S, 47°06' W). Average altitude is 670 m. The natural forest in that area covers 251,8 ha.

7) The Sítio São Luiz (SSL) is located in the municipality of Jundiá (23°20' S, 46°88' W). Average altitude is 715 m. The area covers 43 ha and consists of natural forest.

Climate diagrams of Santa Rita do Passo Quatro, Campinas, Jundiá and Piracicaba indicated, that in all regions samples were collected, precipitation is well distributed throughout the year with an distinct dry season from June to August. Monthly precipitation in that time is less than 60 mm in all regions. Climate in the different regions is very similar. In Piracicaba, mean annual precipitation for the 1975-2001 period was 1357 mm, mean annual air-temperature was 21.8 °C. With an average of 25°C, February was the hottest month, June and July were the coldest months with an average air-temperature around 17.7°C. The climate diagram of Piracicaba (1981-1990 period) is shown in Figure 2.

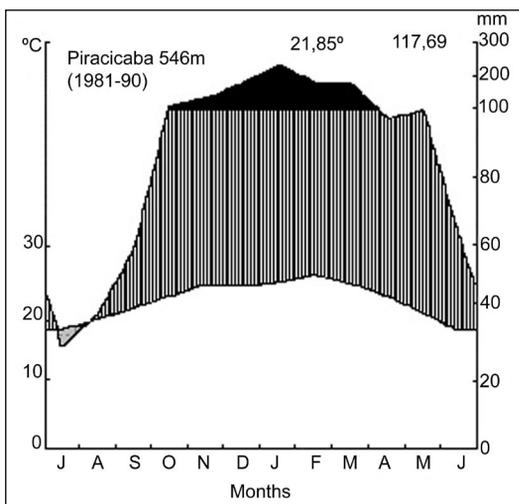


Figure 2

Climate diagram of Piracicaba, São Paulo, Brazil, 1981-1990 period. Walter, 1986).

(Diagrama climático de Piracicaba, São Paulo, Brasil, período de 1981-1990. Walter, 1986)

Wood samples were taken at breast height by a specially developed motorized borer. This borer makes possible an easy sampling of cores, independent of the wood density (Cury, 2002). The samples measured 10 cm length x 1.2 cm diameter, including bark. For each of the 41 tree species investigated, 3 individuals were found and one sample collected out of each tree. Blocks of approximately 2 x 1 x 1 cm were cut out of one

sample per species and softened by boiling in distilled water and glycerine. Transverse, tangential and radial sections (15 µm thick) were cut of the blocks using a sliding microtome and stained with safranin. Microphotographs of the transverse sections were made using a Zeiss Axioskop light microscope.

From each species, 1 or 2 samples were polished with sand paper (150 – 1200 grains per cm²) and observed with the naked eye. Images were scanned, using a HP ScanJet 6100C/T.

The leaf fall pattern of the species investigated were divided into deciduous, semi-deciduous and evergreen, based on the literature (Lorenzi, 1992 e 1998; Morellato, 1991) and phenological observations which were carried out monthly from January 1999 to December 2001.

RESULTS

Three species were collected in the EESRP, 2 species in the REPF, 2 species in the AED, 2 species in the EEI, 3 species in the EET, 2 species in the MSG and 27 species in the SSL (Table 1).

Nine of the 41 tree species investigated showed distinct increment zones, 10 more species showed scarcely distinct increment zones. Thirteen species showed indistinct increment zones, while the remaining 9 species showed no increment zones. Distinct increment zones were found in all leaf-fall categories. However, whereas in each of the two categories deciduous and semi-deciduous 4 tree species with distinct increment zones could be found, in the category evergreen only 1 species showed distinct increment zones. The sampling was made up of 15 deciduous, 15 semi-deciduous and 11 evergreen species. Species with scarcely distinct and indistinct increment zones were found in all leaf-fall categories, too.

