GROWTH RINGS IN CERRADO WOODY SPECIES: OCCURRENCE AND ANATOMICAL MARKERS.

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Abstract

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Growth ring occurrence was investigated in 48 representative species of cerrado in the state of São Paulo, Brazil. We characterized growth ring markers and described the growth layer structure of the basal portion of the most developed stem branches in woody plants. Growth rings were poorly defined in 33%, well defined in 61% and not discernable in 6% of the species studied. Various anatomical features were used as growth markers, such as: thick-walled latewood fibres; radially flattened latewood fibres; fibre zones; distended rays; marginal bands of axial parenchyma; marginal lines of parenchyma; and closeness of the narrow bands of scalariform parenchyma. In a single species, different growth ring markers often occurred together. Within growth layers, variations in the anatomical features were observed. Variations in the axial parenchyma distribution within growth rings in Vochysia cinnamomea, Qualea multiflora, V. rufa and V. tucanorum, wood are here reported for the first time. Variation in the distance of the axial parenchyma in narrow bands along the rays within growth layers in Annona coriacea, A. crassiflora, Diospyrus hispida and Roupala montana wood is also reported. Phenology and habit of the studied species were important aspects related to both growth ring presence and distinctness as well as to the anatomical features’ variations within growth layers.

Key words: Cerrado, increment zones, habit, phenology, wood anatomy

Resumo

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Este estudo investigou a ocorrência de camadas de crescimento em 48 espécies representativas de cerrado no estado de São Paulo, Brasil. Amostras foram obtidas da porção basal de ramos caulinares mais desenvolvidos. Foram caracterizados os marcadores de crescimento, bem como foi descrita a estrutura das camadas de crescimento. As camadas de crescimento apresentaram-se mal definidas em 33% e bem definidas em 61%, sendo ausentes em 6% das espécies analisadas. Várias características anatômicas foram utilizadas como marcadores de crescimento, tais como: fibras de paredes espessas; fibras achatadas radialmente, zonas fibrosas; raios distendidos; faixas marginais de parênquima axial; linhas de parênquima marginal; e proximidade das linhas de parênquima escalariforme. Diferentes marcadores podem ocorrer em uma mesma espécie. Variações na distribuição do parênquima axial nas camadas de crescimento em Vochysia cinnamomea, Qualea multiflora, V. rufa and V. tucanorum, bem como variação na distância das linhas de parênquima axial ao longo dos raios dentro das camadas de crescimento em Annona coriacea, A. crassiflora, Diospyrus hispida e Roupala montana são aqui reportadas pela primeira vez. A fenologia e o hábito das espécies foram aspectos importantes relacionados tanto com a presença e nitidez das camadas de crescimento no lenho quanto com as variações dentro dessas camadas.

Palavras-chave: anatomia da madeira, zonas de incremento, cerrado, fenologia, hábito.
Introduction

Cerrado plants are characterized by slow secondary growth due to diverse factors including limited water availability during the dry season, high irradiation levels, low fertility and acidic soil, high incidence of herbivores and periodic fires (Coutinho 1990, Franco 2002). Additionally, these plants have small size and genuine morphological characteristics such as scleromorphic leaves, and twisted trunks and branches which give a tortuous aspect to the vegetation; however straight trunks may occur in tall trees (Eiten 1993).

The internal structure of cerrado plants is strongly affected by the environmental factors and most of the studies considering the interaction between these factors and plant anatomy have been conducted with leaf (Morretes & Ferri 1959, Morretes 1967, 1969, Oliveira & Marquis 2002). Regarding to the wood features, which are affected mainly by water availability (Franco 2002), the reports are restricted to a few species and have come mainly from studies on mature wood of the main trunk (Machado & Angyalossy-Alfonso 1995; Ceccantini 1996, Machado et al. 1997, Marcati et al. 2001, Machado et al. in press). Growth rings occurrence in cerrado plants was reported in a few species by Coradin (2000) and Tomazello et al. (2004). However, growth rings in these plants are very irregular and with poorly defined boundaries (Coradin 2000).

Growth rings studies are of interest to climatology, as a hydrologic register; to dendrochronology, to estimate the age of trees; to ecology, to recuperate data on fire history; to paleoclimatology; to analyze growth dynamics, and to various other practical applications (see Baas & Vetter 1989, Eckstein et al. 1995, Coradin 2000).

The goal of this study was to verify the occurrence of growth rings in 48 representative species of well-preserved remnants of cerrado in the state of São Paulo, Brazil. We characterized growth ring markers and described the growth layer structure. The analyses were conducted in stem branches because destructive methods were not allowed.

