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Xylem growth rings and leaf phenological patterns in tree species of a subtropical seasonal forest

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ABSTRACT

Growth rings have been reported for several tropical species under seasonal precipitation regimes and have often been related to leaf phenology. We investigated growth ring distinctiveness, wood markers, and leaf shedding and flushing patterns of 16 tree species from a subtropical seasonal deciduous forest under abundant and well-distributed rainfall regime in southern Brazil. Distinct growth rings were found in 13 species, 10 of which presented clear anatomical boundaries. Seven species were deciduous, five semideciduous and four perennial. Leaf shedding peaked during winter and spring months for the deciduous species, while it peaked during spring and summer months for the perennial and semideciduous species. Leaf flushing peaked in spring and summer for all species. All the deciduous species exhibited growth rings with clear boundaries. Marginal parenchyma, associated or not with other anatomical markers, was present in deciduous species but was not present in species with other leaf shedding patterns. Growth rings in *Allophylus edulis, Erythrina falcata, Jacaranda micrantha* and *Luehea divaricata* were described for the first time. The presence of seasonal leaf phenological patterns and growth rings in most of the species suggests that seasonality of the photoperiod and/or temperature influence the development of trees in moist subtropical seasonal deciduous forests.

Keywords: dendrochronology, phenology, seasonal deciduous forest, subtropical forest, tree rings, wood anatomy

Introduction

Growth rhythms in woody plants usually affect the morphology of their secondary tissues, forming radial anatomical patterns in the xylem, phloem and/or rhytidome known as growth layers or growth rings (Fahn *et al*. 1981; IAWA Committee 1964; Silva *et al*. 2019). Growth ring distinctness and periodicity are easier to detect in temperate and boreal floras, where most woody plants produce annual growth rings with conspicuous earlywood and latewood zones because lower temperatures and shorter daylengths toward the winter progressiveely reduce and prevent the mitotic activity of the vascular cambium and affect the differentiation of new cells (Fritts 1976; Schweingruber 2007).

Growth rings that do not follow this periodic and distinct pattern are generally more difficult to detect, especially in tropical floras. The identification of growth rings in taxa from tropical and subtropical regions has been hindered due to conceptual divergences from what is observed in high-latitude floras, which neither incorporate the great diversity of wood anatomy types seen in tropical floras nor their ecological and evolutionary drivers (Worbes 2002; Tarelkin

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et al. 2016; Silva *et al*. 2019). Although xylem growth rings in tropical trees were early recognized (see Worbes 2002), investigated and applied in specific disciplines, notably taxonomy, anatomy and dendrochronology (Stahle 1999; Alves & Angyalossy-Alfonso 2000; Callado *et al*. 2001b; Worbes 2002; Marcati *et al*. 2006a; Tarelkin *et al*. 2016; Silva *et al*. 2017), a definition of growth ring that integrates the anatomical diversity of growth ring distinctness, markers and causal factors of tropical species was only recently proposed (Silva *et al*. 2019).

Formation of conspicuous annual growth rings has been reported for hundreds of tropical species and attributed to seasonal changes in environmental conditions (Worbes 2002; Brienen *et al*. 2016; Schöngart *et al*. 2017), including rainfall in most regions (*e.g.*, Worbes 1995; 1999; Brienen & Zuidema 2005; Marcati *et al*. 2006b) but also flooding in lowland plains (*e.g.*, Worbes 1985; 1989; Callado *et al*. 2001a). Tropical taxa that reach subtropical belts find a contrasting climate environment, with more intense cold and frequent mild frosts in winter (Corlett 2013). In this zone, cambial activity is likely influenced by photoperiod and/or temperature, so that cell division and growth is stimulated by the longer and warmer days of summer (Jacoby 1989; Oliveira *et al*. 2009; Spathelf *et al*. 2010; Shimamoto *et al*. 2015; Kanieski *et al*. 2017; Reis-Ávila & Oliveira 2017). However, other combinations of formation rhythms and distinctness have also been reported for growth rings in tropical and subtropical plants (*e.g.*, Jacoby 1989; Borchert 1999; Alves & Angyalossy-Alfonso 2000; Callado *et al*. 2001a; Tarelkin *et al*. 2016; Baker *et al*. 2017).

Wood formation is a process associated with other vegetative events in a plant because apical and lateral meristems share common and fundamental regulatory mechanisms (Risopatron *et al*. 2010; Immanen *et al*. 2016). Thus, growth ring formation and leaf shedding patterns are likely to be associated, as shown in temperate (*e.g.*, Sass-Klassen *et al*. 2011; Takahashi *et al*. 2015; Guada *et al*. 2019) and tropical species (*e.g.*, Borchert 1999; Callado *et al*. 2001b; Schöngart *et al*. 2002; Singh & Kushwaha 2005; Callado *et al*. 2013; Brienen *et al*. 2016). The cambial activity in deciduous and semideciduous tropical species generally accompanies leaf shedding and flushing, *i.e.*, leaves are shed and the cambium becomes dormant during the dry season, while leaf flushing and cambium activation occur in the rainy season (Borchert 1999; Worbes 1999; Lisi *et al*. 2008; Marcati *et al*. 2006a; Callado *et al*. 2013).

Deciduous and semideciduous forests also occur under ever-wet climate conditions in subtropical belts, such as in southern Brazil (Veloso & Góes Filho 1982; IBGE 2012). In these forests, leaf phenological patterns are associated with seasonal variation in photoperiod and/or temperature, so that leaf shedding is concentrated in the period with shorter days and leaf flushing occurs when photoperiod increases again (Andreis *et al*. 2005; Athayde *et al*. 2009; Ferrera *et al*. 2017). In addition, growth ring formation in subtropical moist forests has been attributed to the same seasonal environmental drivers (Oliveira *et al*. 2009; Spathelf *et al*. 2010; Shimamoto *et al*. 2015; Kanieski *et al*. 2017; Reis-Ávila & Oliveira 2017; Blagitz *et al*. 2019).

Here, we adopt the broader concept of growth ring as defined by Silva *et al*. (2019) to assess and describe the macroscopic features of growth rings in 16 tree species from subtropical deciduous forest and verify relationships between growth ring occurrence and leaf phenological patterns. If subtropical climatic conditions affect the developmental rhythm of trees and/or if this rhythm is conserved in tropical taxa under subtropical conditions, we expect to find distinct growth rings in subtropical trees. Therefore, if leaf phenology is strongly associated with cambium activity, we expect different seasonal leaf phenological patterns to correspond with different incidence and/or anatomical definition of growth rings between species.

Materials and methods

Study area

The study was carried out in a fragment of seasonal deciduous forest in southern Brazil (state of Rio Grande do Sul), within the subtropical belt (Corlett 2013). Due to the mesothermal climatic character, the temperature presents pronounced annual oscillation, with hot summers and cold winters, while the annual rainfall regime has a well-balanced distribution, resulting in high and almost constant humidity throughout the year (Nimer 1989). In this region, the average minimum and maximum temperatures are around 13.7 °C and 24.3 °C respectively and the monthly average rainfall is 142.5 mm (IRGA 2017). Day length ranges from 10.13 h to 14.03 h according to the interactive observatory of the Observatório Nacional (ON 2018) (Fig. 1).

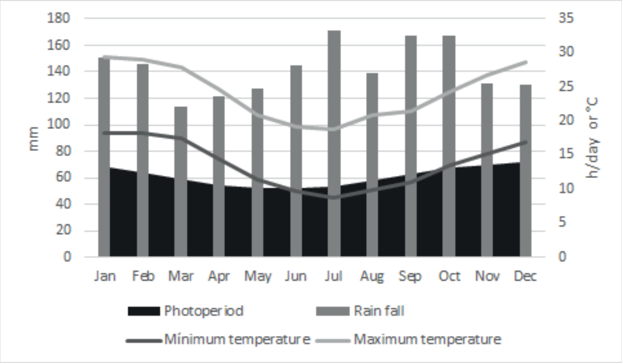

Figure 1. Climate diagram for the region of the study area. Data obtained from climatological averages (IRGA 2017).

