ANATOMICAL FEATURES OF GROWTH RINGS IN FLOOD-PRONE TREES OF THE ATLANTIC RAIN FOREST IN RIO DE JANEIRO, BRAZIL

by
Cátia H. Callado¹, Sebastião J. da Silva Neto², Fábio R. Scarano³, Cláudia F. Barros ⁴ & Cecília G. Costa ⁴

SUMMARY

The anatomical features of growth rings of 13 representative species of the swamp forests within the Atlantic rain forest of the State of Rio de Janeiro, southeastern Brazil, were studied. Most species showed distinct rings. The growth ring boundaries were marked by fibrous zones frequently associated with marginal parenchyma bands, and growth ring boundary features were characteristic of the particular families and genera analysed. Leaf fall can be related to the occurrence of growth rings in seven species, whereas in evergreen species growth rings can be related to flooding. In Euphorbiaceae species, flooding regime differences (periodical or permanent) are related to the shape and distribution of new cells produced by the cambium and, thus, growth ring structure.

Key words: Atlantic rain forest, flooding, growth rings, swamp forest, tropical trees, Brazil.

INTRODUCTION

Annual growth ring formation, which is due to an alternation between cambium activity and dormancy (Fahn 1982), and tree development has frequently been studied in trees of temperate forests (Amobi 1974; Borchert 1999). However, relatively little is known about the prevalence of annual growth rings, and even less about the factors triggering growth ring formation in tropical plants (Baas & Vetter 1989; Jacoby 1989; Priya & Bhat 1999). In Brazil a few studies on growth periodicity in trees have been conducted. These studies examined mostly Amazon forest trees (Botosso 1984; Worbes 1985, 1989; Vetter & Botosso 1988; 1989; Botosso & Vetter 1991). Growth ring studies, by providing information on tree age and on factors influencing tree growth, wood production and quality, can be of great practical value for forest management,
Map 1. Location of the Biological Reserve of Poço das Antas, Rio de Janeiro State, Brazil.

The Brazilian Atlantic rain forest, which once covered most of the Brazilian coastline, is now reduced to about 5% of its original area (Leitão Filho 1993). In the present study, we examined the anatomy of the growth rings of 13 representative species of one of the last well-preserved remnants of swamp forest in the Atlantic forest domain. These species are currently being used in a restoration program at this site. We aim to answer the following questions: a) do representative species of swamp forest in the Atlantic Rain Forest show alternating cambium activity, evidenced by growth ring formation; b) if so, could growth ring occurrence be related to flooding, or to leaf fall behaviour, and/or genetic characteristics?

MATERIALS AND METHODS

Fifty-two trees, belonging to 13 species and 7 families, were sampled in a swamp forest within the Atlantic rain forest domain at the Biological Reserve of Poço das Antas, municipality of Silva Jardim, State of Rio de Janeiro, southeastern Brazil (Map 1). This area had been surveyed floristically and phytosociologically (Guedes-Bruni 1998; Scarano et al. 1998). It is subject to flooding that does not inundate the area in a uniform manner due to gentle relief variations. Scarano et al. (1997) have described this site in the dry season as a mosaic of neighbouring flooded and unflooded patches. Thus, while some plants are permanently flooded, others are flooded for circa 100

Fig. 1. Mean monthly temperature and precipitation in the Biological Reserve of Poço das Antas, Rio de Janeiro, Brazil (data from the Atlantic Rain Forest Program).
Table 1. Growth ring characteristics, diameter at breast height (DBH) in cm, leaf fall pattern, and flooding regime for each individual sampled of the species studied.

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Rain is well distributed throughout the year with a dry season from June to August (precipitation less than 60 mm). Mean annual precipitation for the 1993–1998 period was 2260 mm, mean annual temperature was 25 °C. February was on average the hottest month (up to a maximum of 38 °C) and June to August the coldest months (down to a minimum 14 °C) (Fig. 1).
The trees selected for this study were adults, straight-boled, with no bifurcation or apparent deformities. The number of samples per species differed (Table 1) due to the varying number of individuals with the appropriate characteristics at each collection site.

Wood samples were collected at breast height (approximately 1.30 m above the ground). The samples were complete ones, measuring about 15 × 7 × 10 cm, including bark, sapwood and heartwood. Blocks of approximately 2.5 cm³ were softened by boiling in water and glycerine. Transverse, tangential, and radial sections about...
17 μm thick were prepared with a Spencer 860 sliding microtome. Afterwards the sections were bleached, stained with safranin and astra blue, dehydrated, and mounted in Permount resin on permanent slides (Johansen 1940; Sass 1958; Burger & Richter 1991) for observation with light microscopy.

Terminology used herein follows the IAWA List of Microscopic Features for Hardwood Identification (IAWA Committee 1989). The wood anatomical characteristics of most species studied are described in Barros et al. (1997). Wood samples and permanent slides are housed in the wood collection of the Rio de Janeiro Botanical Garden.

