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CAMBIAL GROWTH PERIODICITY STUDIES OF SOUTH AMERICAN WOODY SPECIES – A REVIEW

Cátia Henriques Callado[1,*], **Fidel Alejandro Roig**[2], **Mário Tomazello-Filho**[3] and **Claudia Franca Barros**[4]

[1]Laboratório de Anatomia Vegetal, Depto de Biologia Vegetal, Universidade do Estado do Rio de Janeiro. Rua São Francisco Xavier 524. PHLC-224, CEP 20550-013, Rio de Janeiro, RJ, Brazil
[2]Laboratorio de Dendrocronología, Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, Centro Científico Tecnológico CONICET-Mendoza, Mendoza, Argentina
[3]Departamento de Ciências Florestais, Escola Superior de Agricultura Luis de Queiroz, Universidade de São Paulo. Av. Pádua Dias 11, CP 09, CEP 13418-900, Piracicaba, SP, Brazil
[4]Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, Rua Pacheco Leão 915, CEP 22460-030, Rio de Janeiro, RJ, Brazil
*Corresponding author; e-mail: catiacallado@terra.com.br

ABSTRACT

This paper reviews histological studies of cambium activity in South American woody species and provides future research prospects. The majority of the studies almost exclusively describe radial increment and/or its periodicity. There are 15 papers concerning the cambial activity of 17 woody species from the South American flora and 3 exotic species in 4 countries that were published to date. Despite endogenous factors affecting the radial meristem, the seasonality of rains has been identified as the main factor influencing cambial activity in the tropics and subtropics. There is a lack of standardization and a need for improvement and discussion concerning the methods used. Moreover, radial growth studies conducted by monitoring cambium cell production are still scarce in South America, especially when considering the high diversity of the continent's flora and ecosystems.

Keywords: Tree growth, cambium, wood production, tree-ring analysis, environmental signals.

INTRODUCTION

The cambium is the lateral meristem that forms the secondary xylem and phloem. In addition to the phellogen, the cambium promotes growth in thickness or circumference of stems and roots in woody species. This meristem is made of a single layer of initial cells, divided into fusiform and ray cell initials, which undergo periclinal and anticlinal divisions (Evert 1963, 2006; Esau 1977; Raven *et al.* 2010). Some cambial initials sometimes differentiate and become part of the vascular tissues (Gahan 1989; Evert 2006).

Morphologically, cambial cells show a great resemblance to their immediate derivative cells, even at the ultrastructural level under transmission electron microscopy and this fact has led to the adoption of the term cambial zone to describe cambial cells and

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their immediate undifferentiated derivatives (*e.g.*, Evert 1963; Evert & Deshpande 1970; Schmid 1976; Algan 1996; Savidge 2000; Angyalossy & Marcati 2006; Pallardy 2008).

The number of cell layers and the morphological and functional aspects of the cells that form the cambial zone may vary according to local and seasonal environmental conditions. The most important environmental variables that promote cell division and expansion are light, temperature, soil nutrients and water availability (*e.g.*, Kramer 1964; Kozlowski *et al.* 1991; Kozlowski & Pallardy 1997; Savidge 2000; Schweingruber 2007). Regular fluctuations of one or more of these limiting factors provoke a periodic rhythm in plant development, reproduced at the cambium level by active and dormant stages. Thus, cambial production of new cells is genetically controlled but the rhythm is determined by environmental limitations (Avila *et al.* 1975; Kozlowski *et al.* 1991; Kozlowiski & Pallardi 1997). Moreover, competition, pollution and pathogenic attacks may affect and alter cambial activity (Kozlowski *et al.* 1991; Rajput *et al.* 2008).

Although several studies have indicated the existence of periodic rhythms of radial growth in South American woody species (*e.g.*, Roig 2000; Worbes 2002; Rozendaal & Zuidema 2011), seasonal fluctuations in the cambial zone have not been extensively observed or discussed. Terrazas *et al.* (2011), for example, showed that the activity and differentiation of the cambium are important factors in the survival and adaptive strategies of woody plants in diverse ecosystems. Fritts (1976) has already stated that the understanding of periodicity in cambial activity is relevant to studies of wood production and essential to dendroclimatological studies because identification of the beginning of cambial cell production and the length of cambial activity allows for a better understanding of the tree-ring formation process and its relationship with climate. Begum *et al.* (2012) add that a better understanding of the mechanisms of radial growth in trees should aid efforts to improve and enhance the exploitation of commercial woods and to develop effective forest policy that can help in mitigating climatic change.

According to Worbes (2002), a partially unresolved matter in the literature concerns the dynamics of tropical forests, which is associated with the discussion of sustained management, time span of natural regeneration and carbon cycle. The understanding of radial growth dynamics is a relevant part of this question. The issue becomes more relevant in South America, where biodiversity is highlighted by five world hotspots (Conservation International 2011). These hotspots account for 29 % of the known angiosperm species and 12 % of the known plant endemism (Myers *et al.* 2000; Prance *et al.* 2000). In spite of the extraordinary ecological and economic importance of the forests in South America, we do not have a general understanding of the radial growth dynamics of native species. The study of Worbes (1995) is the sole study that proposes a predictive analysis for the growth of species related to climate. This predictive hypothesis is based on the development of true annual growth rings in tropical species from regions with an annual dry season of 2 to 3 months with less than ~60 mm monthly precipitation.

