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ORIGINAL ARTICLE

Stem growth rhythms in trees of a tropical rainforest in Southern Brazil

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Abstract

Key message **We demonstrate that tropical trees growing in wet climates can have a marked seasonality in cambium activity and stem growth associated with high temperature and day length of summer.**

Abstract Monitoring the rhythm of tree growth associated with the growth rings can contribute substantially to understanding forest dynamics and the management of tropical forests. In this study, we monitored the girth increment rhythm and described the wood characteristics (anatomy of growth rings, wood specific gravity) in 10 tropical tree species (103 individuals) naturally occurring in a wet and weakly seasonal region of Atlantic Forest in southern Brazil. We aimed to verify whether tree growth dynamics are associated with climate and woody anatomy in tropical trees with contrasting ecological characteristics. We installed permanent dendrometer bands and monthly assessed the girth increment for 22 months. We collected wood samples (non-destructive method), measured wood specific gravity and prepared permanent slides to characterize the growth ring markers. We found growth rings in all species (distinct in six species); deciduous species produced more distinguishable tree rings compared with semi-deciduous and evergreen tree species. Species varied in their accumulated girth growth (in average, from 1.83 to 62.64 mm), growth rates (1–15 %), and annual radial increment (0.16–5.44 mm). Girth increment was positively related to temperature and day length in five out of ten tree species, indicating the possible effects of these climatic variables in triggering cambial activity in these species. The growth pattern varied among species and was marginally associated to the tree deciduousness. We concluded that even in wet and less seasonal climates, there can be an association in the cambium activity and stem growth with the hotter and longer days of summer months.

Keywords Seasonality · Phenology · Growth ring · Wood anatomy · Wood density · Girth increment

Introduction

Determining the occurrence of annual growth rings and the factors affecting the rhythms of stem growth in tropical trees has been an intriguing question for botanists (Worbes 2002; Lüttge and Hertel 2009). Since the nineteenth century occurrence of growth rings was detected in tropical trees (Worbes 2002). However, at the beginning of twentieth century controversies about the causes of growth rhythms emerged and a series of anatomical and ecological studies have attempted to describe the differences between species and to understand the whole process of periodicity in tropical trees (Mariaux 1995; Worbes 2002; Lüttge and Hertel 2009). Understanding these rhythms is important to predict forest dynamics and their possible effects on food production, conservation and management of tropical forests and predictions in climate change scenarios (Jacoby 1989; Roig 2000; Worbes 2002). Additionally, studies on the ecology, growth dynamics and carbon sequestration of

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tropical forests are often hindered by insufficient information on the structure and periodicity of tree rings (Dié et al. 2012; Shimamoto et al. 2014).

Tree growth is determined by cambium activity during a specific period of the year resulting in the formation of growth rings. In general, tree rings in woody plants are induced by seasonally alternating favorable and unfavorable growth conditions (Worbes 1995). For trees growing in temperate forests earlywood and latewood are easily identified, and the growth rings usually represent their annual increment, which allows the precise dating of the tree age (Mozeto et al. 1988). However, in tropical trees, the growth rings are usually less evident because the wood anatomy is much more complex and variable (Stahle 1999; Détienne 1989). In tropical trees growth rings are apparently restricted to some species growing in seasonal climates (Worbes 1995, 1999; Botosso and Tomazello-Filho 2001; Callado et al. 2001, 2013). Thus, it is expected that growth ring markers in tropical trees rarely represent annual rhythms.

Anatomical features that clearly denote growth rings in temperate trees, such as ring-porosity of some angiosperms and the pronounced changes in cell wall thickness and cell dimensions of earlywood and latewood in confers, are uncommon in tropical species (Gourlay 1995). However, relatively little is known about the prevalence of growth rings, and even less is known about the factors triggering growth ring formation in tropical plants (Baas and Vetter 1989; Jacoby 1989; Priya and Bhat 1999). Despite the high diversity in ecosystems, there are comparatively few studies on growth rhythm and periodicity in the tropics (Worbes 1989; Vetter and Botosso 1989; Botosso and Vetter 1991; Roig 2000; Lisi et al. 2008).

The wood specific gravity may play an important role in determining the growth rate (Suzuki 1999). In general, high growth rates in the tropical trees are associated with low wood specific gravity (Suzuki 1999; Muller-Landau 2004), and low growth rates are associated with high wood specific gravity (Parolin et al. 1998; van Gelder et al. 2006). This relationship occurs because there is a trade-off between constructing high-density woody (and reducing the probability of physical damage) and tree growth (Zimmerman et al. 1994; van Gelder et al. 2006). Several ecological studies emphasize the role of wood density as an important life-history trait, showing much wider variation in tropical lowland communities than in communities at higher latitudes and altitudes (Baas and Wheeler 2011).

The cambium activity and stem growth are potentially affected by temperature, photoperiod and precipitation (Fahn et al. 1981; Botosso and Tomazello-Filho 2001; Callado et al. 2001, 2013). Climate affects the endogenous metabolism of plants (Lüttge and Hertel 2009) and causes inter-annual variations in limiting resources such as water, light and nutrients, affecting plant growth (Billings 1952; Campos 1970; Lamprecht 1990; Worbes et al. 2003). For example, when the dry season reaches precipitation with less than 60 mm per month the soil water availability decreases, affecting the wood growth, the cambial dormancy, consequently leading to the formation of boundaries in the wood (Worbes 1995, 1999). Despite consequences of low precipitation are suggested as a strong limiting factor for cambium activity and stem growth (Worbes 1999), low temperature and day length, considered important constraining climatic factors in temperate climates (Cunningham and Read 2003), may also affect stem growth in tropics.

In this study, we assessed the anatomical structure of growth rings and monitored the girth growth (for 22 months) of 10 tree species with contrasting leaf phenology (deciduous, semi-deciduous and evergreen) in a rainforest of southern Brazil. We aimed to verify whether tree growth dynamics are associated with climate and woody anatomy in tropical trees with contrasting ecological characteristics. Specifically, we asked the following questions: (1) do the species differ in growth rings distinctiveness and in stem growth rhythm? (2) Is the girth growth rhythm related to the current and historical climate (i.e., temperature, precipitation and day length)? (3) Are the girth growth patterns related to wood anatomical features (i.e., latewood fiber wall thickness, growth rings and porosity), wood specific gravity and species deciduousness?