Material and Methods

The study was carried out in a well-preserved remnant area of cerrado located in the west central part of the state of São Paulo, Brazil (22° 55' S, 48° 30' W). We studied 48 trees and shrubs species belonging to 27 angiosperm families. Precipitation and temperature data of the region studied were obtained from the Natural Resources Department Agrometeorological Station, São Paulo State University (UNESP). The vouchers and samples of one specimen from all the species are deposited, respectively, in the Herbarium (BOTU) and in the Wood Collection (BOTw) of the Natural Resources Department, University of the State of São Paulo (Table 1). The family classification follows APGII (Souza & Lorenzi 2005).

Discs of 3 cm in thickness were obtained from the basal portion of the most developed branches (three sampled plants, one branch per plant). For macroscopic analyses, the cross sections were polished with sandpaper and analysed under a stereomicroscope. For microscopic analyses, a sliding micrometre was used to cut transverse, radial, and tangential sections of 15-20 μm in thickness, which were double-stained with safranin and astra blue (Roeser 1972) and mounted permanently in Entellan synthetic medium.

Due to observation of the entire circumference of the discs, the term “growth ring” was used in this study. The analyses were qualitative and followed IAWA Committee (1989) instructions. The term fibre zone, adapted from IAWA Committee (1989), was used here when a distinct decreasing in frequency of vessels and parenchyma was observed in the entire circumference of the branches. On a macroscopic level, such a zone always appeared darker-colored.

The leaf fall pattern of the studied species were classified into evergreen, semi-deciduous and deciduous, according to phenological observations which were carried out weekly during two years (2002-2004). Habit was classified into shrubs, small trees (seemingly shrubs in size, however with just one slender trunk), trees (with a well-developed trunk and crown) and tall trees (emergents with crown above dossel), adapted from Ribeiro et al. (1999).

Results

The climate diagram shows one annual dry season per year in the studied region (Figure 1).

Growth rings were not discernable in 6% of the species studied, were poorly defined in 33% and were well defined in 61% (Table 1). Among the species with growth rings in their wood, 63% of them are semi-deciduous or deciduous (56.5% semi-deciduous, 6.5% deciduous) against 37% evergreen (Table 1). The figure 2 shows the percentage of species lacking growth rings and with poorly defined and well-defined growth rings, within each phenological category.

Regarding to habit, growth rings are present in 83.3% of the shrubs and small trees and in 100% of the trees and tall trees (Table 1). Figure 3 shows the percentage of species lacking growth rings, species with poorly defined and well-defined growth rings within each habit category.

The growth ring markers and variations within growth rings of each of the studied species (Figures 4a-41b) are described in Table 2. The growth ring markers were observed as follows: thick-walled latewood fibres; radially flattened latewood fibres; fibre zones; distended rays; marginal bands of axial parenchyma; marginal lines of axial parenchyma; and closeness of the narrow bands of scalariform parenchyma. In a single species, different growth ring markers often occurred together. In the species with growth rings, the most common markers were thick-walled and radially flattened fibres and fibre zones (62% of the species), followed...
Table 1. Growth rings of the studied species from Brazilian cerrado. 