In Rio Grande do Sul, the seasonal deciduous forest covers the Uruguay River Valley and the southern edge of the Serra Geral (IBGE 2012; Fig. 2). The seasonal deciduous

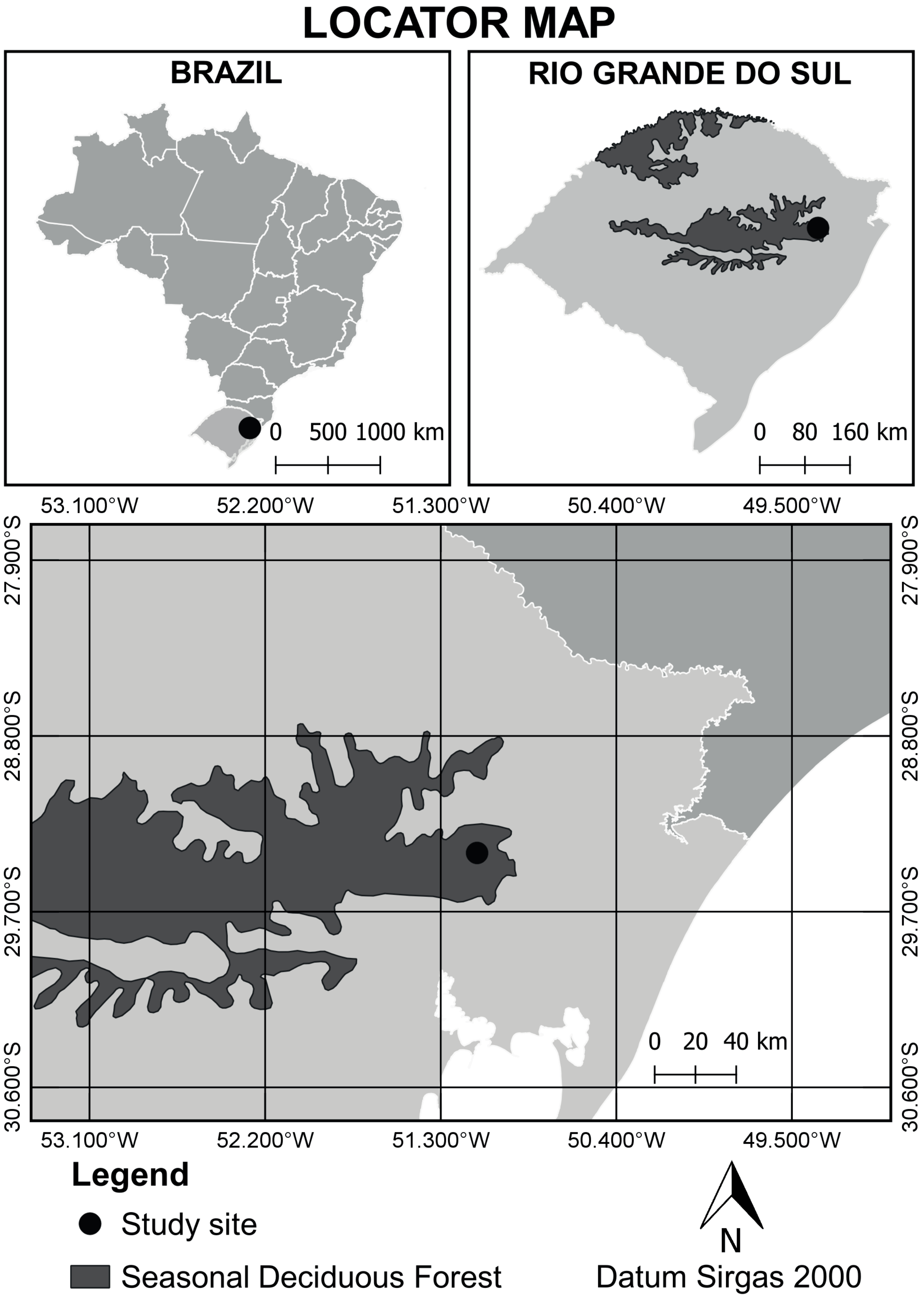

Figure 2. Map of study site location.

Table 1. Growth rings, marker type and leaf shedding pattern of 16 species from subtropical seasonal deciduous forest. Growth rings: DCB – distinct with clear boundaries, DFB – distinct with fuzzy boundaries, IND – indistinct. Marker type: A – absent, MP – marginal parenchyma, TW – thick-walled latewood fibers and thin-walled earlywood fibers, RF – radially flattened latewood fibers and radially elongated earlywood fibers, FB – fibrous band, SR – semi-porous ring. Leaf shedding pattern: DEC – deciduous, SDE – semideciduous, PER – perennial.

Taxa	Growth rings	Marker type	Leaf shedding pattern
BIGNONIACEAE			
Jacaranda micrantha Cham.	DCB	MP, TW, RF	DEC
EUPHORBIACEAE			
Alchornea triplinervia (Spreng.) Müll. Arg.	DFB	RF	SDE
ERYTROXILACEAE			
Erythroxylum argentinum O.E. Schulz	IND	A	SDE
FABACEAE			
Erythrina falcata Benth.	DCB	FB	DEC
Machaerium stipitatum (DC.) Vogel	DCB	MP	DEC
Parapiptadenia rigida (Benth.) Brenan	DCB	MP, TW, RF	DEC
LAURACEAE			
Nectandra megapotamica (Spreng.) Mez	DCB	TW, RF	PER
Nectandra oppositifolia Nees & Mart.	DFB	TW, RF	PER
Ocotea puberula (Rich.) Nees	DFB	TW, RF	SDE

forest is physiognomically defined by tree species that completely shed leaves in a given season of the year, resulting in 50 % or more of the canopy trees to be leafless in autumn and/or winter (Veloso & Góes Filho 1982; IBGE 2012). The seasonal deciduous forest in southern Brazil has been severely devastated since the arrival of European immigrants in 1824 (Rambo 1942) and now consists of fragments in various regeneration stages.

The study site is a seasonal deciduous forest fragment that is regenerating without major disturbances after clearcutting in the 1970s. It is located in the Municipality of Nova Petrópolis (29°23'57" S, 51°06'47" W) at an altitude of 170 m (Fig. 2).

Selection of species and preparation of wood samples

Eighty individuals from 16 species and 10 families were sampled in the study site (Tab. 1). The species were selected because they are widely distributed in areas of seasonal deciduous forest in Rio Grande do Sul (Reitz *et al*. 1988; Sobral *et al*. 2006) and are abundant in the study site. Five adult trees of each species were selected, preferably with rectilinear trunk and without apparent injuries to the stem and crown. The wood samples (two radial cores per tree) were collected from the trunk using a 5.1-mm-diameter increment borer at a height of 1.3 m from the ground. To complement the sample, we analyzed wood discs from recently cut down trees found in nearby sites or from samples in the xylotheque of Herbarium Anchieta that were collected in areas of seasonal deciduous forest in Rio Grande do Sul.

The cores were fixed on wooden supports, identified, dried and polished with sandpaper (grain 80 to 2000) according to the usual methodology for dendrochronological analysis. The disks were polished in the same way. Possible macroscopic features related to the delimitation of growth rings were inspected in the transverse section of the samples under 10 x and 40 x magnifications using a stereomicroscope. Digital photographs of the wood samples were taken using an AxionCam ERc5s camera attached to a Stemi SV6 stereomicroscope under 10 x and 40 x magnifications.

Cell arrangement and anatomical markers of the rings were described according to the IAWA Committee (1989). The classification of the presence of growth rings followed, with adaptations, the proposal of Silva *et al*. (2017) and we considered the pattern seen in most samples obtained from each species. The rings were classified as: **indistinct**, when no pattern of radial anatomical variation was observed; **distinct with clear boundaries**, when there was radial anatomical variation showing growth cycles, usually delimited by abrupt transitions between adjacent growth rings; **distinct with fuzzy boundaries**, when there was radial anatomical variation showing growth cycles, usually delimited by gradual transitions between adjacent growth rings.

Phenological data were obtained from the observation of 10 to 15 trees of each species. All trees had good crown visibility (Morellato *et al*. 2010) and were in seasonal deciduous forest fragments located within a 30-km-radius from the study site, in altitudes from 30 m to 500 m. The selected trees were monthly monitored between December 2017 to November 2018. Leaf shedding, flushing and leaf cover were assessed through direct observation and binoculars. The quantification of the leaf phenological events was performed using the Fournier intensity index (Fournier 1974). Based on the observations, the species were classified as: **deciduous**, when individuals were found leafless in one or more observations; **semideciduous** (brevideciduous), when they presented leaf shedding with partial canopy suppression and concomitant flushing of new leaves; and **perennial** (evergreen), when individuals presented continuous leaf replacement throughout the year, without total or partial canopy suppression (adapted from Morellato *et al*. 1989; Borchert 1999).

Results

The macroscopic anatomical analysis showed that 13 out of 16 species presented distinct growth rings (Tab. 1). Among these, 10 presented distinct growth rings with clear boundaries (63 %) and three presented distinct growth rings with fuzzy boundaries (18 %). Three species showed indistinct growth rings (19 %).

The growth-ring descriptions are presented by species and grouped by family, with emphasis on the anatomical traits that define the boundaries.

Bignoniaceae

Jacaranda micrantha: Growth rings are distinct, with clear boundaries defined by marginal parenchyma and variation in fiber shape and wall thickness (Figs. 3, 4). The boundaries are marked by an abrupt transition zone between radially-flattened thick-walled fibers (typical of latewood) and radially-elongated thin-walled fibers (typical of earlywood), and marginal parenchyma band (Figs. 3A, 4A).

Euphorbiaceae

Alchornea triplinervia: Growth rings are distinct, with fuzzy boundaries defined by variation in fiber shape. The boundaries are marked by a smooth transition zone in the shape of the fibers, which become successively flatter in the radial plane of latewood and then gradually return to the radially and more elongated shape in earlywood (Fig. 3B).

