

RELIABLE ESTIMATES OF RADIAL GROWTH FOR EIGHT TROPICAL SPECIES BASED ON WOOD ANATOMICAL PATTERNS

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LÓPEZ L & VILLALBA R. 2016. Reliable estimates of radial growth for eight tropical species based on wood anatomical patterns. The application of dendrochronological methods based on the precise delimitation of annual bands in tropical trees is vital for implementing precise management practices. This study described the most prominent anatomical features associated with the presence of annual tree rings in *Amburana cearensis*, *Cedrela fissilis*, *Platymiscium ulei*, *Centrolobium microchaete*, *Hymenaea courbaril*, *Anadenanthera colubrina* and *Ficus boliviana*, eight important timber species from the dry tropical Cerrado forest in Bolivia, South America. Initial or marginal parenchyma is the most consistent pattern delimiting annual bands in six of the eight selected species. Wedging and false rings, but more frequently the lack of circular uniformity in ring width, were recorded in most species. Differences in the number of rings between radii from a cross-section were used as reasonable estimates of dating error associated with each species. The rates of growth of cross-dated and non-cross-dated trees with dating errors relatively lower (i.e. around four missing rings per century) were not significantly different, suggesting that the rates of growth from non-cross-dated trees could also be used for complementing the estimates of radial growth derived from cross-dated trees. Given the difficulty of properly dating some tropical woods, measuring growth rates using a combination of cross-dated and non-cross-dated tree rings could provide reliable information to the sustainable forest management in the tropics.

Keywords: Annual growth rings, parenchyma, diffuse porosity, cross dating, tree age estimation, rates of tree growth, tropical trees

INTRODUCTION

The determination of annual growth rings in the wood is essential for the application of dendrochronological techniques (Fritts 1976, Schweingruber 1996). Although many species from tropical rainforests do not show anatomical structures that allow easy and rapid determination of annual radial increments, several tropical species growing in regions with marked climatic seasonality show conspicuous and well-defined annual rings (Schöngart 2008, Lopez & Villalba 2011). A common feature in tropical woods is the presence of wedging or incomplete rings resulting from cambial activity in local sectors of the tree circumference (Worbes 2002). In addition to wedging rings, the presence of false rings is also a limitation for precise dating of tropical trees. False rings are intra-annual bands frequently caused by unfavourable climatic

events during the growth cycle or non-periodical biological processes such as massive flowering or fruiting (Villalba 1987, Borchert & Rivera 2001, Wobes 2002). Sometimes, these false rings are difficult to discriminate from true annual rings. In consequence, a previous knowledge of the anatomical arrangements associated with annual rings is needed to properly identify false rings.

Growth ring formation in tropical trees has been associated with the occurrence of annual periods of flood (Schöngart et al. 2002, Dezzeo et al. 2003), changes in day length (Borchert & Rivera 2001), seasonal variation in rainfall (Worbes & Junk 1999) and internal rhythms of growth not always associated with climate (Alvim & Alvim 1978). In most forest areas not subject to floods, growth ring formation is probably

induced by the occurrence of annual dry season (Worbes 2002, Dunisch et al. 2003). Due to water deficit in dry season, most tree species frequently reduce or stop radial growth, inducing a particular arrangement of wood anatomical elements that facilitate the demarcation of rings (Worbes & Junk 1999). Many of the ring-forming species in tropical regions are generally deciduous or shed off their leaves during the dry season (Worbes 2002, Brienen & Zuidema 2005, Lopez & Villalba 2011). However, distinct annual rings have also been determined in evergreen species such as *Ficus boliviana* (Lopez 2011). The occurrence of growth bands in tropical species has been frequently reported during recent decades and most studies have been able to determine, directly or indirectly, the annual nature of these growth bands (Brienen & Zuidema 2005, Rozendaal & Zuidema 2011, Zuidema et al. 2012). For example, six out of eight selected species in the dry Bolivian Cerrado forests had anatomically distinguishable annual rings (Roig 2000). Lopez (2003) also documented the occurrence of annual growth rings demarcated by bands of marginal parenchyma in 11 trees from the Bolivian Cerrado forests. However, in most cases, the precise dating is difficult to achieve due to the presence of wedging rings, false rings or lack of circular uniformity.

Although lack of governance is the major cause of non-achievable sustainable practices for forest management in the tropics, lack of information on basic estimates of forest dynamics including tree-growth rates, also contributes to the impressive rate of tropical growths. Determination of anatomical features that contribute to tree ring demarcation in tropical species will provide rapid solutions to erroneous management practices related to the overestimation of growth rates conducive to extremely short cutting cycles or rotations that jeopardise the sustainability of tropical forest resources (Schöngart 2008, Lopez et al. 2013). In this context, the main objectives of the present study were:

- (1) Association of anatomical patterns with the visibility of annual growth rings in eight forest species commonly used for timber in the Bolivian Cerrado biogeographic province.
- (2) Estimation of dating errors in trees showing wedging (or growth lenses) and false rings.
- (3) Comparison of growth-rate estimates between cross-dated (large common signal between radii of the stem) and non-cross-dated (low or weak common signal between radius of the stem) sections of a particular species from the same site.

Both types of data are valuable and practical tools for implementing sustainable forest management practices in tropical South America.

MATERIALS AND METHODS

Study area

The Bolivian Cerrado represents the southernmost sector of the Cerrado biome as one of the most extensive vegetation formations in tropical South America (Cabrera & Willink 1973). It stretches from the central north of Brazil to the west of Bolivia and north-east of Paraguay. The site collections are located in the Chiquitos and Guarayos vegetation districts (Figure 1) of the Cerrado biome in Bolivia (Navarro & Maldonado 2004). The Inpa and Santa Anita sites are located in the Chiquitano district, whereas Santa Mónica and La Chonta sites belong to the Guarayos district. The Guarayo and Chiquitano forests extend from the tropical Amazonian wet formations in the north to the Pantanal (swamp formation) areas in the east and the deciduous dry forests in the Bolivian Chaco to the south (Killeen et al. 1993). The Guarayo and Chiquitano districts cover a large territory within the Bolivian Cerrado biome and harbour great biodiversity typical of seasonal tropical environments (Navarro & Maldonado 2004). The Chiquitano district is characterised by shallow and very rocky soils on reliefs dominated by hills and plateaus. The Guarayos district, instead, presents moderately to fairly deep soils, with higher water holding capacity (Peña-Claros et al. 2012).

