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Determining the annual periodicity of growth rings in seven tree species of a tropical moist forest in Santa Cruz, Bolivia

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Abstract

To determine the annual periodicity of growth rings in seven tree species from a tropical moist forest in Santa Cruz, Bolivia, a fire scar was used as a marker point to verify the annual nature of tree rings. The number of tree rings formed between the 1995 fire scar and the collection of the cross sections in 2002 was visually identified. The seven species showed annual growth rings. In most cases, boundaries between rings were marked by the presence of marginal parenchyma and wall-thicked fibers formed at the end of the growing season. Growth lenses and false rings were recorded in some species. Tree rings can be carefully used in Santa Cruz forests to determine rates of growth. This information is crucial for defining forest management practices in tropical regions.

Key words: tropical forest; dendrochronology; tree rings; forest management; fire scars.

Resumen

Determinación de la periodicidad anual de anillos de crecimiento en siete especies arbóreas en un bosque tropical húmedo, en Santa Cruz, Bolivia

Se establece el carácter anual de las bandas de crecimiento presentes en el leño de siete especies forestales de un bosque tropical húmedo. Se usó como indicador para la verificación del carácter anual de los anillos la cicatriz dejada por un incendio ocurrido en el año 1995. Los anillos presentes en el leño de estas especies desde la ocurrencia del incendio en 1995 hasta el año de muestreo en 2002 fueron determinados visualmente. Las siete especies estudiadas poseen bandas anuales de crecimiento cuyos límites están generalmente demarcados por la presencia de parénquima marginal y el engrosamiento de fibras al final del período de crecimiento. En algunas especies se observó la presencia de lentes de crecimiento y falsos anillos. Los anillos de crecimiento en especies tropicales, aunque presenta algunas dificultades para su datación, pueden ser usados para determinar tasas de crecimiento en los bosques de Santa Cruz. Esta información es crucial para definir planes de manejo forestal sostenibles.

Palabras clave: bosque tropical; dendrocronología; anillo de crecimiento; gestión forestal; cicatriz de incendio.

Introduction

In Bolivia, early studies of growth rings started in the Andean region, particularly in species with distinguishable rings (Boninsegna *et al.,* 2009). In lowland eastern Bolivia, studies on tree rings are scarce. The misconception that tree species growing in the tropics do not form tree rings is widespread. In addition, it is also assumed that when rings are present in the wood, the formation is not responding to an annual cycle (Stokes and Smiley, 1968, Boninsegna and Villalba, 1996). It is true that in some species, growth rings only appear in sectors of the trunk, i.e. rings form incomplete bands or wedging rings as a result of the partial cambial activity around the stem. This feature reduces the uniform circularity of the growth rings, so whereas in a cross-section there may be relatively thick rings in a sector, they can be thin or absent in other sectors

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(Villalba *et al.*, 1987). The absence of thermal seasonality, typical of tropical regions, seems so be the main reason for the lack of clearly marked tree rings in most of the trees that grow in these regions (Jacoby, 1989, Worbes and Junk, 1999). However, there are tropical and subtropical regions with moderate seasonality in temperature, and more commonly, a strong seasonality in precipitation. This climate seasonality may induced a dormancy period of growth and thus lead to the formation of well-defined annual rings (Worbes and Junk, 1999).

In many tropical regions of Bolivia, there is marked climatic seasonality mainly due to the annual distribution of precipitation (Killeen *et al.*, 1993, Navarro and Maldonado, 2004). In the study area, seasonal rainfall is marked, which greatly increases the chances that woody plants have an annual cycle of growth. If growth rings follow an annual growth cycle, measuring their interannual variations can be used to evaluate the rate of growth of a particular species under different environmental conditions, to reconstruct past climate variations or, if fire scars are present, the history of fires during the last centuries. This technique could also help generate basic ecological information for the development of appropriate guidelines for sustainable forest management, helping the conservation of native forests in Bolivia.

The aim of this study was to determine the annual periodicity of growth rings in seven tropical forest species in moist semi-deciduous forests in lowland Santa Cruz, Bolivia. We used as points of reference the fire scars occurred in 1995, which also helped to establish the anatomical patterns related to the visibility of annual growth bands in each of the seven species studied.

