

TREE-RING FORMATION, RADIAL INCREMENT PERIODICITY, AND PHENOLOGY OF TREE SPECIES FROM A SEASONAL SEMI-DECIDUOUS FOREST IN SOUTHEAST BRAZIL

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SUMMARY

Many tropical tree species produce growth rings in response to seasonal environmental factors that influence the activity of the vascular cambium. We applied the following methods to analyze the annual nature of tree-ring formation of 24 tree species from a seasonal semi-deciduous forest of southeast Brazil: describing wood anatomy and phenology, counting tree rings after cambium markings, and using permanent dendrometer bands. After 7 years of systematic observations and measurements, we found the following: the trees lost their leaves during the dry season and grew new leaves at the end of the same season; trunk increment dynamics corresponded to seasonal changes in precipitation, with higher increment (active period) during the rainy season (October–April) and lower increment (dormant period) during the dry season (May–September); the number of tree rings formed after injuries to the cambium coincided with the number of years since the extraction of the wood samples. As a result of these observations, it was concluded that most study trees formed one growth ring per year. This suggests that tree species from the seasonal semi-deciduous forests of Brazil have an annual cycle of wood formation. Therefore, these trees have potential for use in future studies of tree age and radial growth rates, as well as to infer ecological and regional climatic conditions. These future studies can provide important information for the management and conservation of these endangered forests.

Key words: Tropical tree rings, cambium activity, phenology, wood anatomy, dendrometer, dendrochronology.

INTRODUCTION

Tree rings result from changes in the cambial activity as influenced by temperature, photoperiod, precipitation, and endogenous regulators that control the growth rhythm

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(Fahn *et al.* 1981). Knowledge of the timing of xylem formation may provide useful data for age determination and related environmental controls of tree growth, commonly described by dendrochronological techniques (Fritts 1976). Because delineating the rings of trees from tropical regions is a difficult task, any attempt to discern the periodicity of the secondary xylem formation is a valuable contribution to the knowledge of the dynamics and ecology of these forests (Roig 2000).

In the State of São Paulo, the seasonal semi-deciduous forest is one of the most important types of native vegetation. The semi-deciduous forest is defined by 20–50% of its tree species losing their leaves during alternating dry and wet periods (IBGE 1992). The São Paulo region is characterized by seasonal climate changes, with rain-fall exceeding 230 mm during summer and intense drought (rainfall less than 30 mm) during winter. These contrasting conditions accentuate physiologic responses of plant growth to climate, affording an interesting opportunity to identify cycles of tree growth. The region is strongly affected by agricultural activities and only remnant fragments of native forests remain. However, these forests still contain countless native plants and animals.

To study the periodicity of xylem formation, several methods can be used. The cambial marking method demonstrates the annual formation of tree rings if the number of rings formed after the injury of cambial cells corresponds to the year of extracting wood samples. Also, permanent dendrometers are used to measure the rate and periodicity of the radial increment by changes in circumference (Botosso & Tomazello F^o 2001). Phenological studies can be used to interpret the occurrence of repetitive biological events in trees and their relationship with biotic and abiotic factors (Matthes 1980). In this sense, particular growth strategies (*e.g.* dormancy, leaf swelling) and their relationships to growth ring formation in tree species may be interpreted by comparing phenological stages in conjunction with seasonal climate (Jacoby 1989; Roig 2000).

These methods have been successfully applied to tropical trees of the Amazonian “terra firme” forests to show that species such as *Cedrela odorata*, *C. fissilis*, *Copaifera multijuga*, and *Parkia nitida* form annual tree rings in response to seasonal precipitation changes (Worbes 1989; Botosso *et al.* 2000). Similarly, *Amburana cearensis*, *Cedrela odorata*, and *Cedrelinga catenaeformis*, from the tropics of Bolivia, produce tree-ring variations in response to seasonal climate changes (Roig 2000; Brienen & Zuidema 2005). This is also the case in the Peninsula of Yucatan, Mexico, where the annual precipitation gradient and seasonal rainfall impact tree physiological processes, including leaf fall, tree growth, and tree-ring formation (Roig *et al.* 2005).

In this study, we integrated data from observations of the wood anatomy, phenology, cambial markings, and measurements from dendrometers to interpret the increment behavior of 24 tree species from a seasonal semi-deciduous forest in southeast Brazil. These methods were sufficiently precise to evaluate the seasonal behavior of tree growth in response to changes in climatic conditions.

MATERIAL AND METHODS

Selecting forest fragments

Three fragments of native forest and three experimental plantations were considered for this study. The sites consist of native tree species characteristic of the seasonal semi-

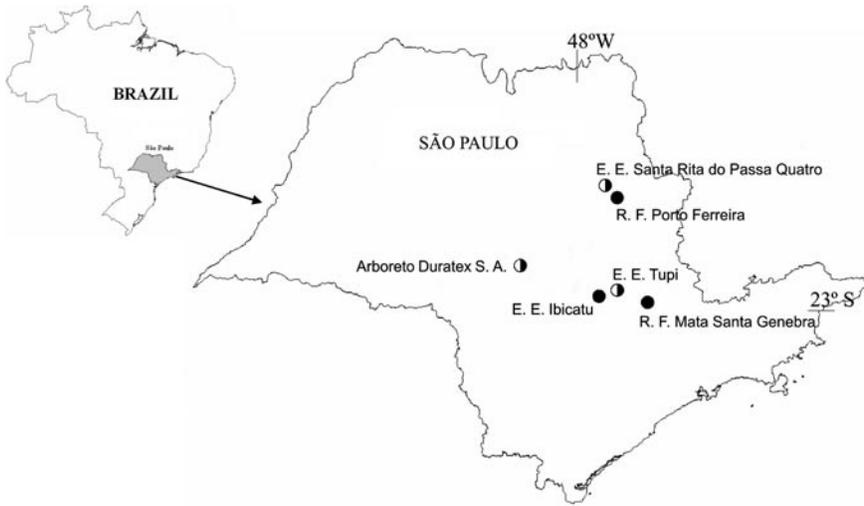


Figure 1. Map of the São Paulo State showing the location of the sampled sites. Black circles represent fragments of native forest and the half-black circles the experimental plantations.

deciduous forests of the southeastern plateau of São Paulo, Brazil (Fig. 1). The native forest sites are located in the Ecological Station of Ibicatu ($22^{\circ} 47' S$, $47^{\circ} 43' W$; 500 m altitude), the State Park of Porto Ferreira ($21^{\circ} 50' S$, $47^{\circ} 28' W$; 540 m altitude), and the Santa Genebra Reserve Forest ($22^{\circ} 44' 45'' S$, $47^{\circ} 06' 33'' W$; 670 m altitude). The experimental plantation sites are in the Experimental Station of Tupi ($22^{\circ} 43' 21'' S$, $47^{\circ} 31' 47'' W$; 535 m altitude), the Experimental Station of Santa Rita do Passa Quatro ($21^{\circ} 40' S$, $47^{\circ} 30' W$; 725 m altitude), and the Arboretum of Duratex S.A. ($22^{\circ} 25' S$, $48^{\circ} 50' W$; 600 m altitude). The study sites have red-yellow podzol and yellow-red latossol soils (Bertonni 1984).