Erytroxilaceae

Erythroxylum argentinum: indistinct growth rings (Fig. 3C).

Fabaceae

Erythrina falcata: Growth rings are distinct, with clear boundaries marked by a continuous fibrous band that is wider than the other bands, and macroscopically characterized as a darker band. Growth-ring boundaries are visible in transverse discs of the trunk but it was not possible to define them in transverse core samples because the continuous dark-colored bands of the growth ring boundaries cannot be differentiated from discontinuous fibrous zones within the growth rings in narrow core samples (Fig. 3D).

Machaerium stipitatum: Growth rings are distinct, with clear boundaries marked by marginal parenchyma. The latewood has axial parenchyma, while the earlywood has winged-aliform axial parenchyma (Figs. 3E, 4B). The innermost growth rings may also have fiber-wall thickening in the latewood.

Parapiptadenia rigida: Growth rings are distinct, with clear boundaries defined by a marginal parenchyma layer and variation in fiber shape and wall thickness between latewood and earlywood. Smaller-diameter vessels are present in latewood (Fig. 3F, 4C). Sometimes, the abrupt transition between radially-flattened thick-walled fibers (latewood) and radially-elongated thin-walled fibers (earlywood) was absent.

Lauraceae

Nectandra megapotamica: Growth rings are distinct, with clear boundaries defined by variation in fiber shape and wall thickness. The boundaries are marked by an abrupt transition zone between radially-flattened thick-walled fibers (latewood) and radially-elongated thin-walled fibers (earlywood) (Figs. 3G, 4D).

Nectandra oppositifolia: Growth rings are distinct, with fuzzy boundaries defined by variation in fiber shape and wall thickness. The boundaries are marked by a smooth transition zone between radially-flattened thick-walled fibers (latewood) and radially-elongated thin-walled fibers (earlywood) (Fig. 3H).

Ocotea puberula: Growth rings are distinct, with fuzzy boundaries defined by variation in fiber shape and wall thickness (Fig. 5). The boundaries are marked by a smooth transition zone between radially-flattened thick-walled fibers (latewood) and radially-elongated thin-walled fibers (earlywood) (Fig. 5A).

Malvaceae

Luehea divaricata: Growth rings are distinct, with clear boundaries marked by a conspicuous marginal parenchyma band. There is a greater incidence of diffuse axial parenchyma forming aggregates in earlywood compared to latewood (Figs. 5B, 4E).

Meliaceae

Cabralea canjerana: indistinct growth rings (Fig. 5C).

Cedrela fissilis: Growth rings are distinct, with clear boundaries defined by conspicuous marginal parenchyma and semi-porous ring. Larger vessels are present in the earlywood and smaller vessels are present in the latewood (Figs. 5D, 4F).

Moraceae

Maclura tinctoria: Growth rings are distinct, with clear boundaries defined by continuous axial parenchyma in a seemingly marginal band (Figs. 5E, 4G). Growth-ring boundaries are visible in transverse discs of the trunk but it was not possible to define them in transverse core samples because the continuous axial parenchyma bands of growth-ring boundaries cannot be differentiated from discontinuous axial parenchyma bands occurring within the growth rings. Growth rings can be indistinct in the sapwood due to a lack of contrast between parenchyma and fibers.

Salicaceae

Casearia sylvestris: Indistinct growth rings (Fig. 5F).

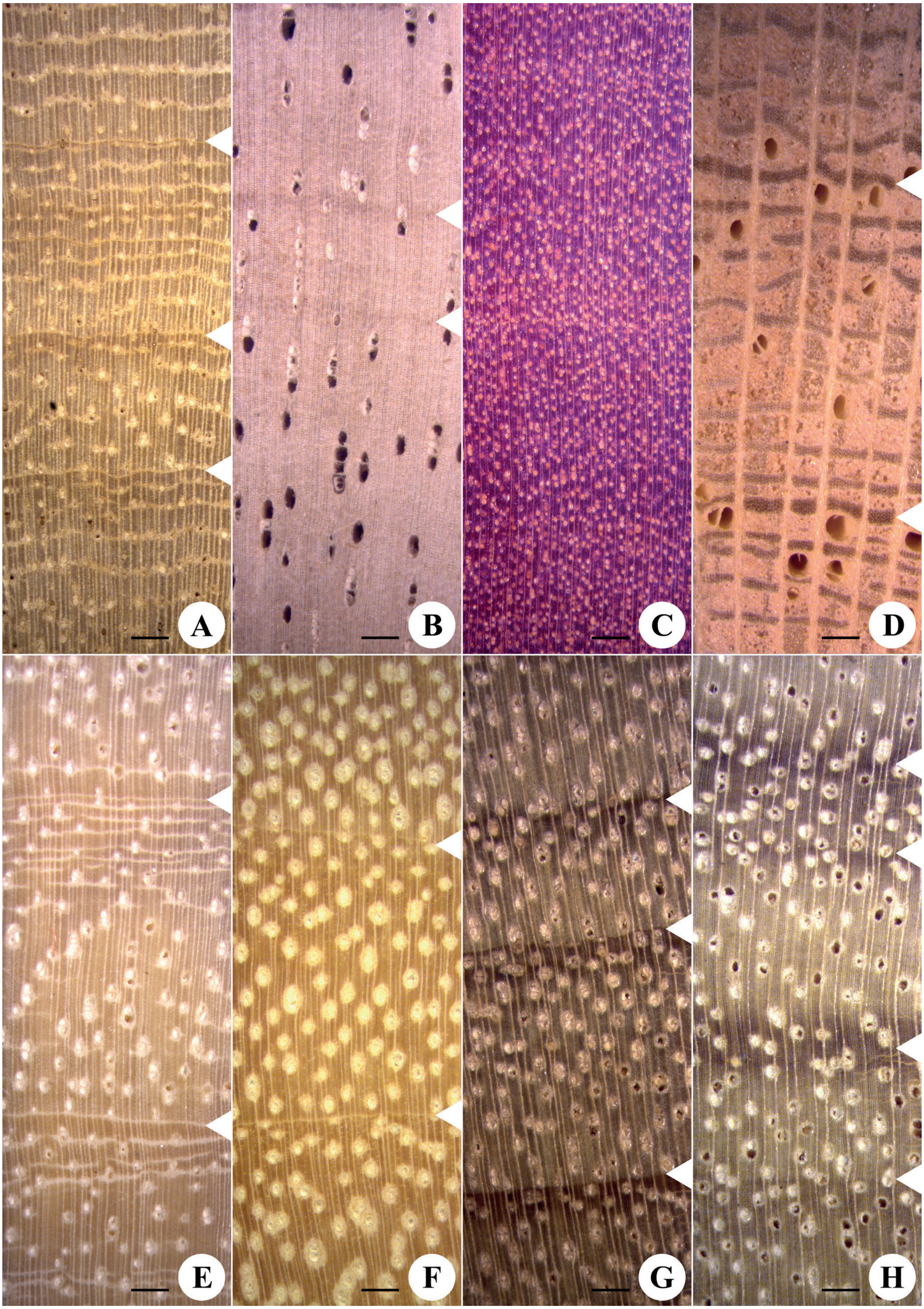

Figure 3. Macroscopic view of transverse xylem sections of tree species from subtropical seasonal deciduous forest. Arrows indicate growth ring boundaries. Magnification: 10x. **(A)** *Jacaranda micrantha;* **(B)** *Alchornea triplinervia*; **(C)** *Erythroxylum argentinum;* **(D)** *Erythrina falcata;* **(E)** *Machaerium stipitatum;* **(F)** *Parapiptadenia rigida;* **(G)** *Nectandra megapotamica;* **(H)** *Nectandra oppositifolia.* Scale: 0.5 mm.

