

## Age and Long-term Growth of Trees in an Old-growth Tropical Rain Forest, Based on Analyses of Tree Rings and $^{14}\text{C}$ <sup>1</sup>

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### ABSTRACT

In an old-growth tropical wet forest at La Selva, Costa Rica, we combined radiocarbon ( $^{14}\text{C}$ ) dating and tree-ring analysis to estimate the ages of large trees of canopy and emergent species spanning a broad range of wood densities and growth rates. We collected samples from the trunks of 29 fallen, dead individuals. We found that all eight sampled species formed visible growth rings, which varied considerably in distinctiveness. For five of the six species for which we combined wood anatomical studies with  $^{14}\text{C}$ -dates (ring ages), the analyses demonstrated that growth rings were of annual formation. The oldest tree we found by direct ring counting was a *Hymenolobium mesoamericanum* Lima (Papilionaceae) specimen, with an age of ca. 530 years at the time of death. All other sampled individuals, including very large trees of slow-growing species, had died at ages between 200 and 300 years. These results show that, even in an everwet tropical rain forest, tree growth of many species can be rhythmic, with an annual periodicity. This study thus raises the possibility of extending tree-ring analyses throughout the tropical forest types lacking a strong dry season or annual flooding. Our findings and similar measurements from other tropical forests indicate that the maximum ages of tropical emergent trees are unlikely to be much greater than 600 years, and that these trees often die earlier from various natural causes.

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### RESUMEN

En una area de bosque muy húmedo tropical localizado en La Selva, Costa Rica, usamos una combinación de análisis de radiocarbono ( $^{14}\text{C}$ ) y análisis de anillos de crecimiento, para estimar las edad de árboles del dosel con un amplio espectro de tasas de crecimiento y de densidades de la madera. Analizamos la madera de ocho especies muestreada de troncos de 29 individuos muertos (árboles caídos). Encontramos que las ocho especies estudiadas forman anillos de crecimiento visibles, pero que estos varían en la distinción del límite de sus anillos. Para cinco de las seis especies para las cuales combinamos un estudio anatómico de la madera con fechado de  $^{14}\text{C}$  (edades de los anillos), nuestro análisis demostró que los anillos de crecimiento fueron anuales. El árbol más viejo en nuestra muestra fue un ejemplar de *Hymenolobium mesoamericanum* Lima (Papilionaceae), que murió a la edad de aproximadamente 530 años. Las edades a las que murieron los demás individuos analizados, incluyendo árboles de gran tamaño y de lento crecimiento, fueron entre 200 y 300 años. Estos resultados demuestran que, aún en un bosque tropical muy húmedo, el crecimiento de muchas especies de árboles puede presentar un crecimiento anual rítmico. Este estudio demuestra que es posible extender el análisis de anillos de crecimiento por todo el trópico, incluyendo las zonas de bosque que no experimentan ni una estación seca fuerte ni inundación anual. Nuestros resultados, y los de otros estudios en bosques tropicales, indican que es poco probable que las edades máximas de árboles tropicales emergentes lleguen a ser mucho mayores a los 600 años, y que tales árboles frecuentemente mueran a edades menores por causas naturales.

*Key words:* emergent trees; La Selva; Costa Rica; old canopy; radiocarbon dating; tree ring analysis; tropical wet forest.

UNDERSTANDING THE PAST AND CURRENT DYNAMICS OF THE WORLD'S TROPICAL rain forests is a pressing challenge for ecologists. Tropical evergreen forests are disproportionately important in the global carbon cycle. They have been estimated to account

for 32 percent of terrestrial net primary productivity (Field *et al.* 1998), and combined with tropical dry forests, they comprise an estimated 59 percent of forest biomass globally (Dixon *et al.* 1994). In this context, the nature of tropical tree growth rhythms, the maximum age attained by the lowland rain forest trees, and their response to climate variability are still questions under discussion.

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The very large trees in tropical rain forests play important roles in ecosystem structure and function. In spite of their low densities (usually <3% of stems  $\geq 10$  cm diam), they can comprise 25–40 percent of the total aboveground biomass (Brown & Lugo 1992, Brown *et al.* 1995, Clark & Clark 1996). Likely to be among the oldest trees present, these individuals could serve as valuable indicators of stand history. Very little is currently known about the growth histories and maximum ages of these large, tropical rain forest trees. In two recent studies, individual large trees from Amazonian forests were aged by  $^{14}\text{C}$ -dating at 190 to 1380 years (1 tree, de Camargo *et al.* 1994; 20 trees, Chambers *et al.* 1998; *cf.* Worbes & Junk 1999). The relatively few ongoing studies involving repeated measurements of large samples of such trees in tropical rain forests have spanned only 20 years or less (Condit *et al.* 1995, Clark & Clark 2000).

Given the importance of obtaining a better understanding of how tropical forests have grown in the past, methods are needed for extending the existing knowledge base. One approach is through the study of tree rings. When trees form annual growth rings, the ring patterns can be used in various ways to gain information on historical growth rates, tree age, and past environmental conditions (Cain & Suess 1976, Worbes 1999). Although numerous studies have demonstrated annual ring formation in the tropics (Coster 1927, 1928; Berlage 1931; Mariaux 1981; Devall *et al.* 1995; Drew 1998; Worbes 1999; Dünisch *et al.* 2002; Worbes *et al.* 2003), these cases have been restricted to forests with a strong annual dry season or with annual flooding. Until now, it has been concluded (*cf.* Bormann & Berlyn 1981, Swaine 1994, Kurokawa *et al.* 2003) that reliable annual growth rings are not produced in forests of the everwet tropics.