Mean annual temperatures for Chiquitos and Guarayos are 24.2 and 23.8 °C respectively (period 1950–2014). Rainfall presents a marked seasonality and ranges from 1100 to 1300 mm in Concepción, Chiquitos, and from 1400 to 1600 mm in Guarayos (Figure 2). At both weather stations, precipitation during January (the wettest month) is six times greater than in July (the driest month). Due to lower precipitation in Concepción, the dry

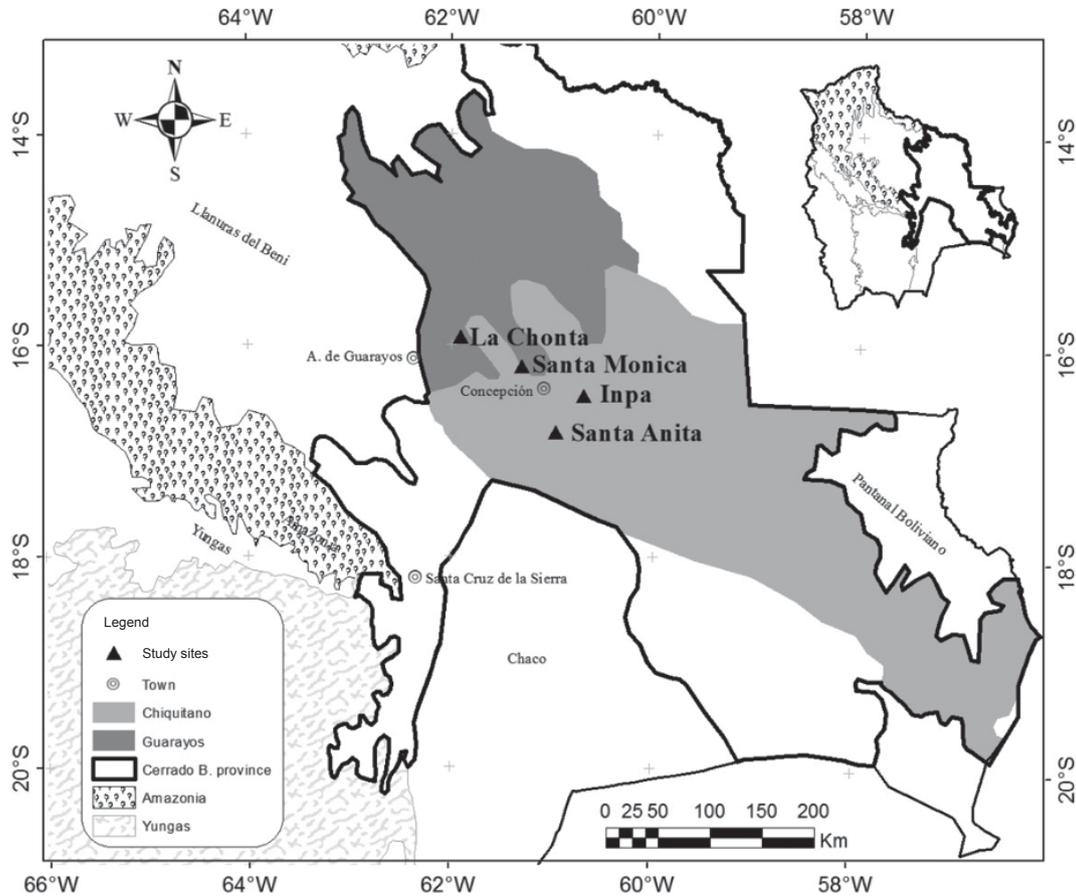


Figure 1 The Cerrado Boliviano biogeography province in Bolivia (Navarro & Maldonado 2004) is delimited by a continuous thick black line; the two biomes Chiquitano and Guarayos, where samples were collected, are indicated by dark and light grey colours, respectively

winter season extends for six months (April–September), one month longer than in Guarayos (May–September). The differences in the amount of total rainfall and the length of the dry season cause the forests in the Guarayos to have more components of tropical wet forests than those recorded in the Chiquitano district (Figure 2). The upper canopy reaches greater heights in the Guarayos (20–30 m) than in the Chiquitos forests (15–25 m). Forests in both regions are particularly dominated by legume species (Killeen et al. 1993).

Selected species

The eight selected tree species are intensively used in the Bolivian timber industry. In consequence, cross-sections for anatomical and dendrocronological studies were collected at logging areas in the Cerrado region

(Table 1). These species are easily identified in the mature stages of the forest with crowns commonly forming the upper canopy. In the Bolivian Cerrado, wood from *Amburana cearensis*, *Cedrela fissilis*, *Platymiscium ulei* and *Centrolobium microchaete* are very appreciated for their excellent quality (Killeen et al. 1993). *Hymenaea courbaril*, *Anadenanthera colubrina* and *Copaifera chodatiana* have wood with higher densities and more diverse uses. In contrast, *Ficus boliviana* has soft wood of low density, mostly used for wooden drawers and wood laminates.