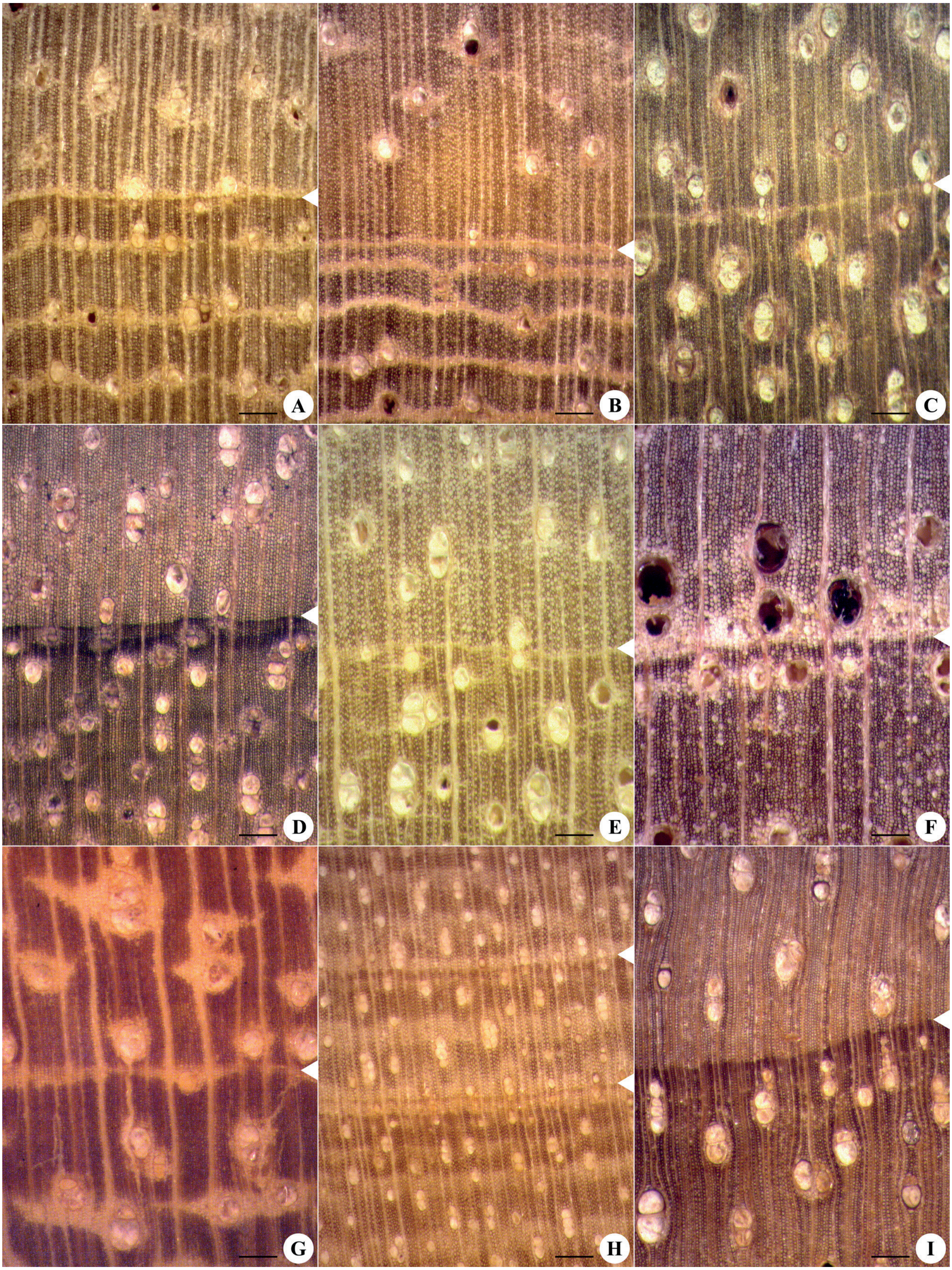

Figure 4. Detail of growth ring with clear boundaries for tree species from subtropical seasonal deciduous forest. Arrows indicate growth ring boundaries. Magnification: 40x. **(A)** *Jacaranda micrantha*; **(B)** *Machaerium stipitatum*; **(C)** *Parapiptadenia rigida*; **(D)** *Nectandra megapotamica*; **(E)** *Luehea divaricata*; **(F)** *Cedrela fissilis*; **(G)** *Maclura tinctoria*; **(H)** *Allophylus edulis*; **(I)** *Cupania vernalis*. Scale: 2 mm.

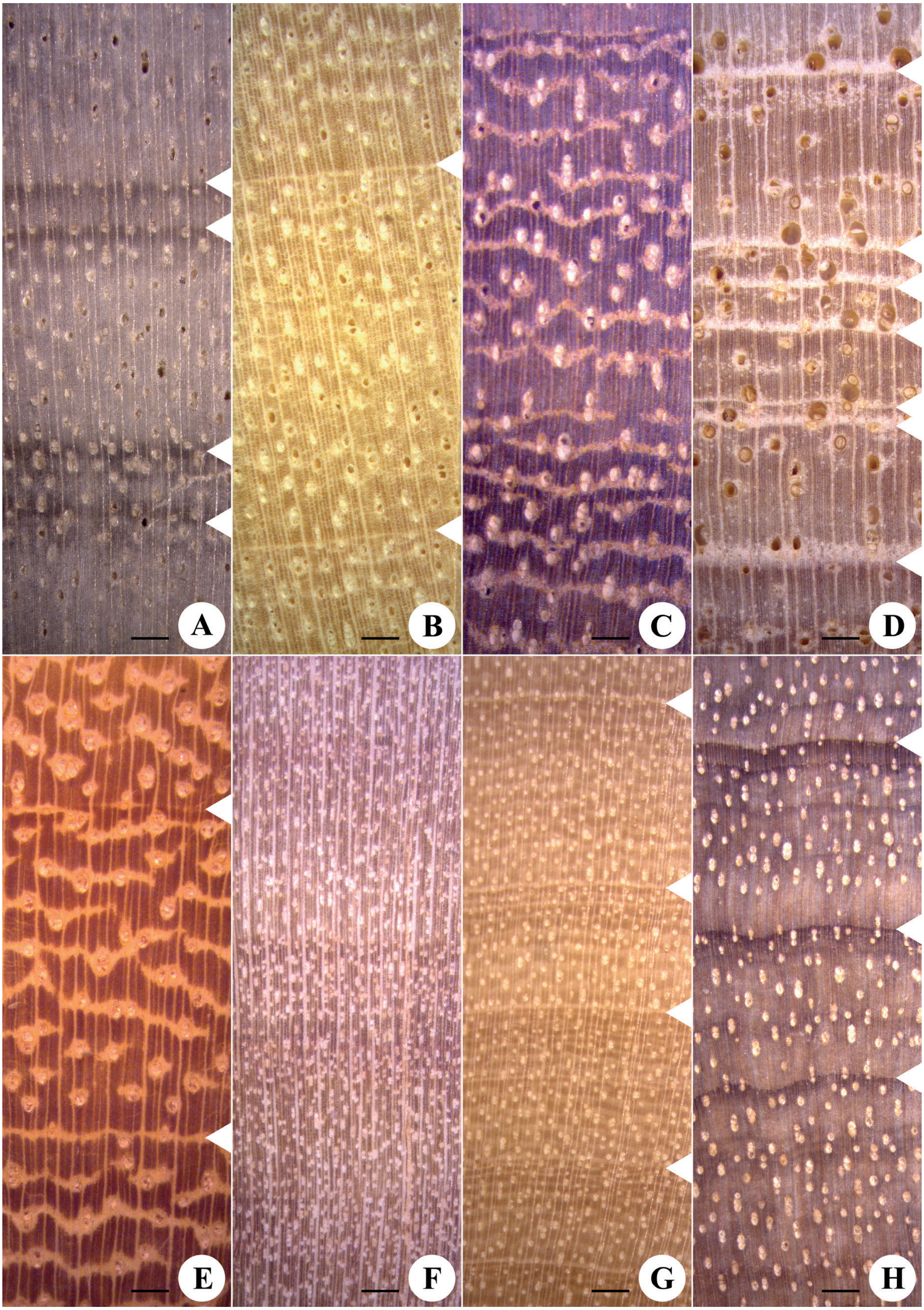

Figure 5. Macroscopic view of transverse xylem sections of tree species from subtropical seasonal deciduous forest. Arrows indicate growth ring boundaries. Magnification: 10x. **(A)** *Ocotea puberula;* **(B)** *Luehea divaricata*; **(C)** *Cabralea canjerana*; **(D)** *Cedrela fissilis*; **(E)** *Maclura tinctoria*; **(F)** *Casearia sylvestris*; **(G)** *Allophylus edulis*; **(H)** *Cupania vernalis*. Scale: 0.5 mm

Sapindaceae

Allophylus edulis: Growth rings are distinct, with clear boundaries defined by variation in fiber shape and wall thickness. The boundaries are marked by an abrupt transition between radially-flattened thick-walled fibers (latewood) and radially-elongated thin-walled fibers (earlywood) (Figs. 5G, 4H).

Cupania vernalis: Growth rings are distinct, with clear boundaries defined by varying fiber shape and wall thickness. The boundaries are marked by an abrupt transition between radially-flattened thick-walled fibers (typical of latewood) and radially-elongated thin-walled fibers (typical of earlywood) (Figs. 5H, 4I).

Regarding leaf-shedding patterns, seven species were deciduous, five were semideciduous and four were perennial (Tab. 1). All species presented a period of more intense leaf loss and replacement in the year of observation and a continuous or discontinuous occurrence of the leaf phenological events (Fig. 6).

Perennial and semideciduous species showed continuous leaf shedding and flushing through the year, while these phenophases were discontinuous in deciduous species. In *E. falcata*, all individuals presented discrete periods of leaf shedding and flushing but these phenophases were asynchronous among the trees and, thus, continuous at the population level. Leaf-shedding peaks occurred in late winter or early spring in deciduous species, and in spring or early summer in perennial and semideciduous species. Leaf-flushing peaks occurred in spring or early summer (except in *A. edulis*) (Fig. 6).

All deciduous species had distinct growth rings with clear boundaries (Tab.1, Fig. 7). A greater proportion of species with distinct growth rings with clear boundaries was observed in perennial species than in semideciduous species (Fig. 7). Species with indistinct or fuzzy-boundary growth rings seem to have a shorter leaf-exchange period (the time-lapse between the peaks of leaf shedding and leaf flushing) than species showing growth rings with clear boundaries (Fig. 8).