The increment zones – distinct and indistinct – of those 93 species which showed distinct increment zones is described below:

Bombacaceae

Both species of the family Bombacaceae studied in the scope of this investigation had distinct increment zones. The increment zones in *Bombax grandiflorum* Cav. (Figure 3) as well as in *Chorisia speciosa* (A. St. -Hil.) Dawson (Figure 4) were

marked by marginal parenchyma bands and thick-walled and radially flattened latewood versus thin-walled early wood fibres. Furthermore, in both species the increment zones showed distended rays.

Lauraceae

The two Ocotea species investigated *Ocotea puberula* (Rich.) Nees (Figure 5) and *Ocotea porosa* (Ness & Mart. Ex Ness) L. Barroso (Figure 6) had distinct increment zones, marked by thick-walled and radially flattened latewood versus thin-walled early wood fibres.

Leguminosae-Caesalpinaceae

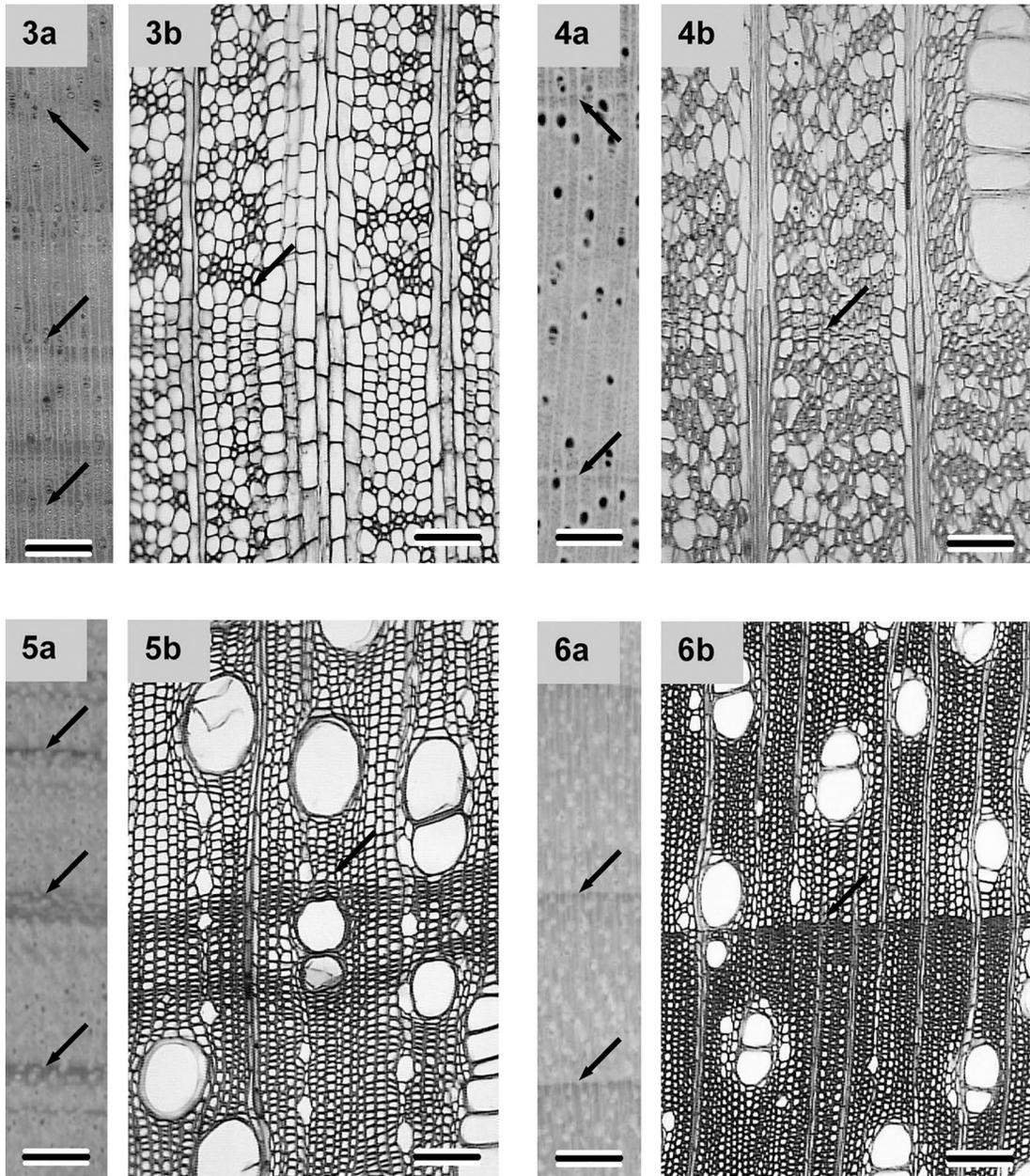
From the 6 species of the family Leguminosae-Caesalpinaceae investigated, *Copaifera langsdorffii* Desf., *Hymenaea courbaril* L. and *Schizolobium parahyba* (Vell.) Blake had distinct increment zones. *Cassia ferruginea* (Schrad) Schrad. Ex DC. and *Caesalpinia ferrea* Mart. Ex Tul. showed indistinct increment zones while *Bauhinia forficata* Link showed no increment zones. The increment zones in *Schizolobium parahyba* (Vell.) Blake (Figure 7) were marked by thick-walled and radially flattened latewood versus thin-walled early wood fibres. Including also a thin-marginal parenchyma. *Copaifera langsdorffii* Desf. (Figure 8) and *Hymenaea courbaril* L. (Figure 9) had increment zones marked by marginal parenchyma bands.