The species sampled were divided into deciduous, semi-deciduous and evergreen groupings, based on the literature (Lorenzi 1992, 1998; Costa et al. 1998) and on field observations conducted monthly from May 1997 to April 1999. Deciduous trees were identified as those which lost 90–100% of their leaves in a given season, semi-deciduous trees as those which lost 60–80% and evergreen trees as those with a continuous leaf turnover.

RESULTS

Table 1 shows that 10 of the 13 species studied showed distinct growth rings, while the remaining three species showed scarcely distinct or indistinct rings. Distinct rings were found in all leaf-fall categories (deciduous, semi-deciduous and evergreen), while scarcely distinct and indistinct rings were not found in deciduous plants but were found in the other leaf-fall categories.

Leaf-fall behaviour was determined for Tabebuia cassinoides, T. umbellata, Alchornea sidifolia, A. triplinervia and Citharexylum myrianthum (Table 1). For T. cassinoides leaf fall took place at the rainiest season, whereas for the others it occurred at the driest season or during the transition to the rainy season. This pattern was not associated to the flooding regime trees were subject to.

Periodically and permanently flooded individuals of the same species showed similar growth ring features and leaf-fall phenology, except in the Euphorbiaceae. Specimens of this family showed indistinct or poorly defined rings in permanently flooded soil and well defined rings in periodically flooded soil, although leaf-fall phenology did not vary according to the flooding regime. The structure of the growth rings of each of the studied species is described below.

Bignoniaceae

Tabebuia cassinoides (Lam.) DC. (Fig. 2) and Tabebuia umbellata (Sond.) Sandwith (Fig. 3) had distinct growth rings. The growth ring boundaries in T. cassinoides were marked by thick-walled and radially flattened latewood versus thin-walled earlywood fibres, whereas in T. umbellata growth ring boundaries were marked by marginal

Fig. 2–5. Transverse sections. – 2: Tabebuia cassinoides. – 3: T. umbellata. – 4: Eriotheca pentaphylla. – 5: Calophyllum brasiliense. Arrows indicate the growth ring boundaries. – Scale bar = 200 μm.
parenchyma bands (1–3 cells wide) associated with thick-walled and radially flattened latewood versus thin-walled earlywood fibres. In *T. umbellata*, there also was a decrease in the frequency of aliform and confluent axial parenchyma in the latewood (Fig. 3).

**Bombacaceae**

*Eriotheca pentaphylla* (Vell. emend. K. Schum.) A. Robyns (Fig. 4) had growth ring boundaries marked by a decrease in the size of the axial parenchyma, an increase of thick-walled fibres, and distended rays.

**Clusiaceae**

*Calophyllum brasiliense* Cambess. (Fig. 5) had indistinct growth rings, whereas *Symphonia globulifera* L. (Fig. 6) showed indistinct or scarcely distinct growth rings. In the latter, the growth ring boundaries were marked by a decrease in the frequency of vessel elements and parenchyma bands towards the latewood, resulting in distinct fibre zones, best observed at low magnification.

**Euphorbiaceae**

While the two *Alchornea* species had distinct growth rings, *Pera glabrata* (Schott) Baill. had scarcely distinct or indistinct growth rings. The growth ring boundaries of *Alchornea triplinervia* (Spreng.) Müll. Arg. (Fig. 7) and *A. sidifolia* Müll. Arg. (Fig. 8 & 9) were marked by thick-walled and radially flattened latewood fibres versus thin-walled earlywood fibres. Both species, on periodically flooded soil, had gelatinous fibres in the earlywood versus non-gelatinous fibres in the latewood, while the permanently flooded trees showed irregular gelatinous fibre zones in the ring. In the case of *P. glabrata* (Fig. 10), the periodically flooded specimen had scarcely distinct growth rings. They were marked by continuous, straight and narrow marginal parenchyma bands (1 or 2 cells of width), associated with thickening of the fibre walls and decreasing frequency of axial parenchyma in the latewood. In the permanently flooded specimen, the growth rings were indistinct.

**Leguminosae–Papilionoideae**

*Andira fraxinifolia* Benth. (Fig. 11), *Lonchocarpus cultratus* (Vell.) A.M.G. Azevedo et H.C. Lima (Fig. 12) and *Platymiscium floribundum* Vogel (Fig. 13) showed distinct growth rings. These species showed thick-walled fibres in the latewood associated with straight and narrow marginal parenchyma bands (1 or 2 cells wide in *A. fraxinifolia*, 1–4 cells wide in *L. cultratus*, and 2–4 cells wide in *P. floribundum*). Numerous prismatic crystals occurred in the chambered marginal parenchyma bands of *A. fraxinifolia*. *Andira fraxinifolia* had large, wavy and discontinuous bands of axial parenchyma, with few prismatic crystals; *L. cultratus* had large, continuous and

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Fig. 6–9. Transverse sections. – 6: *Symphonia globulifera*. – 7: *Alchornea triplinervia*. – 8 & 9: *A. sidifolia*; 8: periodically flooded specimen; 9: permanently flooded specimen. Arrows indicate the growth ring boundaries. – Scale bar = 200 μm.
slightly wavy bands; *P. floribundum* had mostly aliform and confluent axial parenchyma. In *L. cultratus* we observed differences in vessel size between earlywood and latewood. Random gelatinous fibre zones occurred in the growth rings of *A. fraxinifolia* and *L. cultratus*.