Discussion

Distinct growth rings had already been recorded in subtropical species in southern Brazil (Oliveira *et al*. 2009; Spathelf *et al*. 2010; Shimamoto *et al*. 2015; Andreacci *et al*. 2017; Kanieski *et al*. 2017; Reis-Ávila & Oliveira 2017; Granato-Souza *et al*. 2018; Blagitz *et al*. 2019). In this study, distinct growth rings were also observed in most studied species, being absent only in *C. sylvestris*, *C. canjerana* and *E. argentinum*. This result points to a rhythmic cambium activity in the tree species that is possibly triggered by variations in temperature and/or photoperiod (Morales *et al*. 2004; Yanez-Espinosa *et al*. 2006; Figueiredo-Filho *et al*. 2008; Oliveira *et al*. 2009; Kanieski *et al*. 2012; 2013) since regular intra-annual periods of water stress are not observed in this subtropical region (Nimer 1989; Peel *et al*. 2007).

The presence of distinct growth rings is not directly related to phenology, as rings were observed in species with different leaf-shedding patterns. However, indistinct rings were only observed among semideciduous and perennial species, indicating that the episodic leafless phase (deciduous phenology) is strongly associated with the presence of distinct growth rings in subtropical species (Fig. 7).

In perennial or semi-deciduous species, the greatest intensity of leaf shedding and leaf flushing accompanied the increase in temperature and photoperiod in spring and summer. These species keep their leaves during the annual period of lower temperature and shorter day length and undergo a quick (semideciduous) or a partial replacement (perennial) of the crown when the climatic conditions become more favorable for metabolic activity. The deciduous species showed intense leaf shedding during winter and early spring, with total crown loss in most individuals, and flushing between spring and summer (Fig. 6). Crown loss in deciduous species accompanied the decrease in photoperiod and temperature in the study region. Leaf shedding is a phenological strategy for these species to support physiological drought caused by the decrease in temperature in winter, which causes a stop in growth and photosynthesis (Givnish 2002). Leaf flushing occurs when the length of the day and the temperature increase, leading to photosynthetic activity and growth. Crown reconstitution/replacement after a period with low or no photosynthetic activity results in the resumption of growth, anatomically marking the cellular elements of the earlywood (Fahn *et al* 1981) and allowing the visualization of the ring boundaries.

In deciduous species, growth-ring markers are defined by marginal parenchyma (except *E. falcata*) accompanied or not by fiber wall thickness and/or shape or even a semi-porous ring. In perennial or semi-deciduous species, when present, growth rings are defined by wall thickness and shape of the latewood fibers. The species that showed distinct growth rings had marginal parenchyma bands and thickness and/or variation in the fiber shape in the latewood as main markers. These results from subtropical species are similar to the ones described for tropical species where the most common markers of the growth rings are wall thickening and radial flattening of the fibers, which are often associated with the marginal parenchyma (Worbes 1989; Roig 2000). The marginal parenchyma more precisely defines the limit of a growth ring (Lisi *et al*. 2008) and was the marker observed in most species of the study that showed distinct rings with clear boundaries.

Deciduous species tend to show a better distinctness of the growth rings (Coster 1927; 1928; Tomlinson & Logman 1981; Callado *et al*. 2001a; Shimamoto *et al*. 2015; Blagitz *et al*. 2019) resulting from cambial dormancy caused by leaf loss and consequent reduction in metabolism during the

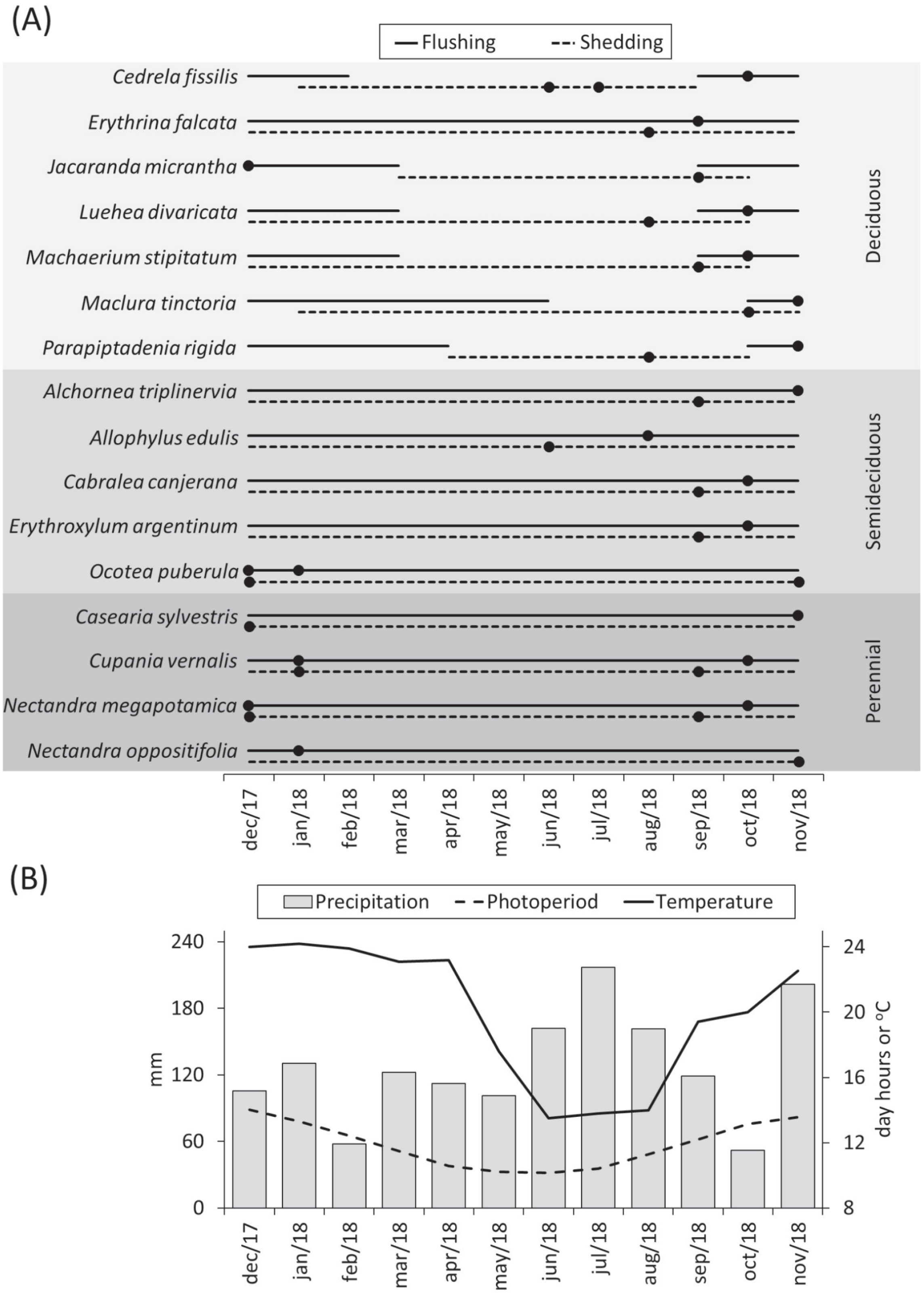

Figure 6. (A) Leaf shedding and flushing phenophases of tree species from subtropical seasonal deciduous forest. The lines in the graph indicate the occurrence of the phenophases and the markers indicate the months of greatest event intensity (Fournier Index). **(B)** Climate diagram for the study area in the period between December 2017 and November 2018. Right axis: photoperiod (h/light/day) and mean temperature; left axis: accumulated monthly rain.

unfavorable period. In tropical regions, the cambial activity of *C. fissilis*, a deciduous tree, is related to phenology and precipitation. Cambial dormancy occurs during leaf shedding in the dry season and earlywood formation occurs along with leaf flushing during the rainy season (Marcati *et al*. 2006b). The leaf phenophases presented by *C. fissilis* in subtropical climatic conditions show a relationship between leaf renewal and increase in photoperiod, and leaf shedding and reduction and photoperiod. In the month following the reduction of the day length by approximately 30 minutes (January) from its maximum (December), senescence and leaf shedding begin, and in the month following the increase of day length by about 2 h (September) from its minimum length (June), leaf flushing begins (Fig. 6). The presence of distinct growth rings combined with this phenological pattern observed in the species reinforce the idea that, in subtropical climatic conditions, day length plays an important role as a seasonal determinant of growth (Andreacci *et al*. 2017) like that observed in temperate deciduous species (Fu *et al*. 2019).