Material and methods

Study area

The study was carried out in the forest of La Chonta, Guarayos province, Department of Santa Cruz, Bolivia (15° 41.5’ S y 62° 46.6’ W; Fig. 1). This property covers an area of 100,000 ha. of sub-humid tropical forest with species from the low, Amazon forest, and Chiquitano dry rainforest (Killeen *et al.*, 1993). Mean temperature is 24°C. Precipitation is concentrated (85%) between November and March. Average annual rainfall is 1,580 mm, ranging between 2,200 and 1,300 mm. The dry period extends for four months (< 100 mm per month from May to September, Fig 1), with evapotranspiration exceeding precipitation during July. The region lies on the southwestern border of the Brazilian pre-Cambrian shield. Soils show medium textured, relatively high nutrients contents and high pH. Occasionally, soil patches are shallow, and poor in organic matter. The relief is slightly sinuous with altitudes ranging from 200 to 480 m (Peña-claros *et al.*, 2012).

Fires are common in the forest landscape around La Chonta. Most of them have been caused by uncontrolled fires from agricultural areas adjacent to the forest concession. There have been two recent fire events, in 1995 and 2004, when about 30% of the concession was burned (Blate, 2005). In the area burned in 1995, it was found that although trees were affected by fire, many of them survived and presented fire scars. In some trees fire scars at the time of our sampling in 2002 were still visible on the bark, while in others cases they were only recorder in cross sections that externally appeared completely healed.

Collection of samples

The wood collections were defined base on the fire map of 1995. Forest species included in this study

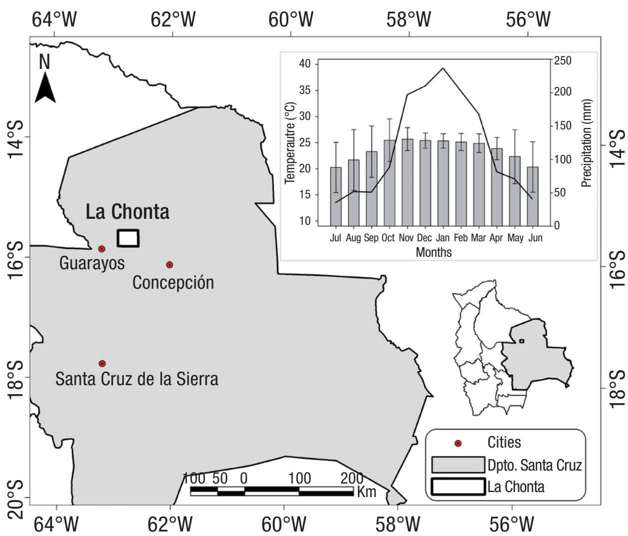


Figure 1. Map of the study area, forest concession La Chonta (Guarayos province, Santa Cruz department, Bolivia). The 30% of 100,000 ha. of this area was burned in 1995. On the right top, a climate diagram is constructed with precipitation and temperature data from Guarayos meteorological station. Heavy rainfall observed from October to April (rainy season) and nearly constant temperature throughout the year.

were: *Ampelocera ruizii* Klotzsch, *Albizia niopioides* (Benth.) Burkart, *Cariniana ianeirensis* R. Knuth, *Centrolobium microchaete* (C. Martius ex Benth.) Lima ex G. P. Lewis, *Ficus boliviana* C.C.Berg, *Hura crepitans* L. and *Pseudolmedia laevis* (Ruiz and Pavón) J.F. Macbr.

Nine to 12 trees per species were sampled, at 30-80 cm height from the soil (tree diameter varied between 30 and 90 cm). Depending on tree size, half of the stem cross section or at least two partial sections (wedges) were taken from each tree using a chainsaw. The sections collected always included the fire scar as a reference point. The material was air-dried and then taken to the Wood Anatomy Laboratory of the University UAGRM in Santa Cruz, Bolivia. In the lab the wedges surfaces were sanded until most of the rings were clearly visible. The samples with relatively visible bands and fire scars from the 1995 fire were then cut to section of 10 cm-width for transportation to the Laboratorio de Dendrocronología e Historial Ambiental del IANIGLA-CONICET in Mendoza, Argentina.