Leguminosae-Faboideae

Of all 41 tree species investigated, the species *Centrolobium tomentosum* Guill. Ex. Benth. (Figure 10) showed the most distinct increment zones. They were marked by thick-walled and radially flattened latewood versus thin-walled early wood fibres.

Euphorbiaceae

Were investigated 4 tree species of the family Euphorbiaceae. *Alchornea sidifolia* Müll. Arg. (Figure 11) was the only one where the increment zones were found to be distinct. *Pachystroma ilicifolium* Müll. Arg. showed scarcely distinct increment zones while *Croton* sp. and *Securinega guarayuva* Kuhl. had no increment zones. The increment zones in *Alchornea sidifolia* were marked by thick-walled and radially flattened latewood versus thin-walled early wood fibres.



Figures 3a-6b

Transverse sections. - 3: *Bombax grandiflorum* (Bombacaceae). - 4: *Chorisia speciosa* (Bombacaceae). - 5: *Ocotea puberula* (Lauraceae). - 6: *Ocotea porosa* (Lauraceae). Figures named with the letter a are macrographs. - Scale bar = 1.5 mm. Figures named with the letter b are micrographs (magnification 40x) - Scale bar = 500 μm. The arrows indicate the increment zones.

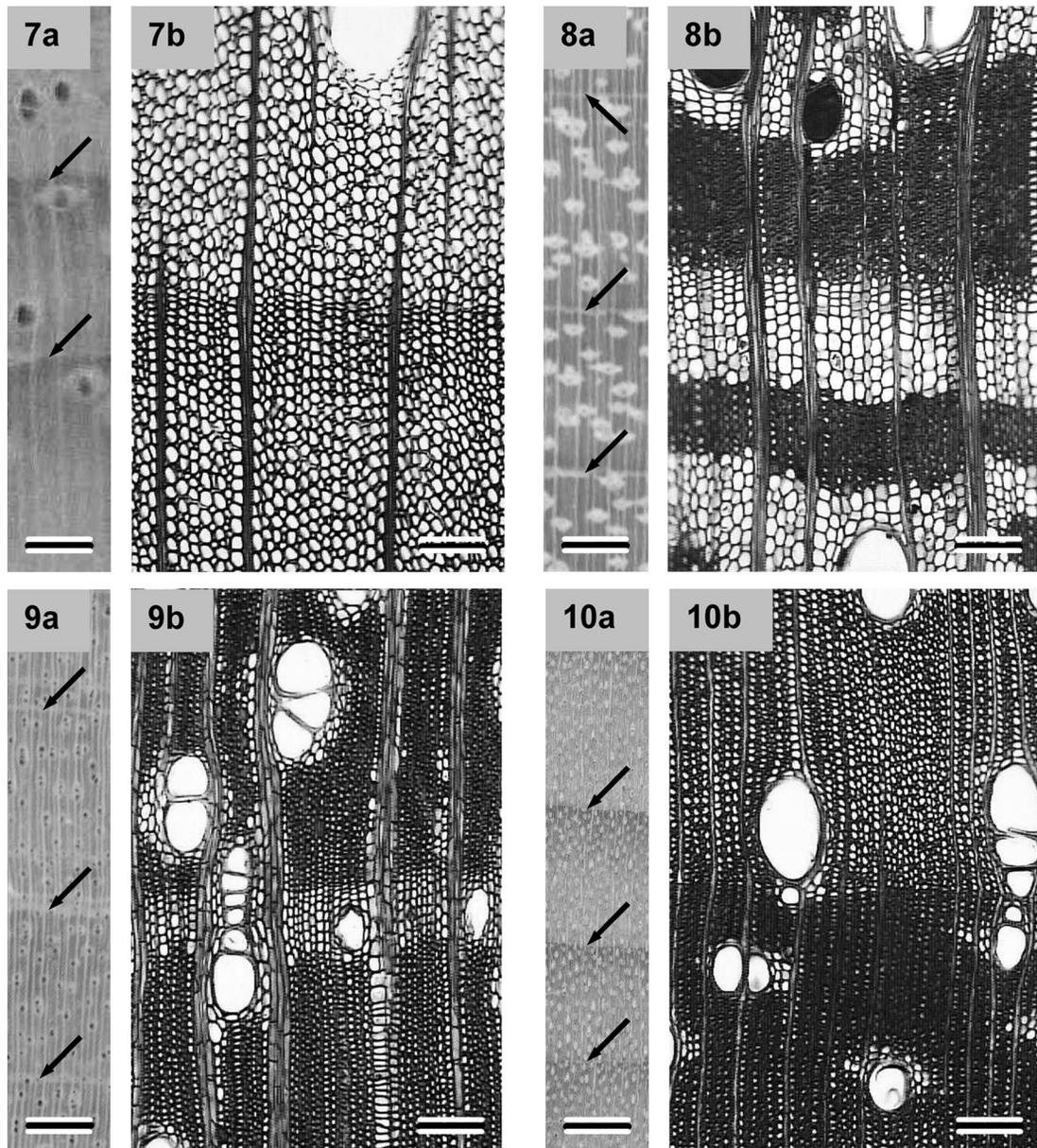
(Seções transversais - 3: *Bombax grandiflorum* (Bombacaceae). - 4: *Chorisia speciosa* (Bombacaceae). - 5: *Ocotea puberula* (Lauraceae). - 6: *Ocotea porosa* (Lauraceae). Figuras nomeadas pela letra a são fotomacrografias - barra de escala = 1,5 mm. Figuras nomeadas pela letra b são fotomicrografias (aumento de 40x) - barra de escala = 500 μm. As setas indicam as zonas de incremento)

Table 1

Distinctness of the increment zones and leaf fall pattern for each species investigated.
(Descrições das zonas de incremento no lenho e padrão de caducifolia das diversas espécies estudadas)