| Family                  | Species                                | Family | Species | BOT w | H    | PhB | GR     |
|-------------------------|----------------------------------------|--------|---------|-------|------|-----|--------|
| Anacardiaceae           | Tapirira guianensis Aubl.              |        |         | 1321  | T    | E   | P      |
| Annonaceae              | Annona coriacea Mart.                 | Annona | crassiflora Mart. | 1322  | ST   | SD  | W      |
| Araliaceae              | Didymopanax vinosum (Cham. & Schlecht.) March. |         |         | 1323  | ST   | SD  | P      |
| Asteraceae              | Gochnatia barrosii Cabrera            |        |         | 1324  | S    | E   | P      |
| Bombacaceae             | Eriotheca gracilipes (K. Schum.) A. Robyns |         |         | 1325  | S    | E   | W      |
| Boraginaceae            | Cordia sellowiana Cham.               |        |         | 1326  | S    | E   | W      |
| Caryocaraceae           | Caryocar brasiliense Cambess.         |        |         | 1327  | T    | SD  | P      |
| Chrysobalanaceae        | Couepia grandiflora (Mart. & Zucc.) Benth & Hook. f. |        |         | 1328  | T    | SD  | W      |
| Clusiaceae (Guttiferae) | Kielmeyera rubriflora Cambess.         |        |         | 1329  | T    | SD  | W      |
| Combretaceae            | Terminalia brasiliensis Raddi          |        |         | 1330  | T    | D   | W      |
| Ebenaceae               | Diospyrus hispida DC.                 |        |         | 1331  | S    | D   | W      |
| Erythroxylaceae         | Erythroxylum suberosum A. St.-Hill.    | Erythroxylaceae | suberosum A. St.-Hill. | 1332  | T    | SD  | W      |
| Euphorbiaceae           | Pera glabrata (Schott.) Bail.          |        |         | 1333  | T    | E   | W      |
| Fabaceae - Caesalpinioideae | Copaifera langsdorffii Desf.      | Fabaceae | - Caesalpinioideae | 1334  | S    | D   | W      |
| Fabaceae – Cercideae    | Bauhinia rufa (Bong.) Stud.            |        |         | 1335  | T    | D   | W      |
| Fabaceae - Faboideae    | Machaerium villosum Vog.              |        |         | 1336  | S    | D   | P      |
| Fabaceae - Mimosoideae  | Anadenanthera falcata (Benth.) Spec.   | Fabaceae | - Mimosoideae | 1337  | S    | E   | W      |
| Lauraceae               | Nectandra sp.                         |        |         | 1338  | S    | D   | W      |
| Malpighiaceae           | Byrsonima basiloba A. Juss.            |        |         | 1339  | T    | E   | P      |
| Melastomataceae         | Miconia albicans (Sw) Triana          |        |         | 1340  | S    | D   | W      |
| Myrsinaceae             | Raphanea umbellata (Mart.) Mez.        |        |         | 1341  | S    | D   | W      |
| Ochnaceae               | Ouratea spectabilis (Mart.) Engl.      |        |         | 1342  | S    | D   | W      |
| Proteaceae              | Ronpa montana Aubl.                   |        |         | 1343  | T    | E   | W      |
| Rutaceae                | Zanthoxylum rhoifolium Lam.           |        |         | 1344  | T    | E   | W      |
| Sapotaceae              | Pouteria torta (Mart.) Radik.         |        |         | 1345  | T    | E   | P      |
| Styracaceae             | Styrax camporum Pohl.                 |        |         | 1346  | T    | E   | P      |
| Tiliaceae               | Luehea grandiflora Mart.              |        |         | 1347  | S    | D   | A      |
| Verbenaceae             | Aegiphila sellowiana Cham.            |        |         | 1348  | S    | D   | W      |
| Vochysiaceae            | Qualea dichotoma (Mart.) Warm.        |        |         | 1349  | S    | D   | W      |
|                         | Qualea grandiflora Mart.              |        |         | 1350  | S    | D   | W      |
|                         | Qualea multiflora Mart.               |        |         | 1351  | S    | D   | W      |

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Figure 1. Climate diagram of the west central part of the state of São Paulo, according to Walter et al. (1975) methodology.

* as the number of deciduous species was small, deciduous and semi-deciduous species were pooled.

Figure 2. Percentage of species lacking growth rings, species with poorly defined and well-defined growth rings within each phenological category. As the number of deciduous species was small, deciduous and semi-deciduous species were pooled. E = evergreen. SD + D = semi-deciduous plus deciduous. A = growth rings absence. P = poorly defined growth rings. W = well defined growth rings.
Figure 3. Percentage of species lacking growth rings, species with poorly defined and well-defined growth rings within each habit category. $S =$ shrubs. $ST =$ small tree. $T =$ tree. $TT =$ tall tree. $A =$ growth rings absence. $P =$ poorly defined growth rings. $W =$ well defined growth rings.

Figure 4. a-b. Transverse section of Nectandra sp. wood. a) Photomacrograph showing growth layers boundaries (arrows). b) Photomicrograph. Arrows indicate thick-walled and radially flattened latewood fibres. Gelatinous fibres occur along the growth layer and can be noted in detail above in the figure.
Figure 5. a-b. Transverse section of Miconia ligustroides wood. a) Photomacrograph. Arrows indicate growth layers boundaries. Parenchyma-like fibre bands can be noted lighter in the figure. b) Photomicrograph. Arrow indicates thick-walled and radially flattened latewood fibres.

Figure 6. a-b. Transverse section of Zanthoxylum rhoifolium wood. a) Photomacrograph. Arrows indicate growth layers boundaries. b) Photomicrograph. Arrow indicates thick-walled and radially flattened latewood fibres.
Figure 7. a-b. Transverse section of *Eriotheca gracilipes* wood. a) Photomacrograph. Arrows indicate growth layers boundaries. b) Photomicrograph. Arrows indicate thick-walled and radially flattened latewood fibres.