In view of the relevance of the radial growth dynamics of woody plants in the different ecosystems of South America and the importance of cambial activity for a better understanding of these dynamics, we surveyed the histological cambial activity research in this region.

Applied methodology

Studies on cambial periodicity in South America are mostly performed using band dendrometers to measure radial growth (*e.g.*, Alvim & Alvim 1964; Prévost & Puig 1981; Détienne *et al.* 1988; Botosso & Vetter 1991; Worbes 1999; Botosso *et al.* 2000; Tomazello-Filho *et al.* 2000; Schöngart *et al.* 2002; Dünisch *et al.* 2002, 2003; Callado *et al.* 2004; Ferreira-Fedele *et al.* 2004; Dünisch 2005; Figueiredo-Filho *et al.* 2008; Lisi *et al.* 2008; Bräuning *et al.* 2009; Pérez *et al.* 2009; Volland-Voigt *et al.* 2011; Cardoso *et al.* 2012) or using cambium mechanical injury techniques, such as the Mariaux window or the pinning method (*e.g.*, Détienne *et al.* 1988; Botosso & Vetter 1991; Détienne 1995; Worbes 1997, 1999; Bauch & Dünisch 2000; Tomazello-Filho *et al.* 2000; Callado *et al.* 2001a; Dünisch *et al.* 2002; Lisi *et al.* 2008; Brandes *et al.* 2011). Oliveira *et al.* (2007, 2009) used one of the oldest methods to study cambial activity: periodical sampling of the last growth rings by conventional increment borers and assessing the radial tree growth by visual inspections and measurements of the sequential formation of earlywood and latewood layers, associated with a formula that allows the evaluation of radial growth and the relationship between seasonal climate variation and tree-ring formation.

1: Mendoza: Ñacuñán.
2: Mendoza: Telteca.
3: Minas Gerais: Viçosa.
4: Amazonas: Manaus.
5: Pará: Santarém.
6: Mato Grosso: Aripuanã.
7: São Paulo: Botucatu.
8: São Paulo: Piracicaba.
9: São Paulo: São Paulo.
10: Rio de Janeiro: Rio de Janeiro.
11: Cordillera de la Costa.
12: Santa Laura.
13: Reserva Laipuna.
14: Reserva Biológica San Francisco.

Figure 1. Locations where cambial studies were performed in South America.