Collection of climate data

We used data for monthly mean temperature and monthly total precipitation recorded at the meteorological stations of the cities of Campinas (Forest of Santa Genebra), Piracicaba (E. S. Tupi), Anhembi (E. S. Ibicatu), Santa Rita do Passa Quatro (E. S. Santa Rita do Passa Quatro), Pirassununga (S.P. Porto Ferreira), and Agudos (A. Duratex). The source of these data was the Department of Physics and Meteorology, ESALQ/USP.

Selecting species and individuals

We selected 24 tree species (see Table 1) for this study. In native forest sites, the number of trees and species we selected was related to their frequency of occurrence in the forest. We made observations and measurements on 109 individuals from native forests and 140 individuals from the experimental plantation areas. A total of 249 individuals were considered in this study.

Collecting phenological data

The month of flowering, fruiting, seed dispersion, and leaf swelling and abscission for 249 trees was recorded between the years 1999 and 2006.

Table 1. Tree species ordered by families and number of individuals per study site within the seasonal semi-deciduous forests of Brazil and their phenology.

Family / Species	Study sites (no. of individuals)		Leaf fall time (phenology)		
	Native	Plantation	D	SD	EG
Anacardiaceae					
<i>Astronium graveolens</i> Jacq.	PF (3), SG (3)			May-Oct	
Apocynaceae					
<i>Aspidosperma polyneuron</i> Muell. Arg.	EI (3), SG (14)	ET (5), SR (6)			Aug-Oct
Bignoniaceae					
<i>Tabebuia serratifolia</i> (Vahl) Nichols.		AD (5)	Aug-Sep		
<i>Zeyheria tuberculata</i> (Vell.) Bureau	PF (1)			Aug-Nov	
Euphorbiaceae					
<i>Savia dictyocarpa</i> Muell. Arg.	EI (5)				Jul-Aug
Lauraceae					
<i>Ocotea porosa</i> (Nees & Mart. ex Nees) L.Barroso	SR (6)		May-Oct		
Lecythidaceae					
<i>Cariniana estrellensis</i> (Raddi) Kuntze	PF (4)	AD (6), ET (4), PF (4)		Jun-Nov	
<i>Cariniana legalis</i> (Mart.) Kuntze	PF (6)			Aug-Dec	
Leg. Caesalpinioideae					
<i>Caesalpinia ferrea</i> Mart. ex Tul.		ET (5)		Jun-Oct	
<i>Copaifera langsdorffii</i> Desf.	PF (8), SG (3)	AD (6)		Jul-Oct	
<i>Hymenaea courbaril</i> L.	PF (3)	SR (6)		Jun-Oct	
<i>Peltophorum dubium</i> (Spreng.) Taub.		SR (6)	Apr-Aug		
<i>Schizolobium parahyba</i> (Vell.) Blake		ET (2)	Apr-Oct		
Leg. Mimosaceae					
<i>Anadenanthera macrocarpa</i> (Benth.) Brenan		AD (3)	Jul-Jan		
<i>Piptadenia gonoacantha</i> (Mart.) J.F. Macbr.	EI (6), SG (4)	AD (5)		Jun-Nov	
Leg. Papilionoideae					
<i>Centrolobium tomentosum</i> Guill. ex Benth.	EI (6), SG (5), PF (13)	SR (6)	Jul-Oct		
<i>Dipteryx alata</i> Vogel		AD (5)			Sep-Feb
<i>Myroxylon balsamum</i> (L.) Harms		AD (2)		Sep-Nov	
<i>Platycyamus regnellii</i> Benth.		SR (6)	May-Sep		
Rhamnaceae					
<i>Colubrina glandulosa</i> Perkins	SG (4)	AD (5)		Jun-Nov	
Rutaceae					
<i>Balfourodendron riedelianum</i> Engl.	SG (2)	AD (5), ET (9), SR (6)		Jul-Nov	
<i>Esenbeckia leiocarpa</i> Engl.	EI (12), SG (4)	AD (6), ET (9), SR (6)			May-Nov
Sterculiaceae					
<i>Guazuma ulmifolia</i> Lam.		PF (2)		May-Sep	
Verbenaceae					
<i>Aegiphila sellowiana</i> Cham.		PF (4)		May-Dec	
Total	109 trees	140 trees			

Study sites: AD = Arboreto da Duratex; EI = Est. Ecol. de Ibicatu; ET = Est. Exp. de Tupi; PF = Parque Est. de Porto Ferreira; SG = Res. Florestal Mata de Santa Genebra; SR = Est. Exp. de Santa Rita do Passa Quatro – D = deciduous; SD = semideciduous; EG = evergreen.

Collecting dendrometer data

The increment of trunk and timing of growth for each of the 249 trees were recorded at DBH by using steel permanent dendrometer bands with a precision of 0.2 mm (Mariaux 1977; Botosso & Tomazello F^o 2001). We recorded data monthly between the years 1999 and 2006. Independently of the tree diameter, the first reading was adjusted to the 0 value to highlight the subsequent increase and lowering of the growth periods resulting from the seasonal availability of water.

Sampling and analyzing the wood anatomical structures

We collected 48 radial wood strips oriented from pith to bark and positioned at DBH (1.3 m above ground level) by using non-destructive methods, including sampling with Pressler increment borers (core diameter 5.15 mm) and a motorized extractor (core diameter 18 mm). From these samples we obtained thin (10–15 μm) wood cross sections using a sliding microtome. Permanent histological slides were prepared according to standard techniques. The macro- and microscopic anatomical structures were described following the IAWA Committee (1989).

Cambial marking and dating scars

We applied the “window method” described by Mariaux (1977), which consisted of removing the bark and phloem (5 cm height \times 0.5 cm length) in the longitudinal direction of the trunk. We made yearly three to six windows per species in winter (June) and spring (December). A total of 48 trees (two individuals per species) were scarred. The wood samples containing scars were extracted with a motorized extractor in two periods (October and December, 2004). We cut the wood cross sections using a sliding microtome and analyzed its surface with a stereoscopic microscope ($\times 10$ –40). The scars were dated by counting the number of rings formed since marking the cambium.