Figure 8. a-b. Transverse section of *Annona coriacea* wood. a) Photomacrograph. The arrows indicate the largest vessels in tangential arrangement in earlywood. Note the closeness of the parenchyma narrow bands just before the largest vessels in each growth layer. b) Photomicrograph shows distended rays in the boundary of the growth layers (arrows).
Figure 9. a-b. Transverse section of Annona crassiflora wood. a) Photomacrograph. The arrows indicate growth layers boundaries. b) Photomicrograph. Arrow indicates thick-walled latewood fibres in the boundary of the growth layers.

Figure 10. a-b. Transverse section of Erythroxylum tortuosum wood. a) Photomacrograph. b) Photomicrograph. Arrow indicates thick-walled and radially flattened latewood fibres and small vessels.
Figure 11. a-b. Transverse section of Terminalia brasiliensis wood. a) Photomacrograph. Arrows indicate growth layers boundaries. b) Photomicrograph. Arrow indicates thick-walled and radially flattened latewood fibres.

Figure 12. a-b. Transverse section of Qualea grandiflora wood. a) Photomacrograph. Arrows indicate marginal lines of axial parenchyma marking growth layers boundaries. b) Photomicrograph. Arrow indicates thick-walled and radially flattened latewood fibres.
Figure 13. a-b. Transverse section of *Rapanea umbellata* wood. a) Photomacrograph. Arrows indicate growth layers boundaries. b) Photomicrograph. Arrows indicate thick-walled and slight radially flattened latewood fibres.

Figure 14. a-b. Transverse section of *Tapirira guianensis* wood. a) Photomacrograph. The arrows indicate growth layers boundaries. b) Photomicrograph shows thick-walled latewood fibres (arrow).
Figure 15. a-b. Transverse section of Vochysia cinnamomea wood. a) Photomacrograph. Note the variation within growth layers in the axial parenchyma distribution. b) Photomicrograph. Note the variation within growth layers in the axial parenchyma distribution and the tangential arrangement of the traumatic canals above in the figure.

Figure 16. a-b. Transverse section of Caryocar brasiliense wood. a) Photomacrograph. Arrows indicate marginal lines of axial parenchyma. b) Photomicrograph. Arrow indicates marginal lines of axial parenchyma.
Figure 17. a-b. Transverse section of Qualea multiflora wood. a) Photomacrograph. Arrows indicate marginal lines of axial parenchyma. b) Photomicrograph. Note variation within growth layers in the axial parenchyma distribution.

Figure 18. a-b. Transverse section of Didymopanax vinosum wood. a) Photomacrograph. Arrows indicate fibre zones. b) Photomicrograph. Thick-walled and radially flattened latewood fibres in fibre zones (arrows).
Figure 19. a-b. Transverse section of *Couepia grandiflora* wood. a) Photomacrograph. Arrows indicate fibre zones. b) Photomicrograph. Arrow indicates thick-walled and radially flattened latewood fibres in fibre zones.

Figure 20. a-b. Transverse section of *Diospyrus hispida* wood. a) Photomacrograph. Arrows indicate fibre zones. b) Photomicrograph. Note that the narrow bands of axial parenchyma tend to come closer towards the end of the growth ring.
Figure 21. a-b. Transverse section of *Pera glabrata* wood. a) Photomacrograph. Arrows indicate fibre zones. b) Photomicrograph. Note irregular zones of gelatinous fibres adjacent to the growth layers. Gelatinous fibres in detail.

Figure 22. a-b. Transverse section of *Styrax ferrugineus* wood. a) Photomacrograph. Arrows indicate fibre zones. b) Photomicrograph. Arrows indicate thick-walled latewood fibres in fibre zones.
Figure 23. a-b. Transverse section of *Byrsonima cocclobifolia* wood. a) Photomacrograph. Arrows indicate fibre zones. b) Photomicrograph. Small stars indicate thick-walled and radially flattened latewood fibres in fibre zone. Note that the rays become narrow in this region.

Figure 24. a-b. Transverse section of *Ouratea spectabilis* wood. a) Photomacrograph. Arrows indicate fibre zones. b) Photomicrograph. Arrow indicates thick-walled and radially flattened latewood fibres in fibre zone.
Figure 25. a-b. Transverse section of Kielmeyera rubriflora wood. a) Photomacrograph. Arrows indicate fibre zones. b) Photomicrograph. Arrows indicate straight lines of marginal parenchyma.

Figure 26. a-b. Transverse section of Pouteria torta wood. a) Photomacrograph. Arrows indicate fibre zones. b) Photomicrograph. Arrows indicate straighter and thinner lines of marginal parenchyma.
Figure 27. a-b. Transverse section of Gochnatia barrosii wood. a) Photomacrograph. Arrows indicate marginal bands of axial parenchyma. b) Photomicrograph. Arrows indicate marginal bands of axial parenchyma. Note higher frequency of vessels in earlywood.