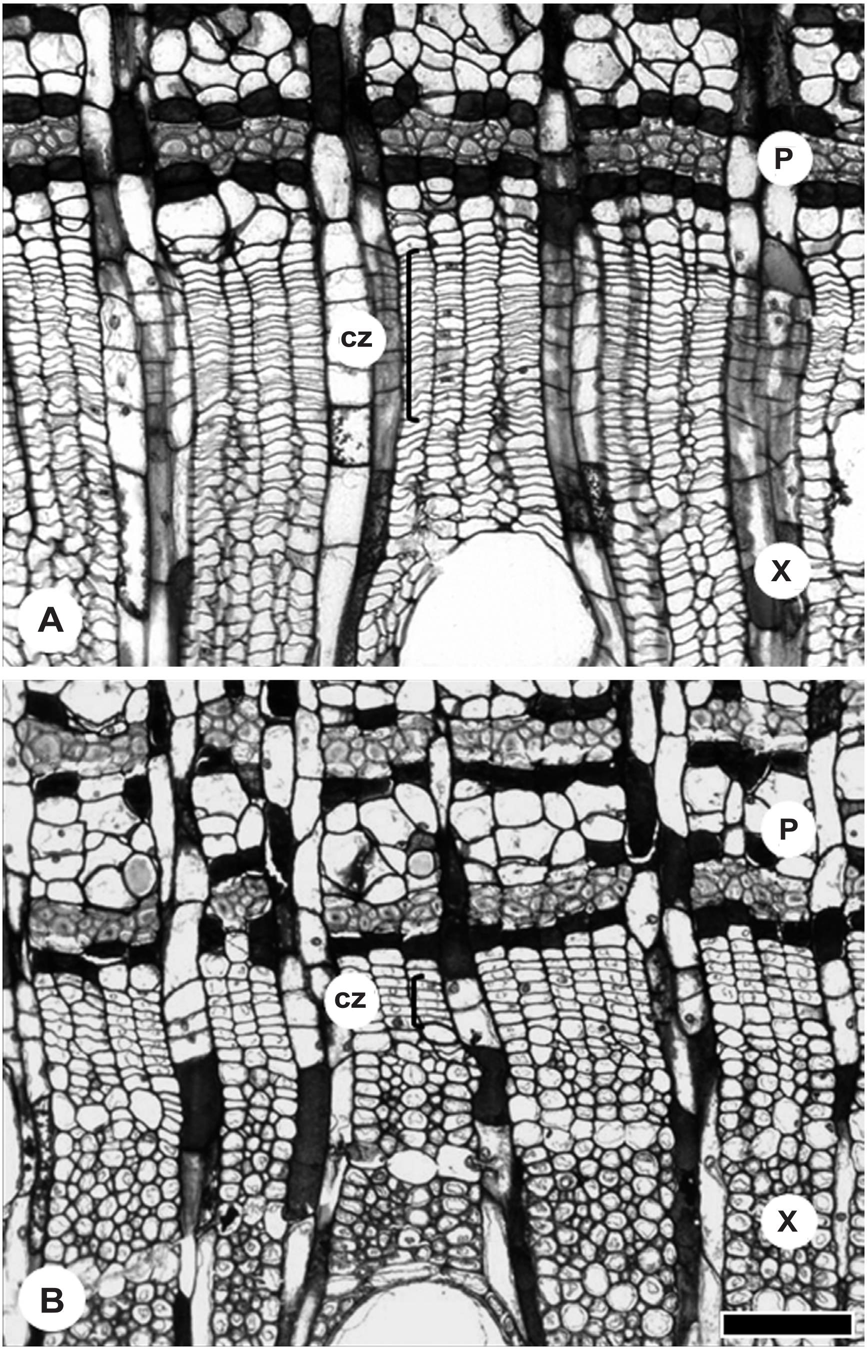

Figure 2. An example of the seasonal cambial activity in *Cariniana estrellensis*. Transverse section showing the number of cells of the cambial zone (cz) in both the growth (A) and dormant period (B), respectively. P = secondary phloem; X = secondary xylem. — Scale bar = 100 μm.

The literature includes many papers that report misinterpretations of results obtained with the dendrometer band approach (*e.g.*, Kuroda & Kiyono 1997; Deslauriers *et al.* 2003; Mäkinen *et al.* 2008), which can be misleading because the method shows the total growth of the stem circumference, including secondary phloem and phellem increment, and ignores the effects of seasonal fluctuations of the water status of stems. Therefore, mechanical injury of cambial cells is considered a more reliable technique to examine periodical wood formation (Kuroda & Kiyono 1997; Mäkinen *et al.* 2008).

Monitoring studies on cambial seasonal activity using histological approaches are still scarce in South America and we were able to find only 15 papers in the literature. These studies were developed in Argentina, Brazil, Chile and Ecuador (Fig. 1), in natural or cultivated woody species in different phytogeographic regions (Fig. 1; Table 1). The monitoring of seasonal cambial activity in these studies, according to the classification of Jura *et al.* (2005), can be divided into direct observations, when the data effectively show the stage of cell division and the development of the cambial zone (Fig. 2; Table 2), or indirect observations, when the secondary xylem ontogeny is considered as a consequence of cambial activity (Table 2).

Cambial studies using histological approaches

Aljaro *et al.* (1972) published the first article on histological cambial dynamics in South American species and described the annual rhythm of the cambial activity of *Proustia cuneifolia* D.Don (Asteraceae) and *Acacia caven* (Molina) Molina (Fabaceae), two typical shrubs of the 'matorral' in the semi-arid region of central Chile (Fig. 1; Tables 1 & 2). In this study, they compared phenological behavior and cambial activity during one year and related this with climatic data. *Proustia cuneifolia*, which is semi-deciduous during drought, showed an annual rhythm of cambial cell production, revealing its sensitivity to rain. *Acacia caven*, an evergreen species, showed a cambial activity that was apparently not synchronized with precipitation. These results indicate that shrubs growing in the same xeric environment may show different patterns of cambial activity.

Avila *et al.* (1975) compared the seasonal cambial activity of sclerophyllous evergreen shrubs from central Chile (Fig. 1; Tables 1–3) and southern California. They established four pairs of species (Table 3) with analogous characteristics based on morphological traits: crown architecture, size, texture and the anatomy of leaves and xylem. The authors measured the number of cell layers formed in the secondary xylem and observed a coincidence of seasonal fluctuations in cambial activity between the species of each ecological pair established.

Villalba (1985) described the cambial activity of *Prosopis flexuosa* DC. (Fabaceae) trees growing in the xerophytic open forests in the eastern deserts of Mendoza, Argentina (Fig. 1; Tables 1 & 2). Cambial activity was related to vegetative and reproductive phenology, monthly precipitation and temperature data. This analysis revealed that the growth of *P. flexuosa* is directly related to fluctuations of the local climate, although the start of cambial activity may partially respond to an endogenous stimulus. Giantomasi *et al.* (2012) demonstrated, for the same tree species, a rapid response of cambial activity to changes in rainfall, at optimum temperatures between 18 and 20 °C.

Table 1. Localities and ecofloristic zones of the studied areas and cited references.