RESULTS

Analysis of climatic conditions

The regional climate is mesothermal with dry winters and hot summers (Cwa according to Köppen 1948). The average temperature is 23°C in the warmer months (January–February) and 15°C in colder months (June–July). The annual average precipitation is 1370 mm, but with a wide seasonal variation: the greatest monthly average (230 mm) occurs during December through February, and the smallest (30 mm) occurs during June through August. Figure 2 shows the annual cycle of mean temperature and precipitation from all the meteorological stations. Although monthly mean temperature values vary slightly, the monthly total precipitation values vary widely, with highest values during December and January (250 mm) and lowest values during July and August (20 mm).

Analysis of wood anatomy

With respect to porosity (P), four species showed semi-ring porosity, and the other 20 species had diffuse porosity. With respect to latewood cell wall thickness (LWF),

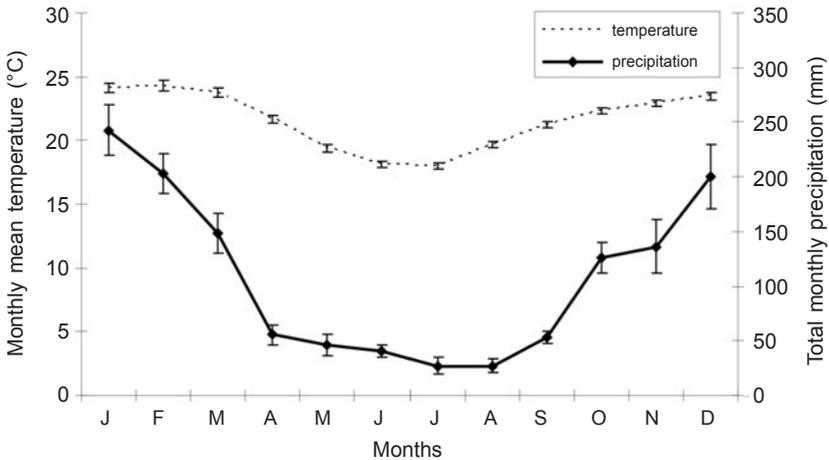


Figure 2. Composite from six meteorological stations of the monthly mean temperature and monthly total precipitation in the southeast region of São Paulo State, Brazil. Axial bars represent the standard deviation between the meteorological stations (source: Depto. de Ciências Exatas, ESALQ/USP).

20 species had tree-ring boundaries distinguishable by thicker walls of the latewood fibers. We observed concentric and continuous layers of marginal parenchyma (MP) in 19 species, discontinuous marginal parenchyma in four species, and no marginal parenchyma in one species (Table 2; Fig. 3).

We classified the species by anatomical features that indicate the boundary between rings: 23 species had marginal parenchyma; 14 species had thicker-walled latewood fibers; 4 species had radial parenchyma with local tangential distention, and only one species, *Schizolobium parahyba*, had thick-walled and radially flattened latewood fibers (instead of thin-walled earlywood fibers) (Table 2; Fig. 3).

We also classified the species by our ability to distinguish individual annual growth rings by observing anatomical characteristics of the wood: 16 species had easily distinguishable tree rings; 8 species had rings that were difficult to distinguish (Table 2; Fig. 3).

Analysis of cambial marks

Macroscopic examination of the polished wood cross sections revealed the scars resulting from injuries to the cambium (Fig. 4). These scars were covered by new layers of xylem tissue in the form of tree rings. For the species with easily distinguishable rings, we were able to confirm their annual nature by counting the number of rings since injury. Similarly we were able to confirm the annual nature of rings of species that previously had been difficult to study because of their anatomical structures. For *Astronium graveolens*, *Colubrina glandulosa* and *Guazuma ulmifolia*, ring counting was extremely difficult due to the poor distinctiveness of the growth rings.

Table 2. Tree-ring anatomical characteristics of 24 species of the seasonal semi-deciduous forests of Brazil.

Family / Species	Wood characters					
	GR	P	LWF	MP	RB	WR
Anacardiaceae						
<i>Astronium graveolens</i>	B	3	3	–	FZ	1
Apocynaceae						
<i>Aspidosperma polyneuron</i>	B	3	3	1	FZ, MP	1
Bignoniaceae						
<i>Tabebuia serratifolia</i>	A	3	3	1	MP	1
<i>Zeyheria tuberculata</i>	A	3	3	1	MP	1
Euphorbiaceae						
<i>Savia dictyocarpa</i>	C	3	2	2	FZ, MP	2
Lauraceae						
<i>Ocotea porosa</i>	A	3	3	1	MP	1
Lecythidaceae						
<i>Cariniana estrellensis</i>	B	3	3	1	FZ, MP	2
<i>Cariniana legalis</i>	B	3	3	2	FZ, MP	2
Leg. Caesalpinioideae						
<i>Caesalpinia ferrea</i>	A	3	3	1	MP, FZ	1
<i>Copaifera langsdorffii</i>	A	3	2	1	MP	2
<i>Hymenaea courbaril</i>	A	3	3	1	MP	1
<i>Peltophorum dubium</i>	A	3	3	1	MP, FZ	1
<i>Schizolobium parahyba</i>	A	3	1	1	MP, FW	1
Leg. Mimosaceae						
<i>Anadenanthera macrocarpa</i>	A	3	3	1	MP, FZ	1
<i>Piptadenia gonoacantha</i>	A	2	3	1	MP, FZ, VD	1
Leg. Papilionoideae						
<i>Centrolobium tomentosum</i>	A	3	3	1	MP, FZ	1
<i>Dipteryx alata</i>	A	3	3	1	MP, FZ	1
<i>Myroxylon balsamum</i>	B	3	3	1	MP	1
<i>Platycamus regnellii</i>	A	3	3	1	MP	1
Rhamnaceae						
<i>Colubrina glandulosa</i>	B	3	3	2	MP	2
Rutaceae						
<i>Balfourodendron riedelianum</i>	A	2	3	1	MP, FZ, VD	1
<i>Esenbeckia leiocarpa</i>	A	2	3	1	MP, FZ, VD	1
Sterculiaceae						
<i>Guazuma ulmifolia</i>	C	3	3	2	FZ, MP	2
Verbenaceae						
<i>Aegiphila sellowiana</i>	A	2	2	1	MP, VD	1

GR = Growth rings: A: distinct; B: distinguishable with difficulty; C: indistinct or absent.

P = Porosity: 1: ring-porous; 2: semi-ring-porous; 3: diffuse-porous.

LWF = Latewood fiber wall thickness: 1: thin- to thick-walled; 2: thick-walled; 3: fiber zone.

MP = Marginal parenchyma: 1: continuous; 2: discontinuous.