In this study, we investigated the feasibility of tree-ring analysis in the lowland tropical wet forest at the La Selva Biological Station, Costa Rica. With data from our combined analyses of wood anatomy and  $^{14}\text{C}$ -dates (ring ages), we demonstrated the existence of reliable annual growth rings in five ecologically diverse tree species, and we used the rings to estimate the age and long-term mean growth rates of trees from these species. For three additional species, we demonstrated the existence of recognizable growth zones in the wood.

## STUDY AREA AND SITE CONDITIONS

The 1550 ha La Selva Biological Station of the Organization for Tropical Studies (OTS) is located

in the Atlantic lowlands of Costa Rica at  $10^{\circ}26'\text{N}$ ,  $83^{\circ}59'\text{W}$  (35–150 m elev.). La Selva's soils range from relatively fertile entisols and inceptisols to infertile ultisols (Sollins *et al.* 1994). The flora includes 339 tree species (Hartshorn & Hammel 1994; D. A. Clark & D. B. Clark, pers. obs.). A comprehensive site description is given in McDade *et al.* (1994).

Mean annual rainfall (42 yr) is 4230 mm and all months average at least 100 mm; the highest precipitation falls during June–August, and the lowest average rainfall occurs during February–April (OTS records). Every year during those drier months, there are periods without appreciable rainfall (with daily rainfall <5mm, which does not contribute substantially to soil moisture because of losses through interception and evapotranspiration (McDade & Hartshorn 1994); these rainless periods average 12 days but can last up to 30 days in exceptional cases (Sanford *et al.* 1994). A four-year record of soil moisture (1998–2002; Schwendenmann *et al.* 2003; L. Schwendenmann, pers. comm.) shows a brief but marked drop in soil moisture each year during the drier season.

## MATERIALS AND METHODS

We took samples from 29 trees of eight species (Table 1) that were part of long-term, ongoing studies of either tree demography (TREES Project; Clark & Clark 2000) or ecosystem carbon cycling (CARBONO Project; *cf.* Clark *et al.* 2002). Because we could not use destructive methods on living or standing dead trees, we used fallen dead trees of known species and death year. Using dead material brought some difficulties because many of the samples showed heartrot or were partly decomposed (especially species with lower wood density). Further, many of these trees likely died from senescence and showed extremely small increments in the outer stem regions. All eight species analyzed in this study (Table 1) were non-pioneer species found in old-growth forest; three of them reached the canopy, three were emergent, and two species were subcanopy trees.

We took cross-sectional wood discs or segments with a chainsaw above any buttresses but otherwise as near as possible to the base of the bole. After drying the discs in an air-conditioned laboratory, we polished them with sandpaper using a grit up to 400–600. We examined the wood anatomical structure macroscopically for growth zones and ring boundaries. To improve the contrast of the ring boundaries, we sometimes carefully moistened

TABLE 1. *The eight tree species investigated for tree rings and  $^{14}\text{C}$  content at the La Selva Biological Station, Costa Rica. For each species, a voucher specimen is indicated in brackets (vouchers are at the Herbario Nacional de Costa Rica).*

| Species  | Family        | Stratum attained | No. of individuals |
|--|---------------|------------------|--------------------|
| <i>Guatteria aeruginosa</i> Standl. [Celso Alvarado 50]                      | Annonaceae    | Subcanopy        | 2                  |
| <i>Protium pittieri</i> (Rose) Engl. [James Folsom 10078]                    | Burseraceae   | Subcanopy        | 4                  |
| <i>Balizia elegans</i> (Ducke) Barneby & J. W. Grimes [B. Hammel 17319]      | Mimosaceae    | Emergent         | 2                  |
| <i>Pentaclethra macroloba</i> (Willd.) Kuntze [B. Hammel & J. Trainer 12795] | Mimosaceae    | Canopy           | 11                 |
| <i>Dipteryx panamensis</i> (Pittier) Record & Mell [R. Robles 1199]          | Papilionaceae | Emergent         | 3                  |
| <i>Hymenolobium mesoamericanum</i> H. C. Lima [R. Aguilar 19]                | Papilionaceae | Emergent         | 2                  |
| <i>Minquartia guianensis</i> Aubl. [G. Herrera 2250]                         | Olacaceae     | Canopy           | 3                  |
| <i>Simarouba amara</i> Aubl. [R. Robles 1670]                                | Simaroubaceae | Canopy           | 2                  |

the wood surface. After we interpreted growth zones as annual rings, we optically dated them by ring counting.

The content of radiocarbon ( $^{14}\text{C}$ ) in individual growth zones is a marker that can be used to date the time of wood formation (Worbes 1995). To confirm that growth rings were annual, we carried out  $^{14}\text{C}$ -analyses of selected rings in a given cross section to test them for correspondence with historical changes in atmospheric  $^{14}\text{C}$ -content (Worbes & Junk 1989). During 1950–1965, above-ground explosions of atomic bombs resulted in a doubling of the concentration of atmospheric  $^{14}\text{C}$ , followed by a steady decline to the present (Nydal & Lövsseth 1983). These changes in atmospheric  $^{14}\text{C}$  are detectable by radiocarbon measurements in any tree that was growing during that time and

thus enable annual dating of single growth zones (Worbes & Junk 1989).

