GROWTH RINGS, INCREMENT AND AGE OF TREES IN INUNDATION FORESTS, SAVANNAS AND A MOUNTAIN FOREST IN THE NEOTROPICS

by

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Summary

Investigations on growth zones of tropical trees were carried out and published since the beginning of our century. In tropical regions with severe annual dry seasons or inundation phases trees form annual rings. This is demonstrated for trees from Central Amazonian inundation forests and the Gran Sabana in Venezuela using a combination of several dendrochronological methods (wood anatomy, radiocarbon dating, ring width measurements).

The occurrence of annual rings allows the determination of age and growth rate of trees. The growth rate depends on the growth strategy of the species and the growth conditions. At a given site growth rate shows a weak negative correlation with the specific gravity of the wood of trees from the upper story. Several reported ring width patterns are explained by the vegetation history of different forest stands.

Key words: Tropical trees, inundation forest, Central Amazonia, annual rings, radiocarbon analysis, periodical growth zones, specific gravity, tree ring analysis.

Introduction

Tree ring research on tropical timbers was initiated at the beginning of this century (Ursprung 1900, Klebs 1915), inspired by the general discussion of the nature and causes of tree ring formation and periodical tree growth (Hartig 1853).

Especially in connection with forestry research projects in the former colonies in Africa, India and the Far East very precise and detailed reports were given on tree growth in relation to climatic and edaphic conditions (Geiger 1915). The most comprehensive investigation was carried out on the timbers of Java by Coster (1927 & 1928), who definitively demonstrated the existence of annual rings in many tropical tree species.

Strangely enough the biological and forestry sciences ignored these facts although they were confirmed by more recent studies (Mariaux 1969, 1976). The concept of constant tree growth in a uniform tropical climate was developed very early (e.g. Leeuwenhoek 1680, in: Baas 1982) and widely accepted (e.g. Walter 1973). In fact, however, a distinct seasonality occurs in many regions in the tropics even close to the equator (Walter & Lieth 1967). Severe and periodical dry seasons of several months duration e.g. in Manaus, Brazil or other places (Amobi 1973) as well as annual floodings of great river systems like in Central Amazonia can effect a cambial dormancy in trees (Gessner 1968) which is reflected by annual growth zones in the wood (Worbes 1985).

In the last several years the development of dendrochronological methods (Schweingruber 1988) and the more intense focus on tropical ecosystems have led to an increase in the number of tree-ring-analysis investigations of tropical timbers, some of which were presented at a workshop in New Haven in 1980 (Bormann & Berlyn 1981). In the present investigation several of the methods proposed in Bormann & Berlyn (1981) were combined to an integrated concept of dendrochronology in the tropics. Age determination of tropical trees requires the application of several independent methods and investigations:
— careful research on the site and growth conditions of the trees,
— wood anatomical and macroscopical investigations to clarify the structure of the growth zones and its boundaries,
— radiocarbon analyses and ring width measurements to clarify the nature of the growth rhythm.

When this basic information is available it is possible to apply the results to ecological studies or for other purposes. In the present study this concept is tested on trees of the Central Amazonian inundation forests and transposed to trees of non-flooded areas (terra firme) in Costa Rica and Venezuela.

**Origin of samples, Methods**

**Origin of samples**

a) Central Amazonian inundation forests

Annual fluctuations up to 15 m of the Rio Amazonas and Rio Negro cause flooding over extensive areas of the naturally forested flood plains. The inundations last up to 8—9 months of the year in forest sites of low elevation and rise up to 5—6 m above the forest floor. Stem disks and cores of about 100 different tree species were collected in 1981, 1982 and 1986 in the nutrient-rich white-water inundation forest of the Amazon called Várzea and the nutrient-poor black-water inundation forest of the Rio Negro called Igapó. The study areas are located in the vicinity of Manaus, Brazil (3° 06' S, 60° W). Worbes (1986) gives further information on the tree species and the general ecological conditions in this area.