RB = Ring boundary structure (as observed in the latewood portion): FW: changes in fiber wall thickness or fiber radial size; VD: changes in vessel diameter; MP: presence of marginal parenchyma; FZ: fiber zone.

WR = Wedging rings: 1: rare; 2: abundant.

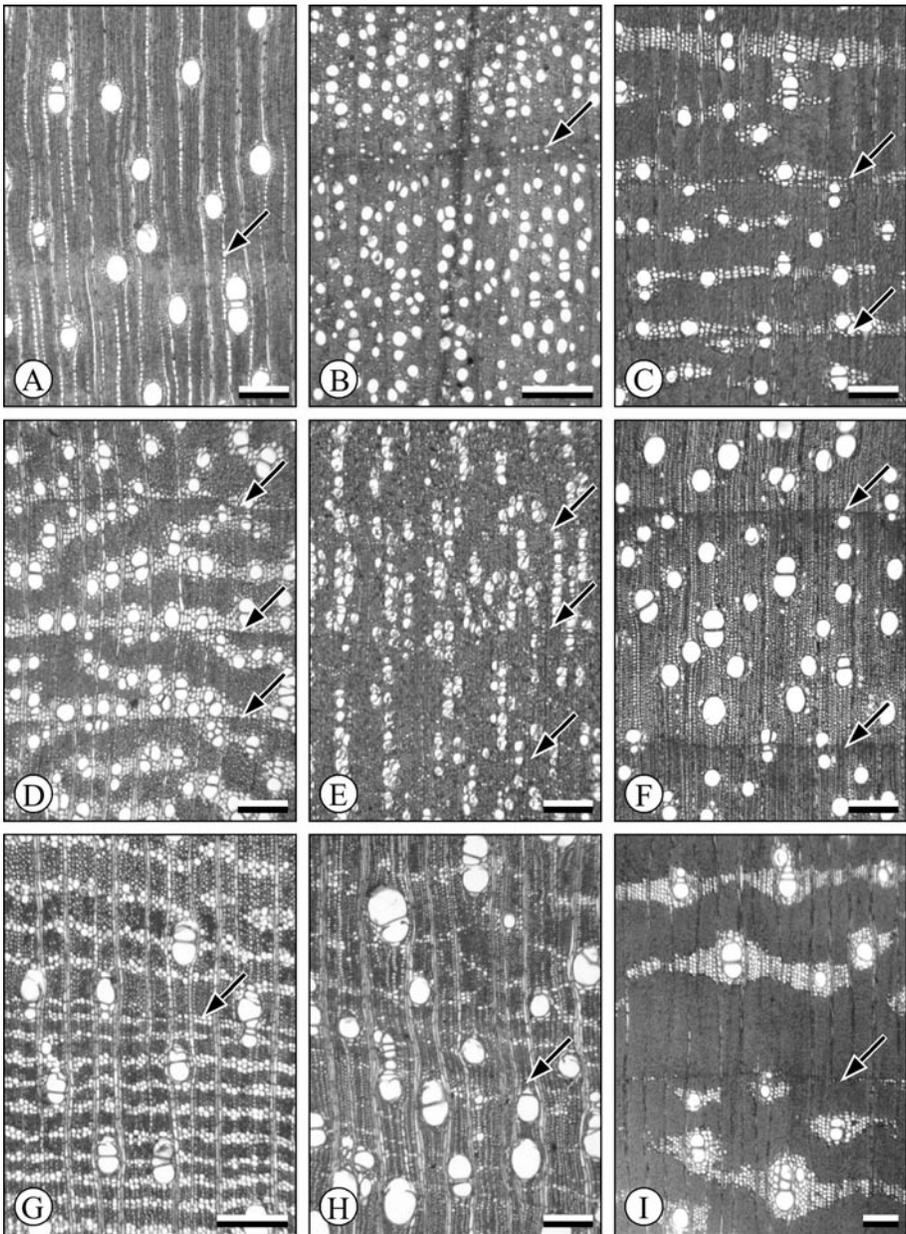


Figure 3. Wood anatomical structure from cross sections of tree species from the seasonal semi-deciduous forest of Brazil. – A: *Astronium graveolens*. – B: *Aspidosperma polyneuron*. – C: *Tabebuia serratifolia*. – D: *Zeyheria tuberculata*. – E: *Savia dictyocarpa*. – F: *Ocotea porosa*. – G: *Cariniana estrellensis*. – H: *Cariniana legalis*. – I: *Caesalpinia ferrea*. – Arrows indicate tree-ring boundaries. – Scale bars = 0.1 mm.