The use of radiocarbon to date wood formed before 1950 requires different methods than those used for dating based on the atomic bomb effect. Dating older wood can be difficult, because single samples formed between 1640 and 1950 cannot be dated directly (Stuiver & Becker 1986). Radiocarbon dating is based on the measurement of the decay of  $^{14}\text{C}$  in organic material; however, a simple linear extrapolation based on the half-life of radiocarbon cannot be used because there has been substantial temporal variation in atmospheric  $^{14}\text{C}$ . The greatest temporal variation occurred with industrial fossil fuel burning, which involved large emissions of million-year-old  $^{14}\text{C}$ -free carbon (the “Suess effect”; Tans *et al.* 1979). The incorporation in living tissues of  $\text{CO}_2$  from the period of the Suess effect produces an overestimation of the tissues’ radiocarbon age. A calibration curve (Fig. 1) to address this problem was constructed by analyzing the  $^{14}\text{C}$ -content of tree rings having a known age (Stuiver & Becker 1986). The graph shows the radiocarbon age in years before present (years BP; “present” is arbitrarily defined as 1950 AD) versus the actual dendro-age in years (years AD). As seen in Figure 1, the radiocarbon age of a sample can correspond to up to five possible dendro-ages. Using such a calibration curve for dating a single wood sample is only appropriate for dates from the present back to 1950 (when the atomic bomb effect led to the extreme increase of  $^{14}\text{C}$  in the atmosphere during the 1960s; *cf.* Fig. 6). Larger trees in old-growth tropical forests will include wood formed during the period influenced by the Suess effect. To confirm that such trees’ rings are annual requires the use of multiple radiocarbon dating from an individual tree and/or validating ring-count estimates with a radiocarbon dating from the period for

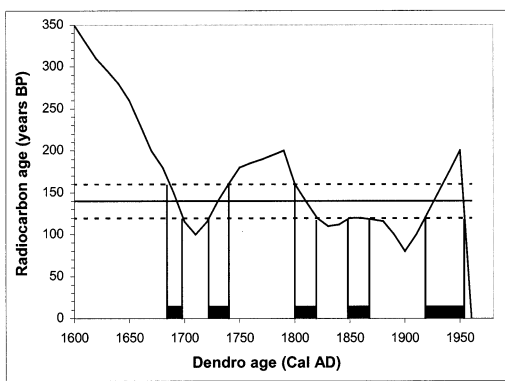


FIGURE 1. Calibration of  $^{14}\text{C}$  dates from dendrochronologically calibrated standard curve (after Stuiver & Becker 1986). Shown is a mean  $^{14}\text{C}$ -value of 140 yr BP (horizontal line) with a standard deviation of  $\pm 20$  yr BP (dotted lines). All values of the calibrated curve that fell in the band  $140 \pm 20$  yr BP are considered as possible absolute dates of formation (black areas).