b) Gran Sabana in Venezuela

Eighty stem disks of *Tapirira cf. guianensis*, Anacardiaceae, *Ficus* sp., Moraceae and other species from the area of the Coroní divide in the Guyana highlands in Venezuela (5° 06' N, 61° 01' W). The Gran Sabana is characterised by distinct regular drought periods and extremely poor nutrient supply (Fölster 1986).

c) Tropical mountain rain forest in Costa Rica

About 50 stem disks of *Quercus costaricensis*, Fagaceae and other species were cut in 1986 in a tropical mountain rain forest in the Costa Rican cordillera (9° 30' N, 83° 30' W, 2700 m above sea level, 2500 mm/yr precipitation, 2—5 months dry period). A detailed description of this area can be found in Blaser (1987).

**Methods**

The stem disks were cut at breast height and sanded carefully.

Microtome sections of 20—30 μm thickness were stained with safranin and astra blue, when the natural coloration was too weak.

Duplicates of the Brazilian wood samples are kept in the wood collection of the Instituto Nacional de Pesquisas da Amazônia (INPA), Dep. CPPF, Manaus, Brazil. Duplicates of the microscopic sections are deposited in the Institute of Wood Biology and Wood Protection, Hamburg, F. R. G.

For the radiocarbon analyses single growth zones of 4—9 g wood matter were sawn out (Fig. 13). The analyses were carried out at the Gliwice Radiocarbon Laboratory, Institute of Physics, of the Silesian Technical University in Poland. The results are documented in laboratory reports 91/85, 64/86, 36/87, 37/87, and 38/87. The samples were pretreated with 2% HCl and 2% NaOH solutions. A proportional and in some cases a microproportional counter were used to measure the radiocarbon content. The calculation of the data followed international conventions (Stuiver & Pollach 1977).

Ring width analyses were carried out with a measuring device following Eklund. Ring width curves are presented as raw data or as index curves. Indexing means in this case: the raw curves are smoothed by moving average (eleven value window) and then every value of the raw curve is divided by its smoothed value (index = raw value/smoothed value).

The specific gravity was estimated from entire stem disks, dried at 105°C. The area of a disk was estimated using a leaf area measuring device.

From the disk area the mean radius was calculated. Mean radius devided by the age resulted in the mean annual increment.
Site selection

The success of dendrochronological work in the tropics depends to a great extent on careful site selection and sampling strategy. It works favourably at sites where seasonal growth limiting factors are strengthened by local characteristics. In the inundation forests flooding has the greatest effect at sites of low elevation with a long submersion phase. In regions with dry seasons, stands far from rivers or creeks – perhaps on slopes with a poor water supply – should be chosen.

At the present state of our knowledge it is not possible to indicate how many months of a dry period, and which (low) amount of precipitation are necessary to cause a cambial dormancy in certain tree species. In the ever-wet rain forests, however, with humid or perhumid climate during the entire year, dendrochronological studies are undoubtedly not successful (Wrobel 1977).

The sampling strategy at a new site must be a compromise between taking samples of many different species to find those with the most distinct rings and obtaining as many samples as possible from one interesting species.

Wood anatomy

Above all it is necessary to define the structure of the growth zones and the character of its boundaries wood anatomically. The great diversity of tree species in the tropics is correlated with a similar diversity in wood structure.

According to Coster (1927 & 1928), however, it is possible to define four basic types of growth ring formation.

a) In the most common case a growth zone boundary is marked by several rows of fibres with a shortened radial diameter and thickened walls. This results in a more or less distinct difference in ‘early-’ and ‘latewood’ density. Distinct examples of this type can be found in Annonaceae, Lauraceae, Euphorbiaceae and other families (Figs. 1, 2).

b) Boundaries formed by uni- or multiseriate marginal parenchyma bands, the cells of which are often filled with various amorphous substances or crystals (Figs. 3–5) are also widespread, e.g. in many Leguminosae and Euphorbiaceae.

c) In several families a growth zone is characterised by periodically recurring patterns of alternating parenchyma and fibre bands. In particular in Sapotaceae, Moraceae, Euphorbiaceae and Lecythidaceae, a broad band of fibre tissue marks the beginning of an increment zone. The alternating bands usually become narrower toward the end of a growth zone (Figs. 6–8).

d) Ring-porous structure is described in Coster (1927) for some tropical timbers but does not occur in wood from the inundation forests.