Methods

Study site

The study was conducted in the *Rio Cachoeira* Reserve (25°19′15″S and 45°42′24″W; total area of 8600 ha) and in the *Morro da Mina* Reserve (25°21′16″S and 48°46′17″W; total area of 3300 ha) in the municipality of Antonina, Paraná State, southern Brazil. These reserves are located in a large protected environmental area (PEA Guaraqueçaba) that comprises preserved areas (68 % of the total) of one of the largest fragments of Atlantic Forest in Brazil (Kauano et al. 2012). The soils in the region are Neosols, Gleysols, Cambisols and Argisols (Ferretti and Britez 2006). The climate is humid subtropical (Cfa in the Köppen climate classification), with an average annual temperature of 21.4 °C, an average annual rainfall of 2778 mm, no dry season and rare occurrence of frosts (Fig. 1a). For the study period, 2011 was wetter (3319 mm) and 2012 was drier (2567 mm) than historical records, but average temperatures were similar (20.8 and 20.4 °C, respectively) (Fig. 1c). For this region, differences in day length are ∼3 h along the year (Fig. 1b). Considering that

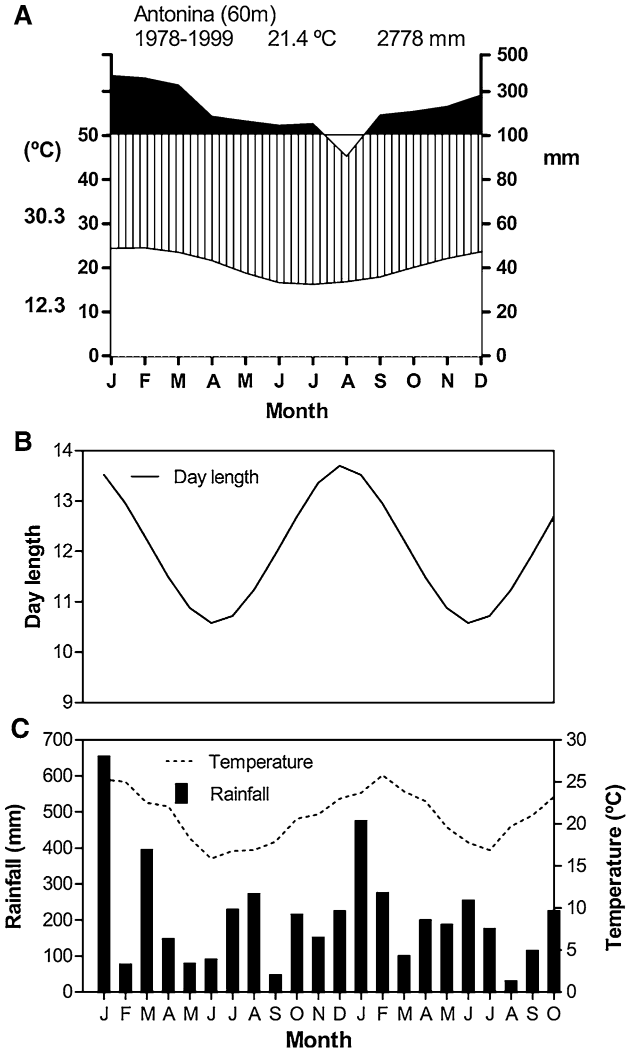


Fig. 1 Climatic diagram for the period of 1978 to 1999 (**a**), day length (**b**), and climate for the studied period from January 2011 to October 2012 (**c**). Source: **a** IAPAR (http://www.iapar.br/arquivos/Image/monitoramento/Medias_Historicas/Antonina); **b** US Naval Observatory (http://aa.usno.navy.mil); **c** SIMEPAR (http://www.simepar.br/)

monthly rainfall is always higher than 60 mm, even during the winter, the region can be considered aseasonal with regard to water availability (Walter 1983). However, it is possible to recognize climatic differences between the wetter and hotter spring and summer seasons (October to March; averages 297 mm and 23 °C) and the less wet and colder autumn and winter seasons (April–September; averages 134 mm, 18 °C).

The reserves comprise primary and secondary forests distributed in lowland and montane areas, characterized by high species richness, including a total of 306 tree species (Liebsch et al. 2008; Borgo et al. 2011). In the lowland areas, the forest was logged over 30 years and converted into pasture areas for livestock. After pasture abandonment (10 years before starting the experiment), the forests were restored through direct seedling planting and assisted natural regeneration (Ferretti and Britez 2006; Bruel et al. 2010).

Studied species

Ten tree species naturally occurring in the lowland and slope successional areas (20–60 years old) of the Atlantic forest were selected based on their high frequency in the region (Liebsch et al. 2007; Borgo et al. 2011). We selected species representing different leaf phenology: six semi-deciduous, three deciduous and one evergreen (Table 1). We labeled 6–19 individuals of each species (total 103 individuals, Table 1) to ensure the inclusion of individuals belonging to different diameter classes. In general, an effort was made to select adult trees with straight-boled stems, no bifurcations and no apparent trunk deformities. For some species, it was not possible to collect a more representative number of specimens due to the varying number of individuals with the appropriate characteristics at each growth condition.

Growth ring markers and wood specific gravity

To characterize growth ring markers and describe the growth layer boundary, small wood samples 5 mm in diameter containing the tree ring time series (radial increment from pith to bark) were collected at breast height through a non-destructive method (Pressler's increment borer). The number of sampled radii varied among species (Table 1). To recognize growth rings we used the characteristics of the increment zones by inspection of the anatomical features of the wood. We only identified if growth rings were distinguishable or not in the studied region, independently of their frequency (annual or not).