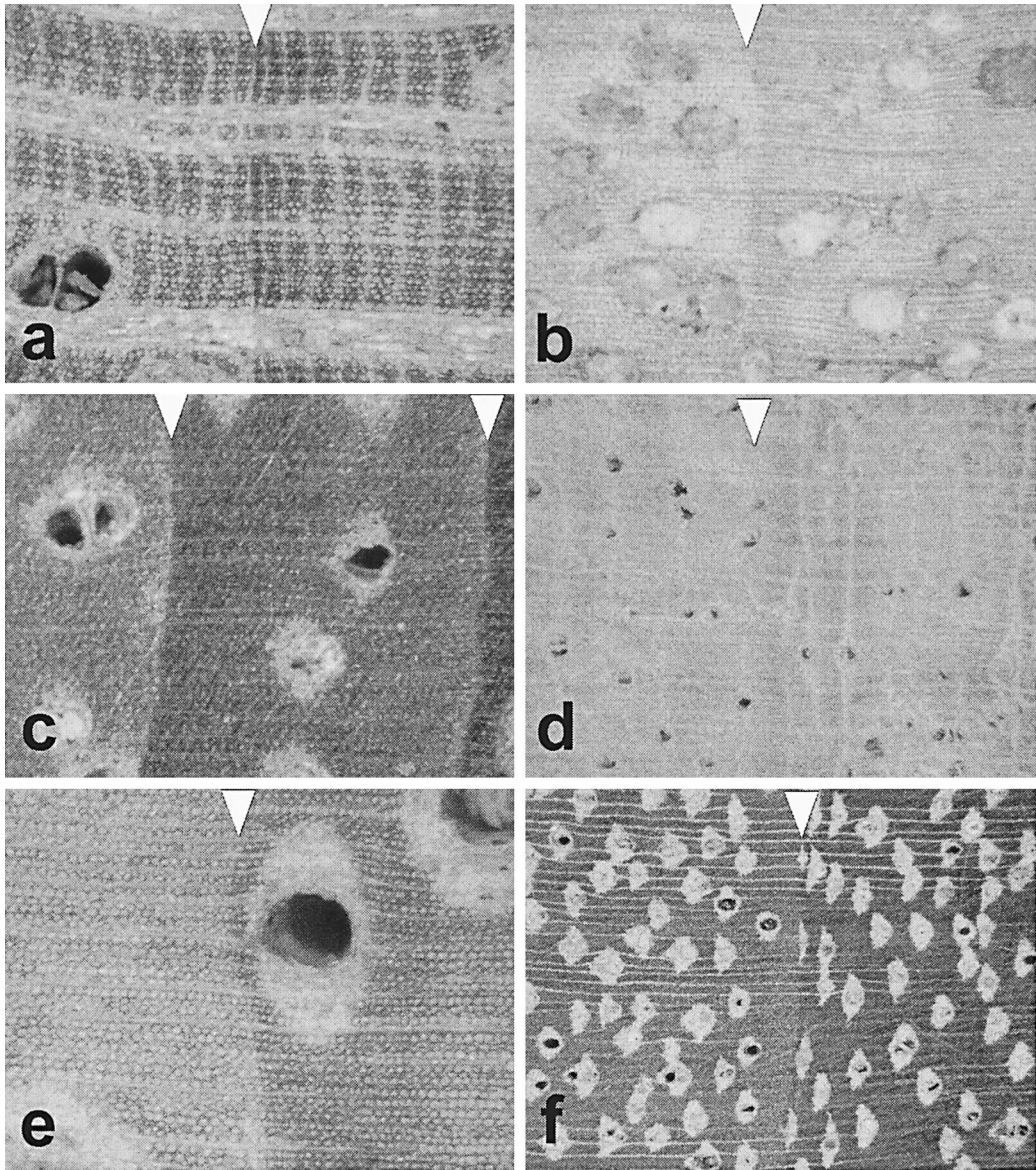


FIGURE 2. Growth zone type 1 (density variations): *Guatteria aeruginosa* (a; 50x), *Protium pittieri* (b; 66x), *Pentaclethra macroleoba* (c; 50x), *Simarouba amara* (d; 50x), *Balizia elegans* (e, 66x), *Dipteryx panamensis* (f; 16x).

which  $^{14}\text{C}$ -dates are not affected by the Suess effect.

The samples for radiocarbon dating were isolated with an electric band saw. To prevent any contamination of the wood sample with chainsaw oil, we removed all parts of the samples that were in contact with the chain. For a given tree, we tried to get a series of three to five growth zones that were probably formed after 1950, to compare the inferred growth periodicity to dates around the

1964 "bomb peak." When we counted more than 300 rings in a tree's cross section, we isolated the innermost growth ring and additional rings. In the case of one tree (*Hymenolobium mesoamericanum*), we isolated only the innermost ring. Although we tried in all cases to isolate single rings, in some trees the very narrow growth zones forced us to include several rings in a sample. The radiocarbon analyses of the samples were performed by means of an accelerator mass spectrometer at the University of Er-

TABLE 2. Phenology, distinctiveness of the growth zones, mean increments (calculated by dividing the diameter by the number of rings) of the analyzed individuals, and growth zone types (1 = density variations; 2 = marginal parenchyma bands; 3 = patterns of parenchyma bands; 4 = variation in vessel distribution) of the studied species.

| Species                            | Phenology |           | Growth zone |            | Mean increment (mm) | Growth zone type |
|------------------------------------|-----------|-----------|-------------|------------|---------------------|------------------|
|                                    | Deciduous | Evergreen | Distinct    | Indistinct |                     |                  |
| <i>Guatteria aeruginosa</i>        |           | X         | X           |            | 3.25                | 1                |
| <i>Protium pittieri</i>            |           | X         | X           |            | 1.97                | 1                |
| <i>Balizia elegans</i>             | X         |           | X           |            | 3.97                | 1                |
| <i>Dipteryx panamensis</i>         | X         |           | X           |            | 3.46                | 1, 2, 4          |
| <i>Hymenolobium mesoamericanum</i> | X         |           | X           |            | 2.81                | 3                |
| <i>Pentaclethra macroloba</i>      |           | X         | X           |            | 2.57                | 1, 2             |
| <i>Minquartia guianensis</i>       |           | X         |             | X          | 1.67                | 4                |
| <i>Simarouba amara</i>             |           | X         |             | X          | 6.96                | 1, 3             |

langen-Nürnberg (Germany) and at Beta Analytic Inc. (Miami, Florida). The pretreatment of the samples followed usual procedures to isolate cellulose.

## RESULTS

WOOD STRUCTURE AND GROWTH ZONES.—All investigated species formed visible rings that varied considerably in distinctiveness (Figs. 2–5). *Balizia elegans*, *Dipteryx panamensis*, *H. mesoamericanum*, *Pentaclethra macroloba*, and the two subcanopy species, *Guatteria aeruginosa* and *Protium pittieri*, all showed distinct rings. *Minquartia guianensis* and *Simarouba amara* formed indistinct rings. All three deciduous species showed distinct rings (Table 2). The distinctiveness of the growth rings varied among the evergreen species and was not clearly related to tree growth rate; even the indistinct growth zones, however, could be identified and were therefore suitable for tree ring analysis.

We classified the ring structure of all studied species (Table 2) according to growth zone type (Coster 1927, 1928; Worbes 1995): (1) density variations (Fig. 2); (2) marginal parenchyma bands (Fig. 3); (3) patterns of parenchyma bands (Fig. 4);

and (4) variations in vessel distribution and/or vessel size (Fig. 5). Three species (*D. panamensis*, *P. macroloba*, and *S. amara*) combined multiple growth zone types (Table 2). *Dipteryx panamensis* also showed ontogenetic changes in growth zone structure: in juvenile wood, density variations were combined with variation in vessel distribution; most mature wood showed marginal parenchyma bands combined with variation in vessel distribution, but wood in the outermost stem region only showed marginal parenchyma bands (a similar ontogeny of wood structure occurs in the tropical tree species *Carapa guianensis*; Bauch & Dünisch 2000).