Familie	Species	Site	Increment zones	Leaf fall pattern
Anacardiaceae	<i>Astronium graveolens</i> Jacq.	SSL	scarcely distinct	deciduous
Anacardiaceae	<i>Schinus terebinthifolius</i> Raddi	SSL	scarcely distinct	evergreen
Apocynaceae	<i>Aspidosperma cylindrocarpon</i> Müll. Arg.	SSL	without	deciduous
Apocynaceae	<i>Aspidosperma polyneuron</i> Müll. Arg.	EEL	indistinct	evergreen
Apocynaceae	<i>Aspidosperma ramiflorum</i> Müll. Arg.	SSL	scarcely distinct	deciduous
Bignoniaceae	<i>Tabebuia chrysotricha</i> (Mart. ex DC.) Standl.	SSL	scarcely distinct	deciduous
Bombacaceae	<i>Bombax grandiflorum</i> Cav.	SSL	distinct	deciduous
Bombacaceae	<i>Chorisia speciosa</i> (A. St. -Hil.) Dawson	SSL	distinct	deciduous
Boraginaceae	<i>Cordia sellowiana</i> Cham.	SSL	scarcely distinct	semi-deciduous
Combretaceae	<i>Terminalia brasiliensis</i> Cambess	SSL	scarcely distinct	deciduous
Compositae	<i>Gochnatia polymorpha</i> (Less.) Cabrera	SSL	scarcely distinct	semi-deciduous
Erythroxylaceae	<i>Erythroxylum</i> sp.	REPF	scarcely distinct	deciduous
Euphorbiaceae	<i>Alchornea sidifolia</i> Müll. Arg.	SSL	distinct	evergreen
Euphorbiaceae	<i>Croton</i> sp.	SSL	without	semi-deciduous
Euphorbiaceae	<i>Pachystroma ilicifolium</i> Müll. Arg.	MSG	scarcely distinct	evergreen
Euphorbiaceae	<i>Securinega guarayuva</i> Kuhlmann	EEL	without	evergreen
Lauraceae	<i>Ocotea porosa</i> (Ness & Mart. Ex Ness) L. Barroso	EESRP	distinct	semi-deciduous
Lauraceae	<i>Ocotea puberula</i> (Rich.) Nees	SSL	distinct	semi-deciduous
Lecythidaceae	<i>Cariniana estrellensis</i> (Raddi) O. Kuntze	EET	scarcely distinct	semi-deciduous
Lecythidaceae	<i>Cariniana legallis</i> (Mart.) O. Kuntze	REPF	indistinct	semi-deciduous
Leg.-Caesalpinoideae	<i>Bauhinia forficata</i> Link	SSL	without	semi-deciduous
Leg.-Caesalpinoideae	<i>Caesalpinia ferrea</i> Mart. Ex Tul.	EET	indistinct	semi-deciduous
Leg.-Caesalpinoideae	<i>Cassia ferruginea</i> (Schrad) Schrad. Ex DC.	EESRP	indistinct	deciduous
Leg.-Caesalpinoideae	<i>Copaifera langsdorffii</i> Desf.	SSL	distinct	semi-deciduous
Leg.-Caesalpinoideae	<i>Hymenaea courbaril</i> L.	SSL	distinct	semi-deciduous
Leg.-Caesalpinoideae	<i>Schizolobium parahyba</i> (Vell.) Blake	SSL	distinct	deciduous
Leg.-Mimosoideae	<i>Piptadenia gonoacantha</i> (Mart.) J. F. Macbr.	SSL	indistinct	semi-deciduous
Leg.-Mimosoideae	<i>Piptadenia macrocarpa</i> Benth.	AED	indistinct	deciduous
Leg.-Papilionoideae	<i>Centrolobium tomentosum</i> Guill. Ex. Benth.	MSG	distinct	deciduous
Leg.-Papilionoideae	<i>Dipteryx</i> sp.	AED	indistinct	evergreen
Leg.-Papilionoideae	<i>Machaerium aculeatum</i> Raddi	SSL	without	deciduous
Leg.-Papilionoideae	<i>Machaerium villosum</i> Vogel.	SSL	indistinct	evergreen
Leg.-Papilionoideae	<i>Platycyamus regnelli</i> Benth.	EESRP	indistinct	deciduous
Melastomataceae	<i>Tibouchina granulosa</i> Cogn.	SSL	without	evergreen
Meliaceae	<i>Cabralea canjerana</i> (Vell.) Mart.	SSL	without	deciduous
Myrsinaceae	<i>Rapanea umbellata</i> (Mart.) Mez.	SSL	without	evergreen
Myrtaceae	<i>Eugenia uniflora</i> L.	SSL	indistinct	semi-deciduous
Rutaceae	<i>Esenbeckia leiocarpa</i> Engl.	EET	indistinct	evergreen
Rutaceae	<i>Zanthoxylum rhoifolium</i> Lam.	SSL	scarcely distinct	semi-deciduous
Sterculiaceae	<i>Guazuma ulmifolia</i> Lam.	SSL	scarcely distinct	semi-deciduous
Ulmaceae	<i>Trema micrantha</i> (L.) Blume	SSL	without	evergreen