The characteristics described above often occur in various combinations depending on the specific wood structure of a given species. Particular ring types are predominant in certain families. For example, the growth zones of all Leguminosae are separated by marginal parenchyma bands, even though in several species additional structural zonation is also present.

All dendrochronological work is impeded by the fact that wood structure varies considerably within one species depending on the growth conditions of a tree. Figure 9 shows distinct growth zones of a young, fast growing Piranhea trifoliata, Euphorbiaceae; the wood formation corresponds ideally with that described under growth ring types b) and c). The same species shows extremely indistinct rings in the wood of an old tree which grew at a higher site in a dense forest and was inundated comparatively seldomly (Fig. 10). Similar variations occur in the wood of Tabebuia barbata from sites with good or poor light conditions (Figs. 11 & 12), and often trees show more indistinct ring boundaries in the juvenile wood than in mature tissues. This can result in slight errors in the exact determination of tree age (cf. Coster 1927 & 1928).

Almost all investigated species from inundation forests and from the terra firme show more or less distinct growth zones. The structures at the boundaries primarily indicate

(text continued on page 116)
Common legend to Figures 1–16: All species without indicated origin from Central Amazonian inundation forests. Black arrows mark some ring boundaries. Magnification: all microphotos (1–4, 7, 8, 15, 16): × 160; all macrophotos (5, 6, 9–12, 14): × 2.5; Fig. 13 with scale bar.

Figs. 1 & 2. *Mabea nitida* (Euphorbiaceae) and *Matayba macrolepis* (Sapindaceae): growth rings are delimited by radially flattened fibres. — Figs. 3 & 4. *Trichilia singularis* (Meliaceae) and *Pithecellobium inaequale* (Mimosoideae, Leg.): growth rings are delimited by marginal parenchyma bands. *T. singularis* also shows radially flattened fibres and represents therefore growth ring types a and b.
Fig. 5. *Macrolobium acaciaefolium* (Caesalpinioidae, Leg.): growth rings are mainly delimited by marginal parenchyma bands. — Figs. 6–8. *Ficus* sp. (Moraceae) from Gran Sabana, *Neoxythecel elegans* (Sapotaceae) and *Eschweilera* sp. (syn. *Jugastrum*) (Lecythidaceae): growth zones are characterised by patterns of alternating parenchyma and fibre bands.
Figs. 9 & 10. *Piranhea trifoliata* (Euphorbiaceae) from a light stand of low elevation (9) and from a dense stand of high elevation (10) in the inundation forests. — Figs. 11 & 12. *Tabebuia barbata* (Bignoniaceae) from a light stand (11) and a dense stand (12). Fig. 11 shows also the result of cambial wounding one year before the tree was felled.
Fig. 13. *Tapirira cf. guianensis* (Anacardiaceae) from the Gran Sabana in Venezuela. The disk shows very fine increment zones. For the radiocarbon analysis a strip of wood representing the period from 1964/65 to 1967/68 was investigated, the radiocarbon content concurred with the mean level in the air during this period. — Fig. 14. *Duguetia* sp. (Annonaceae) with extreme lobate growth. — Fig. 15. Very dense wood of *Piranhea trifoliata* (Euphorbiaceae) (spec. grav. ≈ 0.9). — Fig. 16. Extreme light wood of *Pseudobombas munguba* (Bombacaceae) (spec. grav. ≈ 0.2).
deceleration or even cessation of cambial activity (dormancy, Roth 1981). This means that all these trees show periodical growth.