Locality	Geographic coordinates	Ecofloristic zones	Mean annual rainfall	Mean temperature	References
Argentina					
Mendoza	34° 02' S, 67° 58' W	Xerophytic Open Forest	330 mm	16 °C	Villalba 1985
Mendoza	32° 21' S, 68° 20' W	Xerophytic Open Forest	155 mm	18 °C	Giantomasi *et al*. 2012
Brazil					
Minas Gerais	20° 45' S, 42° 51' W	Cultivated in urban area	1,250 mm	20 °C	Silva *et al*. 1991
Amazonas	03° 08' S, 59° 52' W	Amazon Forest (Terra Firme) and Plantation areas	2,500 mm	26 °C	Dünisch *et al*. 2002
Pará	02° 52' S, 54° 45' W	Amazon Forest (Terra Firme) and Plantation areas	2,000 mm	26 °C	Dünisch *et al*. 2002
Mato Grosso	10° 09' S, 59° 26' W	Amazon Forest (Terra Firme) and Plantation areas	3,000 mm	25 °C	Dünisch *et al*. 2002, 2003
São Paulo	22° 55' S, 48° 26' W	Atlantic Rain Forest (Semi-deciduous Seasonal Forest)	1,400 mm	22 °C	Marcati *et al*. 2006, 2008; Marcati & Angyalossy 2005
São Paulo	22° 42' S, 47° 38' W	Atlantic Rain Forest (Semi-deciduous Seasonal Forest)	1,300 mm	21 °C	Tomazello Filho & Cardoso 1999
São Paulo	23° 58' S, 48° 52' W	Atlantic Rain Forest (Semi-deciduous Seasonal Forest)	1,300 mm	21 °C	Lima *et al*. 2010
Rio de Janeiro	22° 28' S, 43° 13' W	Atlantic Rain Forest (Dense Ombrophilous Forest)	1,380 mm	24 °C	Callado 2010
Chile					
Santa Laura	33° 04' S, 71° 00' W	Mediterranean Semi-arid Region (Matorral)	300 mm	14 °C	Avila *et al*. 1975
Ecuador					
Reserva Laipuna	04° 12' S, 79° 53' W	Seasonal Tropical Dry Forest	900 mm	23 °C	Volland-Voigt *et al*. 2011
Reserva Biol. San Francisco	03° 58' S, 79° 04' W	Humid Tropical Lower Montane Forest	2,176 mm	16 °C	Bräuning *et al*. 2009; Volland-Voigt *et al*. 2011

Table 2. The applied methods (according to Jura *et al.* 2005) for monitoring seasonal cambial activity (Methods), time intervals of cambial sampling (Sampling), starting period of cambial activity (Start of cambial activity), period of new xylem formation (New xylem), type of parenchyma bands (Parenchyma bands), and respective reference (R) of the 17 native species studied in South America.

Species studied	Methods	Sampling	Start of cambial activity	New xylem	Parenchyma bands	R
Anacardiaceae						
Lithraea caustica	Indirect	Monthly	*	Throughout the year	*	1
Asteraceae						
Proustia cuneifolia	Direct	Weekly	June	July		2
Bignoniaceae						
Tabebuia chrysantha	Direct	Monthly	Montane: April Dry: Mid-February	Montane: April Dry: February	Initial?	3
Tynanthus cognatus	Direct	Cambial dormancy and activity	Mid-March	April	Initial	4
Fabaceae						
Acacia caven	Direct	Weekly	August	November		2
Prosopis flexuosa	Direct[5]; Indirect[6]	Monthly[5]; Weekly (growing season) and monthly (dormant period)[6]	End-October[5]	November[5] Early-October[6]	Terminal	5, 6
Schizolobium parahyba	Direct	Cambial dormancy and activity	*	January	Initial	7
Lauraceae						
Cryptocarya alba	Indirect	Monthly	*	End-July	*	1
Lecythidaceae						
Cariniana estrellensis	Direct	Cambial dormancy and activity	*	*	Marginal[a]	8
Meliaceae						
Carapa guianensis	Direct	Monthly	December	February; March	Terminal	9
Cedrela fissilis	Direct	Cambial dormancy and activity	*	*	Terminal & Initial	10
Cedrela montana	Direct	Monthly	January	January–April	Initial?	11
Cedrela odorata	Direct	Monthly[9]; Periods without increase in stem circumference[12]	January[9]	January[9]	Initial[9]	9, 12
Swietenia macrophylla	Direct	Monthly[9, 13]; Periods without increase in stem circumference[12]	December[9]	January[9]	Terminal[9]	9, 12; 13
Quillajaceae						
Quillaja saponaria	Indirect	Monthly	*	End-July	*	1
Rosaceae						
Kageneckia oblonga	Indirect	Monthly	*	Mid-June	*	1
Verbenaceae						
Citharexylum myrianthum	Direct	Dormancy and activity	*	*	Marginal[b]	14

1: Avila *et al.* 1975; 2: Aljaro *et al.* 1972; 3: Volland-Voigt *et al.* 2011; 4: Lima *et al.* 2010; 5: Villalba 1985; 6: Giantomasi *et al.* 2012; 7: Marcati *et al.* 2008; 8: Callado 2010; 9: Dünisch *et al.* 2002; 10: Marcati *et al.* 2006; 11: Bräuning *et al.* 2009; 12: Dünisch *et al.* 2003; 13: Silva *et al.* 1991; 14: Marcati & Angyalossy 2005. Additional reference: [a] = Lisi et al. 2008 and [b] = Callado *et al.* 2001b. * = Data unknown.