ANNUAL GROWTH PERIODICITY.—The macroscopic age estimation of the wood samples from one individual of each of four species (*S. amara*, *B. elegans*, *D. panamensis*, and *P. macroloba*) was performed by counting the rings between a  $^{14}\text{C}$ -dated ring sample and the outermost ring, which was dated according to the year of death. Because most of the sampled trees had been lying on the forest floor for several years before sampling, some discs had lost the bark and we could not exclude the possibility that some of the sapwood had been lost

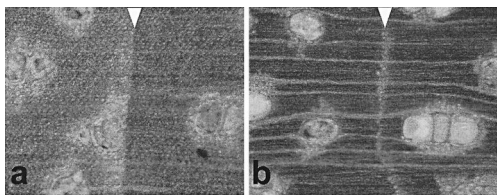


FIGURE 3. Growth zone type 2 (marginal parenchyma bands): *Pentaclethra macroloba* (a; 66x), *Dipteryx panamensis* (b; 32x).

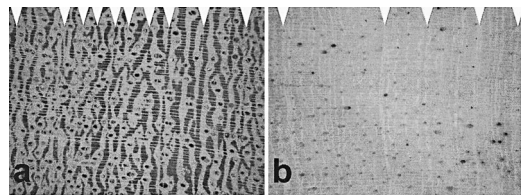


FIGURE 4. Growth zone type 3 (patterns of parenchyma bands): *Hymenolobium mesoamericanum* (a; 6x), *Simarouba amara* (b; 6x).

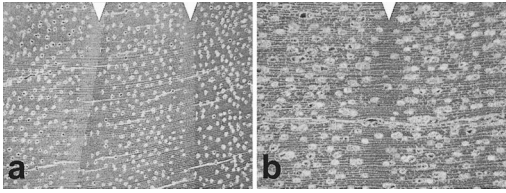


FIGURE 5. Growth zone type 4 (variation in vessel distribution): *Dipteryx panamensis* (a; 8x), *Minquartia guianensis* (b; 20x).

through decomposition. For these trees, we radiocarbon-dated three to five different growth rings, so that we could subsequently correct the macroscopic age estimate with a high degree of certainty.

Such a correction was illustrated by the *S. amara* individual (tree 234, 54.7 cm diam, 25.4 cm disc radius; Fig. 6). The disc from this tree lacked bark, and the disc's reduced radius (compared to its last measured diameter while alive) indicated that some of the outermost growth rings had also been lost. For the macroscopic ring-count age estimate, we treated the outermost ring on the disc as if it were the last ring formed by the tree before its death in 1998. As expected, the results of the  $^{14}\text{C}$ -analyses did not confirm this dating sequence. After interpreting the  $^{14}\text{C}$ -values of the analyzed growth rings (Fig. 6), we corrected our ring dating by 12 years under the prediction that 12 years of sapwood had been lost through decomposition. To confirm this interpretation, we isolated the growth ring that was, after the corrected dating, identified as formed in 1964. The  $^{14}\text{C}$ -content subsequently determined for that growth ring was equivalent to the atmospheric  $^{14}\text{C}$ -content in 1964; this agreement validated our ring interpretation for the entire disc and demonstrated the existence of annual growth rings in *S. amara*.

For the wood samples from the analyzed individuals of *B. elegans* and *D. panamensis*, in all cases the  $^{14}\text{C}$ -content of the tested rings corresponded with the  $^{14}\text{C}$ -values of the atmosphere at the time of their predicted formation (Fig. 7), thus confirming that the identified growth rings were annual.

For *P. maculoba*, however, the results from such test radiocarbon dating of the wood samples did not confirm our ring-count predictions for the time of formation. One possible explanation is the great prevalence of wedging rings in this species. Further studies will be needed to determine if *P. maculoba* can be reliably aged by ring counts.

AGE DATING.—For two additional species, we confirmed the existence of annual rings by two differ-

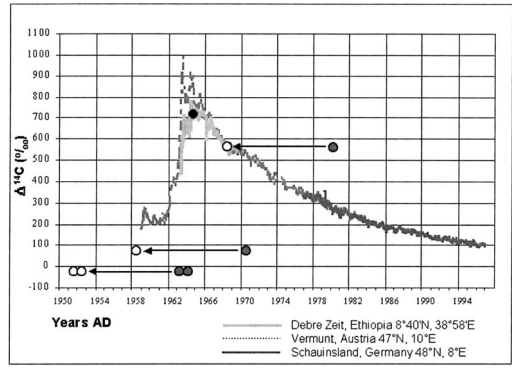


FIGURE 6. Results of radiocarbon dating from wood samples of *Simarouba amara*. Shown are the  $^{14}\text{C}$  values of the atmosphere (lines) in the Northern Hemisphere at various latitudes (from Hua *et al.* 1999, adopted) and the  $^{14}\text{C}$  values of the predated growth rings (gray circles). After correcting the macroscopic dating, the samples were dated 12 yr older (white circles). To confirm the correction of the macroscopic dating, the growth ring from 1964 was analyzed (black circle).

ent approaches, depending on whether the sampled individual's lifetime exceeded 350 years (the period over which radiocarbon dating of wood is affected by the Suess effect; see Methods).

According to our count of the growth rings for one individual of *H. mesoamericanum* (530 growth rings; tree 8058, 1983 diam: 128.0 cm, death yr: 1992), this tree was old enough to be aged by radiocarbon dating the center of the disc. The radiocarbon date of the disc center ( $570 \pm 40$ yr BP) confirmed our ring counting.