**Determination of the growth rhythm**

The existence of periodical growth zones in tropical trees does not imply the occurrence of an annual growth rhythm. The present lack of knowledge requires that the periodicity of the increment zones has to be investigated in different species at an unknown site.

Three independent methods for determining the growth rhythm are described below. In all cases the prerequisite is that the trees show regular growth around the entire stem. Species which show lobate growth or rings which disappear in certain regions of the stem cannot be used (Fig. 14). On carefully sanded stem disks suitable samples were selected by means of macroscopical investigations (a species list is given by Worbes 1985).

**Cambial wounding**

One of the safest but most time consuming ways is marking by mechanical wounding (Mariaux 1976) or poisoning of the cambium. After some time the tree has to be felled and the number of rings can then be compared with the time difference between marking and felling. One *Tabebuia barbata* tree was marked some weeks before the submersion phase began and was felled one year later. Figure 11 shows that little wood was produced until the next ring boundary. It can be presumed that wood production stopped shortly after the flooding water covered the roots of the tree.

**Radiocarbon analysis**

More complicated is the age dating of already felled trees by radiocarbon analysis based on the nuclear weapon effect (Cain & Suess 1976; Stuiver et al. 1981). As one result of the more than 400 above-ground atomic bomb explosions in the fifties and the early sixties the C$^{14}$-level in the air nearly doubled in the Northern Hemisphere. In the Southern Hemisphere the increase of radiocarbon amounted about 1.6 times the 1950 level (Nydal & Lövseth 1983; Levin et al. 1985). Since the late sixties the C$^{14}$-level of the air has been decreasing because of the exchange with the ocean surface and the uptake by the biosphere. Every plant incorporates radiocarbon in the same concentration as in the air; this allows the age determination of a certain growth zone of any tree that grew between 1950 and the present.

Two stem disks of *Sawtia laevicarpa* and *Rourea* sp. were split ring by ring to compile a continuous time series of the annual radiocarbon content in the wood for the period from 1952 to 1982. The results show that the radiocarbon contents of the rings follow those of the air (Fig. 17) and prove the existence of annual rings in trees of the Amazonian inundation forests.

The shape of the radiocarbon air curve demonstrates that – with the exception of the maximum value – one C$^{14}$-value represents two different ages of a sample. This means that in most cases an exact age determination requires several estimations. A careful anatomical predating can minimise the analytical effort to one measurement, if the peak of the radiocarbon curve in the middle of the sixties can be determined (cf. Mozeto et al. 1988). On this basis the existence of an annual growth rhythm of ten species from inundation forests (Worbes & Leuschner 1987) and one species (*Tapirira* cf. *guianensis*, Fig. 13) from Gran Sabana in Venezuela could be proven with one estimation each.

Samples from Costa Rican oaks (*Quercus costaricensis*) showed very indistinct growth zones. The radiocarbon investigation established a more or less biannual growth rhythm corresponding with the irregular periodicity of precipitation in the Costa Rican mountain cloud forests.

**Ring width analysis**

The method of ring width analysis is feasible and often used in temperate zones. The ring width patterns of different individuals of one species are similar when tree growth is influenced regionally by strong climatic factors or events (Schweingruber 1988). The comparison of the ring width curve of a sample with unknown age with a regional standard chronology allows an exact age dating in most cases (cross dating).

In the tropics, however, it seems that the method is restricted to certain cases; several problems must be considered:
1) In many tree species one increment zone can vary its width considerably in different regions of the stem so that results of ring width measurements may be reversed depending on the selected radius (Fig. 14).

2) Especially in old, slow growing trees the short radii (depressions) of a stem disk often show a smaller number of rings than the longer radii (missing rings) on which the measurements should be carried out.

3) At the present stage of research the described difficulties require investigations of stem disks. When wood structure and growth behaviour of certain species are clarified completely this destructive method should be replaced by the use of core samples.