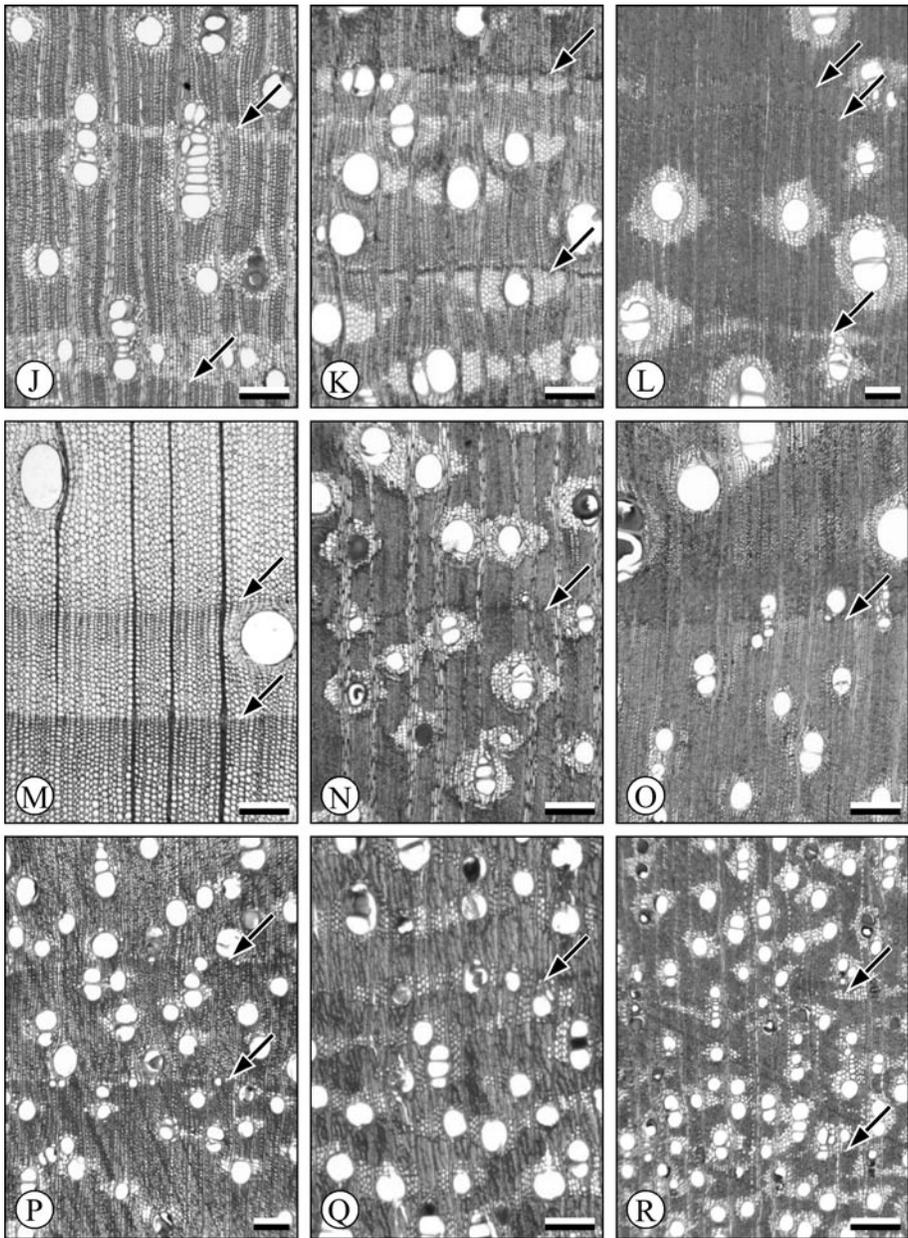


Figure 3 continued. – J: *Copaifera langsdorffii*. – K: *Hymenaea courbaril*. – L: *Peltophorum dubium*. – M: *Schizolobium parahyba*. – N: *Anadenanthera macrocarpa*. – O: *Piptadenia gonocantha*. – P: *Centrolobium tomentosum*. – Q: *Dipteryx alata*. – R: *Myroxylon balsamum*. – Scale bars = 0.1 mm.

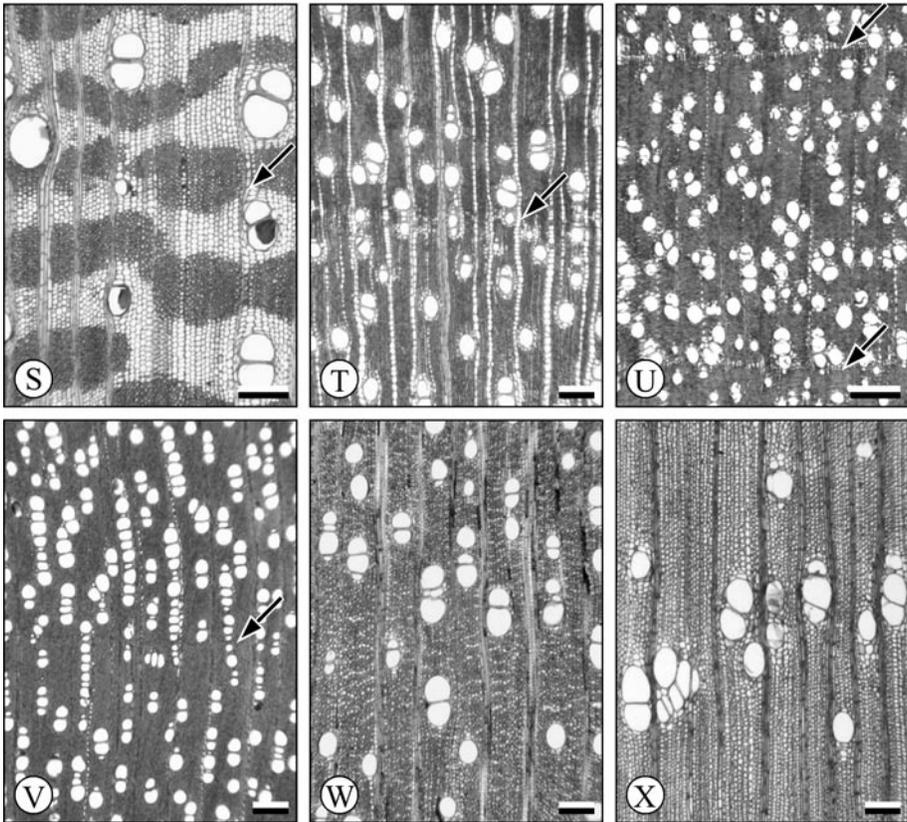


Figure 3 continued. – S: *Platycyamus regnellii*. – T: *Colubrina glandulosa*. – U: *Balfourodendron riedelianum*. – V: *Esenbeckia leiocarpa*. – W: *Guazuma ulmifolia*. – X: *Aegiphila sellowiana*. – Scale bars = 0.1 mm.