Table 3. Species studied by Avila *et al*. (1995) in the arid sites of Chile and California.

Pairs*	**Chilean species****	**Californian species**
1	*Kageneckia oblonga* Ruíz & Pavón (Rosaceae)	*Heteromeles arbhatifolia* (Lindl.) M. Roemer (Rosaceae)
2	*Quillaja saponaria* Molina (Quillajaceae)	*Rhus ovata* S.Watson (Anacardiaceae)
3	*Lithraea caustica* (Molina) Hook. & Arn. (Anacardiaceae)	*Quercus dumosa* Nutt. (Fagaceae)
4	*Cryptocarya alba* Looser (Lauraceae)	*Quercus agrifolia* Née (Fagaceae)

* Pairs of the analogous shrubs compared. ** Only Chilean species were considered in this study.

Dünisch *et al*. (2002) investigated the cambial activity of *Carapa guianensis* (evergreen - Dünisch & Moraes 2002), *Cedrela odorata* (deciduous - Dünisch & Moraes 2002) and *Swietenia macrophylla* (semi-deciduous - Dünisch & Moraes 2002) in both natural and plantation areas in the Amazon Forest (Fig. 1; Tables 1 & 2). The authors followed cambial activity through four growing seasons and did not observe differences between the cambial seasonality of natural and planted trees; both cambial activity and vegetative phenology were strongly influenced by photoperiod and precipitation. They also observed differences in the development of the growth ring markers: the marginal parenchyma bands of *S. macrophylla* are formed during the dryer periods prior to cambial dormancy while the marginal parenchyma bands of *C. guianensis* are formed in wet conditions –but without inundation and episodic droughts–, and *C. odorata* forms a the thicker-walled latewood fiber zone during dry periods prior to cambial dormancy and large earlywood vessels sheathed by axial parenchyma during cambial reactivation in this ring-porous species.

In a subsequent study, Dünisch *et al*. (2003) established tree-ring chronologies of *Swietenia macrophylla* and *Cedrela odorata* growing in primary forests of the southern Amazon basin. They determined tree ages and growth periodicity by dendrometer bands and the relationship between monthly precipitation and cambial activity. The correlation analyses revealed a significant relationship between precipitation at the beginning and at the end of the growing season of the cambium, which was correlated with the width of the increment zones in the adult xylem of *S. macrophylla*. In contrast, the width of the growth increment in the xylem of *C. odorata* was significantly correlated with the precipitation in March and May of the previous growing period.

In a semi-deciduous seasonal forest of São Paulo, Brazil (Fig. 1; Tables 1 & 2), Marcati and Angyalossy (2005) analyzed the seasonal formation of acicular calcium oxalate crystals in fusiform and ray cell initials and their immediate derivative cells in *Citharexylum myrianthum* Cham. (Verbenaceae) and suggested that this characteristic is a probable consequence of droughts.

Marcati *et al*. (2006) analyzed the seasonality of cambial activity in *Cedrela fissilis* Vell. (Meliaceae) from a semi-deciduous seasonal forest in São Paulo, Brazil (Fig. 1;

Tables 1 & 2) and described the different phases of the cellular cycle and the seasonal modifications in the number of cell layers in the cambial zone. The annual rhythm of the cambial activity of this species was associated with the rainy season and complete leaf expansion, while the dormancy period was related to the dry season and leaf loss. The analysis of intra-annual variations of the secondary xylem showed the formation of parenchyma bands and small diameter vessels at the beginning of the dry season, just before the cambium becomes dormant. When the cambium becomes reactivated during the next growing season, new layers of axial parenchyma appeared close to and around the large earlywood vessels. Therefore, the formation of this banded axial parenchyma occurs both at the end of the previous growing season and at the beginning of the following growing season.

Marcati *et al*. (2008) studied the seasonality of the cambial activity and development of secondary xylem and phloem in *Schizolobium parahyba* (Vell.) Blake trees (Fabaceae), growing in a semi-deciduous seasonal forest in São Paulo, Brazil (Fig. 1; Tables 1 & 2). In this study, a standardization of terminology was presented and characteristics of the cambial zone and the recently formed xylem and phloem cells of *S. parahyba* trees were discussed. Seasonal differences in the cambial zone were observed, including a reduction of the cambial activity coincident with the dry season and leaf loss. High cambial activity was correlated with the rainy season and the leaf maturity phase. In the secondary xylem, a narrow band of axial parenchyma indicates the beginning of a new growth ring.