Laboratory analysis

Following Stokes and Smiley's (1968) standard methods for dendrochronological studies, the samples were sanded with increasingly fine sandpaper (80-1200) until reaching a clear view of the anatomical arrangement that determines growth rings. As samples were collected between May and November 2002, the last completely formed growth ring was assigned to 2001, given that the growth period in this region extends from November to April (López and Villalba, 2010).

Rings were identified in a chronological order to reach the 1995 fire scar. In all cases, two radii per tree were analyzed. As the fire occurred in the period August-September 1995 (i.e. the dry season), the effect of the fire on the wood should have been recorded at the beginning of the growth period of 1995.

Once the anatomical pattern related to the growth rings presence was determined for each species, the individual growth rings were dated on two radii from each cross-section. For cross-dating the two radii, growth rings carefully were identified based on the anatomical characteristics previously recorded, trying to get the same number of rings in each of the two radii.

Results

Visibility of growth rings

The results of this study indicate that all seven species examined form annual growth rings. In general, the rings of four species are strongly demarcated by a line of marginal parenchyma. However, other three species are distinguished by the presence of vascular elements (usually fiber), smaller and thickened walls, contrasting with lighter fabrics (higher proportion of parenchyma tissue) with larger vessels at the beginning of the growth cycle (Table 1). A brief description of the most important macroscopic woody characteristics of the studied species is found below.

The rings of *Ampelocera ruizii* (blanquillo) are delimited by a marginal parenchyma band associated with a line larger diameter vessels formed at the beginning of the growth period (Fig. 2A). The vessels decrease in size gradually towards the end of the growing season. The parenchyma forms thick bands in the early wood and thin bands in the latewood, which can be

Table 1. Description of the most important macroscopic growth ring characteristics of the studied species *Ampelocera ruizii, Albizia niopioide, Cariniana ianeirensis, Centrolobium microchaete, Ficus boliviana, Hura crepitans* and *Pseudolmedia laevis.*

Species	No. of trees	Wedging ring	False rings	Limit between rings
Ampelocera ruizii	10	obs. not	always	marginal parenchyma
Albizia niopioides	11	obs. not	obs. not	marginal parenchyma
Cariniana ianeirensis	12	always	always	compressed fibers
Centrolobium microchaete	10	obs. not	obs. not	marginal parenchyma
Ficus boliviana	13	occasionally	occasionally	compressed fibers
Hura crepitans	10	always	always	compressed fibers
Pseudolmedia laevis	12	always	obs. not	marginal parenchyma

confused with the parenchyma tissue defining the growth ring. The marginal parenchyma band can be, however, recognized by the fact that it is not continuous. Finally, this species is characterized by wedging ring, which is more commonly found at juvenile stages. This characteristic, together with the presence of poorly defined parenchyma bands in sections with thin growth rings, and the presence of buttresses, makes cross-dating of different trunk sections of the same tree and among trees very difficult.

The growth rings of *Albizia niopioides* (jebió) are easily determined as they are bordered by a thin band of marginal parenchyma (Fig. 2B). *A.niopioides* has diffuse porosity with vessels evenly distributed throughout the width of the growth ring. It has paratracheal vasicentric parenchyma, with medium-sized rays and high abundance of fibers. As this species does not present missing or false growth rings, cross-dating among individuals is very feasible, regardless of tree size.