All eight studied species are restricted to tropical/subtropical forests in South America (Killeen et al. 1993). *Ficus boliviana* and *C. microchaete* are endemic to the Cerrado region (Killeen et al. 1993, Mostacedo et al. 2003), whereas *C. chodatiana* is distributed between 200 and 500 m elevation in the Cerrado and also in nearby biogeographic regions from central

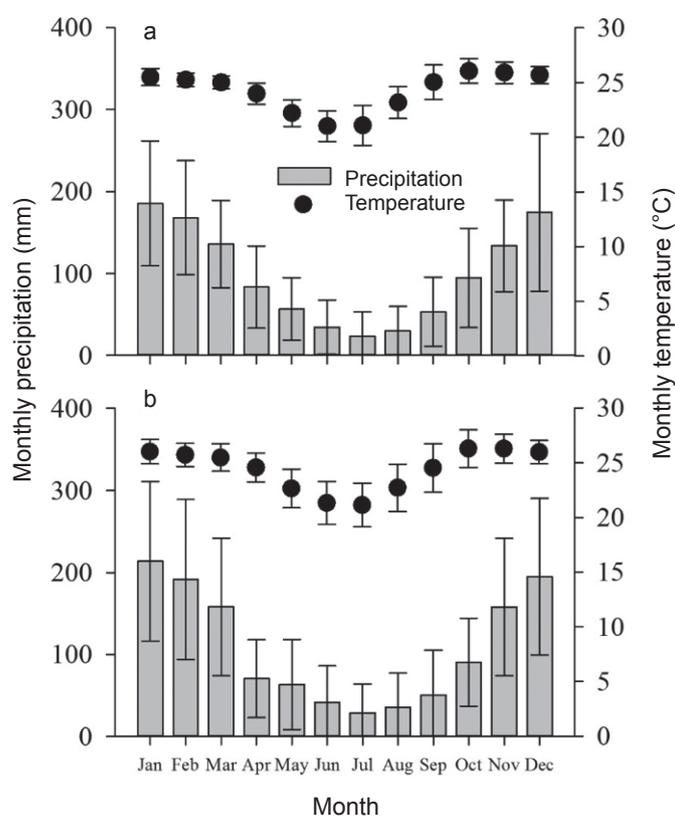


Figure 2 Climatic diagrams (1950–2014) for (a) the Concepción and (b) Guarayos meteorological stations, Santa Cruz, Bolivia; monthly total precipitation and their standard deviations are indicated by bars and cupped lines; monthly mean temperature variations and their standard deviations are shown by circles and cupped lines

Table 1 Selected species and geographic location of collection sites within the Bolivian Cerrado biogeographic province, Santa Cruz de la Sierra, Bolivia

Family	Species	Geographic location				
		Vegetation district	Site	Location (S)	Location (W)	Elevation (M)
Fabaceae	<i>Amburana cearensis</i>	Chiquitos	Santa Anita	16° 32'	61° 55'	423
Mimosaceae	<i>Anadenanthera colubrina</i>	Chiquitos	Inpa	16° 22'	61° 55'	503
Meliaceae	<i>Cedrela fissilis</i>	Guarayos	Santa Anita	16° 32'	61° 55'	423
Fabaceae	<i>Centropodium microchaete</i>	Chiquitos	Santa Mónica	16° 22'	61° 55'	503
Caesalpiniaceae	<i>Copaifera chodatiana</i>	Chiquitos	Inpa	16° 22'	61° 55'	503
Moraceae	<i>Ficus boliviana</i>	Guarayos	La Chonta	15° 38'	62° 46'	250
Caesalpiniaceae	<i>Hymenaea courbaril</i>	Guarayos	La Chonta	15° 38'	62° 46'	250
Fabaceae	<i>Platymiscium ulei</i>	Chiquitos	Santa Anita	16° 32'	61° 55'	423

and western Bolivia (Justiniano & Fredericksen 1999). *Amburana cearensis* and *A. colubrina* are widely distributed across Bolivia and also occur in bordering countries like Brazil, Peru and the northern sector of Argentina. *Hymenacea courbaril*, *P. ulei* and *C. fissilis* occur in many regions of Bolivia and have widespread distribution across tropical America, from Mexico down to Paraguay and north of Argentina (Killeen et al. 1993).

Sample collection

Cross-sections were collected from trees in logging areas. The trees exhibited good morphological features in both stem and crown characteristics. Wood samples were collected using chainsaw and the number of samples per species varied according to the logging intensity at each site. Studies conducted in the dry or semi-dry areas of South America showed the difficulty of obtaining wood samples using traditional increment bores (Lopez 2003). Since the increment borers have been designed for sampling wood of low densities, they cannot be used to core hard- and high-density wood. In addition, difficulties in ring delimitation are reduced with cross-sections instead of the traditional 5-mm wide increment borers. Entire or partial cross-sections allowed better view of the cell arrangements and increased the accuracy in determining and measuring growth-ring widths. The identification of false and wedging rings was also facilitated by the inspections of these anomalous features in cross-section rather than in samples from increment borers. Most cross-sections were taken between 1.5–2 m above ground level, depending on the length of stem buttresses and practices used during tree cutting.

Tree-ring anatomy

After drying at room temperature, samples were polished with sandpapers of increasingly finer grains (80–1200 cm²), for achieving smooth surfaces with no imperfections for good visualisation under binocular magnifying microscope (50 ×). The most prominent wood features were described for each species. Spatial arrangements of the different wood elements (vessels, fibre, parenchyma), and the associated differences in colour and texture between earlywood and latewood were recorded. Also

recorded were the distribution of vessels and their variations in size between earlywood and latewood, type of parenchyma, its shape, size and distribution across the annual bands, fibrous elements and differences in size, shape and colour between sectors in the wood. Identification of growth rings were based on the type and arrangement of wood elements that define tree rings in each species. For species with wedging or false rings, these elements were closely monitored across the whole circumference in the cross-sections. This pattern was visually compared among the different radii in a cross-section and among trees of the same species at each of the sampled sites. Growth rings were assigned at the year in which the radial growth starts following the South Hemisphere dating convention (Schulman 1956).

Dating process

Once the anatomical patterns defining the growth rings were established, the number of growth rings, along different radii of the same cross-section, were counted. When the number of rings were equal between radii, we assumed that the dating was correct (no dating error). However, we anticipate that an equal number of rings between different radii does not always confirm an exact dating. Cross dating between samples from several trees is the valid method to establish a precise dating of wood (Schulman 1956, Stokes & Smiley 1968, Fritts 1976).