Callado (2010), studying the radial growth dynamics of selected Atlantic rainforest trees (Fig. 1; Tables 1 & 2), showed the usefulness of fluorescence microscopy to better characterize the seasonality of the cambial activity in *Cariniana estrellensis* (Raddi) Kuntze (Lecythidaceae) (Fig. 2). With this technique, it was possible to determine that during dormancy, the conductive tissues adjacent to the cambial zone showed completely lignified xylem cell walls and callose deposits in sieve plates in the secondary phloem.

Lima *et al*. (2010) analyzed the seasonality of cambial activity and the differentiation process of derived cells in *Tynanthus cognatus* Miers (Bignoniaceae) from the semi-deciduous forest of southeast Brazil (Fig. 1; Tables 1 & 2). This species shows cambial variants, with formation of four phloem wedges in the xylem, and unlike other tropical trees and shrubs, the cambium of this liana reactivates at the phloem wedges through the end of the rainy season to the beginning of the dry period. However, this cambial behavior induced new questions: 1) is the start of cambial activity toward the end of the rainy season a feature common to most Bignonieae lianas or particular to *T. cognatus*? 2) what is the exact role of the secondary phloem, given that it influences the cambium so strongly and is this role related to either photosynthate transport or hormone translocation? and 3) in the context of development, does the short period of cambial activity explain why lianas have such narrow stems? All these questions should be addressed in future research (Lima *et al*. 2010).

Volland-Voigt *et al*. (2011) studied the stem diameter increments of *Tabebuia chrysantha* G. Nicholson in a tropical lower montane forest and in a dry forest in southern Ecuador (Fig. 1; Tables 1 & 2). The authors used high-resolution dendrometers to measure the growth increment and they evaluated the interrelation of stem diameter increment with cambial activity by anatomical analysis of secondary xylem formation. These wood anatomical studies allow the determination of periods of active cambial growth and the timing of annual growth boundary formation. The period of cambial activity varied between the two studied sites and was shorter in the dry forest. The results indicate that rainfall plays a key role for tree growth, even in the lower montane forest.

Bräuning *et al.* (2009) constructed a tree-ring chronology of *Cedrela montana* Moritz *ex* Turcz. (Meliaceae). This chronology was the first tree-ring series established from southern Ecuador and the longest one from humid tropical mountain areas in South America (Fig. 1; Table 1). The chronology covers the time until 1840 but is only statistically robust back to 1910. In this study, the combination of dendrometer data and histological approaches shows the periods of intensive cambial activity and new xylem formation (Table 2). The authors described growth boundaries marked by marginal parenchyma bands, including more or less tangentially arranged vessels that seem to be formed at the beginning of the growing periods. They also observed that parenchyma bands are difficult to detect in some of the sections, suggesting the occurrence of missing or partly missing rings.

Planted trees of native and exotic species have also shown annual rhythms of cambial activity even outside their areas of occurrence, a feature observed by Silva *et al.* (1991) and Tomazello-Filho & Cardoso (1999) in southeast Brazil for *Swietenia macrophylla* King (Meliaceae, from northern Brazil), *Gmelina arborea* Roxb. *ex* Sm. (Lamiaceae, from Asia), *Terminalia ivorensis* A.Chev. (Combretaceae, from western Africa) and *Tectona grandis* L.f. (Verbenaceae, from southeast Asia) (Fig. 1; Table 1). The cambial growth of these species was observed by a direct method and the results obtained were correlated with the local climate in which the plants were developing.

SYNTHESIS AND DISCUSSION

Among the 20 woody species reported here in studies of cambium activity, 17 are native to South America. The cambial activity of the Meliaceae family is the best known, involving five tree species (*Carapa guianensis*, *Cedrela fissilis*, *C. montana*, *C. odorata* and *Swietenia macrophylla*).

Concerning the sampling time intervals used in these studies, this varied (Table 2) between weekly (Aljaro *et al.* 1972; Giantomasi *et al.* 2012 - during the growing season), monthly (Avila *et al.* 1975; Villalba 1985; Silva *et al.* 1991; Tomazello-Filho & Cardoso 1999; Dünisch *et al.* 2002; Bräuning *et al.* 2009; Volland-Voigt *et al.* 2011) or seasonal intervals in pre-defined periods during dormancy and/or cambial growth (Dünisch *et al.* 2003; Marcati & Angyalossy 2005; Marcati *et al.* 2006, 2008; Callado 2010; Lima *et al.* 2010; Giantomasi *et al.* 2012).

Cambial monitoring experiments were performed at different time lengths and in periods of one (Aljaro *et al.* 1972; Avila *et al.* 1975; Silva *et al.* 1991; Bräuning *et al.* 2009), two (Villalba 1985; Tomazello-Filho & Cardoso 1999; Marcati & Angyalossy 2005; Marcati *et al.* 2006, 2008; Lima *et al.* 2010), three (Dünisch *et al.* 2003; Volland-Voigt *et al.* 2011; Giantomasi *et al.* 2012) or four years (Dünisch *et al.* 2002).