Small wood samples were embedded in Historesin® (Leica, Heidelberg), and transverse sections were performed on a rotation microtome with a thickness of 7 µm. The sections were stained with toluidine blue O (O'Brien et al. 1965), permanently mounted and thereafter observed under an optical microscope and photographed with a digital camera. For macroscopic wood observations, small wood samples were superficially sanded with micro-abrasive paper. The macro- and microscopic features descriptions of the tree rings structures were made following the terminology proposed by IAWA (1989). We considered growth ring boundaries according to family descriptions present in IAWA (1989), Metcalfe and Chalk (1950) and in the Insidewood web resource (Wheeler 2011). For some species, atypical wood anatomical patterns differing from the typical growth ring boundaries (e.g., intra-ring density fluctuation, fiber density fluctuation, among others;

Table 1 List of 10 tree species studied in the Atlantic Forest, southern Brazil

Acronym	Species	Family	Deciduousness	*N*	*n*	DBH (cm)
C_myr	*Citharexylum myrianthum* Cham.	Verbenaceae	Deciduous	8	8	22.17 ± 8.25
S_par	*Schizolobium parahyba* (Vell.) Blake	Fabaceae	Deciduous	15	10	30.21 ± 19.94
S_mul	*Senna multijuga* (L.C. Richard) H.S. Irwin e Barneby	Fabaceae	Semi-deciduous	6	6	14.57 ± 5.24
V_bic	*Virola bicuhyba* (Schott ex Spreng.) Warb.	Myristicaceae	Semi-deciduous	19	18	24.33 ± 16.26
H_ser	*Handroanthus serratifolius* (Vahl) S. O. Grose	Bignoniaceae	Deciduous	6	6	31.80 ± 18.82
C_can	*Cabralea canjerana* (Vell.) Mart.	Meliaceae	Semi-deciduous	11	8	17.56 ± 10.88
C_est	*Cariniana estrellensis* (Raddi) Kuntze	Lecythidaceae	Semi-deciduous	12	7	17.94 ± 11.42
I_edu	*Inga edulis* Mart.	Fabaceae	Evergreen	9	6	24.38 ± 10.92
I_ mar	*Inga marginata* Willd.	Fabaceae	Semi-deciduous	8	6	9.95 ± 3.15
M_cor	*Myrsine coriacea* (Sw.) R. Br. ex Roem. & Schult.	Primulaceae	Semi-deciduous	9	6	14.11 ± 8.69

N number of trees, *n* number radius samples, *DBH* variation (mean ± SD) of diameter at breast height

Table 2 Wood characteristics of 10 tree species studied in the Atlantic Forest, southern Brazil

Species	ρ (g cm^{-3})	*N* (*n*)	Growth rings distinction	Porosity	LWF	GR boundary structure	Marginal parenchyma[a]
C_myr	0.43 ± 0.11	8 (36)	Distinct	Semi-ring	1	MP, VD, FW	Continuous
S_par	0.32 ± 0.11	8 (34)	Distinct	Diffuse	1	MP, FW	Continuous
S_mul	0.44 ± 0.05	6 (26)	Distinct	Diffuse	1	MP, FW	Discontinuous
V_bic	0.53 ± 0.05	12 (48)	Distinct	Diffuse	1	FW	–
H_ser	0.70 ± 0.02	3 (8)	Distinct	Diffuse	3	FW, MP	Continuous
C_can	0.60 ± 0.06	7 (27)	Scarcely	Diffuse	1	FW, FZ, VD	Discontinuous
C_est	0.67 ± 0.08	6 (26)	Distinct/scarcely	Diffuse	3	FW, FZ, MP	Discontinuous
I_edu	0.51[b]	–	Scarcely	Diffuse	1, 2	FW, VD	–
I_ mar	0.50 ± 0.07	6 (19)	Scarcely	Diffuse	1, 2	FW, VD	–
M_cor	0.56 ± 0.07	5 (12)	Scarcely	Diffuse	2, 3	FW, FZ	–

ρ wood specific gravity (mean ± SD), *N* number of trees (and n = radius samples) used for ρ measures, *LWF* latewood fiber wall thickness (*1* thin-to-thick-walled; *2* thick-walled; *3* fibrous zone); growth ring (*GR*) 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* fibrous zone

[a] Or in seemingly marginal bands

[b] Data from Zane et al. (2013)

Copenheaver et al. 2006; Speer 2010), were considered as "false" ring.

Additionally, these same wood samples were also used to determine the wood specific gravity of studied species. For this, small wood samples (5 mm in diameter) were collected from 61 individual trees (8–48 samples per species, Table 2) and applied the maximum moisture content method (Smith 1954). First, the weight of water-saturated samples and the weight of the oven-dried samples (105 ± 2 °C for 48 h) are taken. Then, by dividing the weight of oven-dried samples (g) by the green volume of samples (cm^3), the wood specific gravity is calculated by the formula proposed by Smith (1954), and using the density of wood substance constant (1.53 g cm^3). We did not collect wood samples from *Inga edulis* to avoid injuries to small trees. Thus, the wood specific gravity of this species was used as reported by Zanne et al. (2013). Wood samples and permanent slides are housed in the wood collection of Embrapa Forestry.

Tree growth monitoring

The girth growth increment for each of the 103 trees was recorded at DBH (diameter at breast height, 1.3 m above ground level) by using steel permanent dendrometer bands with a precision of 0.2 mm (Mariaux 1977; Botosso and Tomazello-Filho 2001; Cardoso et al. 2012). We recorded data monthly, for 22 months (from January 2011). All readings were performed in the early morning when stem size is at a maximum, thus minimizing possible effects of water movement in the trunk (Chitra-Tarak et al. 2015). One month after installation, we adjusted the band dendrometer to the stem in order to minimize eventual measurement errors. This procedure is necessary because band dendrometers have a tendency to underestimate growth or not measure any growth at all, for a period after installation (Keeland and Sharitz 1993; O'Brien et al. 2008; David and Downes 2009). Thus, the first data were taken 2 months after band dendrometer installation. Despite all these methodological control, water-induced fluctuations can potentially affect dendrometer readings, and all girth growth results have to be interpreted cautiously.