Figure 28. a-b) Transverse section of Bauhinia rufa wood. a) Photomacrograph. Arrows indicate marginal bands of axial parenchyma. b) Photomicrograph. Arrows indicate marginal bands of axial parenchyma. Note higher frequency of vessels adjacent to the marginal bands.
Figure 29. a-b. Transverse section of Cordia sellowiana wood. a) Photomacrograph. Arrows indicate marginal bands of parenchyma. b) Photomicrograph. Arrow indicates small latewood vessels absorbed in marginal parenchyma.

Figure 30. a-b. Transverse section of Alibertia concolor wood. a) Photomacrograph. Arrows indicate marginal bands of axial parenchyma. b) Photomicrograph. Arrows indicate marginal bands.
Figure 31. a-b. Transverse section of *Copaifera langsdorffii* wood. a) Photomacrograph. Arrows indicate marginal bands of axial parenchyma. b) Photomicrograph. Small stars indicate axial canals in marginal bands of axial parenchyma.

Figure 32. a-b. Transverse section of *Aegiphilla sellowiana* wood. a) Photomacrograph. Arrow indicates marginal bands of axial parenchyma. b) Photomicrograph. Arrow indicates marginal band of axial parenchyma.
Figure 33. a-b. Transverse section of Piptocarpha rotundifolia wood. a) Photomacrograph. Arrows indicate marginal bands of axial parenchyma. Note the higher frequency of vessels adjacent to the marginal bands. b) Photomicrograph. Arrows indicate distended rays in the boundary of a growth layer.

Figure 34. a-b. Transverse section of Vochysia rufa wood. a) Photomacrograph. b) Photomicrograph. Note axial parenchyma variation within growth layers.
Figure 35. a-b. Transverse section of *Dimorphandra mollis* wood. a) Photomacrograph. Arrows indicate marginal lines of axial parenchyma. b) Photomicrograph. Arrows indicate marginal lines of axial parenchyma.

Figure 36. a-b. Transverse section of *Bowdichia virgilioides* wood. a) Photomacrograph. Arrows indicate marginal lines of axial parenchyma. b) Photomicrograph. Marginal lines of axial parenchyma in detail (arrow).
Figure 37. a-b. Transverse section of *Anadenanthera falcata* wood. a) Photomicrograph. Arrows indicate marginal lines of axial parenchyma. b) Photomicrograph. Arrow indicates marginal lines of axial parenchyma in detail.

Figure 38. a-b. Transverse section of *Qualea dichotoma* wood. a) Photomacrograph. Arrow indicates marginal lines of axial parenchyma. b) Arrow indicates marginal lines of axial parenchyma in detail.
Figure 39. a-b. Transverse section of Machaerium villosum wood. a) Photomacrograph. Arrows indicate marginal lines of axial parenchyma. Note the variation within growth layers in the axial parenchyma distribution. b) Photomicrograph. Arrows indicate marginal lines of axial parenchyma.

Figure 40. a-b. Transverse section of Roupala montana wood. a) Photomacrograph. Arrows indicate closeness of the narrow bands of scalariform parenchyma. b) Photomicrograph. Arrow indicates the region of the closeness of the narrow bands of scalariform parenchyma.
Figure 41. a-b. Transverse section of *Luehea grandiflora* wood. a) Photomacrograph. Absence of growth ring markers. b) Photomicrograph.
Table 2. Growth rings of the studied species from Brazilian cerrado. Growth ring visibility: W = well defined, P = poorly defined, A = growth ring absent.