Concerning the fixation methods used to preserve the cambial zone and the recently formed tissues, the majority of the articles refer the use of 70 % alcohol formalin-acetic acid-alcohol (FAA), CRAF III and/or Karnovzky solution. The protocols included dehydration in ascending series of alcohol or acetone and embedding in paraffin, polyethylene glycol and/or resin glycol methacrylate. These techniques varied according to the type of analysis and the equipment and materials available in the various laboratories. Samples were sectioned by hand or by rotary or sliding microtomes and variable stain formulations were used, including Astrablue and basic Fuchsin, Astrablue and Chrysoidine, Safranin, Safranin and Alcian Green, Safranin and Astrablue, Safranin and Fast Green, or Toluidine Blue O and fluorochromes (*e.g.*, Auramine O and Aniline Blue), according to standard protocols in plant anatomy defined by, *e.g.*, Johansen (1940), Sass (1958), O'Brien *et al.* (1964), Karnovzky (1965), Feder & O'Brien (1968), Bennet *et al.* (1976), Berlyn & Miksche (1976), Gerlach (1977), O'Brien & McCully (1981), Tolivia & Tolivia (1987), and Ruzin (1999).

The methods used directly influence the results. The fixative solution influences the preservation of the tissue content and cells, including their organelles, such as nuclei and vacuoles, which is crucial to understand cambium seasonal growth. The use of coagulating fixatives (*e.g.*, Formalin-Acid-Alcohol, Chromium-containing fixatives or CRAF) results in a so-called acid fixation image, which is good for preserving chromatin, nucleoli and spindles; however, some organelles are dissolved (*e.g.*, mitochondria) and the cytoplasm becomes a stringy, coagulated mass (Ruzin 1999; Souza 2007). In these conditions, it could be difficult to evaluate cell division and impossible to differentiate cambial cells from their derivatives because cambial cells are characterized by the presence of small vacuoles in the dormant stage and by intense Golgi activity and plasma membrane invaginations during reactivation (Evert 2006).

The different microscopy contrast methods allow a better understanding of the cell differentiation processes, highlighting aspects of cell division and development. Microscopic analysis was carried out in bright field (Aljaro *et al.* 1972; Avila *et al.* 1975; Villalba 1985; Silva *et al.* 1991; Tomazello-Filho & Cardoso 1999; Dünisch *et al.* 2002, 2003; Marcati & Angyalossy 2005; Marcati *et al.* 2006, 2008; Bräuning *et al.* 2009; Callado 2010; Lima *et al.* 2010; Giantomasi *et al.* 2012; Volland-Voigt *et al.* 2011), in bright field combined with polarized light (Dünisch *et al.* 2002; Marcati & Angyalossy 2005), and the previous techniques combined with fluorescence microscopy (Callado 2010). We strongly recommend the use of different microscopy contrast methods, which allow a better understanding of a process as complex as radial growth.

The staining methods also can influence the interpretation of the radial growth. There are many hystochemical and cytochemical staining methods that can detect proteins, lipids and cell wall components as well as some organelles. In the study of cambial cells, the use of fluorescent proteins to tag nuclei, plasma membrane, plastids and cell wall components could be valuable (*e.g.*, Kitin *et al.* 2000; Kato *et al.* 2008; Thomas *et al.* 2013). Cytological methods should be introduced in the study of cambial activity in South American tree species, as suggested by Chaffey (2002). Moreover, observations based on transmission electron microscopy techniques may introduce new insights for analyzing seasonal changes in the cambial zone as revealed by Rao & Dave (1983), Farrar & Evert (1997a, b), Rensing & Samuels (2004), and Prislan *et al.* (2011).