Data analysis

The monthly girth increment for individuals of each species was used to calculate the species month average (with sample size varying between six and 19 individuals). From the accumulate girth increment (total in 22 months) we also calculated the girth growth rate (% of girth growth in the studied period) and the annual radial increment (by interpolating for a period of 12 months), in order to facilitate future comparisons with other studies. We tested for differences among species in accumulate total girth growth for the studied period (22 months; January 2011–October 2012) by a Kruskal–Wallis test. We tested for the relationship between girth current (monthly) increment and climate using a Spearman correlation test (Zar 1999). We correlated the average monthly girth increment of each species with monthly day length (standard measure for region, Fig. 1b), monthly rainfall and mean temperature for the studied (2011–2012, Fig. 1c) and historical period (1978–1999, Fig. 1a). The correlations considering current (annual) and historical climates were performed in order to test if trees respond differently to this two different trigging. Also, considering that plants can show a delayed response to climate variation (Marques and Oliveira 2004), we also correlated girth increment with the lagged rainfall (current and historical), temperature (current and historical) and day length, from 1 to 3 months. In all tests we assumed $\alpha = 0.05$.

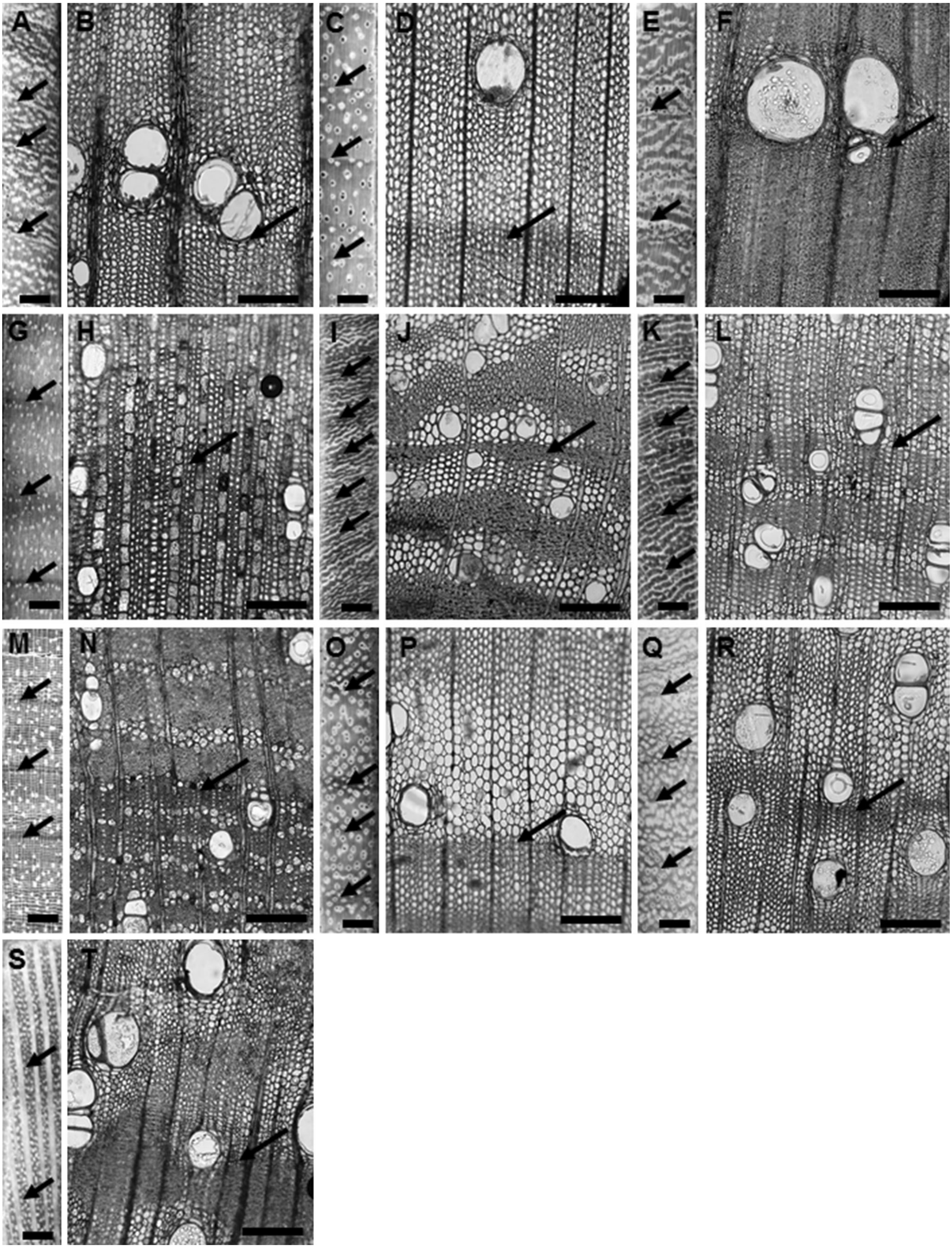
Results

Anatomical structure

The 10 studied species showed different wood anatomical patterns (Fig. 2; Table 2) and wood specific gravity, which, on average, varied from 0.32 g cm^{-3} (in *Schizolobium parahyba*) to 0.70 g cm^{-3} (*Handroanthus serratifolius*) (Table 2). Nine species showed diffuse-porous and *Citharexylum myrianthum* presented semi-ring porous. Five of the species showed distinct growth rings: *C. Myrianthum*, *S. Parahyba, Senna multijuga, Virola bicuhyba,* and *H. serratifolius.* In *C. myrianthum*, growth rings were marked by gradual differences in vessel diameter between latewood and earlywood, associated with marginal parenchyma bands as well as radially flattened and thick-walled latewood fibers (Fig. 2a, b). *S. parahyba* had distinct growth rings marked by marginal parenchyma band and by thickening of fiber walls in latewood (Fig. 2c, d). In *S. multijuga*, the growth rings were characterized by thickening fiber walls and radially flattened latewood fiber, sometimes combined with marginal parenchyma bands (Fig. 2e, f). *V. bicuhyba* showed distinct growth rings marked by slight and gradual increases in fiber wall thickness (Fig. 2g, h). In *H. serratifolius* the growth rings were marked by thick-walled latewood fiber, associated with marginal parenchyma bands (Fig. 2i, j). Four species presented scarcely distinct growth rings. In *C. canjerana*, when visible, these growth rings were characterized by one or more of the following features: differences in fiber wall thickness, changes in vessel diameter and/or fibrous zone (Fig. 2k, l). *C. estrellensis*, had growth rings with different levels of distinction: distinct and scarcely distinct. Distinct growth rings were marked by gradual fiber wall thickness and decreasing frequency of parenchyma bands towards the latewood, associated with marginal parenchyma bands and fibrous zones (Fig. 2m, n). In some areas these anatomical features were scarcely distinct. *Inga edulis*, *I. marginata* and *Myrsine coriacea* had marked changes in fiber wall thickness, fiber radial size, vessel diameter and/or fibrous zone (Fig. 2o–t). In these species we also observed "false" rings (sometimes forming diffuse ring boundaries), characterized by intra-growth ring density fluctuations, fiber density fluctuations and/or irregular tangential bands of vessels.