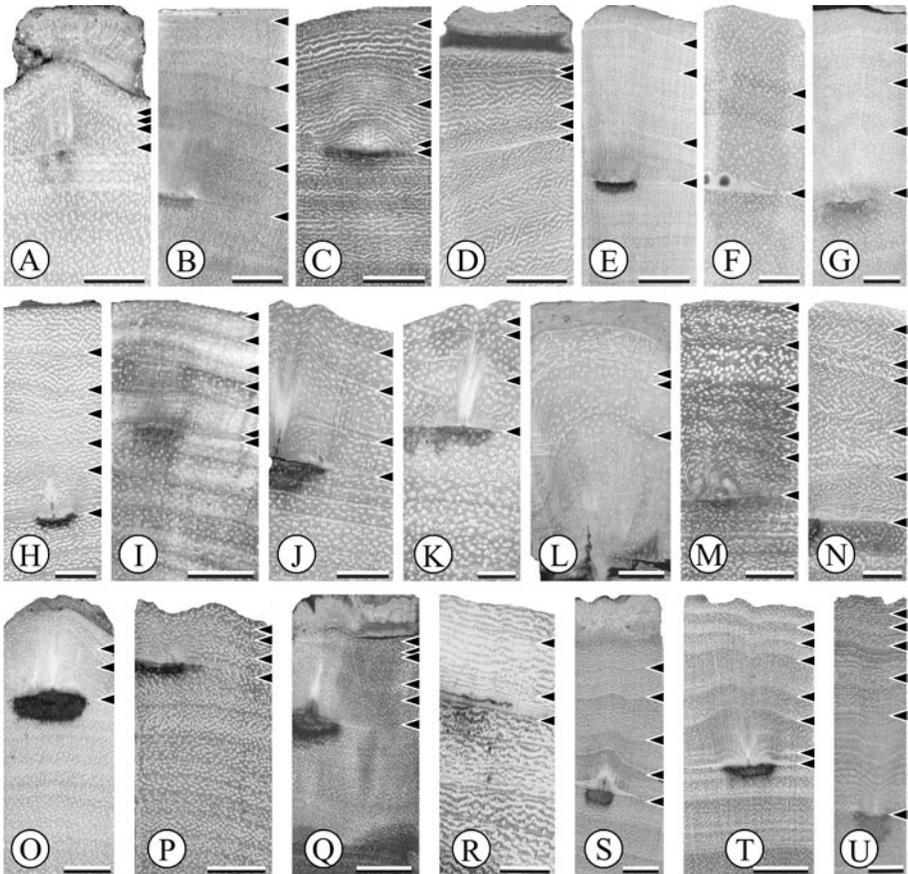
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Figure 4. Xylem scars induced by the Mariaux's window method in tree species from the seasonal semi-deciduous forest of Brazil. The year of the cambium marking and the year of the wood sampling is indicated between brackets. – A: *Astronium graveolens* (Oct/00; Oct/04). – B: *Aspidosperma polyneuron* (Sep/99; Dec/04). – C: *Tabebuia serratifolia* (Jul/98; Dec/04). – D: *Zeyheria tuberculata* (Sep/99; Oct/04). – E: *Savia dictyocarpa* (Sep/00; Dec/04). – F: *Cariniana estrellensis* (Sep/01; Oct/04). – G: *Cariniana legalis* (Oct/00; Oct/04). – H: *Caesalpinia ferrea* (Dec/98; Oct/04). – I: *Copaifera langsdorffii* (Jul/98; Dec/04). – J: *Hymenaea courbaril* (Oct/00; Oct/04). – K: *Peltophorum dubium* (Oct/00; Oct/04). – L: *Schizolobium parahyba* (Dec/00; Oct/04). – M: *Anadenanthera macrocarpa* (Jul/98; Dec/04). – N: *Piptadenia gonocantha* (Sep/99; Dec/04). – O: *Centrolobium tomentosum* (Sep/01; Oct/04). – P: *Dipteryx alata* (Sep/01; Dec/04). – Q: *Myroxylon balsamum* (Jul/99; Dec/04). – R: *Platycyamus regnellii* (Sep/01; Oct/04). – S: *Balfourodendron riedelianum* (Oct/99; Dec/04). – T: *Esenbeckia leiocarpa* (Sep/98; Dec/04). – U: *Aegiphila sellowiana* (Sep/98; Oct/04). – Arrows indicate tree-ring boundaries. Due to the low quality of some wood samples affected by fungal attack and reaction wood, the woods of *Ocotea porosa*, *Colubrina glandulosa*, and *Guazuma ulmifolia* were not included in the figure. – Scale bars = 5.0 mm.

Phenological analysis

Most of the species studied lost their leaves in response to seasonal drought between April and May. The new leaves developed between September and October, which coincided with the beginning of the rainy season (Table 1). As stress increased during the dry season (especially between July and September), the loss of leaves intensified in more tree species (Fig. 5). Most of the tree species had fully developed their new foliage between October and March.

Copaifera langsdorffii, *Tabebuia serratifolia* and *Peltophorum dubium* began to develop new leaves between August and September, before the end of the dry season, which demonstrated a different adaptation to regional climatic conditions. In contrast, *Cariniana legalis* and *C. estrellensis* developed new leaves after the first rains in spring (October and November). The semi-deciduous tree species (for example, *Esenbeckia leiocarpa* and *Aspidosperma polyneuron*) lost some leaves during the winter (July and August) and developed new leaves at the beginning of the rainy period. The timing of flowering, fruiting, and seed dispersion was similar to that observed in other semi-deciduous forests in the São Paulo region (Matthes 1980; Morellato *et al.* 1989).



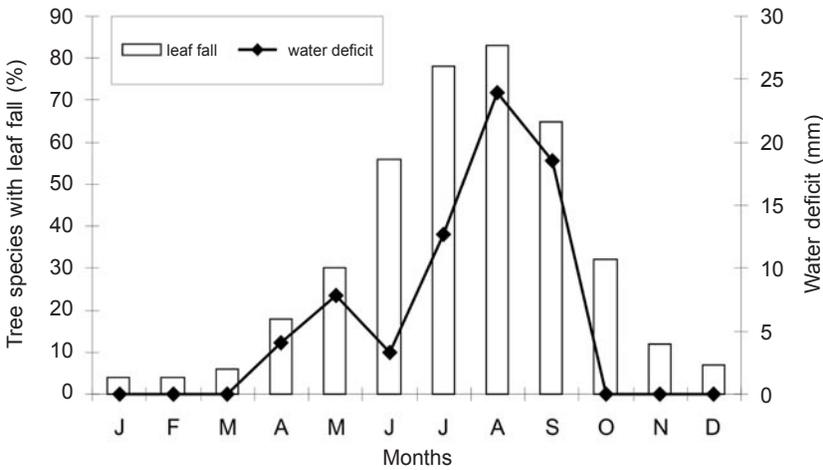


Figure 5. Tree species (%) with leaf fall in response to water stress. The rapid response to the increment of water deficit is the increase in the number of species with leaf fall activity, particularly during the dry season (between July and September).

Dendrometer data analysis

The annual rhythm of radial increment, measured by trunk girth increment, is shown as cumulative increment in Table 3 and Figure 6. Each year, the radial increment decreased during the winter drought season (May and June), which was probably the result of bark retraction by dehydration in addition to reduction and cessation of cambial activity. Each year, growth was re-activated after the first rains in spring (October and November) (see Fig. 6).

We compared growth measured by dendrometers with precipitation and temperature data. Temperatures below 10 °C were infrequent between 1999 and 2005 (Fig. 7). However, 1999, 2000, and 2003 had periods with a monthly precipitation below 10 mm during the dry season. Radial growth was positively correlated with the annual precipitation (Fig. 7). Significant shrinkage (radial decrease) occurred when rains did not occur during the dry seasons (1999, 2000, and 2003 at the Ibicatu site). However, when rains occurred during the dry period (in 2004 and 2005), much less shrinkage occurred (Fig. 7). These results demonstrate the influence of precipitation on the rhythm of the cambium and thus its corresponding seasonal effect on the growth ring formation of species from tropical semi-deciduous forests.

The average annual radial increment of species is shown in Table 3. *Aspidosperma polyneuron* had the greatest and the least radial growth among the species from native forest sites (Ibicatu = 15.2 mm/year and Santa Genebra = 5.4 mm/year) and an intermediate radial increment among trees of this species from plantation sites (Tupi = 11.6 mm/year and Santa Rita = 13.8 mm/year). *Piptadenia gonoacantha* and *Centrolobium tomentosum* showed this same pattern. *Cariniana estrellensis*, *Copaifera langsdorffii*, and *Esenbeckia leiocarpa* had similar growth in both native forest and plantation sites, although growth may have been influenced by factors other than climate or inter-tree

Table 3. Annual trunk girth increment of tree species in native and plantation forests. Period from 1998 to 2006.