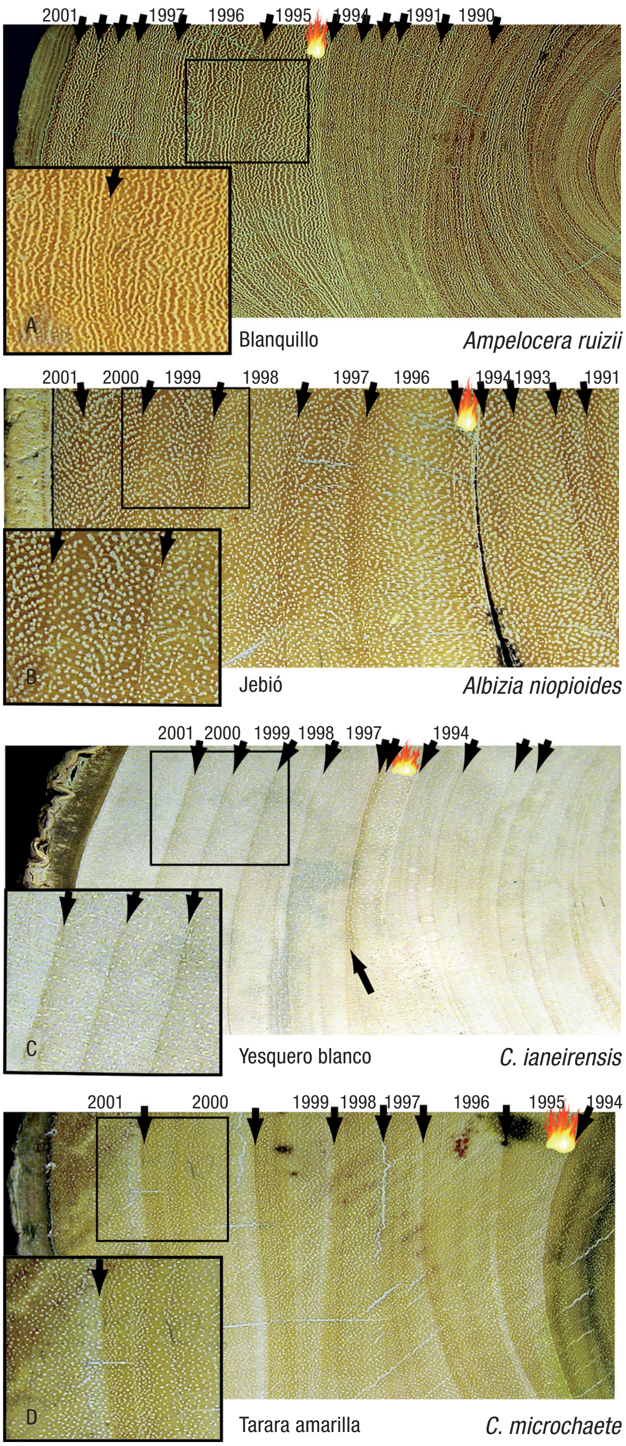
The growth rings of *Cariniana ianeirensis* (yesquero blanco) are visible and are determined by bands of narrow fibers that are tangentially compressed and are located at the marginal part of the latewood (Fig. 2C). Growth rings are diffuse-porous, with medium-sized vessels, narrow rays, and vasicentric parenchyma. Wedging ring is also commonly found in this species, making ring dating difficult. The growth rings formed after the 1995 fire scars are more visible compared to those formed before the fire. It is possible that the release of resources (e.g., more light) resulting from the death of some of the neighboring trees (due to the fire) has resulted in thicker growth rings that are more easily identified.

The growth rings of *Centrolobium microchaete* (tarara amarilla) are visible only after sanding with very fine sandpaper, and with the aid of a magnifying glass due to the fact that the wood grain runs parallel to the growth rings. Growth rings are defined by a very thin layer of marginal parenchyma and by the arrangement of vessels with larger lumens at the beginning of the growing season (circular to semicircular porosity) and a larger percentage of fibers in the latewood (Fig. 2D). The parenchyma is paratracheal vasicentric with thick rays. In most individuals the circular uniformity between the bands is consistent. In this species no wedging ring or false growth rings was observed in this and other studies (Lopez and Villalba 2012). The variation in tree ring width within and among individuals is highly correlated.