SSL = Sitio São Luiz, EET = Estação Experimental de Tupi, EESRP = Estação Experimental de Santa Rita do Passa Quatro, MSG = Mata de Santa Genebra, AED = Arboreto Experimental da Duratex S.A., REPF = Reserva Estadual de Porto Ferreira, EEI = Estação Ecológica de Ibicatu



Figures 7a-10b

Transverse sections. – 7: *Schizolobium parahyba* (Leguminosae-Caesalpinaideae). – 8: *Hymenaea courbaril* (Leguminosae-Caesalpinaideae). – 9: *Copaifera langsdorfii* (Leguminosae-Caesalpinaideae). – 10: *Centrolobium tomentosum* (Leguminosae-Papilionoideae). Figures named with the letter a are macrographs. – Scale bar = 1.5 mm. Figures named with the letter b are micrographs (magnification 40x) – Scar bar = 500 μ m. The arrows indicate the increment zones.

(Secções transversais - 7: *Schizolobium parahyba* (Leguminosae-Caesalpinaideae). – 8: *Hymenaea courbaril* (Leguminosae-Caesalpinaideae). – 9: *Copaifera langsdorfii* (Leguminosae-Caesalpinaideae). – 10: *Centrolobium tomentosum* (Leguminosae-Papilionoideae). Figuras nomeadas pela letra a são fotomacrografias – barra de escala = 1,5 mm. Figuras nomeadas pela letra b são fotomicrografias (aumento de 40x) – barra de escala = 500 μ m. As setas indicam as zonas de incremento)

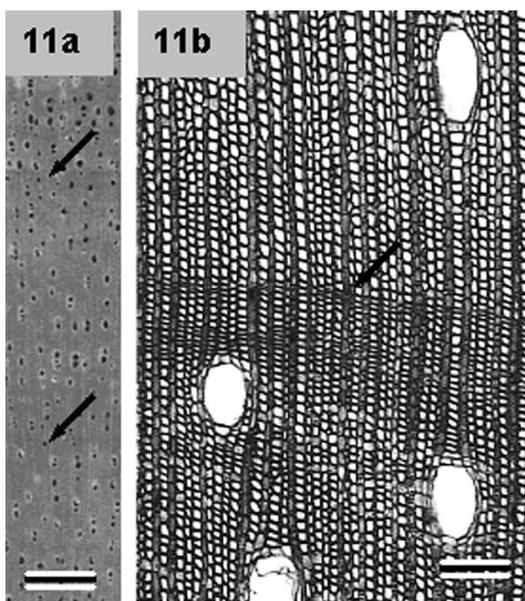


Figure 11a, b

Transverse sections - *Alchornea sidifolia* (Euphorbiaceae). a: macrograph. - Scale bar = 1.5 mm. b: micrographs (magnification 40x) - Scar bar = 500 μ m. The arrows indicate the increment zones.

(Seções transversais *Alchornea sidifolia* (Euphorbiaceae). a: fotomacrografia - barra de escala = 1,5 mm. b: fotomicrografias (aumento de 40x) - barra de escala = 500 μ m. As setas indicam as zonas de incremento.)