| Growth ring marker | Variation within growth ring | Species |
|--------------------|-----------------------------|---------|
| Thick-walled and radially flattened latewood fibres. | Not observed. | Nectandra sp. (W) (Fig. 4a, 4b), Ocotea corymbosa (P), Miconia ligustroides (W) (Fig. 5a, 5b), Zanthoxylum rhoifolium (W) (Fig. 6a, 6b). |
| Thick-walled and radially flattened latewood fibres. | Within the growth layers there is a higher frequency in the amount of axial parenchyma cells in the earlywood, decreasing to the latewood. In the areas where axial parenchyma is abundant, the fibres seem to be in a diffuse arrangement in relation to the parenchyma cells. Also, there is a variation in the size of axial parenchyma cells, being smaller in the end of the growth ring. | Eriotheca gracilipes (P) (Fig. 7a, 7b). |
| Thick-walled latewood fibres and distended rays. | The wood of species show scalariform axial parenchyma. These narrow bands of parenchyma tend to come closer periodically along the rays. Additionally there is a tangential arrangement of the largest vessels in earlywood. | Annona coriacea (W) (Fig. 8a, 8b), Annona crassiflora (P) (Fig. 9a, 9b). |
| Thick-walled and radially flattened latewood fibres. Also, together to these fibres we can note small vessels. | Not observed. | Erythroxylum tortuosum (P) (Fig. 10a, 10b). |
| Thick-walled and radially flattened latewood fibres. Eventually, in some regions, marginal lines of axial parenchyma can be noted. | Not observed. | Terminalia brasiliensis (W) (Fig. 11a, 11b). |
| Thick-walled and radially flattened latewood fibres. Marginal lines of axial parenchyma can be noted tangentially to these fibres. | Not observed. | Qualea grandiiflora (W) (Fig. 12a, 12b). |
| Thick-walled and slight radially flattened latewood fibres. | Not observed. | Rapanea umbellata (P) (Fig. 13a, 13b). |
| Thick-walled latewood fibres. | Not observed. | Tapirira guianensis (P) (Fig. 14a, 14b). |
| Thick-walled latewood fibres. | Variation within growth layers in the axial parenchyma distribution were observed: axial parenchyma ranging from simple aliform to short aliform-confluent and finally to long aliform confluent. | Vochysia cinnamomea (P) (Fig. 15a, 15b). |
| Species                          | Description                                                                 | Reference/Notes |
|---------------------------------|-----------------------------------------------------------------------------|-----------------|
| *Caryocar brasiliense* (P)       | Thick-walled latewood fibres and marginal lines of axial parenchyma.        | Fig. 16a, 16b.  |
| *Qualea multiflora* (W)          | Fibre zone and thick-walled and radially flattened latewood fibres.          |                 |
| *Didymopanax vinosum* (P)        | Fibre zone and thick-walled and radially flattened latewood fibres.          |                 |
| *Couepia grandiflora* (W)        | Fibre zone and thick-walled and radially flattened latewood fibres.          |                 |
| *Licania tomentosa* (W)          | Fibre zone and thick-walled and radially flattened latewood fibres.          |                 |
| *Diospyrus hispida* (W)          | Fibre zone and thick-walled and radially flattened latewood fibres.          |                 |
| *Pera glabrata* (P)              | Fibre zone and thick-walled and radially flattened latewood fibres.          | Fig. 21a, 21b.  |
| *Styrax ferrugineus* (P)         | Fibre zone and thick-walled and radially flattened latewood fibres.          |                 |
| *Styrax camporum* (P)            | Fibre zone and thick-walled and radially flattened latewood fibres.          |                 |
| *Byrsonima coccolobifolia* (W)   | Fibre zone and marginal lines.                                              |                 |
| *Byrsonima basiloba* (P)         | Fibre zone and marginal lines.                                              |                 |
| *Ouratea spectabilis* (P)        | Fibre zone and marginal lines.                                              |                 |
| *Kielmeyera rubriflora* (W)      | Fibre zone and straighter and narrower bands of marginal parenchyma.         |                 |
| *Pouteria torta* (W)             | Fibre zone and straighter and narrower bands of marginal parenchyma.         |                 |
| *Gochnata barrosii* (W)          | Marginal bands of axial parenchyma.                                         |                 |
| *Bauhinia rufoa* (W)             | Marginal bands of axial parenchyma.                                         |                 |
| Marginal bands of axial parenchyma. | Semi-ring porosity. | Cordia sellowiana (W) (Fig. 29a, 29b). |
|-------------------------------------|---------------------|---------------------------------------|
| Marginal bands of axial parenchyma. | Not observed. | Alibertia concolor (W) (Fig. 30a, 30b). |
| Terminal bands of axial parenchyma. | Not observed. | Copaifera langsdorffii (W) (Fig. 31a, 31b). |
| Marginal bands of axial parenchyma and radially flattened latewood fibres. | Semi-ring porosity. | Aegiphila sellowiana (W) (Fig. 32a, 32b). |
| Marginal bands of axial parenchyma and distended rays. | Not observed. | Piptocarpha rotundifolia (W) (Fig. 33a, 33b). |
| Marginal bands formed by long aliform confluent. | Variations within growth layers in the axial parenchyma distribution were observed: axial parenchyma ranging from long aliform confluent forming marginal bands to a decreasing in the parenchyma frequency and type, i.e. to the simple aliform. | Vochysia rufa (W) (Fig. 34a, 34b), Vochysia tucanorum (W). |
| Marginal lines of axial parenchyma. | Not observed. | Dimorphandra mollis (P) (Fig. 35a, 35b), Bowdichia virgoides (W) (Fig. 36a, 36b), Sweetia subelegans (W), Anadenanthera falcata (W) (Fig. 37a, 37b), Stryphnodendron polyphyllum (W), Qualea dichotoma (P) (Fig. 38a, 38b). |
| Marginal lines of axial parenchyma. | Variation within growth layers in the axial parenchyma distribution were observed: axial parenchyma ranging from simple aliform to short aliform-confuent and finally to long aliform confluent. | Machaerium villosum (W) (Fig. 39a, 39b). |
| Closeness of the narrow bands of scalariform parenchyma. | Along the rays the narrow bands of scalariform parenchyma tend to come closer periodically. | Roupala montana (W) (Fig. 40a, 40b). |
| Absent. | Not observed. | Luehea grandiflora (A) (Fig. 41a, 41b), Erythroxylum suberosum (A), Miconia albicans (A). |
by marginal bands (20%), marginal lines (16%) and close-
ess of the narrow bands of scalariform parenchyma (2%).