For samples with different number of rings, resulting from counting on several radii in a cross-section, the differences were averaged, and the value taken as estimate of dating error. For example, if ring counting values between three radii in a cross-section were $a = 60$, $b = 58$ and $c = 55$ years, the mean value of the differences [2 years (radius $a-b$), 3 years (radius $b-c$) and 5 years (radius $a-c$)], provided an estimation of the dating error (in this case 3.3 years). To make dating errors comparable between trees with variable ages, we scaled the estimated errors to 100-year-old trees. However, since the distinctiveness of tree rings may change with increasing tree age, linear extrapolation of the dating error over the current age of the trees was taken with caution. The larger the error, the higher the difference between radii of the same tree. The mean from all

individual tree-dating errors for a species in a site provided a local estimate of the dating error for a particular species. This local error reflected the number of wedging and false rings present in all cross-sections from a given species in a sampling site.

Once the age of each tree was determined, total ring widths were measured on a UniSlide stage connected to a Quick-Chek 10V digital readout with 0.001 mm precision. For samples with equal number of rings between different radii (corrected dated), the quality of visual dating was verified using the program COFECHA. To facilitate dating error identification, tree-ring series were previously detrended by COFECHA using spline function, designed to reduce 50% of the variance in a sine wave with a periodicity of 32 years. Series with dating and measurement problems were reinspected. Dating problems associated with wedging and false rings or absence of local ring visibility were occasionally corrected, and some of the samples initially classified as not precisely dated were corrected and included in the cross-dated group. An inter-correlation value of $r = 0.32$ ($p < 0.05$ for a 50-year time window comparison) was set as the threshold for the cross-dated group. Mean values of ring widths for cross-dated and non-cross-dated trees were compared to determine differences in the rates of growth between both groups. Diametric increments (shown in Figure 3) were estimated by averaging the growth increments from two or more radii in a cross section and multiplying by two. Mean cross-dated and non-cross-dated chronologies were developed by averaging raw individual series from each group for each species (Figure 3). Mean rates of growth over common interval between cross-dated and non-cross-dated chronologies were used for comparison for each species. No missing rings were considered in the estimation of the non-cross-dated chronologies.

RESULTS

Wood characteristics

Amburana cearensis presented distinct growth rings visible to the naked eye. They were best defined during the juvenile stage of growth.

Ring boundaries were marked by dense fibrous zone at the end of each growth period, which produced marked contrast with the light-coloured earlywood composed by a large percentage of vessels mixed with both confluent and aliform paratracheal parenchyma (Figure 4a). No false rings or growth lenses were observed in *A. cearensis*. Outer rings were increasingly narrow in large-diameter trees, with frequent clusters of microrings. In these narrow rings, the parenchyma covered most of the entire ring surface and the fibrous zone separating adjoining rings partially disappeared.

Growth rings in *A. colubrina* were marked by marginal parenchyma which were observed as a thin but continuous line of light-coloured cells at the end of the ring (Figure 4b). Overall, growth rings were readily visible in young trees. However, counting of tree rings was more problematic as trees increased in diameter and age. The abundance of vessels during periods of reduced radial growth hindered the visibility of the narrow bands of marginal parenchyma. Intra-annual bands with large proportion of fibres were present in the wood of *A. colubrina*. No wedging rings were recorded in this species.

Growth rings in *C. fissilis* were visible to the naked eye, even before conducting a careful polishing of the cross-section. The wood of *C. fissilis* exhibited semicircular to circular porosity with numerous, large solitary or multiple vessels. A conspicuous parenchyma band, formed at the beginning of growing season, demarked the rings (Figure 4c). The light-colour parenchyma surrounding the large vessels at the beginning of the growth period contrasted the dark late-wood dominated by small vessels and large proportion of fiber. As trees increased in diameter, growth rings usually became narrower making ring counting more difficult. In cluster of microrings, the initial parenchyma from contiguous rings tended to merge, making ring determination problematic (Figure 4c). Wedging rings were occasionally recorded in *C. fissilis*.

Growth rings in *C. microchaete* were visible after careful polishing of the wood surface. Boundaries between growth rings were marked by a narrow line of marginal parenchyma formed at the end of the growing season (Figure 4d).