DISCUSSION

Nine out of the 41 tree species investigated showed distinct increment zones. Four species belonged to the leaf-fall category deciduous, 4 to the category semi-deciduous and 1 to the category evergreen. It is known that evergreen tree species also can show distinct increment zones (Alvim, 1964, Worbes, 1999).

The increment zones in the 2 *Ocotea* species (Lauraceae) were marked by thick-walled and radially flattened latewood versus thin-walled early wood fibres. Worbes (1989) already mentioned, that this type of increment zone is common in species of the family Lauraceae. He also mentioned that marginal parenchyma bands are common in species of the family Leguminosae, which were detected in this study. Tree species with a ring-porous or semi-ring-porous structure and marginal parenchyma, as can be found for example in *Cedrela fissilis* and *C. odorata* (Boninsegna et al., 1989; Roig, 2000; Botosso et al., 2000; To-

mazello Filho et al., 2000; Botosso e Tomazello Filho, 2001), could not be found within the 41 trees species investigated. Worbes (1989) wrote, that this type of increment zone does not occur in tree species from the Central Amazonian inundation forests. Therefore, it looks like that this type of increment zone is not very common. Alves et al. (2000) investigated 491 tree species of the 22 most representative families of the Brazilian flora. They already found that *Ocotea puberula*, *Copaifera langsdorffii*, *Hymenaea courbaril* and *Centropogon tomentosum* showed increment zones.

According to Worbes (1995), the formation of increment zones in woody plants in general can be induced by seasonally changing favourable and unfavourable growth conditions. In the tropics, dry seasons and inundations were found to be triggering climate factors (Jacoby, 1989, Worbes, 1995). The relationship between precipitation and the formation of increment zones in tropical trees was found early. At the beginning of the last century Coster (1927 e 1928) recognized that trees of the same species showed distinct increment zones when they were grown under seasonal monsoon climate, whereas individuals of the ever wet climate only showed indistinct increment zones. According to Worbes (1995), a dry season width a length of two to three months and monthly precipitation with less than 60 mm can induce the formation of increment zones in tropical trees. In all areas under investigation in which trees were sampled in the scope of this study, precipitation is well distributed throughout the year with a distinct dry season of 3 months and monthly precipitation with less than 60 mm.

Luchi (1998) investigated the growth periodicity of *Hymenaea courbaril* in the State of São Paulo, using the method of cambial wounding (Wolter, 1968; Shiokura, 1989). She found that the growth rhythm is annual, triggered by the annual hydric deficit and the parenchyma layer is characterised as terminal, because is formed during dry period. Marcati (2000) investigated the growth rhythm of *Copaifera langsdorffii* and found an annual growth rhythm, triggered by the water regime. She also found that the cambial activity during the rainy season was higher and that a typical marginal parenchyma band was formed during the dry season.

The results of those two investigations already indicate that tree ring studies in tropical and subtropical tree species in the eastern parts of the State of São Paulo, where precipitation is

well distributed part of the year and with dry period, seems to be possible. However, even when it seems to be highly likely that the periodicity of the increment zones in other tree species which show distinct increment zones also will found to be annual, it should be proofed in further investigations. The results of this investigation indicate that *Bombax grandiflorum* Cav., *Chorisia speciosa* (A. St. -Hil.) Dawson, *Ocotea puberula* (Rich.) Nees, *Ocotea porosa* (Ness & Mart. Ex Ness) L. Barroso, *Copaifera langsdorffii* Desf., *Hymenaea courbaril* L., *Schizolobium parahyba* (Vell.) Blake, *Centrolobium tomentosum* Guill. Ex. Benth. and *Alchornea sidifolia* Müll. Arg. are species which should be further investigated in terms of their potential for tree ring analysis. Concerning *Alchornea sidifolia* the anatomic features and periodicity of growth rings in flood-prone trees of Atlantic rain forest were already described by Callado et al., 2001 a and b).

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