In *Miconia ligustroides*, parenchyma-like fibre bands
(lighter regions in macroscopical view) alternating with or-
dinary fibres (Fig. 5a) were observed.

Within the growth layers, variations in the anatomical
features were observed (Table 2), such as: variation in
the amount of gelatinous fibres (Fig 21b); variations in
the axial parenchyma distribution (Figures 15, 17b, 34, 39); varia-
tion in the distance between the narrow bands of axial pa-
renchyma (Figures 8, 9a, 20, 40a); variation in the amount
and in the size of axial parenchyma cells (Fig. 7); variation in
the size and amount of vessels (Figures 27, 28, 33); semi-
ring porosity (Figures 29, 32).

**Discussion**

For this study we were able to analyse 70% from all
wood species that, according to the floristical studies of
Bicudo (1987) and Silberbauer-Gottsbeger & Eiter (1983),
occur in cerrado areas in the west central of the São Paulo
state, Brazil. We noticed that more than 60% of all species
studied showed clearly defined growth rings. This factor
should therefore be accounted for conservation and man-
agement programs of cerrado, a much threatened vegeta-
tion type. This incidence of growth rings in tropical wood
species is comparable with 48% found by Alves &
Angyalossy-Alfonso (2000) in stem wood of 491 Brazilian
tropical and subtropical wood species. However, the inci-
dence of growth rings in cerrado species is relatively high if
it is compared with the study of Mainieri et al. (1983) who
found growth rings in approximately 35% of the stem wood
of nearly 300 Brazilian tropical and subtropical species (see
Alves and Angyalossy-Alfonso 2000). The high occurrence
of species with growth rings in cerrado might be related to a
distinct annual dry season, lasting about one to four months.
According to Worbes (1995), a period of two or three months
with precipitation below 60 mm is an environmental condi-
tion necessary for species to form growth rings in their wood.

In this study both evergreens and deciduous or semi-
deciduous plants had high ratios of species with growth
rings. Similar observations were reported by Alvim (1964)
and Worbes (1985) on tropical rain forest trees and by
Coradin (2000) for deciduous and evergreens species from
cerrado of Brazil Central region. In addition, Coradin (2000)
observed that species with a single period of flushing, in-
cluding the deciduous and some of the evergreen species,
showed generally distinct growth rings while those ever-
green species which showed more than one period of flush-
ing during the year presented indistinct or poorly defined
growth rings. The phenological methodology used in the
present study does not allow us to relate growth ring dis-
tinctness with flushing periods during the year in a species.

We observed clear differences among tree and shrub
species related to both growth rings percentage and dist-
tinctness, with attention to trees and tall trees with 100% of
well defined growth rings. The high frequency of small trees
and shrubs in cerrado points out the relevance of habit for
the analysis of the growth rings formation in this vegeta-
tion type.

All combinations of microscopic anatomical features
used to detect the growth layers were already mentioned by
other authors (Détienne & Mariaux 1977, Bornmann & Berly
1981, Worbes 1985, Carlquist 1988, Baas & Vetter 1989, IAWA
Committee 1989, Fahn & Werker 1990 and Wheeler & Baas
1991). Thick-walled and radially flattened latewood fibres
and fibre zones bounding the growth rings were the most
common features observed in the wood of the branches of
the species studied. Extensive analyses are in course to
determine if these markers are predominant in the woody
plants of cerrado vegetation.