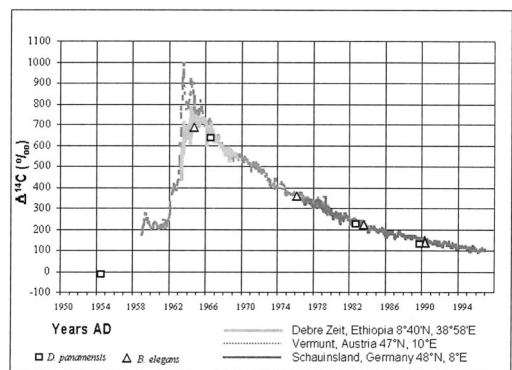


FIGURE 7. Results of radiocarbon dating test rings (see text) sampled from one individual of *Balizia elegans* (tree 3345, 67 cm diam; triangles) and one individual of *Dipteryx panamensis* (tree CES 350, 103 cm diam; squares) compared with the atmospheric  $^{14}\text{C}$  in the Northern Hemisphere at various latitudes (lines; from Hua *et al.* 1999, adopted).

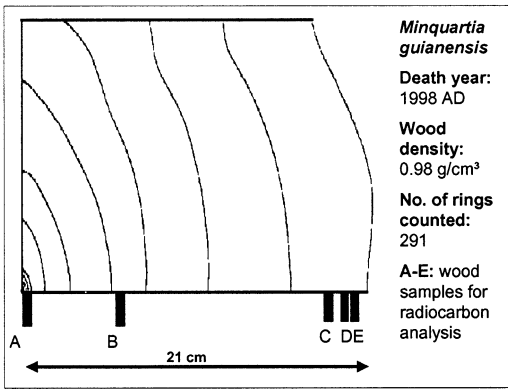


FIGURE 8. Sketch of half cross section of *Minquartia guianensis* on which 291 rings were counted (wavy lines are for orientation and do not indicate individual rings) Wood samples predicted to various ages for radiocarbon analyses were isolated from this disc (black squares).

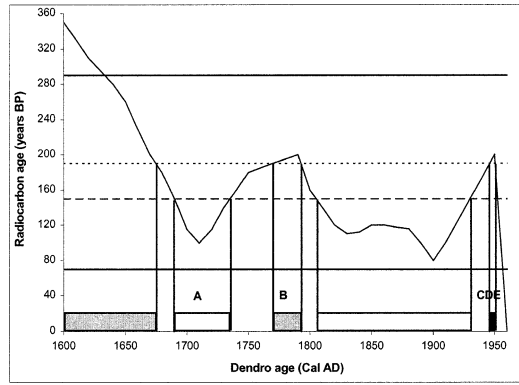


FIGURE 9. Calibration of the <sup>14</sup>C dating of wood samples dendrochronologically predicted to 1700 AD and 1780 AD from *Minquartia guianensis*. Shown are the calibrated standard curve and the radiocarbon age for the sample predated to 1700 AD (sample A: horizontal line at 70 yr BP) and to 1780 AD (sample B: horizontal line at 290 yr BP), with the corresponding standard deviations for both results (dashed line: sample A; dotted line: sample B). The corresponding possible dates of formation are for the sample 1700 AD, the periods 1690–1730 AD, and 1805–1930 AD (white areas), while for the sample 1780 AD, the periods 1600–1670 AD and 1770–1790 AD (gray areas) are considered possible times of formation. For samples C, D, and E, only the period ca. 1950 AD can be considered as the possible time of formation (black area).

We aged the one *M. guianensis* individual (tree 50268, diam: 38.2 cm, death yr: 1998) through interpretation of radiocarbon-dates for the innermost and several other rings, in combination with dendrochronological analysis of the growth zones. The calibration curve of Stuiver and Becker (1986) shows that a given <sup>14</sup>C-concentration in a wood sample corresponds to several real (dendro-) ages (Fig. 1). We used this calibration curve to compare the ages we predicted for the *Minquartia* rings based on optical counts, to subsequent radiocarbon dates for these rings. We isolated five wood sections (Fig. 8): two individual rings with the predicted times of formation of 1700 AD and 1780 AD, respectively; and three multiple-ring samples from the outer stem region, which we expected to show contrasting <sup>14</sup>C-values from before and after the 1964 bomb peak based on our ring counts. The sample B (predicted to 1780 AD by tree ring analysis) has three theoretically possible dendro-ages (Fig. 9; year ranges indicated by shaded bars). The time between 1940–1950 AD could be tentatively excluded, however, because the sample was taken 170 mm in from the stem periphery, and 170 mm of radial growth in 60 years (5.6 mm diam growth/yr) was unlikely based on the very low median diameter increments measured for *Minquartia* at La Selva (0.7–2.8 mm/yr, depending on size class; Clark & Clark 1992). The dendro-age 1600–1670 AD could also be excluded for sample B because this sample was formed later than sample A. The period 1805–1930 AD for sample A could be excluded because A was formed earlier than sample B (Figs. 8 and 9). The samples C, D, and E did

not hit the curve of the <sup>14</sup>C-concentration in the atmosphere before and after the bomb peak in 1964. Sample C was calibrated to 1680–1730 AD, 1810–1930 AD, and 1950 AD. The samples D and E were both calibrated to all the following date ranges: 1670–1710 AD, 1720–1770 AD, 1800–1880 AD, 1910–1940 AD, and 1950 AD. All periods prior to 1900 could be excluded because of these three samples' peripheral position in the disc; even considering extremely low increments, samples taken 5–20 mm from the bark could not be hundreds of years old, when the stem center, which is 210 mm from the bark, was only 300 years old. The similar calibrated dating ca. 1930–1950 of the three samples was influenced by the fact that it was not possible to isolate single rings from before and after the bomb peak, but also indicates that the optical predating deviated ca. 10–20 years. These results do, however, demonstrate how reduced the increments in the outer stem regions were in the last four decades before the tree died.