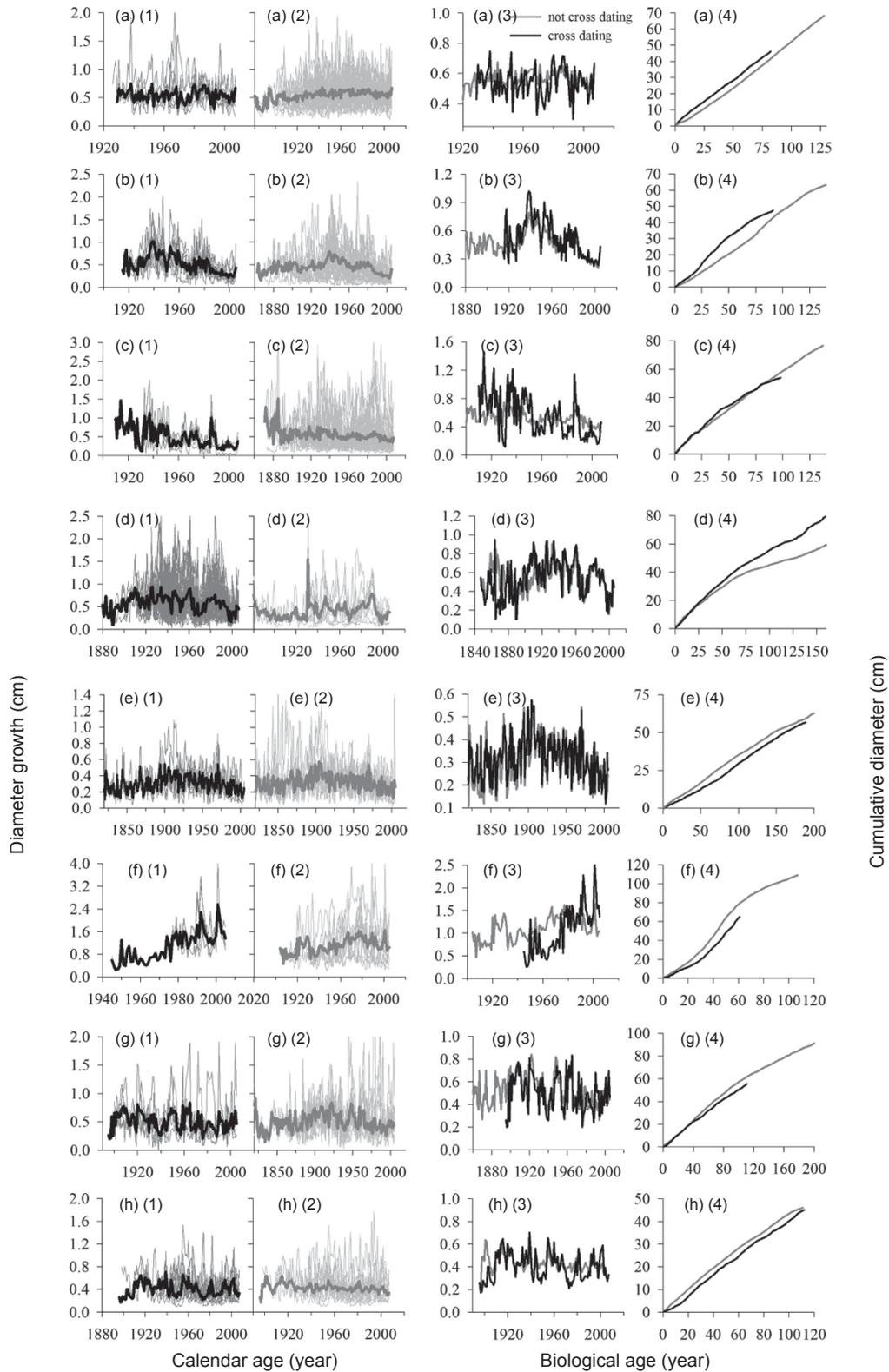


Figure 3 Temporal variations in diametric growth of cross-dated (1) and non cross-dated (2) trees for eight species from the tropical dry forest in the Cerrado, Bolivia; (a) *Amburana cearensis*, (b) *Anadenanthera colubrina*, (c) *Cedrela fissilis*, (d) *Centrolobium microchaete*, (e) *Copaifera chodatiana*, (f) *Ficus boliviana*, (g) *Hymenaea courbaril* and (h) *Platymiscium ulei*; in (1) and (2) inter-annual variations for individual trees (thin grey lines) and the mean (thick black and grey lines) are shown; comparisons of temporal variations in mean (3) and accumulated (4) diametric growth between cross-dated (black line) and non-cross-dated (grey line) trees are shown

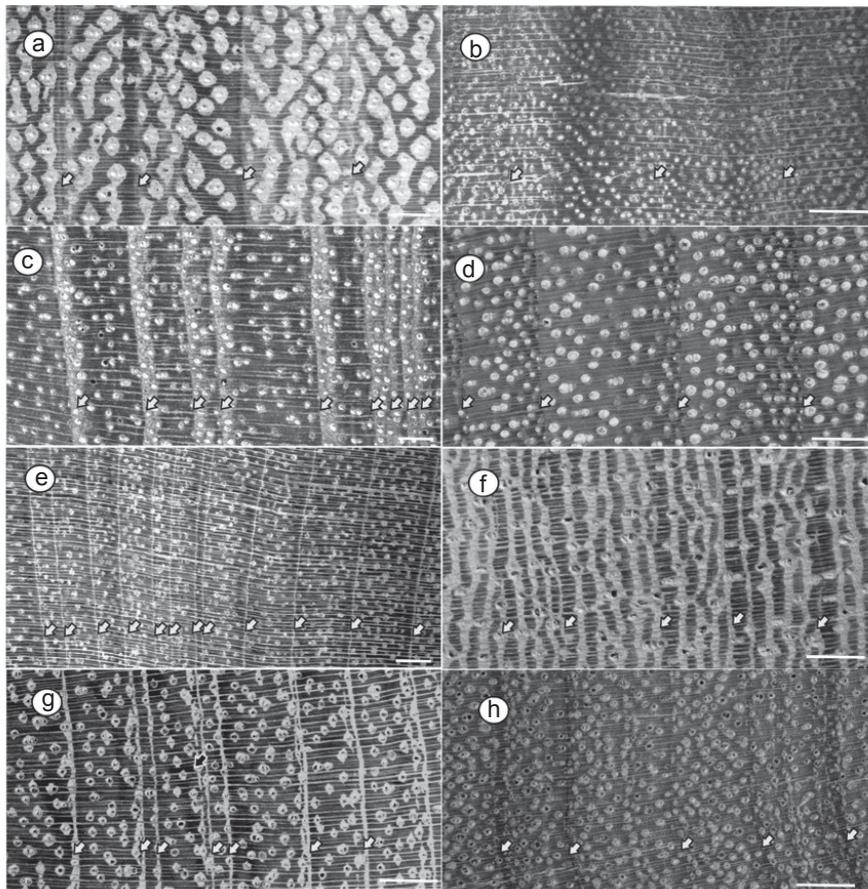


Figure 4 Growth rings in (a) *Amburana cearensis*, (b) *Anadenanthera colubrina*, (c) *Cedrela fissilis*, (d) *Centrolobium microchaete*, (e) *Copaifera chodatiana*, (f) *Ficus boliviana*, (g) *Hymenaea courbaril* and (h) *Platymiscium ulei*; white arrows indicate growth boundaries, black arrows indicate wedging or false rings; scale (white bars) = 5 mm

In addition, determination of growth ring was facilitated by the contrast between vessels with larger and smaller diameters in the earlywood and latewood respectively. The change in vessel size across the annual ring was accompanied by gradual increase in fibre, giving a darker colour to the latewood. Although difficulties in ring identification increased with tree age and size, neat polishing allowed the distinguishing of all growth bands on cross-sections. In general, this species presented dark purple coloured bands in the heartwood. Frequently, these purple bands covered more than a single annual ring. No false rings or lenses were recorded in this species.