Cumulative and current girth increment

The 10 species showed different patterns of cumulative girth increment along the 22 studied months (Fig. 3). Four species (*C. myrianthum, S. parahyba*, *S. multijuga,* and *C. estrellensis*) exhibited seasonal stem growth, characterized by a period of girth increment and a period with no observed growth (Figs. 3, 4a–c, g). All of these species showed clear growth peaks and the higher increment rates generally during the wettest and hottest period of the year (October–March) and no girth growth during the end of the less wet season and the beginning of the wettest season (June to November) (Fig. 4a–c, g). *V. bicuhyba* showed a seasonal growth pattern (Fig. 3), with a reduced growth in the winter months (Fig. 3b, d). Three species (*M. coriacea*, *I. marginata* and *I. edulis*) had a continued growth pattern (Fig. 3a), and more than one girth increment events were observed during the year (Fig. 4j, i, h). *C. canjerana* and *H. serratifolius* had several small growth peaks during the year (Figs. 3, 4f, e).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◀**Fig. 2** Macroscopic (*left*) and microscopic (*right*) wood transverse sections tree species. **a**, **b** *Citharexylum myrianthum*; **c**, **d** *Schizolobium parahyba*; **e**, **f** *Senna multijuga*; **g**, **h** *Virola bicuhyba*; **i–j** *Handroanthus serratifolius*; **k–l** *Cabralea canjerana*; **m–n** *Cariniana estrellensis*; **o–p** *Inga edulis*; **q–r** *Inga marginata*; **s–t** *Myrsine coriacea*. *Arrows* indicate the growth ring boundaries. *Scale bar* 2500 and 200 μm for macroscopic and microscopic views, respectively

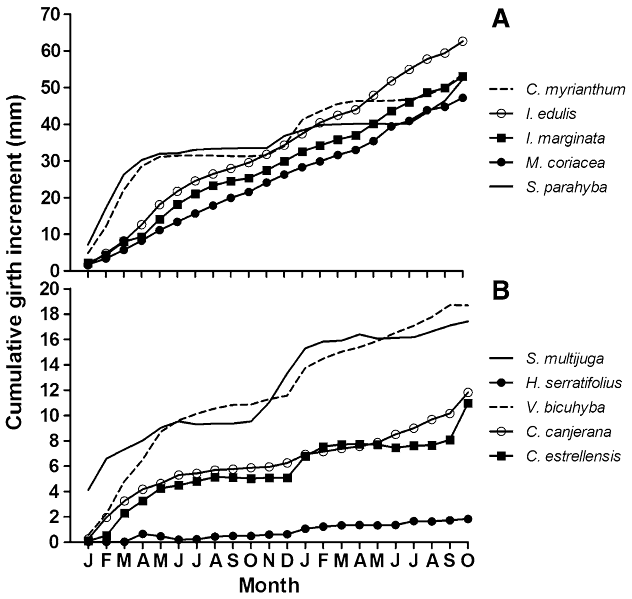

Fig. 3 Cumulative girth increment of 10 tree species over 22 months (from January 2011 to October 2012), in the Atlantic Forest, southern Brazil. Note differences in scale in **a** (fast growing species) and **b** (slow growing species)

Tree species differed in their accumulated girth growth average ($H = 46.28$; $P < 0.0001$; Table 3). For example, the girth increment (or annual radial increment) of *H. serratifolius* was approximately 35 times lower than *I. edulis*, the species with the highest increment. Higher girth growth were found in *I. edulis*, *C. myrianthum, I. marginata, S. parahyba* and *M. coriacea* and lower girth increment were observed for *V. bicuhyba*, *S. multijuga*, *C. canjerana, C. estrellensis* and *H. serratifolius* (Table 3). During the observed period, species varied in their growth rates from 1 ± 0.5 % (*H. serratifolius*) to 15 ± 4.0 % (*I. edulis*) (Table 3).

Girth increment and climate

The girth increment of the 10 species were, in general, weakly or not related to rainfall (current or historical), but strongly and positively related to temperature (current and historical) and day length for most of species (Table 4). The relationship between growth and climate differed among species: the girth increment of *C. myrianthum* and *S. multijuga* and *V. bicuhyba* was more strongly related to mean temperature and day length (and weakly with rainfall); the increment of *I. edulis* and *S. parahyba* were more related to temperature, and the increment of *H. serratifolius* was related only to rainfall (Table 4). For four species (*I. marginata*, *M. coriacea*, *C. canjerana* and *C. estrellensis*), no significant correlation was observed ($P > 0.05$). In general, the girth increment was strongly correlated with the temperature and day length of the same or previous month, suggesting a small delay in growth response (Table 4).