**TREE AGES.**—The ring counts provide a basis to determine the (minimum) ages of the sampled trees for the five species found to produce annual rings

TABLE 3. Minimum tree ages and lifetime mean diameter growth rates, based on ring counting of the studied trees, and estimated maximum ages for these species. Mean annual increments were calculated by dividing the tree's diameter by the total number of rings counted; when parts of the disc were missing, the increments were calculated on the base of the analyzed radius. The total number of rings gives an estimated age in years; however, for trees in which the disc showed loss of outer sapwood or the core due to decomposition, the age is underestimated. For each species, we divided the largest observed diameter at La Selva (Clark & Clark 1999) by mean annual diameter increment for the slowest-growing individual of the analyzed trees of that species, to estimate a theoretical maximum age.

| Species                            | Diameter of sampled disc at death year (cm) | No. of rings counted (= age, yr) | Mean annual diameter increment (mm/yr) | Largest observed diameter (cm) | Theoretical maximum age (yr) |
|------------------------------------|---|----------------------------------|--|--------------------------------|------------------------------|
| <i>Balizia elegans</i>             | 96.2  | 211 <sup>a,b</sup>               | 4.27                                   | 137                            | 372                          |
|                                    | 108.0                                       | 182 <sup>b</sup>                 | 3.68                                   |                                |                              |
| <i>Dipteryx panamensis</i>         | 116.0                                       | 229 <sup>a,b</sup>               | 2.90                                   | 187                            | 645                          |
|                                    | 103.0                                       | 252                              | 4.09                                   |                                |                              |
|                                    | 91.8  | 270 <sup>a,b</sup>               | 3.40                                   |                                |                              |
| <i>Hymenolobium mesoamericanum</i> | 90.0  | 301 <sup>a</sup>                 | 3.20                                   | 156                            | 645                          |
|                                    | 128.0                                       | 530                              | 2.42                                   |                                |                              |
| <i>Minquartia guianensis</i>       | 38.2  | 291 <sup>a</sup>                 | 1.26                                   | 82                             | 651                          |
|                                    | 42.6  | 223 <sup>a</sup>                 | 1.72                                   |                                |                              |
|                                    | 51.5  | 274 <sup>a</sup>                 | 2.05                                   |                                |                              |
| <i>Simarouba amara</i>             | 51.6  | 63 <sup>a</sup>                  | 7.24                                   | 81                             | 121                          |
|                                    | 54.7  | 76 <sup>a</sup>                  | 6.68                                   |                                |                              |

<sup>a</sup> Some outer sapwood appeared to have been lost from the disc through decomposition.

<sup>b</sup> Center missing from disc.

(Table 3). For the cases in which the analyzed discs had lost either heartwood or outer sapwood by decomposition, these ages are underestimates. At La Selva, young trees of these species show very slow diameter-growth rates (Clark & Clark 1992, 1999); such processes in the very young stages could be missed from the discs with missing cores. Similarly, adult trees can show very slow diameter increments prior to death (D. A. Clark & D. B. Clark, pers. obs.); discs missing part of the outer sapwood could miss periods of such slowed growth.

## DISCUSSION

The growth and dynamics of tropical trees and forests remain poorly understood. Little is known about the age and the age structure of old-growth tropical forests. In a review of recent literature on forest dynamics and carbon fluxes, the maximum age reported for the oldest tropical forest trees was found to increase rapidly among successive studies (Worbes & Junk 1999). These studies calculate or model the maximum age of tropical trees and tend to overestimate considerably (Condit *et al.* 1995), with the focus on the oldest theoretically possible age.

In the temperate zone, the easiest way to determine a tree's age is ring counting. Annual growth

rings represent a reliable basis for age determination and interpretation of tree growth under different ecological conditions or management regimes (Stahle *et al.* 1999). It is a continuing paradigm in the literature (*cf.* Studhalter 1955, Roth 1981, Whitmore 1984, Richards 1996) that tropical trees do not show annual rings because of the lack of seasonality in the tropics; however, in many tropical regions, drought periods exist. That these annual drought periods are reflected by annual rings in the wood has been shown now for tropical moist and tropical dry forests in all tropical regions (Coster 1927, 1928; Berlage 1931; Mariaux 1981; Worbes 1984, 1995, 1997, 1999; Dünisch *et al.* 2002).

The climate in La Selva is classified as everwet. Under such conditions, continuous growth of the trees has been often assumed (*cf.* Raven *et al.* 1999). Usually, however, the everwet tropics actually experience distinct seasonal variations in rainfall each year (*e.g.*, long-term averages of monthly rainfall totals for La Selva [OTS records] of 156–271 mm/mo for the four months of the drier season; 353–524 mm/mo for the eight months of the wetter season).

Phenological observations of the tree and shrub communities in La Selva (Frankie *et al.* 1974) indicate a distinct seasonality in phenology. A large

annual peak in leaf litter fall occurs during March–April, the latter part of the drier season (D. A. Clark, pers. obs.). Lieberman and Lieberman (1987) found the highest seedling mortality during the drier season. Tree growth studies at La Selva, however, have produced contradictory results. Hazlett (1987) found the highest diameter increment for the evergreen tree species *P. macroloba* in the drier period between January and April, while Breitsprecher and Bethel (1990) found cambial dormancy in observations of small samples of *Pentaclethra macroloba* and other species in the same period of the year. In a recent two-year study on leaf phenology and monthly growth of canopy and emergent tree species at La Selva, O'Brien (2002) found diverse patterns for several of our study species. *Dipteryx panamensis* showed annual deciduousness in the first half of the year, although individuals were not closely synchronous; these trees showed significantly reduced growth rates immediately following the drier season. *Simarouba amara*, an evergreen species, showed a synchronized flushing of new leaves in the early part of the drier season. For two other species for which we found annual growth rings (*B. elegans* and *H. mesoamericanum*), however, O'Brien (2002) found individuals to be strongly asynchronous in their leaf phenology, with individuals being deciduous during diverse parts of the year (some *Hymenolobium* trees were deciduous more than once in a year).