Copaifera chodatiana showed readily visible growth rings, particularly in freshly cut cross-sections. Although vessels, mostly of medium size,

did not show contrasting changes in size between earlywood and latewood, distinguishable and highly contrasting lines of marginal parenchyma delimited contiguous annual rings. Wedging rings (or growth lenses) were very common in this species (Figure 4e). The vessel number decreased towards the end of the ring, but this characteristic was not always present, particularly when tree rings were narrow.

Ficus boliviana had comparatively wider growth rings than other species. Rings were more visible to the naked eye than under a microscope. This was due to the presence, within an annual ring, of concentric bands of apotracheal parenchyma, which were easily confused with annual growth bands under magnification. Growth rings were defined by the contrast between the thick walled and radially

flattened fibre at the beginning of the growing season and the light and narrow parenchyma bands in the latewood (Figure 4f). In some sectors of the wood with relatively narrow rings, thick parenchyma bands blurred the dark brown fibre bands making it difficult to accurately define the beginning and end of each ring. Overall, the visibility of growth rings was larger in young trees or in those sectors of the cross-section with wider growth rings. As trees increased in diameter and rings decreased in size, their identification was more difficult.

Hymenaea courbaril had growth rings visible to the naked eye. Most vessels were surrounded by aliform confluent parenchyma. Tree rings were defined by the presence of a continuous line of marginal parenchyma. However, semi-continuous bands of parenchyma tissue resembling annual rings were also observed. Although presented across the annual band, these false rings were common in the late-wood where the abundance of confluent and aliform paratracheal parenchyma increased (Figure 4g). No differences in vessel diameter were observed between earlywood and latewood.

Platymiscium ulei showed growth rings visible under magnifying glass after a neat polish of the surface with fine-grain sandpaper. The boundary between annual rings was defined by the presence of a narrow band of marginal parenchyma at the end of each growth period (Figure 4h). However, in some parts of the stem other intra-annual

bands were formed by changes in position and shape of the parenchyma and/or grouping of thick-wall fibres. These false rings were generally less demarcated and showed gradual transitions in wood arrangements compared to annual rings. Different anatomical arrangements between earlywood and latewood were recorded in sectors of the wood, but the pattern was highly variable. Vessels were surrounded by confluent parenchyma and aligned forming tangential transversal lines with vessel sizes larger at the beginning of the rings. Some rings exhibited increase in the darker fibrous tissue at the end of the annual growth band.

Tree-ring dating

Only 8 of the 18 sampled trees of *A. cearensis* showed a common ring-width pattern of growth (mean inter-correlation $r = 0.49$, Table 2). In the remaining trees, lack of circular uniformity was the principal cause for absence of cross-dating. In spite of differences in inter-annual variations in radial growth, the rate of diametric growth between cross-dated and non-cross-dated trees showed no significant differences between groups (Figures 3a and 5a).

Of the 31 sampled trees of *A. colubrina*, 9 showed a common pattern of growth (Table 2). The mean inter-correlation between cross-dated trees ($r = 0.39$) was significantly higher than non-cross-dated samples ($r = 0.11$). However, both

Table 2 Tree-ring delimitations and statistics of cross-dated and not-cross-dated trees

Scientific name	a	Cross-dated				Non-cross-dated				n	Error
		n	r*	ms	sd	n	r*	ms	sd		
<i>Amburana cearensis</i>	1, 2	8	0.49	0.31	0.50	10	0.31	0.39	0.54	0	0
<i>Anadenanthera colubrina</i>	1	9	0.39	0.43	0.56	22	0.11	0.44	0.53	0	0
<i>Cedrela fissilis</i>	1, 3	5	0.51	0.47	0.58	15	0.07	0.45	0.53	3	4
<i>Centrolobium microchaete</i>	1, 3	49	0.60	0.36	0.48	5	0.30	0.38	0.45	0	0
<i>Copaifera chodatiana</i>	1	5	0.50	0.41	0.48	18	0.31	0.42	0.48	6	4
<i>Ficus boliviana</i>	1, 2	5	0.68	0.32	0.56	4	0.15	0.31	0.52	0	0
<i>Hymenaea courbaril</i>	1	7	0.32	0.41	0.48	9	0.26	0.41	0.52	0	0
<i>Platymiscium ulei</i>	1, 2	6	0.32	0.29	0.49	14	0.17	0.30	0.52	0	0

a = Anatomical pattern associated with growth delimitation: 1 = parenchyma 2 = compressed fibre 3 = semicircular to circular porosity, n = number of cross-sections analysed, r = Pearson’s correlation coefficient, correlation coefficients $r > 0.325$ are statistically significant at 95% confidence level, ms = mean sensitivity; sd = standard deviation; error dating error reported in non-cross-dated trees

groups showed similar mean rates of diametric growth (Figures 3b and 5b). Despite good visibility and consistent dating of wood samples, lack of circular uniformity was the principal cause for the differences in radial growth patterns between *A. colubrina* non-cross-dated trees.

Twenty individuals of *C. fissilis* were analysed. The number of rings counted along two opposing radii in the cross-section differed in three trees, with differences of three, four and five rings. These differences were due to the presence of growth lenses. Only five trees were cross-dated (mean inter-correlations $r = 0.51$). In the remaining 12 trees, number of rings was similar along opposing radii. However, lack of circular uniformity in ring width accounted for by the low series inter-correlation ($r = 0.07$). The comparison between the five cross-dated against the twelve non-cross-dated trees indicated that both groups showed similar mean rates of growth, even when the three trees with differences in ring numbers between radii were considered (Figures 3c and 5c).