Although the presence of distinct growth-ring boundaries is expected in species that have a period of absence of leaves, it is common for species with this phenological leaf pattern not to present distinct growth rings (Coster 1927; 1928; Worbes 1999; Venugopal & Liangkuwang 2007), so that a clear relationship between leaf shedding patterns and distinct tree-ring boundaries was not always observed (Marcati *et al*. 2006a). However, in this study, all deciduous species showed distinct growth rings with clear boundaries (Fig. 7). This result agrees with previous results (Coster 1927; 1928; Tomlinson & Logman 1981; Callado *et al*. 2001a; Shimamoto *et al*. 2015; Blagitz *et al*. 2019) and indicates that leaf-shedding patterns are linked to wood formation in trees from tropical and subtropical regions and is a good indicator for the distinctness of growth rings. Complementing this idea, it is interesting to note that all species with indistinct growth rings had a short leaf exchange, a phenological behavior that would facilitate a strategy of continuous growth (Fig. 8). Leaf exchange was also associated with growth ring distinctness in the flora of the Cerrado biome (Coradin 2000), where distinct growth layers occurred mainly in species showing one leaf-flushing event per year.

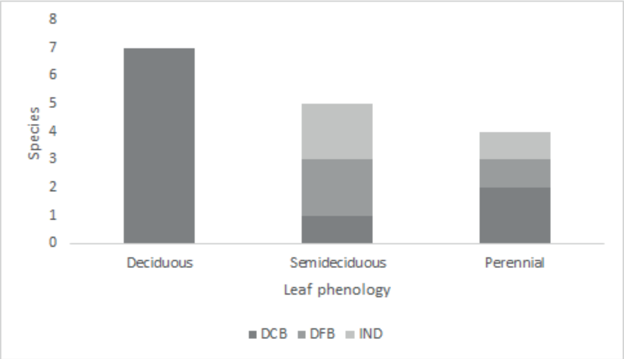

Figure 7. Number of deciduous, semideciduous and perennial species that present growth rings with different degrees of distinctiveness for trees from a subtropical seasonal forest. Growth rings: DCB – distinct with clear boundaries, DFB – distinct with fuzzy boundaries, IND – indistinct.

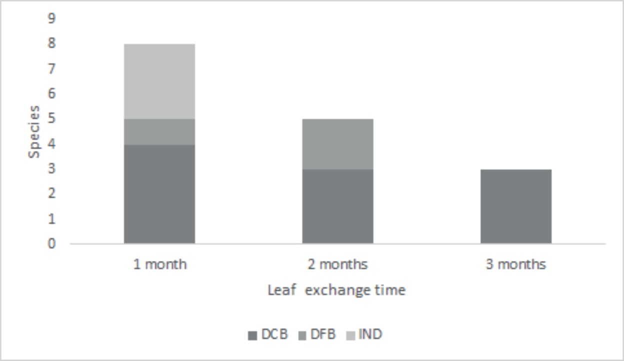

Figure 8. Leaf exchange time in tree species that present growth rings with different degrees of distinctiveness in a subtropical seasonal forest. Growth rings: DCB – distinct with clear boundaries, DFB – distinct with fuzzy boundaries, IND – indistinct.

The results found herein for the presence, absence and/or degree of distinctness of the rings agree with those observed in studies with the species *M. stipitatum* (Alves & Angyalossy-Alfonso 2000), *P. rigida* (Boninsegna *et al*. 1989), *M. tinctoria* (Alves & Angyalossy-Alfonso 2000), *C. fissilis* (Boninsegna *et al*. 1989; Alves & Angyalossy-Alfonso 2000; Dunisch 2005; Marcati *et al*. 2006b; Lopéz & Villalba 2016; Andreacci *et al* 2017; Pereira *et al*. 2018), *C. canjerana* (Alves & Angyalossy-Alfonso 2000 and Tomazello Filho *et al*. 2004), *C. vernalis* (Alves & Angyalossy-Alfonso 2000) and *O. puberula* (Boninsegna *et al*. 1989; Oliveira *et al*. 2001). These similar results found in species from subtropical and other climatic conditions suggest that growth rings are typical or genetically fixed for a species and/or that different restrictive climatic factors may act similarly on the growth rate of the trees, anatomically marking the wood.

On the other hand, our results differ from the results obtained in previous studies on growth rings of *A. triplinervia* (Callado *et al*. 2001a; Granato-Souza *et al*. 2018), *C. canjerana* (Shimamoto *et al*. 2015; Blagitz *et al*. 2019), *N. megapotamica* (Reis-Ávila *et al*. 2017), *N. oppositifolia* (Alves & Angyalossy-Alfonso 2000), *O. puberula* (Alves & Angyalossy-Alfonso 2000; Oliveira *et al*. 2001; Tomazello Filho *et al*. 2004; Reis-Ávila *et al*. 2017) and *C. sylvestris* (Absy & Scavone 1973, Sonsin *et al*. 2013, Avila *et al*. 2017). Several factors can be responsible for these divergences. The distinctness of growth rings may vary depending on the classification criteria adopted by the author, which are usually different, showing the need for uniformity in this sense (Silva *et al*. 2019). Factors such as the number of sampled specimens, genetic variations, endogenous rhythm, edaphic and local climatic conditions (Fahn *et al*. 1981; Vetter 2000; Callado *et al*. 2001a; Tarelkin *et al*. 2016; Silva *et al*. 2017; Blagitz *et al*. 2019; Silva *et al*. 2019) may influence the anatomy of growth rings and can partly explain the variations observed in the delimitation of rings between different studies. Therefore, the possible influence of sex on the distinction of growth rings in dioecious species, such as *O. puberula* (Carvalho 2002) and *A. triplinervia* (Carvalho 2004), should be investigated. In the Atlantic Forest, annual and distinct growth rings were observed in *A. triplinervia* (Callado *et al*. 2001a; Granato-Souza *et al*. 2018) but the studies do not mention whether the analyzed samples were from male or female individuals. In our study, two male and three female individuals from this species were sampled and it was observed that in the latter the boundaries of the rings were more defined.

Besides that, the methodology used for the anatomical analysis must also be considered. The 5-mm wood sections may be inadequate when there is variation in size or distance between the layers (Marcati *et al*. 2006b; Lisi *et al*. 2008; Silva *et al*. 2017), and, for a better view of the cell arrangements and greater precision of the determination and measurement of the growth rings width, cross-sections are more appropriate (López & Villalba 2016). Regarding this aspect, species that initially did not show distinct growth rings in the samples obtained using the Pressler probe (*E. falcata*, *M. tinctoria*, *C. canjerana, E. argentinum* and *C. sylvestris*) were also analyzed through cross-sections, and *E. falcata* and *M. tinctoria* showed distinct boundaries, reinforcing the limitation of the Pressler probes in such cases (Tarelkin *et al*. 2016).

To the best of our knowledge, this is the first study to describe growth rings and their anatomical characteristics in *E. falcata*, *J. micrantha*, *L. divaricata* (deciduous) and *A. edulis* (semideciduous), and the first wood anatomical investigation in *E. argentinum* (semideciduous), which showed indistinct growth rings. These novel results highlight the relevance of conducting basic research with subtropical species.

This study contributes to consolidating the idea that most subtropical trees forma distinct growth rings, which are probably marked when there is a reduction in temperature and photoperiod, considering the climatic conditions of the study area (Alves & Angyalossy-Alfonso 2000; Dünisch *et al*. 2003; Dünisch 2005; Lisi *et al*. 2008; Yanez-Espinosa *et al*. 2006; Venugopal & Liangkuwang 2007; Oliveira *et al*. 2009; Shimamoto *et al*. 2015). A periodicity pattern was also observed in the leaf phenophases of the studied species, as all species presented a period of more intense shedding and flushing during the year that was related to the subtropical climatic seasonality.

Although it was not possible to establish a direct relationship between leaf-shedding pattern and the presence of rings, since distinct rings were observed in deciduous, semideciduous and perennial species, leaf loss likely promotes an increase in growth-ring distinctness in deciduous species. Most deciduous species showed tree rings limited by marginal parenchyma, associated or not with other anatomical markers, while semideciduous and perennial species with distinct rings did not show this boundary marker, indicating a possible relationship between the type of ring marker and leaf-shedding pattern presented by the species.

Conclusion

This study confirmed the hypothesis that most tree species sampled from the subtropical seasonal deciduous forest have distinct growth rings, as found in tropical seasonal deciduous forests. It suggests that the widespread growth ring formation in this forest type may emerge under different seasonal climatic conditions, i.e., photoperiod and/or temperature in the subtropics and rainfall in the tropics. The rhythm of growth ring formation (if seasonal or other) and the role of climatic conditions as seasonal growth drivers need to be further investigated.

About the second hypothesis, we did not observe a clear relationship between leaf phenology and the presence of growth rings since growth rings were found in all leaf phenological patterns. However, all deciduous species had distinct growth rings with clear boundaries, suggesting that complete leaf loss has a strong influence on the wood anatomy of subtropical trees, similar to what is observed in tropical and temperate species.

Allophylus edulis, *Erythrina falcata*, *Cedrela fissilis*, *Cupania vernalis, Jacaranda micrantha*, *Luehea divaricata*, *Machaerium stipitatum*, *Maclura tinctoria*, *Nectandra megapotamica* and *Parapiptadenia rigida* constitute a group of tree species that can be explored for dendrochronological studies in subtropical moist forests in South America because they were found to have distinct growth rings with clear boundaries. Therefore, further dendrochronological investigations would shed light on the periodicity of growth ring formation and climatic drivers.