Discussion

Distinctiveness of tree rings varied among the studied species, but was sufficiently clear to mark individual rings in most of species. These rings were delimited by a growth period and non-growth (or less expressive) growth periods. Growth rings were observed in the secondary xylem of reveling anatomical growth marker in all species, as previously seen in other tropical tree species (Alves and Angyalossy-Alfonso 2000). The presence of thick-walled and radially flattened latewood fibers versus thin-walled earlywood was the most common growth ring boundary, commonly found in a great number of tropical species (Worbes 1989; Callado et al. 2001; Lisi et al. 2008). “False” rings as observed in some studied species (especially *Inga edulis*, *I. marginata* and *Myrsine coriacea*) are a ring anomaly relatively frequent in species growing in weakly seasonal tropical regions (Heinrich and Banks 2005). They are explained by temporary growth limitation in a stressful period caused, for example, by low temperatures, flooding (Speer 2010), drought stress (Priya and Bhat 1999; Wimmer et al. 2000), and by abrupt variation from dry to wet period (Masiokas and Villalba 2004). False growth rings are also common in young individuals of pioneer species (Wimmer et al. 2000; Vogel et al. 2001; Lopez et al. 2012) which is the case of *I. marginata, M. coriacea* and *I. edulis* (Shimamoto et al. 2014).

Growth ring boundaries can be marked by one or more structural changes or by a combination of characteristics (IAWA 1989; Worbes 1989). This association of two or more wood anatomical features is useful for identifying tree-ring boundaries in tropical species (Stahle 1999; Roig 2000; Vetter 2000). *C. myrianthum* is a semi-porous species demarcated by marginal parenchyma; this parenchyma was also verified in other tropical trees (Callado et al. 2001). *S. multijuga, S. parahyba* and *H. serratifolius* have a combination of latewood thick-walled fibers and marginal parenchyma, previously described for other tropical species (Tomazello-Filho et al. 2004; Marcati et al. 2008; Lisi et al. 2008). *C. estrellensis* has a decreasing frequency of

Fig. 4 Girth current increment (mean ± SD) of 10 tree species over 22 months (from January 2011 to October 2012), in the Atlantic Forest, southern Brazil. Species with distinct growth rings: **a** *Citharexylum myrianthum*, **b** *Schizolobium parahyba*, **c** *Senna multijuga*, **d** *Virola bicuhyba*, **e** *Handroanthus serratifolius*; species with scarcely distinct (or distinct/scarcely*) growth rings: **f** *Cabralea canjerana,* **g** *Cariniana estrellensis*, **h** *Inga edulis*, **i** *Inga marginata*, **j** *Myrsine coriacea*. *Black and grey bars* represent the rainiest (October to March) and the less rainy (April to September) seasons, respectively. *Dotted lines* represent the period with lowest growth rates and/or dormant period for each species. Note the difference in the y-axis scales. Negative error bars were omitted

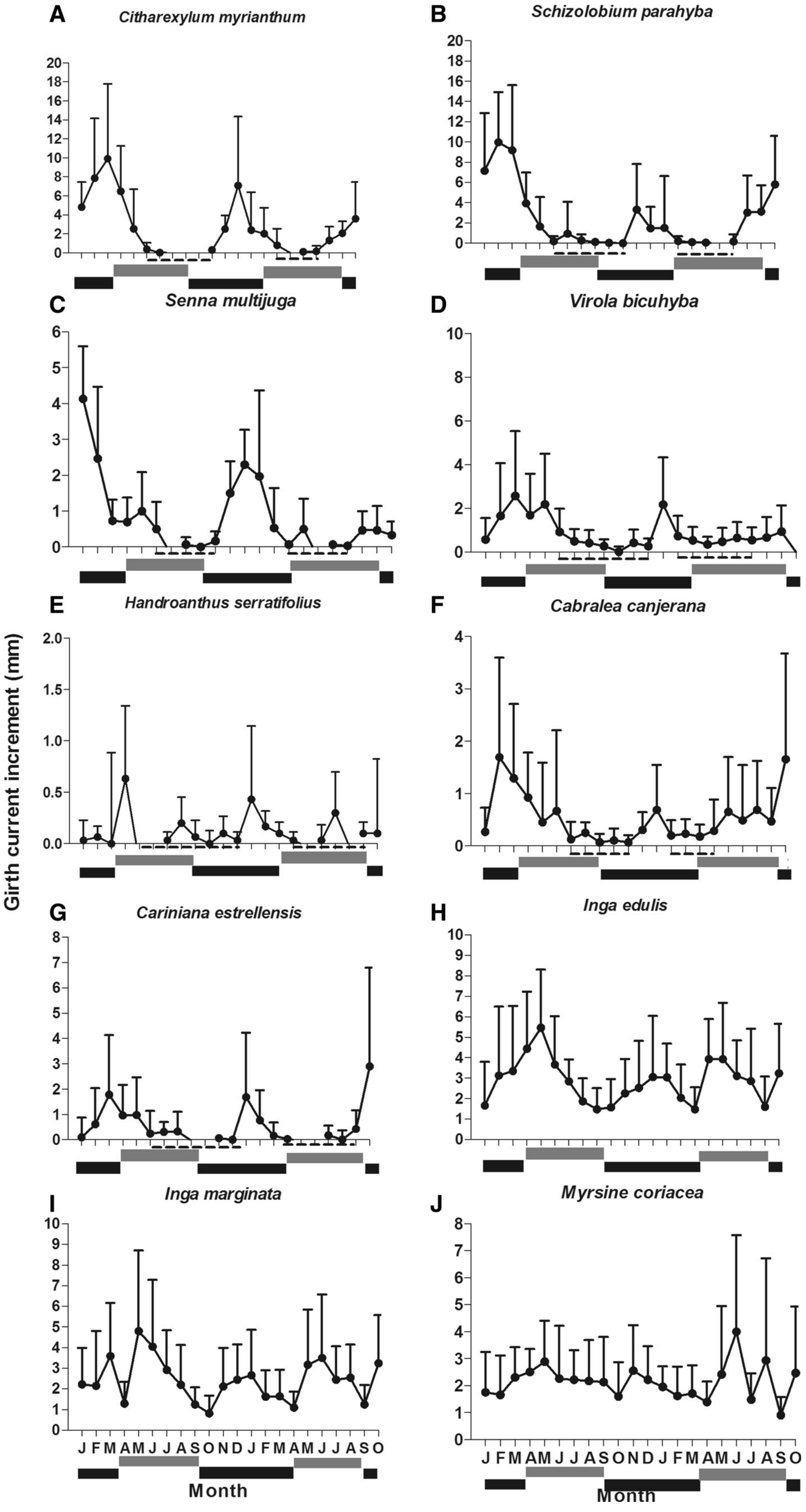

Table 3 Accumulated girth increment, rate of girth increment, annual radial increment (mean ± SE) and resumed characteristics of the 10 studied tree species in the Atlantic Forest, southern Brazil