For *C. microchaete*, five out of the 54 trees analysed showed low inter-correlations ($r = 0.30$, Table 2) due to lack of circular uniformity in ring width. In all cases, the number of rings were similar along the different radii in the cross-sections. Mean inter-correlation between cross-dated trees was highly significant ($r = 0.60$; Figure 3d). The rates of growth between cross-dated and non-cross-dated trees was comparatively similar (Figure 5d).

Eighteen trees of *C. chodatiana* were analysed. The number of rings on opposing radii of six trees showed differences of up to four rings over a 100-year interval. Although the number of rings on opposing radii for the remaining trees was similar, lack of circular uniformity made the search for common patterns of growth difficult (Table 2). Only five trees of this species showed similar ring-width patterns (inter-correlation $r = 0.50$). Despite the differences in growth patterns, both cross-dated and non-cross-dated trees showed similar rates of radial growth (Figures 3e and 5e).

For *F. boliviana*, five of nine trees analysed were successfully cross-dated with mean inter-correlation of $r = 0.68$. The number of rings was similar along opposing radii of the remaining trees. However, the lack of circular uniformity, mainly during the juvenile and mature stages of

trees limited the cross-dating of different radii in the cross-sections. However, the mean rates of diameter growth between the two groups showed similar pattern (Figure 5f).

Seven of the 16 sampled trees of *H. courbaril* exhibited relatively weak, common pattern of ring-width variations ($r = 0.30$, Table 2, Figure 3g). Although the number of rings was similar in opposing radii of the remaining trees, lack of circular uniformity appeared to be the major limiting factor hampering cross-dating in this species. Similar to previous species, there was no statistical differences in the rates of growth between cross-dated and non-cross-dated trees (Figure 5g).

Six of the 20 trees of *P. ulei* analysed, were cross-dated showing a decent pattern of common ring-width variations (mean inter-correlation $r = 0.31$). In the remaining trees, the presence of false rings and less circular uniformity severely reduced cross-dating ($r = 0.17$). Trees, with and without common signal, showed similar mean values of inter-annual variation in radial growth. (Figures 3h and 5h).

DISCUSSION

A detailed observation of complete and fully polished cross-sections was found vital to the initial determination of annual bands in woods of tropical/subtropical species from South America (Figure 4). The microscopic description of wood, with emphasis on spatial arrangements of wood anatomy that contributed to ring delimitation, was an additional step required to clearly define annual tree rings in tropical species. The combination of these techniques was fundamental to the identification of particular structures in wood such as false or wedging rings that represent main limitation to cross-dated tropical species (Boninsegna et al. 1989, Worbes 2002).

The diversity of wood elements in broadleaf tropical species create diverse anatomical arrangements, defining growth ring boundaries. In broadleaf species from temperate and cold regions, tree ring limits were defined by the presence of larger vessels in earlywood, that contrast with very few to nearly absent vessels in latewood (Villalba 1985, Worbes 2002, Lopez 2011). This transitional pattern in vessel size across tree rings was commonly accompanied

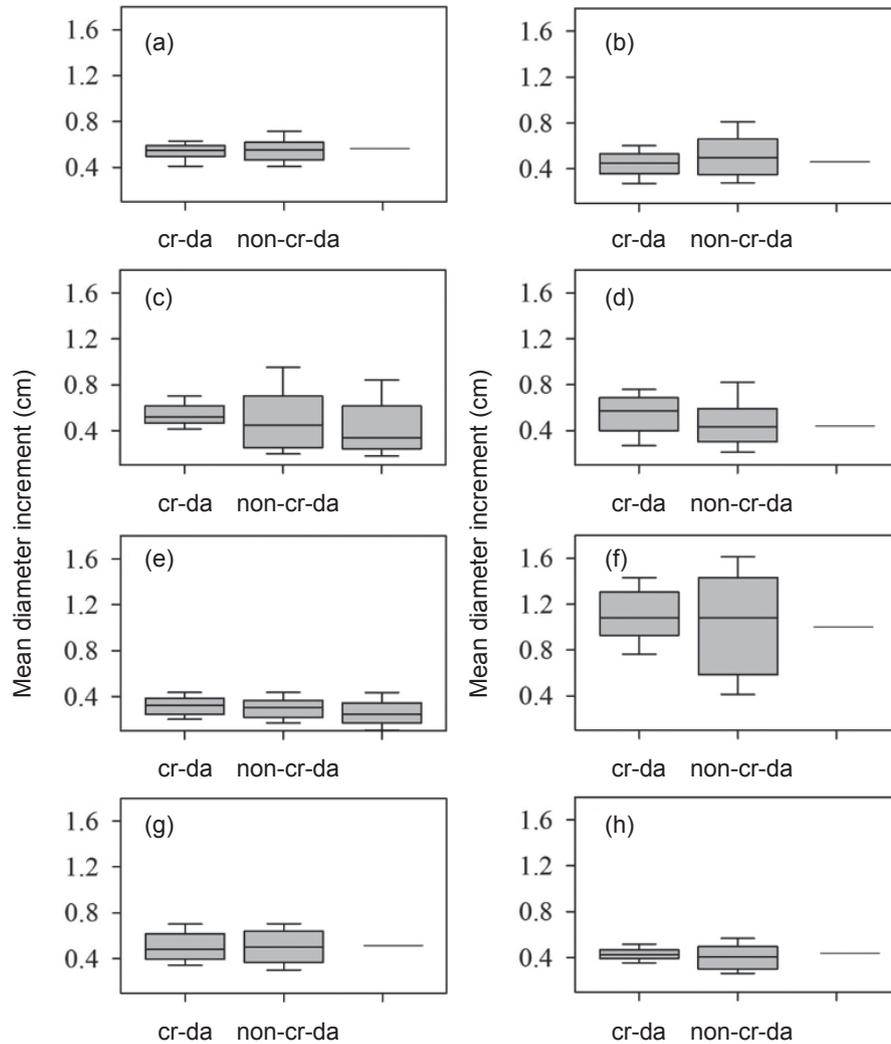


Figure 5 Comparison of rates of growth (diameter increment) between cross-dated (cr-da) and non-cross-dated (non-cr-da) trees for eight different species from the tropical dry forest in the Cerrado, Bolivia; mean rates of growth for cross-dated, non-cross-dated trees and trees with different number of rings between radii in a cross-section are shown, (a) *Amburana cearensis*, (b) *Anadenanthera colubrina*, (c) *Cedrela fissilis*, (d) *Centrolobium microchaete*, (e) *Copaifera chodatiana*, (f) *Ficus boliviana*, (g) *Hymenaea courbaril* and (h) *Platymiscium ulei*