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References

Absy ML, Scavone O. 1973. Sobre a anatomia e morfologia de *Casearia sylvestris* Swartz. Boletim de Zoologia e Biologia Marinha 30: 641- 676.

Alves ES, Angyalossy-Alfonso V. 2000. Ecological trends in the wood anatomy of some Brazilian species. 1. Growth rings and vessels. International Association of Wood Anatomists Journal 21: 3-30.

Andreacci F, Botosso PC, Galvão F. 2017. Fenologia Vegetativa e Crescimento de *Cedrela fissilis* na Floresta Atlântica, Paraná, Brasil. Floresta e Ambiente 24: e20150241. doi: 10.1590/2179-8087.024115

Andreis C, Longhi SJ, Brun EJ, Wojciechowski A, Vaccaro S, Cassal CZ. 2005. Estudos fenológico em três fases sucessionais de uma Floresta Estacional Decidual no município de Santa Tereza, RS, Brasil. Revista Árvore 29: 55-63.

Athayde EA, Giehl ELH, Budke JC, Gesing JPA, Eisinger SM. 2009. Fenologia de espécies arbóreas em uma floresta ribeirinha em Santa Maria, sul do Brasil. Revista Brasileira de Biociências 7: 43-51.

Avila A, Giongo C, Schell-Ybert R. 2017. Anatomia do lenho carbonizado de 10 espécies nativas da planície costeira do Rio Grande do Sul – subsídio a pesquisas arqueobotânicas e paleoecológicas. Cadernos do Laboratório de Antropologia e Arqueologia UFPel 14: 481- 499.

Baker JCA, Santos GM, Gloor M, Brienen RJW. 2017. Does Cedrela always form annual rings? Testing ring periodicity across South America using radiocarbon dating. Trees 31: 1999-2009.

Blagitz M, Botosso PC, Longhi-Santos T, Bianchini E. 2019. Tree rings in tree species of a seasonal semi-deciduous forest in southern Brazil: wood anatomical markers, annual formation and radial growth dynamic. Dendrochronologia 55: 93-104.

Boninsegna JA, Villalba R, Amarilla P, Ocampo J. 1989. Studies of tree rings, growth rates and age-size relationships of tropical tree species in Misiones, Argentina. International Association of Wood Anatomists Journal 10: 161-169.

Borchert R. 1999. Climatic periodicity, phenology, and cambium activity in tropical dry forest trees. International Association of Wood Anatomists Journal 20: 239-247.

Brienen RJW, Zuidema PA. 2005. Relating tree growth to rainfall in Bolivian rain forests: a test for six species using tree ring analysis. Oecologia 146:1-12.

Brienen RJW, Schöngart J, Zuidema PA. 2016. Tree rings in the tropics: insights into the ecology and climate sensitivity of tropical trees. In: Goldstein G, Santiago LS. (eds.) Tropical tree physiology. Adaptations and responses in a changing environment. Switzerland, Springer International Publishing, Switzerland. p. 439-446.

Callado CH, Silva Neto SJ, Scarano FR, Costa CG. 2001a. Periodicity of growth rings in some flood-prone trees of the Atlantic Rain Forest in Rio de Janeiro, Brazil. Trees 15:492-497.

Callado CH, Silva Neto SJ, Scarano FR, Barros CF, Costa CG. 2001b. Anatomical features of growth rings in flood-prone trees of the Atlantic rain forest in Rio de Janeiro, Brazil. International Association of Wood Anatomists Journal 22: 29-42.

Callado CH, Goig FA, Tomazello-Filho M, Barros CF. 2013. Cambial growth periodicity studies of South American woody species - a review. International Association of Wood Anatomists Journal 34: 213-230.

Carvalho PER. 2002. Canela-Guaicá – *O. puberula*. Embrapa Florestas, Circular Técnica 62: 1-11.

Carvalho PER. 2004. Tapiá – *Alchornea triplinervia*. Embrapa Florestas, Circular Técnica 99: 1-12.

Coradin VTR. 2000. Formação de anéis de crescimento e sazonalidade da atividade cambial de dez espécies lenhosas do cerrado. PhD Thesis, Universidade de Brasília, Brasília.

Corlett RT. 2013. Where are the Subtropics? Biotropica 45: 273-275.

Coster C. 1927. Zur Anatomie und Physiologie der Zuwachszonen und Jahresbildung in den Tropen. Annales du Jardin Botanique de Buitenzorg 37:49-160.

Coster C. 1928. Zur Anatomie und Physiologie der Zuwachszonen und Jahresbildung in den Tropen. Annales du Jardin Botanique de Buitenzorg 38:1-114.

Dünisch O, Montóia VR, Bauch J. 2003. Dendroecological investigations on *Swietenia macrophylla* King and *Cedrela odorata* L. (Meliaceae) in the central Amazon. Trees 17: 244-250.

Dünisch O. 2005. Influence of the El-niño southern oscillation on cambial growth of *Cedrela fissilis* Vell. in tropical and subtropical Brazil. Journal of Applied Botany and Food Quality 79: 5-11.

Fahn A, Burley J, Longman KA, Mariaux A. 1981. Possible contributions of wood anatomy to the determination of the age of tropical trees. In: Bormann FH, Berlyn G. (eds.) Age and growth rate of tropical trees: new directions for research. Vol. 94. New Haven, Yale University. p. 31-54

Ferrera TS, Pelissaro TM, Eisinger SM, Righi EZ, Buriol GA. 2017. Fenologia de espécies nativas arbóreas na região central do estado do Rio Grande do Sul. Ciência Florestal 27: 753-766.

Figueiredo-Filho A, Rode R, Figueiredo DJ, Machado AS. 2008. Seasonal diameter increment for 7 species from an Ombrophyllous Mixed Forest, Southern state of Paraná, Brazil. Floresta 38: 527-543.

Fournier LA. 1974. Un método cuantitativo para la medición de características fenológicas en árboles. Turrialba 24: 422-423.

Fritts HC. 1976. Tree Rings and Climate. 1st. edn. London, Academic Press. 567 p.

Fu YH, Zhang X, Piao S, *et al*. 2019. Daylengtt helps temperate deciduous trees to leaf-out at the optimal time. Global Change Biology 25: 2410-2418.

Givnish TJ. 2002. Adaptive Significance of Evergreen vs. Deciduous Leaves: Solving the Triple Paradox. Silva Fennica 36: 704-743.

Granato-Souza D, Adenesky-Filho E, Barbosa ACMC, Esemann-Quadros K. 2018. Dendrochronological analyses and climatic signals of *Alchornea triplinervia* in subtropical forest of southern Brazil. Austral Ecology 43: 385-396.

Guada G, Vásquez-Ruiz RA, García-González I. 2019. Response patterns of xylem and leaf phenology to temperature at the southwestern distribution boundary of *Quercus robur*: A multi-spatial study. Agricultural and Forest Meteorology 269: 46-56.

IAWA Committee – International Association of Wood Anatomists. 1964. Multilingual glossary of terms used in wood anatomy. https://www.iawa-website.org/uploads/soft/Abstracts/IAWA_glossary.pdf

IAWA Committee – International Association of Wood Anatomists. 1989. IAWA list of microscopic features for hardwood identification. International Association of Wood Anatomists Journal 10: 219-332.

IBGE – Instituto Brasileiro de Geografia e Estatística. 2012 Manual Técnico da Vegetação Brasileira. Manuais Técnicos em Geociências número 1. 2nd. edn. Rio de Janeiro, Instituto Brasileiro de Geografia e Estatística-IBGE.

Immanen J, Nieminen K, Smolander O, *et al*. 2016. Cytokinin and auxin display distinct but interconnected distribution and signaling profiles to stimulate cambial activity. Current Biology 26: 1990-1997.

IRGA – Instituto Riograndense do Arroz. Previsão do tempo. http://www.irga.rs.gov.br/conteudo/764/previsao-em-graficos. 07 Nov. 2017.

Jacoby GC. 1989. Overview of tree-ring analysis in tropical regions. International Association of Wood Anatomists Journal 10: 99-108.

Kanieski MR, Longhi-Santos T, Graf Neto J, *et al*. 2012. Influência da precipitação e da temperatura no incremento diamétrico de espécies florestais aluviais em Araucária-PR. Floresta e Ambiente 19: 17-25.

Kanieski MR, Longhi-Santos T, Milani JEF, *et al*. 2013. Crescimento diamétrico de *Blepharocalyx salicifolius* em remanescente de Floresta Ombrófila Mista Aluvial, Paraná. Floresta e Ambiente 20: 197-206.

Kanieski MR, Galvão F, Roig FA, Botosso PC. 2017. Dendroecologia de Sebastiania commersoniana (Baill.) L.B.Sm. & Downs e Hovenia dulcis Thunb. em uma área degradada na Floresta Ombrófila Mista aluvial, Sul do Brasil. Ciência Florestal 27: 1201-1215.