**Myrtaceae**

*Marlierea georgeana* (O. Berg.) G.M. Barroso (Fig. 14) showed distinct growth ring boundaries marked by thickness and flatness of latewood fibres and a decrease in the frequency of vessels and axial parenchyma, resulting in conspicuous fibre zones.

**Verbenaceae**

*Citharexylum myrianthum* Cham. (Fig. 15) showed distinct growth rings marked by gradual differences in vessel diameter between latewood and earlywood, associated with marginal parenchyma bands and flattened and thick-walled latewood fibres.
DISCUSSION

In all species studied with distinct growth rings, the rings were delimited by thick-walled and radially flattened fibres in the latewood and were frequently associated with marginal parenchyma bands. These are common characteristics found in a great number of tropical families (Worbes 1989) and the structural patterns of growth rings were similar to the characteristics mentioned for other species belonging to the same families and genera analysed here (Record & Mell 1924; Metcalfe & Chalk 1950; Worbes 1985; Détienne 1989; Mainieri & Chimelo 1989; Vetter & Botosso 1989), thus reflecting inherited phylogenetic characteristics.

Growth ring periodicity was not verified in this study. However, a parallel can be traced between the anatomical features of growth rings of some species analysed here and those found by Détienne (1989) for other tropical species (Guinean-Congolese and French Guyana) belonging to the same families and/or genera. In that study, annual growth rings were well-delimited in species with semi-ring-porous wood or with marginal parenchyma bands. The marginal parenchyma bands were easily detected when they were associated with shorter, discontinuous and/or wavy bands, or when they were associated with other paratracheal parenchyma types, such as: vasicentric, confluent and aliform. In a tropical species of *Acacia*, studied by Gourlay and Kanowski (1991) and Gourlay (1995), the boundaries of the annual growth rings were marked by marginal parenchyma bands with numerous crystalliferous chains. Such features were to some extent observed here in *Citharexylum myrianthum*, *Tabebuia cassinoides*, *T. umbellata*, *Andira fraxinifolia*, *Lonchocarpus cultratus* and *Platymiscium floribundum* and could represent typical annual growth rings.

In Euphorbiaceae species studied, ring distinctiveness varied between individuals submitted to different flooding regimes. Worbes (1985) attributed distinctiveness of tree rings to differences of leaf-fall behaviour for flooding species from *várzea* (white-water, mainly deciduous species) and *igapó* (black-water, mainly evergreen species) forests at the Amazon. However, in our study distinctiveness of tree rings seemed to be influenced by flooding regimes. In periodically flooded *Pera glabrata*, an evergreen species, cambial dormancy could be promoted by seasonal flooding; permanently flooded specimens showed indistinct growth rings, probably due to lack of cyclic growth. In *Alchornea sidifolia* and *A. triplinervia*, both semi-deciduous species, the individuals subjected to seasonal flooding and leaf shedding showed well defined growth ring boundaries, while the individuals subjected only to seasonal leaf shedding showed poorly defined ring boundaries.

Reaction wood formation can be induced by flooding (Kozlowski et al. 1991). In deciduous species gelatinous fibres are reported to be more abundant in earlywood, not extending throughout the latewood (Kozlowski & Pallardy 1997). This was observed in individuals from periodically flooded soils of both semi-deciduous species of *Alchornea*. According to Kozlowski and Pallardy (1997), gelatinous fibres often extend throughout both the earlywood and latewood in evergreen species. Random zones of gelatinous fibres were observed throughout the rings of *Andira fraxinifolia* (evergreen), *Lonchocarpus cultratus* (deciduous) and *Pera glabrata* (evergreen), and also in permanently flooded specimens of *Alchornea sidifolia* and *A. triplinervia* (both
Thus, the distribution of gelatinous fibres was similar for all three leaf-fall categories, and probably the differences found within *Alchornea* reflect differences in flooding regimes.

Although it was not always possible to identify which was the primary factor determining cambial dormancy, it appeared that flooding influenced growth ring formation in evergreen species, while leaf-fall was related to growth ring formation in deciduous and semi-deciduous species. Defoliation followed by cambial dormancy with formation of fibre zones in the latewood as a result of flooding could be the case of *Tabebuia cassinoides*. Leaf-fall of this species took place in the rainy season, when flooding is permanent. This pattern has already been observed by Worbes (1985) for flood-prone Amazonian species.

We believe that *Tabebuia umbellata*, *Lonchocarpus cultratus*, *Platymiscium floribundum* and *Citarexylum myrianthum* (all deciduous), *Tabebuia cassinoides*, *Alchornea sidifolia* and *A. triplinervia* (all semi-deciduous) may provide interesting material for future research on dating of tropical trees, due to the conspicuous growth ring boundaries observed, and to well defined periodicity of leaf-fall. Moreover, monitoring cambial activity in these and in the evergreen species with distinct growth rings, may further enhance the understanding of growth dynamics in tropical ecosystems.

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