Radial growth is closely associated with whole plant physiology and a way to observe the physiological status of a plant is through phenology. Eight of the 15 papers showed aspects of the reproductive and vegetative phenology in the studied plants (Aljaro *et al.* 1972; Villalba 1985; Tomazello-Filho & Cardoso 1999; Marcati & Angyalossy 2005; Marcati *et al.* 2006, 2008; Volland-Voigt *et al.* 2011; Giantomasi *et al.* 2012). In association with the analysis of the seasonal climate records, the monitoring of the leaf-shedding and budbreak stages is important for a better understanding of the cambial activity phases. It is important to establish if endogenous annual rhythms are under the control of internal clocks or calendars (Lüttge & Hertel 2009), as seems to be the case with the start of cambial activity in *Prosopis flexuosa* (Villalba 1985). Lüttge and Hertel (2009) also observed that purely environmentally controlled rhythms may be indicators of endogenous rhythms. It has been observed that arid, semi-arid and dry regions of Argentina, Chile and Ecuador are strongly affected by seasonal variations in precipitation, which induced radial growth rhythms that form annual rings in most woody species (Aljaro *et al.* 1972; Avila *et al.* 1975; Villalba 1985; Roig 2000; Volland-Voigt *et al.* 2011; Giantomasi *et al.* 2012). In the humid tropics of Brazil and Ecuador, cambial dormancy was observed in trees and lianas from different phytogeographic regions (Tomazello-Filho & Cardoso 1999; Dünisch *et al.* 2002, 2003; Marcati & Angyalossy 2005; Marcati *et al.* 2006, 2008; Bräuning *et al.* 2009; Callado 2010; Lima *et al.* 2010; Volland-Voigt *et al.* 2011). Although these reports indicate a mean annual rainfall well above 1,200 mm, a water deficit arises when less than ~60 mm of precipitation per month occurs yearly, in at least 2 to 3 consecutive months. According to Worbes (1995), this water threshold may induce cambial dormancy with a consequent annual ring formation in tropical trees. In a site near Manaus (Brazilian Amazon) where the annual rainfall is approximately 2,500 mm and no water deficit is observed throughout the year, trees such as *Carapa guianensis* (evergreen - Dünisch & Moraes 2002), *Cedrela odorata* (deciduous - Dünisch & Moraes 2002) and *Swietenia macrophylla* (semi-deciduous - Dünisch & Moraes 2002), experience seasonality of their cambial growth (Dünisch *et al.* 2002).

Similar cambial seasonality was observed for *Cedrela odorata* and *Swietenia macrophylla* in other Brazilian phytogeographic regions (Silva *et al.* 1991; Dünisch *et al.* 2002, 2003). Radial periodicity in growth, without histological approaches but with dendrometers, Mariaux's windows and/or dendrochronological techniques, was observed for these two species in other rain forests from Bolivia and Venezuela (Worbes 1999; Brienen & Zuidema 2005, 2006). These results may be related to the concept of paradormancy (Lang *et al.* 1985), where physiological factors outside the affected structure (in this case the cambial cells) regulate dormancy (Lang 1994; Pallardy 2008).

Another aspect that received attention in the South American studies of cambial seasonality is the formation of marginal parenchyma (*e.g.*, Dünisch *et al.* 2002; Marcati *et al.* 2006; Bräuning *et al.* 2009). The presence of these parenchyma cells may be explained by the need of fast availability of carbohydrates and nutrients (*e.g.*, Zimmermann & Brown 1971; Zimmerman 1983; Langenfeld-Heyser 1987; Kozlowski *et al.* 1991; Dünisch *et al.* 2002) at the stage of reactivation of cambial cell divisions after dormancy (Larson 1995). However, this marginal parenchyma band may be terminal or initial according to the tree species. For example, in *Cedrela fissilis* it was observed that the marginal band is formed both at the beginning and the end of the growing season (Marcati *et al.* 2006). However, recent results (Callado *et al.* in press) reinforce the need to characterize the nature of the marginal parenchyma to accurately determine the growth ring boundary, increasing the confidence of correlations with inductive or inhibiting growth factors.

CONCLUDING REMARKS AND RECOMMENDATIONS

Despite the fact that only 15 papers referring to cambial activity have been produced up to now in South America, these studies highlight the importance of histology in monitoring the seasonal activity of the cambium in order to better understand resulting tissue reproductive rates and environmental factors influencing the intra- and inter-annual radial growth dynamic of woody species.

These results show that the annual periodicity of the radial growth of the studied species is strongly influenced by rainfall seasonality. Moreover, they also prove that cambial activity is periodic, resulting in a proof that growth rings in these species are annual despite the climate and ecosystem characteristic. Nevertheless, the studies of radial growth by monitoring cambial cell production are still scarce in South America, especially considering the high diversity of the continent's flora and biomes.

It is also clear that we need to standardize observational and sampling methodologies (Table 2) as well as histological procedures. As plant growth processes include three distinct phases of the cell development, division, expansion and differentiation (Evert 2006), indirect methods cannot describe cambial activity itself. Thus, the use of direct methods is recommended if the objective is the understanding of cambial behavior.

As the steps of differentiation occur within a short time interval, we also recommend weekly or monthly sampling intervals, which are considered adequate time intervals for xylogenesis studies. However, a high-frequency sampling might be difficult in plants with breast height stem diameters less than 20 cm. This is because the risk of injury, which may influence cambial activity and the consequent anomalous tissue formation in new sampling portions close to the former ones (cf. Sass *et al.* 1995). On the other hand, the number of samples per individual and the number of specimens per species must also be considered. The majority of the studies use one sample per tree and one specimen per species. An increase of this number is recommended to allow an analysis of the population behavior and to avoid misinterpretations due to small sample numbers.

Long-term observations (*e.g.* a three-year period or higher) of the cambial phenology may facilitate better interpretations of the cell differentiation phases (*e.g.*, Rossi *et al.* 2012) which in turn may be combined with other analytical approach such as, for example, the analysis of the isotope content variability inside the growth ring, in order to reach a better understanding of the link between cambial seasonality and environmental conditions (Ogée *et al.* 2009).

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