Although the underlying mechanisms are thus still unclear, our results have demonstrated that deciduous and evergreen tree species show growth periodicity at La Selva. All eight investigated species formed visible growth rings in the wood. We showed with complementary radiocarbon dating that these rings were annual, in five of the six tested species. These annual rings indicate a yearly period of slower growth or cambial dormancy. Triggers for such growth periodicity in trees can be flooding, variations in temperature, precipitation, or day length (Worbes 1995, Borchert & Rivera 2001, Schöngart *et al.* 2002), possibly supplemented by an unidentified internal rhythm (Alvim & Alvim 1978, Roth 1981). The trees investigated in this study were from upland forest at La Selva, thus not influenced by flooding. We believe that the slight variation in mean monthly temperatures of 1 to 2°C is unlikely to trigger growth periodicity, because (1) diurnal variation is much higher and (2) temperature never falls to growth-limiting values. Internal rhythms that could produce such growth periodicities have never been demonstrated for tropical trees. There are some indications that at

least stem-succulent tropical tree species (Burseraeae, Bombacaceae) react to changes in photoperiod (Borchert & Rivera 2001), but growth periodicity of deciduous and evergreen species has been linked to seasonal stress factors (*i.e.*, drought, flooding) clearly independent of photoperiod (Schöngart *et al.* 2002). The trigger of growth ring formation in La Selva trees cannot be attributed to the extreme stress situations (*i.e.*, at least two arid months, or annual floods) that have been assumed to be required for the formation of reliable annual rings in the tropics (Stahle *et al.* 1999, Worbes 1999). Although the climate at La Selva is classified as everwet, the forest may experience major drought stress during short periods without appreciable rainfall (*i.e.*, <5 mm) in the drier season between February and April (Sanford *et al.* 1994); such periods lead to a brief but marked drop in soil moisture content (Schwendenmann *et al.* 2003). Limitation in soil water can inhibit root growth and affects root metabolism (Mulkey & Wright 1996, Sanford & Cuevas 1996). Such short dry periods (10–21 d) may be effective triggers for growth periodicity in trees (*cf.* Medway 1972). The existence of an annual growth periodicity was demonstrated by our dendrochronological analysis of the canopy and emergent tree species we investigated at La Selva. The seasonality of their growth may reflect the effects of predictable, moderately long rainless periods in the annual “drier season” in this tropical wet forest.

Our results show that dendrochronological studies can be extended to all parts of the tropics. This will lead to great progress in understanding the dynamics and history of tropical forests. The existence of annual rings in tropical wet forest trees opens wide prospects for age and growth determination. The problems of age dating with indirect methods have been discussed elsewhere (Worbes & Junk 1999). Our findings illustrate why single radiocarbon-dates cannot be used to determine the age of a tree that is between 50 and 350 years old, although such findings are reported in the literature (Ogden 1981; Chambers *et al.* 1998, 2001). Aging trees of this age range requires either multiple radiocarbon dating from the same disc, or the combination of <sup>14</sup>C-dating with wood anatomical and dendrochronological methods, as performed in our study.

The oldest tree among the 12 individuals we aged in this study was an *H. mesoamericanum* with a diameter of 128 cm and an age of 530 years. The four other investigated very large trees (>70 cm diam) from La Selva were *ca.* 200–300 years old

when they died. Lieberman *et al.* (1985) estimated a mean life span of 190 years (range: 42–442 yr) for trees 10 cm diameter or greater based on simulated growth trajectories of trees at La Selva. Our preliminary findings, although based on small samples, suggest that large trees at La Selva often die at ages considerably below the maximum possible age. The maximum theoretical life expectancies we calculated for the La Selva trees (Table 3) parallel those found for broadleaf tree species in the temperate zone (Loehle 1988). There, the definitely oldest tree species (*Quercus* spp.) have a maximum life expectancy of *ca.* 600 years, and the typical age at mortality (= rotation period of the long living species) is 200–300 years less than that maximum. Similar estimates have been reported for seasonal dry and flooded tropical forests based on direct ring counting. In an old-growth forest in Cameroon the mean age of trees 10 cm diameter or greater was estimated to be only 60 years, although trees with a theoretical maximum age of 220 years were found (Worbes *et al.* 2002). In Amazonian floodplain forests, the species *Piranhea trifoliata* reaches ages up to 500 years in stands where all other trees are much younger (Worbes 1997). In a Central Amazonian forest, however, three individual trees were reported to be between 900 and 1400 years old (Chambers *et al.* 1998). Those findings are clear outliers to all other findings to date from tropical forests, and they were based on single samples from

each tree and single radiocarbon estimations, without any corroborating data or replicated analyses; thus, to confirm such widely greater longevities for tropical trees will require more data than currently exist. Together with our results from La Selva, the existing data present a picture of old-growth tropical forests in which relatively low average tree longevity (Korning & Balslev 1994) combines with much greater maximum tree ages. It is very reasonable that in a highly diverse broadleaf forest, very few species with very few individuals can survive for centuries when the overall stand is very dynamic. This is probably true for the La Selva forest and should be confirmed in the future by more extensive tree sampling and direct ring counting.

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