Marginal bands in *Copajaera langsdorffii* had already
been described by Mainieri et al. (1983) and Détienne &
Jacquet (1993). However, Marcati (2000) studied the forma-
tion of these marginal bands and verified that they are ter-
mal since they are formed in the beginning of the dry
season, before the cambial dormancy.

The growth ring markers described here agree in gen-
eral with most of the results obtained by other authors
(Mainieri et al. 1983, Détienne 1989, Vetter & Botoss 1989,
Boninsegna et al. 1989, Marcati 2000, Callado et al. 2001)
studying stem wood of the same genus or species. Although
Mainieri et al. (1983) have described indistinct growth rings
in the stem wood of *Vochysia* spp., *Rapanea* spp., *Qualea*
spp., *Tapirira guianensis*, *Didymopanax* spp. and *Roupala*
spp., and distinct growth rings in the stem wood of *Luehea*
spp., different to our study, it is important to comment that
the wood analyzed by Mainieri et al. (1983) were collected
from tree stem of different regions of Brazil, so subject to
different environmental conditions.

Comparing our results on growth rings markers to
those of Coradin (2000) from woody plants from cerrado of
Brazil Central region, some differences need further com-
ments. According to this author, *Qualea grandiflora* and
*Ouratea hexasperma* wood show differences in vessel fre-
quency as the main feature in the boundary of the growth
rings in stem and branches, which was not observed nei-
ther in *Q. grandiflora* nor in *Ouratea spectabilis* studied
here. Coradin (2000) did not mention the closeness of the
narrow bands of scalariform parenchyma in *Roupala montana*
wood as noted in our study, but a tangential ar-
angement of vessels in the boundary of growth rings in
stem and branches. *Didymopanax macrocarpum* wood,
according to Coradin (2000), shows indistinct growth rings
in its branches while in the stem wood the author found a
difference in the vessel frequency within growth layers. In
*Vochysia elliptica* wood the author observed fibre zones

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and irregular bands of axial parenchyma in branches and stem wood. The various differences between our study and that of Coradin (2000), listed out above, may be related to the specific environmental conditions of the two cerrados. For instance, unlike the cerrado of São Paulo state, the relative humidity in cerrado from Brazil can reach very low values during the dry season (see Oliveira & Marquis 2002).

Parenchyma-like fibre bands alternating with ordinary fibres were observed in *Miconia ligustroides* wood and it was already mentioned by Coradin (2000) to genus *Miconia*. These parenchyma-like fibre bands, according to the author, are septate fibres which accumulate starch and so have also a storage function.

Gelatinous fibres, although of common occurrence in most of the studied species, were related to the growth rings, forming a regular pattern, only in *Pera glabrata*, an evergreen species. Callado et al. (2001) observed random zones of gelatinous fibres throughout the rings in the stem wood of the same species that occur on periodically flooded soil. According to Kozlowski & Pallardi (1997), gelatinous fibres often extend throughout both earlywood and latewood in evergreen species. Further studies are required to a better comprehension about the differences in the arrangement of gelatinous fibres in *Pera glabrata* occurring in under different water regime. Gelatinous fibres have been observed in different organs of cerrado plants (Paviani 1978) as a result of reaction wood formation (Kozlowski et al. 1991) and may function as water storage (Paviani 1978, Chalk 1989), as well as giving flexibility to the organ.

Variations in the axial parenchyma distribution in *Vochysia cinnamomea*, *Qualea multiflora*, *V. rufa*, *V. tucanorum*, wood were reported for the first time. For *Machaerium villosum* wood this variation had already been reported by Ceccantini (1996). Although Détienne & Jacquet (1983) have observed long aliform confluent forming bands in the wood of others *Vochysia* species and terminal parenchyma in other *Machaerium* species, they did not mention the variation within growth layers as we observed in this study. Variation in the distance between the narrow bands of axial parenchyma periodically along the rays within growth layers in *Annona coriacea*, *A. crassiflora*, *Diospyros hispida* and *Roupala montana* wood was also reported for the first time. Variation in the amount of axial parenchyma and in the size of axial parenchyma cells within growth layers in *Eriotheca gracilipes* was already mentioned by Callado et al. (2001) for *E. pentaphylla* wood occurring in swamp forests of Rio de Janeiro, Brazil. Variation in the amount of vessels within growth layers was observed in *Gochnatiar barrosti*, *Bauhinia rufa* and *Piptocarpha rotundifolia* as described by Coradin (2000) for other cerrado species. Further studies about cambial activity are necessary to a better comprehension about these variations.

Although growth rings occurrence was verified in different cerrado woody species, additional anatomical wood studies of a larger number of species are necessary to determine if the growth rings are annual, widespread and possess taxonomic and/or adaptive value.

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