Family / Species	CBH	Native			Plantation			A	B
		EI	PF	SG	ET	SR	AD		
Anacardiaceae									
<i>Astronium graveolens</i>	895 (±100)		1.8	14.5					8.2
Apocynaceae									
<i>Aspidosperma polyneuron</i>	745 (±228)	15.2		5.4	11.6	13.8			11.5
Bignoniaceae									
<i>Tabebuia serratifolia</i>	629 (±143)							4.9	4.9
<i>Zeyheria tuberculata</i>	342			7.5					7.5
Euphorbiaceae									
<i>Savia dictyocarpa</i>	658 (±243)	10.6							10.6
Lauraceae									
<i>Ocotea porosa</i>	745 (±125)					7.7			7.7
Lecythidaceae									
<i>Cariniana estrellensis</i>	763 (±251)		12.2		12.7			12.0	12.3
<i>Cariniana legalis</i>	1432 (±675)		17.1						17.1
Leg. Caesalpinioidae									
<i>Caesalpinia ferrea</i>	818 (±214)				19.3				19.3
<i>Copaifera langsdorffii</i>	855 (±449)		10.1					9.8	10.0
<i>Hymenaea courbaril</i>	941 (±178)		6.4			9.3			7.9
<i>Peltophorum dubium</i>	968 (±152)					4.9			4.9
<i>Schizolobium parahyba</i>	1280 (±120)				19.6				19.6
Leg. Mimosaceae									
<i>Anadenanthera macrocarpa</i>	1263 (±362)							7.5	7.5
<i>Piptadenia gonoacantha</i>	789 (±207)	22.8		13.0				19.1	18.3
Leg. Papilionoidae									
<i>Centrolobium tomentosum</i>	895 (±279)	3.7	7.1	5.1		7.3			5.8
<i>Dipteryx alata</i>	724 (±66)							5.3	5.3
<i>Myroxylon balsamum</i>	500 (±127)							6.0	6.0
<i>Platycyamus regnellii</i>	862 (±104)					10.8			10.8
Rhamnaceae									
<i>Colubrina glandulosa</i>	472 (±167)			15.7				1.8	8.7
Rutaceae									
<i>Balfourodendron riedelianum</i>	671 (±265)			5.5	9.2	8.7		4.8	7.0
<i>Esenbeckia leiocarpa</i>	653 (±234)	7.3		8.5	7.4	11.8		9.0	8.8
Sterculiaceae									
<i>Guazuma ulmifolia</i>	193 (±43)		19.0						19.0
Verbenaceae									
<i>Aegiphila sellowiana</i>	337 (±125)		19.5						19.5

CBH: Mean circumference at breast height (mm). In parentheses, the standard deviation. Study sites: AD : Arboreto da Duratex; EI: Est. Ecol. de Ibicatu; ET: Est. Exp. de Tupi; PF: Parque Est. de Porto Ferreira; SG: Res. Florestal Mata de Santa Genebra; SR: Est. Exp. de Santa Rita do Passa Quatro. – **A**: Mean increment (mm) for the entire observational period and by site; **B**: Mean increment (mm) for the entire observational period and by species. Anacardiaceae and Apocynaceae showed large differences in their mean radial increments due to strong competition with lianas and injuries by wind.

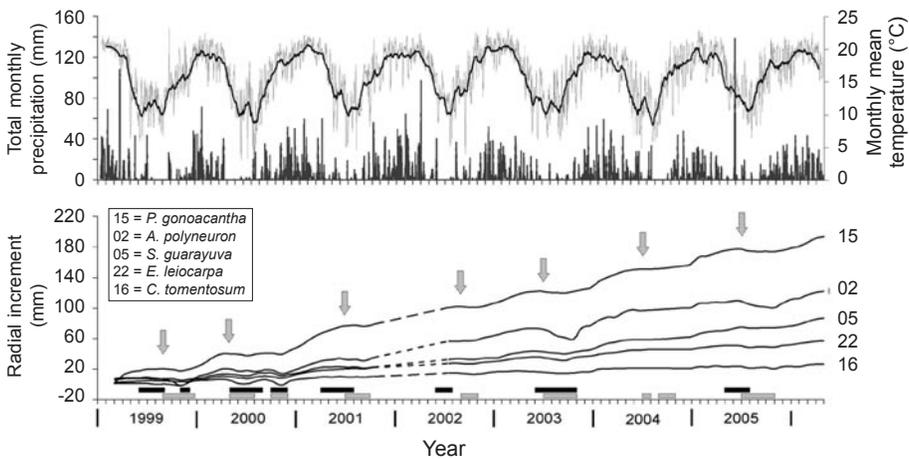


Figure 7. Relationship between climate conditions and the rate of trunk growth of trees species of Ibicatu (source: Depto. de Ciências Exatas, ESALQ/USP). The upper panel shows the total precipitation (histogram) and mean temperature (daily mean temperature with a superposed 5-yr smoothing curve) from the Piracicaba meteorological station. The lower panel represents the accumulated radial growth corresponding to five species (see box). Below the growth curves appear the length of the dry season (black) and the length of the dormant period (shaded). Arrows indicate the beginning of the dormant period.

had the greatest annual radial growth. Dominant tree species such as *Cariniana legalis* (17.1 mm/year) and *Caesalpinia ferrea* (19.3 mm/year) also had high rates of radial increment. In contrast, late secondary tree species such as *Tabebuia serratifolia* (4.9 mm/year) and *Hymenaea courbaril* (7.9 mm/year) showed the lower radial growth (see Table 3).

DISCUSSION

The presence of marginal parenchyma was the most common and most identifiable characteristics that defined tree-ring boundaries. Vetter (2000) also found this to be characteristic of tree species from the “terra firme” forests in Amazonia. As pointed out in previous studies, the marginal parenchyma is a particularly well-defined characteristic in tree rings of *Centrolobium tomentosum* and *Copaifera langsdorffii* (Marcati et al. 2006). Moreover, it has been corroborated by several other studies that *Tabebuia serratifolia* also has marginal parenchyma, even though it is difficult to observe (Roig 2000; Botosso & Tomazello F^o 2001; Ferreira-Fedele et al. 2004). The presence of thick-walled latewood fibers marking tree-ring boundaries was also a common feature of the species we studied, of which *Aspidosperma polyneuron* is one example. A useful strategy for identifying tree-ring boundaries in tropical species is to associate two or more anatomical characteristics of the wood (Worbes 1989; Roig 2000; Vetter 2000). Accordingly, we found rings of semi-porous species demarcated by marginal parenchyma (e.g. *Piptadenia gonoacantha*), by confluent parenchyma with concentric

bands that were thicker at the beginning of the growth rings (*e.g. Cariniana estrellensis* and *C. legalis*), by the combination of latewood thick-walled fibers and marginal parenchyma (*e.g. Caesalpinia ferrea*, *Peltophorum dubium* and *Balfourodendron riedelianum*) or simply by latewood fibers with thick walls (*e.g. Guazuma ulmifolia* and *Savia dictyocarpa*).