Species	Accumulated (22 months) girth increment (mm)	Rate of girth increment (%)	Annual radial increment (mm)	Deciduousness	Growth rings distinction[a]
C_myr	53.62 ± 13.40 bcd	11 ± 3.0	4.65 ± 1.16	Deciduous	Distinct
S_par	52.21 ± 8.37 bd	11 ± 1.0	4.53 ± 0.72	Deciduous	Distinct
S_mul	17.43 ± 2.54 a	3 ± 1.0	1.51 ± 0.22	Semi-deciduous	Distinct
V_bic	18.68 ± 4.91 a	6 ± 2.0	1.62 ± 0.42	Semi-deciduous	Distinct
H_ser	1.83 ± 1.44 a	1 ± 0.5	0.16 ± 0.12	Deciduous	Distinct
C_can	11.82 ± 4.01 a	2 ± 1.0	1.02 ± 0.35	Semi-deciduous	Scarcely
C_est	10.98 ± 4.23 ac	3 ± 1.0	0.95 ± 0.37	Semi-deciduous	Distinct/scarcely
I_edu	62.64 ± 12.67 b	15 ± 4.0	5.44 ± 1.10	Evergreen	Scarcely
I_ mar	53.12 ± 12.71 bcd	4 ± 1.0	4.61 ± 1.10	Semi-deciduous	Scarcely
M_cor	47.22 ± 7.71 bcd	6 ± 1.0	4.10 ± 0.67	Semi-deciduous	Scarcely

Different letters from Kruskal–Wallis test indicate significant differences among species ($P < 0.05$)

[a] According to Fig. 2 and Table 2

Table 4 Spearman coefficients (r_s) between monthly girth increment and climatic variables of 10 tree species from the Atlantic Forest, southern Brazil

Climatic variable	Species									
	C_myr	S_par	S_mul	V_bic	H_ser	C_can	C_est	I_edu	I_mar	M_cor
Rainfall (0)	–	–	–	–	–	–	–	–	–	–
Rainfall (1)	–	–	–	–	0.51	–	–	–	–	–
Rainfall (2)	–	–	–	–	–	–	–	–	–	–
Rainfall (3)	–	–	–	–	–	–	–	–	–	–
Historical rainfall (0)	0.59	–	0.60	–	–	–	–	–	–	–
Historical rainfall (1)	0.65	–	0.61	–	–	–	–	–	–	–
Historical rainfall (2)	0.50	–	–	0.48	–	–	–	–	–	–
Historical rainfall (3)	–	–	–	0.44	–	–	–	0.56	–	–
Temperature (0)	**0.69**	0.50	0.62	–	–	–	–		–	–
Temperature (1)	**0.70**	–	0.56	–	–	–	–	–	–	–
Temperature (2)	0.52	–	–	0.43	–	–	–	0.49	–	–
Temperature (3)	–	–	–	0.53	–	–	–	**0.67**	–	–
Historical temperature (0)	**0.66**	0.45	**0.72**	–	–	–	–	–	–	–
Historical temperature (1)	**0.66**	–	0.59	–	–	–	–	–	–	–
Historical temperature (2)	0.52	–	–	0.44	–	–	–	–	–	–
Historical temperature (3)	–	–	–	0.51	–	–	–	0.57	–	–
Day length (0)	0.49	–	**0.65**	–	–	–	–	–	–	–
Day length (1)	**0.67**	–	**0.74**	–	–	–	–	–	–	–
Day length (2)	**0.66**	–	0.60	–	–	–	–	–	–	–
Day length (3)	0.52	–	–	0.50	–	–	–	–	–	–

n number of lagged months; – non-significant correlation ($P > 0.05$); bold: $P \leq 0.001$

parenchyma bands towards the latewood resulting, sometimes, in distinct fiber zones (Lisi et al. 2008; Tomazello-Filho et al. 2004). Finally, *M. coriacea* and *V. bicuhyba* have latewood fibers with thick walls that are associated or not associated with a fiber zone.

Marginal parenchyma was observed in *C. myrianthum*, *C. estrellensis, S. parahyba* and *S. multijuga*. These cells are related with storage of carbohydrates and transport of nutrients and are necessary for the fast reactivation of cambial cell divisions after a cambial dormancy

(Kozlowski et al. 1991; Larson 1995; Dünisch et al. 2002). The presence of marginal parenchyma band in these species could be explained, in some way, by the fast re-growth observed in months with increased temperature and day length. Furthermore, characterizing the nature of the marginal parenchyma is important to accurately determine the growth ring boundary, increasing the confidence of correlations with inductive or inhibiting growth factors (Callado et al. 2013).

The ring-porous structure is frequently associated to autumnal deciduously in trees growing in temperate climates (Boura and De Franceschi 2007). For the studied species we found only one deciduous species presenting semi-ring porous (*C. myrianthum*), whereas in the two other deciduous species (*S. parahyba* and *H. serratifolia*) and in the semi-deciduous species (*I. marginata*, *M. coriaceae*, *V. bicuyba*, *S. multijuga*, *C. canjerana*, *C. estrellensis*) we found diffuse-porous. Thus, as previously reported in other studies (Wheeler and Baas 1993; Poole and van Bergen 2006; Boura and De Franceschi 2007), the relation between deciduously and porosity is possibly much less clear for tropical trees.