by large number of fibre with thick cell walls formed at the end of the growing season. The fibre gave the wood a dark colour that contrasted with the tissues formed at the beginning of the earlywood, which included larger vessels or higher proportion of parenchyma tissue (Villalba 1985, Worbes 2002, Lopez 2011). These typical arrangements of wood elements in temperate/cold forests were not common in tropical/subtropical trees (Table 2). Although the gradual transition from large to small vessels

from earlywood to latewood in *C. microchaete* (Figures 4c and 4d) or the presence of thick-wall fibre in the latewood of *A. cearensis* and *F. boliviana* (Figures 4a and 4f) facilitated the identification of annual rings, the dominant pattern in growth ring delimitation was the presence of parenchyma. In four of the eight selected species (*A. colubrina*, *C. microchaete*, *C. chodatiana* and *P. ulei*) growth rings were delimited by a narrow band of marginal parenchyma at the end of each growth band.

In *H. courbaril* and *C. fissilis*, a much thicker band of marginal and initial parenchyma (Figures 4g and 4c) respectively delimited tree rings. Worbes (2002) indicated that most Fabaceae and Meliaceae in tropical regions presented tree rings limited by marginal parenchyma and observed these anatomical arrangements. In the Brazilian Cerrado, the same arrangement had also been indicated for *H. courbaril* (Locosselli et al. 2013).

A basic requirement for the application of dendrochronological methods was the determination of annual growth rings in cross-sections of the wood (Stokes & Smiley 1968). By forming one band per year, tree rings can be precisely dated to the year of formation. Some tropical species form incomplete (limited to a sector of the stem circumference) or more than a band per year (Dunish et al. 2003). The incomplete annual bands, known as wedging rings or growth lenses, were mostly present in localised sectors of the stem and more frequent in old trees. By altering the regular pattern of growth between different radii of the same tree, these anatomical structures make precise dating difficult (Figure 4e). Intra-annual bands or false rings represented an additional problem for the accurate dating of growth rings. False rings were common in *H. courbaril* and *P. ulei*. These false rings, partially discontinued and hardly visible in some parts of the stem, were characterised by gradual transition in the anatomical arrangement of the wood elements that normally contrast with marked changes delimiting true growth rings (Figures 4g and 4h). False rings were caused by unfavourable climatic events over the growing season or during physiological processes associated with massive flowering or fruiting (Villalba 1987, Worbes 2002). In *H. courbaril* and *P. ulei*, false rings appear to be related to physiological specific processes to each species rather than unfavourable climatic events. However, additional studies would be necessary to confirm these observations.

Comparative dating of two or more radii per tree was crucial to properly identify wedging or false rings, and facilitating the estimation of tree ages with relatively high precision. Mean differences in the number of rings between radii of around four rings (on a 100-year context) were recorded in cross sections of *C. fissilis* and *C. chodatiana* (Table 2). The mean of the

differences in the number of rings between radii from all available sections of these species provided a reasonable estimate of dating error, since it was clearly consistent with the number of wedging or false rings presented in each section. Although the difference in the number of rings between radii could be taken as an indirect indicator of the dating errors for a particular species, long-term studies of cambial activity or cambial marks in the wood are necessary to provide accurate estimates of dating errors over time (Lopez 2003).

The differences in the number of rings between radii and the lack of circular uniformity recorded in the selected species did not result in large differences in the long-term estimated growth rates. Although no common patterns of inter-annual variability in radial growth were recorded between trees for particular species, the long-term trend in the rates of radial growth were similar between cross-dated and non-cross-dated trees (Figures 3 and 5). Since wedging rings and lack of circular uniformity were more common in old specimens, common patterns of ring-width variations were more frequently associated with young trees.

Considering that the rates of growth between cross-dated and non-cross-dated trees were not significantly different over time (Figure 5), rates of growth from non-cross-dated trees could also be used for complementing the estimates of annual growth rates from cross-dated trees. Information from non-cross-dated trees, with relatively reduced dating errors (around four to six rings in 100 years), could be used for estimating rates of growth, optimal cutting diameters and for designing sound forest management guidelines. The correct determination of annual rings, based on the anatomical arrangement of wood elements in tropical trees, was essential to achieve good estimates on growth rates of several trees of high commercial demand in Bolivia.

CONCLUSIONS

The study has proven that the anatomical identification of growth rings in eight tropical trees from the Bolivian Cerrado was a useful tool to obtain consistent annual rates of growth for sustainable practices of forest management. Since most of the examined

species presented difficulties for dating growth bands at the precise year of formation, it was vital to identify the anatomical patterns that delimited growth bands. A precise determination of the anatomical arrangement of the wood elements that defines annual rings was required to facilitate the identification of false rings. In this study, the presence of marginal and initial parenchyma in five and one from the eight selected species respectively, was the dominant pattern in delimiting growth rings. While annual variability in radial growth in non-cross-dated trees was not strictly precise to the actual year of formation, long-term trend in the rates of growth could not be seriously affected by the absence of cross-dating, with relatively low dating errors (~ 4 missing rings in 100 years). Therefore, although not totally reliable for traditional dendrochronological studies, the information is still valid to assess the rhythms of growth of tropical forests in the Bolivian Cerrado.

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