Lisi CS, Tomazello Filho M, Botosso PC, *et al*. 2008. Tree-ring formation, radial increment periodicity and phenology of tree species from a Seasonal Semi-deciduous forest in Southeast Brazil. International Association of Wood Anatomists Journal 29: 189-207.

López L, Villalba R. 2016. Reliable estimates of radial growth for eight tropical species based on wood anatomical patterns. Journal of Tropical Forest Science 28: 139-152.

Marcati CR, Angyalossy V, Evert RF. 2006b. Seasonal variation in wood formation of *Cedrela fissilis* (Meliaceae). International Association of Wood Anatomists Journal 27: 199-211.

Marcati CR, Oliveira JS, Machado SR. 2006a. Growth rings in cerrado woody species: occurrence and anatomical markers. Biota Neotropica 6: 3. doi: 10.1590/S1676-06032006000300001

Morales MS, Villalba R, Grau HR, Paolini L. 2004. Rainfall controlled tree growth in high-elevation subtropical treelines. Ecology 85: 3080-3089.

Morellato LPC, Rodrigues RR, Leitão Filho HF, Joly CA. 1989. Estudo comparativo da fenologia de espécies arbóreas de floresta de latitude e floresta mesófila semidecídua na Serra do Japi, Jundiaí, São Paulo. Revista Brasileira de Botânica 12: 85-98.

Morellato LPC, Camargo MGG, D'eça Neves FF, Luize BG, Mantovani A, Hudson IL. 2010. The Influence of Sampling Method, Sample Size, and Frequency of Observations on Plant Phenological Patterns and Interpretation in Tropical Forest Trees. In: Hudson IL, Keatley MR. (eds.) Phenological Research. Methods for Environmental and Climate Change Analysis. Dordrecht, Heidelberg, London, New York, Springer Science & Business Media. p. 99-121.

Nimer E. 1989. Climatologia do Brasil. 2nd. edn. Rio de Janeiro, Departamento de Recursos Naturais e Estudos Ambientais, Instituto Brasileiro de Geografia e Estatística-IBGE.

Oliveira CW, Callado CH, Marquete O. 2001. Anatomia do lenho de espécies do gênero *Nectandra* Rol. ex Rottb. (Lauraceae). Rodriguésia 52: 125-134.

Oliveira JM, Santarosa E, Pillar VD, Roig FA. 2009. Seasonal cambium activity in the subtropical rain forest tree *Araucaria angustifolia*. Trees 23: 107-115.

ON – Observatório Nacional. 2018. Anuário do Observatório Nacional, Seção B – Nascer, Passagem Meridiana e Ocaso do Sol, Lua e Planetas. http://euler.on.br/ephemeris/index.php. 28 Feb. 2018.

Peel MC, Finlayson BL, Mcmahon TA. 2007. Updated world map of the Koppen-Geiger climate classification. Hydrology and Earth System Sciences Discussions, European Geosciences Union 4: 439-473.

Pereira GA, Barbosa ACMC, Torbenson MCA, *et al*. 2018. The Climate Response of *Cedrela Fissilis* Annual Ring Width in the Rio São Francisco Basin, Brazil. Tree-Ring Research 74: 162-171.

Rambo B. 1942. A fisionomia do Rio Grande do Sul: ensaio de monografia natural. 1st. edn. Porto Alegre, Imprensa Oficial.

Reis-Ávila G, Oliveira JM. 2017. Lauraceae: a promising Family for the advance of neotropical dendrochronology. Dendrochronologia 44: 103-116.

Reitz R, Klein RM, Reis A. 1988. Projeto Madeira do Rio Grande do Sul. Porto Alegre, SUDESUL, Herbário Barbosa Rodrigues.

Risopatron JPM, Sun Y, Jones BJ. 2010. The vascular cambium: molecular control of cellular structure. Protoplasma 247: 145-161.

Roig FA. 2000. Dendrocronología en los bosques del Neotrópico: revisión y prospección futura. In: Roig FA. (ed.) Dendrocronología en América Latina. Mendonza, Universidad Nacional de Cuyo p. 307-355.

Sass-Klassen U, Sabajo CR, Ouden J. 2011. Vessel formation in relation to leaf phenology in pedunculate oak and European ash. Dendrochronologia 29: 171-175.

Schöngart J, Piedade MTF, Ludwigshausen S, Horna V, Worbes M. 2002. Phenology and stem–growth periodicity of tree species in Amazonian floodplain forests. Journal of Tropical Ecology 18: 581-597.

Schöngart J, Bräuning A, Barbosa ACMC, Lisi CS, Oliveira JM. 2017. Dendroecological Studies in the Neotropics. Ecological Studies 231: 35-73.

Schweingruber FH. 2007. Wood Structure and Environment. Birmensdorf, Springer Science & Business Media.

Shimamoto CV, Botosso PC, Amano E, Marques MCM. 2015. Stem growth rhythms in trees of a tropical rainforest in Southern Brazil. Trees 30: 99-111.

Silva MS, Santos FAR, Callado CH, Barros CF, Silva LB. 2017. Growth rings in woody species of Ombrophilous Dense Forest: occurrence, anatomical features and ecological considerations. Brazilian Journal of Botany 40:281-290.

Silva MS, Funch LS, Silva LB. 2019. The growth ring concept: seeking a broader and unambiguous approach covering tropical species. Biological Reviews 94: 1161-1178.

Singh KP, Kushwaha CP. 2005. Emerging paradigms of tree phenology in dry tropics. Current Science 89: 964-975.

Sobral M, Jarenkow JA, Brack P, Irgang B, Larocca J, Rodrigues RS. 2006. Flora arbórea e arborescente do Rio Grande do Sul, Brasil. São Carlos, Editora Ribeiro Martins e Novo Ambiente.

Sonsin JO, Gasson P, Machado SR, Caum C, Marcati CR. 2013. Atlas da diversidade de madeiras do Cerrado Paulista. São Paulo, Editora Fundação de Estudos e Pesquisas Agrícolas e Florestais.

Spathelf P, Tomazello Filho M, Tonini H. 2010. Dendroecological analysis of *Ocotea pulchella* and *Nectandra megapotamica* on two sites near Santa Maria, Rio Grande do Sul (Brazil). Floresta 40: 777-788.

Stahle DW. 1999. Useful strategies for the development of tropical tree-ring chronologies. International Association of Wood Anatomists Journal 20:249-253.

Takahashi S, Okada N, Nobuchi T. 2015. Relationship between vessel porosity and leaf emergence pattern in ring- and diffuse-porous deciduous trees in a temperate hardwood forest. Botany 93: 31-39.

Tarelkin Y, Delvaux C, Ridder M, Berkani T, Cannière C, Beeckman H. 2016. Growth-ring distinctness and boundary anatomy variability in tropical trees. International Association of Wood Anatomists Journal 37: 275-294.

Tomazello Filho M, Lisi CS, Hansen N, Cury G. 2004. Anatomical features of increment zones in different tree species in the State of São Paulo, Brazil. Scientia Forestalis 66: 45-65.

Tomlinson PB, Longman KA. 1981. Growth Phenology of Tropical Trees in Relation to Cambial Activity. In: Bormann FH, Berlyn G. (eds.) Age and growth rate of tropical trees: new directions for research. Vol. 94. New Haven, Yale University.

Veloso HP, Góes Filho L. 1982. Fitogeografia brasileira: classificação fisionômico-ecológica da vegetação neotropical. Boletim Técnico Projeto Radambrasil, Série Vegetação 1: 1-80.

Venugopal N, Liangkuwang MG. 2007. Cambial activity and annual rhythm of xylem production of elephant apple tree (*Dillenia indica* Linn.) in relation to phenology and climatic factor growing in sub-tropical wet forest of northeast India. Trees 21: 101-110.

Vetter RE. 2000. Growth periodicity and age of Amazonian tree species: Methods for their determination. In: Roig FA. (ed.) Dendrocronología en America Latina. Mendonza, Universidad Nacional de Cuyo. p.135-155.

Worbes M. 1985. Structural and other adaptations to long-term flooding by trees in Central Amazonia. Amazoniana 9: 459-484.

Worbes M. 1989. Growth rings, increment and age of trees in inundation forests, savannas and a mountain forest in the Neotropics. International Association of Wood Anatomists Journal 10: 109-122.

Worbes M. 1995. How to measure growth dynamics in tropical trees: a review. International Association of Wood Anatomists Journal 16: 337-351.

Worbes M. 1999. Annual growth rings, rainfall-dependent growth and long-term growth patterns of tropical trees from the Caparo Forest Reserve in Venezuela. Journal of Ecology 87: 391-403.

Worbes M. 2002. One hundred years of tree-ring research in the tropics: a brief history and an outlook to future challenges. Dendrochronologia 20: 217-231.

Yanez-Espinosa L, Terrazas T, Lopez-Mata L. 2006. Integrated Analysis of Tropical Trees Growth: A Multivariate Approach. Annals of Botany 98: 637-645.