The cambial marking method was reliable for defining the annual nature of tree-ring formation. However, to properly remove the bark and phloem to reach the cambium zone, we needed to accurately determine the outer and inner bark thickness. We also found that, for some species (*e.g. Savia dictyocarpa* and *Colubrina glandulosa*), this method may result in fungal infections that promote the formation of thickened and lignified scar tissues and narrow growth rings after the wounding mark. We successfully used the cambial marking method to delimit annual tree rings in the following species: *Aegiphila sellowiana*, *Anadenanthera macrocarpa*, *Aspidosperma polyneuron*, *Astronium graveolens*, *Balfourodendron riedelianum*, *Caesalpinia ferrea*, *Cariniana legalis*, *C. estrellensis*, *Centrolobium tomentosum*, *Copaifera langsdorfii*, *Dipteryx alata*, *Esenbeckia leiocarpa*, *Hymenaea courbaril*, *Myroxylon balsamum*, *Ocotea porosa*, *Peltophorum dubium*, *Piptadenia gonoacantha*, *Platycyamus regnellii*, *Savia dictyocarpa*, *Schizolobium parahyba*, *Tabebuia serratifolia*, *Zeyheria tuberculata*. Other authors also found that some of these species form annual rings (Borchert 1999; Ferreira 2002; Maria 2002), thus corroborating our observations.

Considering the phenological data analysis, we can generally conclude that these tree species lose their leaves between May and September, which encompasses the dry season. These results indicate that stress provoked by periods of severe drought was the key factor initiating leaf fall for species from the semi-deciduous forests of Brazil (Roig 2000). This phenological phase occurs when the vascular cambium is least active. *Tabebuia serratifolia* also loses its leaves during the dry season, but flowering, fruiting, and seed dispersal also occur during the same period. Other species, such as *Esenbeckia leiocarpa*, lose some of their leaves during the dry season, develop new leaves after the first rains of early spring, and produce fruit and seeds during the summer months (May and September) (Ferreira-Fedele *et al.* 2004). *Aspidosperma polyneuron* partially or totally loses its leaves during the dry season. We observed that the timing of the phenological phases of flowering, fruiting, and seed dispersal differed for the tree species studied. However, this behavior is considered typical for the seasonal climatic conditions of the semi-deciduous forests. Although drought seems to be the major factor influencing leaf phenology, other factors such as day length, temperature variations or genetics may also be involved (Morellato *et al.* 1989).

Several authors claim that lower precipitation during the winter strongly reduces the rate of radial growth of many tree species in the Neotropics (Détienne & Mariaux 1977; Prévost & Puig 1981; Détienne 1989). Our findings of a reduced rate of incremental growth during May and June (dry season) and a faster rate during October and November (early rainy season), confirm these earlier findings. A similar behavior has been previously observed for the same species from the seasonal semi-deciduous forest of São Paulo (Ferreira 2002; Maria 2002) and from the “terra firme” Amazonian forests,

which also have an annual dry season (Vetter 2000). Although the annual rate of radial growth may be influenced by local environmental conditions (*e.g.* topography, nutrient availability, and competition between trees and lianas), water availability seems to be the primary factor. This is suggested by the decreased activity of the vascular cambium during periods of low precipitation during winter. The decrease in cambial activity is also accompanied by changes in the type and morphology of latewood cells, resulting in distinguishable boundaries between annual tree rings for most of the tree species. These findings have been corroborated for many of the presently studied species (Prévost & Puig 1981; Détienne 1989; Worbes 1989; Maria 2002; Ferreira-Fedele *et al.* 2004; Botosso *et al.* 2005).

This study provides evidence that the semi-deciduous forests of São Paulo experience seasonal cycles in radial increment controlled by seasonal climate, and that annual growth increments for most of the studied species can be identified on the basis of anatomically distinguishable features.

Much research related to ecology, paleoclimate, forest production, and conservation in the Neotropics depends on the availability of dendrochronological data sensitive to environmental variations derived from anatomically-distinct annual growth rings (Stahle 1999; Roig 2000). Therefore, many previous studies have searched for the most promising species suitable for dendrochronological applications (Worbes 1989; Boninsegna *et al.* 1989; Jacoby 1989; Tomazello *et al.* 2000). In Brazil, these efforts were first concentrated in the Amazon area and later expanded to the Atlantic Forests (Vetter 2000; Botosso *et al.* 2000; Tomazello *et al.* 2000; Callado *et al.* 2001; Ferreira 2002; Maria 2002). All these studies suggested the use of a multi-proxy approach based on the annual nature of tree-ring formation and growth responses to climatic variables (Roig 2000; Vetter 2000; Tomazello *et al.* 2000; Botosso & Tomazello *et al.* 2001). Therefore, by simultaneously exploring relationships among the timing of leaf fall, cambial activity (measured with dendrometers and cambial markers), and climatic factors, we can better understand the particular growth behavior of tropical tree species, including the rhythm of cambial activity and the formation of annual growth rings (Jacoby 1989; Roig 2000).

ACKNOWLEDGEMENTS

We thank the São Paulo University - USP (Forest Science Department) and IANIGLA-CONICET, for laboratory facilities, the Research Support Foundation of São Paulo State - FAPESP (Proc. 02/14166-3), the Brazilian Council for Superior Education, CAPES - Secretaría de Ciencia, Tecnología e Innovación Productiva of Argentina, SECYT (Grant 106/06), for fellowships, funding and research grants. We thank the Forest Institute of São Paulo (units: Tupi Experimental Reserve, Ibicatu Ecological Reserve, Porto Ferreira Park, Santa Rita do Passa Quatro Experimental Reserve), Forest Park Santa Genebra, and Duratex Arboretum for providing camping facilities and study sites. We thank Maria A.R. Bermudez and Marcio A. Danalesi for providing laboratory and field facilities. We thank R. Bottero and J. Boshoven for help during the manuscript preparation. This paper was developed from research conducted by the first author during a post-doctoral fellowship at the Tree-ring Laboratory of Piracicaba, São Paulo University.

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