My own preliminary investigation on *Macrolobium acaciaefolium*, Caesalpinioidae (*Leg.*), showed that only one of eight core samples (Fig. 18: 1) could be synchronised with the ring patterns of the stem disks of this


Fig. 18. Index curves smoothed by moving average. Ring width patterns of a core sample from *Macrolobium acaciaefolium* (1), from stem disks of the same species (2–4), from *Tabebuia barbata* stem disks (5, 6) and the annual duration of the non-flooded phase in inundation forests (7).
species (Fig. 18: 2-4), because of additional parenchyma bands within one growth zone, which only can be differentiated from ring boundaries in a complete stem disk (Fig. 5).

4) In accordance with the results in the temperate zones in most cases only the synchronisation of ring width patterns within one species is possible as could be shown for *Macrolobium acaciaefolium* (Fig. 18: 1-4) and *Tabebuia barbata* (Fig. 18: 5 & 6). Some carefully selected samples from different species of a delimited stand, however, can also be cross-dated (Fig. 18: 4 & 5). This generally indicates the existence of a strong external factor which influences periodical tree growth of different species in a similar manner. In the present case the duration of the non-flooded phase – the vegetation period of the inundation forests – correlates positively with the ring widths.

**Vegetation history**

In spite of the problems discussed, ring width analysis can be a useful help to clarify questions in tropical forest ecology.

Ring width patterns of individual *Tabebuia barbata* trees typify the shape of many other curves of three different inundation forest stands. In Figure 19 the typical ring curves of the following forest stands are compared:

1) an obviously young stand at the edge of the Ilha de Marchantaria (dotted line),
2) a stand in the centre of the same island (outlined),
3) a stand on the Ilha de Careiro, another larger island in the Amazon (broken line).

The young tree (1) originates from the upper canopy of a young stand with a maximum age of 20-40 years. Good light conditions result in extremely high annual increments.

The fact that curve 3 is damped, i.e., centered around the average, indicates that during its life the tree grew in an undisturbed forest in light competition with the neighbouring trees. The tree reached an age of about 140 years.

A calculation based on the diameters of the thickest trees and the mean annual increment of *Piranhe trifoliata* resulted in an age-estimate of 350-400 years for hollow trees of...
Table 1. Annual increment, specific gravity (density), age, nutrient supply and light conditions (stratum) of trees from Central Amazonia.

<table>
<thead>
<tr>
<th>Species</th>
<th>Family</th>
<th>Annual increment (mm)</th>
<th>Density</th>
<th>Age (years)</th>
<th>Nutrients</th>
<th>Stratum</th>
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<td>0.80</td>
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<td>+</td>
<td>5</td>
</tr>
<tr>
<td>Psidium acutangulum</td>
<td>Myrtaceae</td>
<td>1.2</td>
<td>0.80</td>
<td>71</td>
<td>+</td>
<td>4</td>
</tr>
<tr>
<td>Roucheria sp.</td>
<td>Hugoniaceae</td>
<td>1.1</td>
<td>0.82</td>
<td>27</td>
<td>–</td>
<td>5</td>
</tr>
<tr>
<td>Endlichera arunciflora</td>
<td>Lauraceae</td>
<td>1.5</td>
<td>0.82</td>
<td>38</td>
<td>–</td>
<td>3</td>
</tr>
<tr>
<td>Neoxythece elegans</td>
<td>Sapotaceae</td>
<td>1.3</td>
<td>0.82</td>
<td>45</td>
<td>–</td>
<td>3</td>
</tr>
<tr>
<td>Tabebuia barbata</td>
<td>Bignoniaceae</td>
<td>1.1</td>
<td>0.83</td>
<td>110</td>
<td>+</td>
<td>3</td>
</tr>
<tr>
<td>Tabebuia barbata</td>
<td>Bignoniaceae</td>
<td>1.6</td>
<td>0.85</td>
<td>75</td>
<td>+</td>
<td>1</td>
</tr>
<tr>
<td>Tabebuia barbata</td>
<td>Bignoniaceae</td>
<td>1.2</td>
<td>0.88</td>
<td>94</td>
<td>–</td>
<td>2</td>
</tr>
<tr>
<td>Tabebuia barbata</td>
<td>Bignoniaceae</td>
<td>1.1</td>
<td>0.92</td>
<td>51</td>
<td>–</td>
<td>5</td>
</tr>
<tr>
<td>Piranhea trifoliata</td>
<td>Euphorbiaceae</td>
<td>2.0</td>
<td>0.93</td>
<td>64</td>
<td>+</td>
<td>4</td>
</tr>
<tr>
<td>Poecilanthe amazonica</td>
<td>Papilionoideae (Leg.)</td>
<td>1.1</td>
<td>0.94</td>
<td>46</td>
<td>–</td>
<td>4</td>
</tr>
</tbody>
</table>