The studied species also varied in the timing and magnitude of the girth growth. For example, *C. myrianthum*, *S. parahyba* and *S. multijuga* (and less intensively *V. bicuhyba*) were characterized by an intense girth growth in the hotter and longer days of the summer and a reduction during the colder and shorter days of the winter. Longer lasting period over 3–5 months was especially observed in both deciduous species (*C. myrianthum* and *S. parahyba*), whereas the semi-deciduous and evergreen species presented, in general, a more continuous growth with short interruptions. A similar pattern was previously observed for tropical trees growing in seasonal climates (Mariaux 1969, 1970; Worbes 1995,1999; Botosso et al. 2000) and were associated to a long period of cambial dormancy in deciduous species, and to a short interruption of cambial activity in evergreen species (Alves and Angyalossy-Alfonso 2000; Lisi et al. 2008). However, considering our results, this pattern apparently occurs even in wet and less seasonal climates.

Species with higher accumulated growth, such as *I. edulis* (evergreen), *I. marginata* and *M. coriacea* (semi-deciduous species), were characterized by a continued growing strategy, even in the winter. Meanwhile, a contrasting pattern was observed for both *C. myrianthum* and *S. parahyba* (deciduous trees), which also accumulated a large trunk increment, but with growth restricted to spring and summer months. Considering the deciduousness of these five species presenting higher accumulated girth increment (Table 3), it is possible to suggest that evergreen and some semi-deciduous species growing in aseasonal conditions probably photosynthesize during a longer period, including the unfavorable winter season, as recognized previously for other species (Monk 1966, Chabot and Hicks 1982; Escudero and Del Arco 1987; Jurik et al. 1988; Givnish 2002). On the other hand, individuals of deciduous species such as *C. myrianthum and S. parahyba* presented growth rates similar to growth rates of evergreen and semi-deciduous species. It is possible that these species have a higher rate of photosynthesis per unit leaf mass compared to evergreen species, reducing their transpiration rate during the unfavorable season (Chabot and Hicks 1982; Givnish 2002).

Despite showing a relatively high girth increment in our study (17.43 mm in 22 months), trees of *S. multijuga* growing in experimental plots of restoration areas showed a much higher growth (36.5 mm in 12 month, Cardoso et al. 2012). It is possible that these differences are imposed by small variations in soil characteristics that can severely limit the tree's growth (Cardoso et al. 2012). All other species (*H. serratifolius*, *C. estrellensis*, *C. canjerana* and *V. bicuhyba*) grew very slowly during the year, resulting in a lower accumulated growth after 22 month (<19 mm). Specifically *H. serratifolius* trees grew much less than previously reported for this species in Seasonal Semi-Deciduous Forest (Lisi et al. 2008; Maria 2002), demonstrating a large spatial variation in tree growth for a given species. Furthermore, variations in tree dimension among species, not considered in analyses, may also explain some differences among species.

The correlation between girth increment and climatic variables varied among species, indicating that species have different sensitivities to climate and day length. For example, whereas the growth of trees of *I. edulis, C. myrianthum, S. parahyba, V. bicuhyba, S. multijuga* were seasonal and more strongly associated to the temperature and day length, the growth of other species growing seasonally (*C. canjerana*, *C. estrellensis*) and species with intermittent growth (*I. marginata, M. coriacea, H. serratifolius*) did not relate to climate variables in this study. In general, the trees' growth correlated more tightly with temperature (current or lagged) and day length than to rainfall. This result contrasts previous studies in which cambial growth of tropical trees was associated with the beginning of the wet period (Worbes 1999, 2002). On the other hand, it was already demonstrated that in plants growing in wet tropical climates, small differences in temperature and day length during the year are sufficient to trigger reproductive and vegetative phenological phases (Marques and Oliveira 2008). Thus, it is possible that in tropical areas where there is no dry season, girth increment can potentially occur throughout the year, but the increase in temperature and photoperiod promotes, immediately or lately, a stimulus for the cambium activity for some species.

The growth strategy of the studied species was partially associated with different anatomical and ecological characteristics. *C. myrianthum* and *S. parahyba* are species with moderate accumulate growth concentrated in the summer and deciduous leaves, resulting in clear growth ring distinction. Considering that these species lose their leaves in the winter (personal observation), this growth pattern possibly results from a rapid remobilization of carbohydrates to the stems during the winter (Lüttge and Hertel 2009) following the immediate optimization of the stem growth in hotter and longer days of the summer. The girth growth of *I. marginata*, *I. edulis* and *M. coriacea* is high and distributed through the year (not limited by the climate) and is not related with any anatomical characteristics or deciduousness pattern. This strategy seems to result from a low sensitivity of these species to climate limitations, resulting in rapid growth. The species *H. serratifolius* and *C. estrellensis*, *C. canjerana, V. bicuhyba* and *S. multijuga* grow slowly, resulting in a denser wood with marked growth rings. Probably, this reflects a strategy of slow metabolism and a higher stem resistance to damage or pathogens (Zimmerman et al. 1994).

Our results suggest that these woody species growing in wet climate of the Atlantic forest in southern Brazil, even when there is no water deficit during the less rainy season, can have a marked seasonality in cambium activity and stem growth in the hotter and longer days of summer months. This pattern varies among species and is marginally associated with the tree deciduousness and wood characteristics. In view of the worldwide discussion regarding the future of rainforests, the knowledge of seasonality in tree growth is an important step to dating tropical trees and for providing better comprehension of growth dynamics in tropical ecosystems and its effects on ecosystem processes, such as biomass accumulation, across climate change scenarios.

Author contribution statement MCMM, PCB and CYS designed the experiment. CYS collected field data. EA, CYS and PCB performed the anatomical analysis. CYS and MCMM performed statistical analysis. All authors together wrote the manuscript and interpreted the data.

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Compliance with ethical standards

Conflict of interest The authors declare no conflicts of interest.

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