The growth rings of *Ficus boliviana* (bibosi colorado) are marked by a band of compressed fibers with thick cell walls at the end of the annual growing period. In some cases, a thin discontinuous layer of marginal parenchyma can be observed between these fibers. The vessels have medium-sized lumens, and are uniformly distributed within each annual ring (i.e., the wood is diffuse porous). The parenchyma is present in almost continuous bands, is wider in the early wood and decreases gradually in thickness in the latewood. The woody rays are small to medium in size (Fig. 2E). The individuals of this species have circular uniformity in growth rings. Despite the easiness to visually identify the growth rings, even in fresh section without sanding, it is not always possible to make an exact ring dating. This species is hemi-epiphytic: it starts growing as an epiphyte and after some years it becomes an independent tree. It seems that during the epiphytic stage, the growth rings are not clearly defined, and false growth rings are more common in the vicinity of the pith. In our study, the growth rings formed after the fire scars were clear and very well defined. Finally, in large trees the outer growth rings are more compressed, and the continuous and thin parenchymatic bands are interspersed with bands of fibers, which can be considered as real growth rings by the inexperienced observed.

The growth rings of *Hura crepitans* (ochoó) are best seen when the wood is wet rather than after sanding. The boundary between rings is determined by a band of compressed fibers formed at the end of each growing period; this band is darker in color making the growth rings very well visible in a cross section. Both the porosity and parenchyma are diffuse, the vessels have a medium-sized lumen and the woody rays are also medium in size (Fig. 2F). Although the growth rings counted from the fire scar onwards indicated that rings are annually formed, it was difficult to date the samples collected due to missing and false rings.

The growth rings of *Pseudolmedia laevis* (ojoso colorado) are defined by a thin band of parenchyma. The porosity is semicircular and has a greater visibility in the early wood. The parenchyma is observed in bands, and the rays are thin and numerous. Although the growth rings are easy to define and are annually formed, it was not possible to cross-date samples of the same individual. The first three growth rings after the fire were almost twice as thick as those recorded



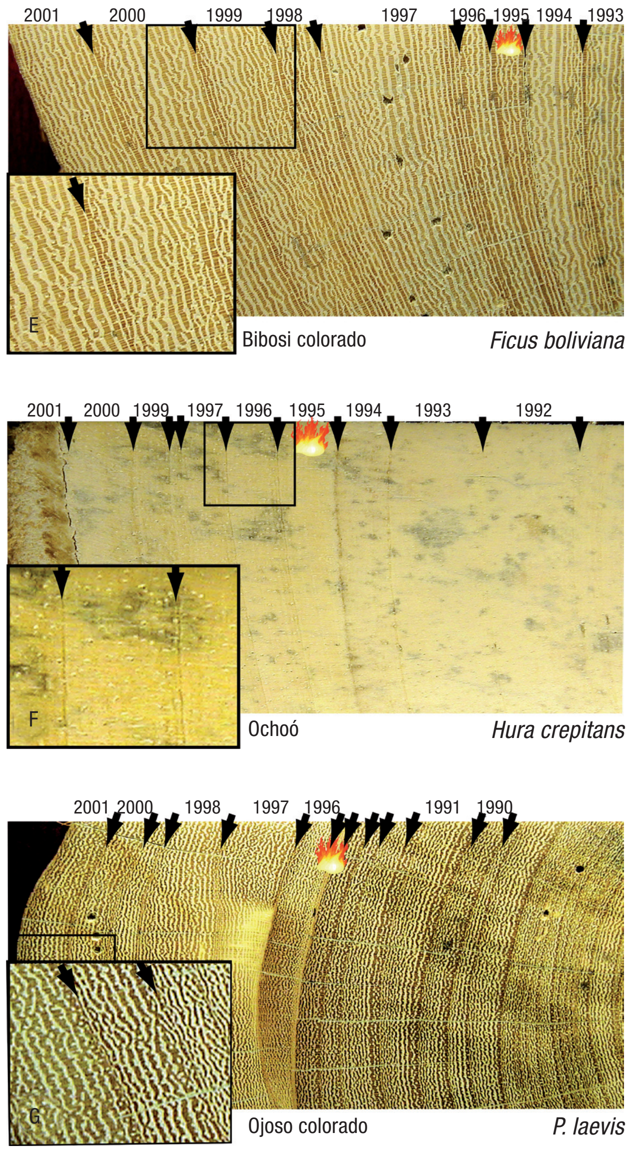


Figure 2. Growth rings in A. *Ampelocera ruizii*. B. *Albizia niopioide*. C. *Cariniana ianeirensis*, D. *Centrolobium microchaete* E. *Ficus boliviana*. F. *Hura crepitans* and G. *Pseudolmedia laevis*. The arrows represent upper limits of growth bands. The arrow in the opposite direction indicates the beginning of a slow growth. The fire symbol indicates the year of forest fire.

before the fire (Fig. 2G). There were no false rings, but wedging ring was found with a higher frequency at the juvenile stages of the species. This means that it is not possible to find a circular uniformity in the whole sample.

Discussion

Although the presence of visible growth bands in tropical South America has begun to be reported in recent decades (Boninsegna *et al.*, 1989, Worbes and Junk, 1999), the annual demarcation of growth rings has been established for few species (López, 2003). Scars in the wood caused by disturbances of known age (as forest fires in this study) represent a valid alternative than the common methods for testing the annual nature of growth rings in tropical species (Villalba *et al.*, 2000). This work is the first to determine the annual frequency of radial growth in the seven forest species under study, using the fire recorded in 1995 as date marker.

Accurate identification of structural wood elements was essential for determining the existence of annual growth bands. For example, the presence of a thin line of marginal parenchyma was the most important feature for establishing the boundaries between growth bands *A. ruizii, A. niopioides, C. microchaete,* and *P. laevis*. In contrast, in *Cariniana ianeirensis, F. boliviana* and *H. crepitans*, the presence of abundant radially compressed fibers at the end of the late wood anatomical arrangement, was the element that allowed determining the presence of growth bands.

Change in the arrangement of structural wood elements along the ontogeny of the trees was also essential for determining the existence of annual growth rings. In some species it is difficult to visualize growth rings in the initial growth stages (*F. boliviana* and *P. laevis*), while in others it is which present more difficulties do so when analyzing the long-lived individuals (*F. boliviana*, *C. microchaete A. niopioides* and *P. laevis*). Consequently, changes in the arrangement of wood structural elements should also be taken into account in tree ring studies aiming to determine growth rates at different ontogeny stages. Additionally, both the accurate determination of growth bands and of wood structural elements and their different arrangement are essential if they are to be used in dendrochronological studies.

Another feature contributing to impede accurate determination of growth rings is the presence of false or missing growth rings. It is common to find false growth rings in the wood of *C.ianeirensis, H. crepitans* and *P. laevis*. Additionally, species can also produce false rings only at certain ontogenetic stages. For example, both *A. ruizii* and *F. boliviana* produce false rings in the first years after establishment, while *F. boliviana* and *P. laevis* produce them during their juvenile stages (López, 2003). Another factor that reduces the possibility of finding common patterns of growth between radii of the same tree and between trees from the same site is the presence of nearly continuous bands of parenchyma in sectors with low stem growth of no circular uniformity.

There were no false or missing growth rings in *A. niopioides* and *C. microchaete*. Both species have clearly visible rings, which will allow precise ring dating in future studies. Moreover, these species could be successfully used to establish not only the age of each tree in the stand (Worbes and Junk, 1999, Brienen *et al.*, 2006) at the time that they reach the minimum cutting diameter, but also the increases in basal area per year, as well as other parameters useful for forest management (Brienen and Zuidema, 2006, Schöngart, 2008, López and Villalba, 2010).

Although it was not possible to find a similar pattern in ring width in the opposite radii of the same tree in five of the species (*C. ianeirensis, F. boliviana*, *H. crepitans A. ruizii* and *P. laevis*), the identification of growth bands measurement of the tree ring thickness in three or more radii of the same tree can provide valuable information for estimating growth rate (c.f. Brienen and Zuidema, 2005). This information could be useful to establish guidelines for the sustainable management of these species (Brienen and Zuidema, 2005, López *et al.*, 2011, 2012).

Conclusions

This study identified the annual character of tree rings of in seven tropical tree species growing in Santa Cruz, Bolivia. For this study the occurrence of a wildfire in 1995 was used as known date marker, as the scars left by the fire in the wood could be easily identified even seven years later. The establishment of the periodicity of growth rings is a crucial step in dendrochronological forestry studies. Other disturbances (e.g., damage caused by during timber harvesting) could also be potentially used for determining the annual nature of growth rings in tropical tree species.

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