Legend: + = trees are from white-water inundation forest; – = trees are from black-water inundation forest. The light supply is ranged from 1 = upper story, to 5 = understory, with gradations (2–4) in between; the light condition of the Vitex cymosa-tree was undetermined.
this species frequently occurring in the same stand.

In recent times the Tabebuia barbata tree 3 grew in a dense and closed canopy overtopped only by a few others. Tree 2 from the centre of the Ilha de Marchantaria grew under almost the same recent light conditions. Its extreme increments in the thirties, however, are only explicable on the assumption that the stand was young and open at this time. The fact, that the maximum tree age at the Ilha de Marchantaria amounts to 100–120 years, confirms the assumption that the stand represents an early stage of succession in the white water inundation forest.

Increment rates

An important result of the age determination of tropical trees is the radial increment rate. The amount of the annual growth reflects the genetic precondition of a tree species and the growth conditions of an individual tree in the stand. The estimates for 48 trees of 28 species from inundation forests, of which the age could be determined relatively easily, shows a very large range of increment rates (Table 1). One has to consider that most of the species in the list are only represented by a single tree but trends are evident: The pioneer tree Pseudobombax munguba, Bombacaceae, can reach an annual and radial increment of 8 mm. Typical trees of the understory such as Psidium acutangulum, Myrtaceae, show in certain cases less than 1 mm radial growth per year. Within one species (Tabebuia barbata) the annual growth varies from 4.7 mm in a young tree growing under good light and nutrient conditions to 1.1 mm in an understory tree growing on poor soil. Species with high increments are generally those from the upper story and from the white water inundation forest where the annual sedimentation supplies the soil with nutrients.

The growth rate can explain various phenomena, such as different colours in species with heartwood formation. The slower a tree grows the more substances can be deposited in the heartwood during its formation (Rudman 1966; Barajas Morales 1985). Therefore the colour of the heartwood of T. barbata varies between almost black in slow growing trees to yellowish/brown in faster growing trees.

The trees in Table 1 are listed in order of increasing specific gravity of the woods. A first look at the increment rates gives an impression of disorder. But by eliminating all young trees with juvenile wood (< 20 years), and those of the understory, a weak correlation of about -0.77 between density and annual increment appears to exist. This correlation holds true especially within a given species (e.g. T. barbata) and corresponds with the observations of Barajas Morales (1985, 1987). She noticed a distinctly higher mean specific gravity in timbers from an arid location compared with those from a humid rain forest, suggesting that the growth rate is lower at the site with little precipitation.

The causes for the correlation may be found on the one hand in differences of growth conditions like water-, nutrient- or light-supply. On the other hand tree species with certain growth strategies are adapted to and at an advantage at certain sites. It is obvious that the wood formation of Pseudobombax munguba (Fig. 16) implies a strategy to settle new sites very rapidly at the cost of stability. Indeed this species is very successful and frequent in young stands but rare in older ones. Pirania trifolia (Fig. 15), however, occurs frequently in old climax forest communities. Its slow growing, dense wood is very stable and protected by an intense heartwood formation against fungal attack and insect damage (Martius 1989). These characteristics suggest longevity which is necessary to play a role in old forest stands.

The example of T. barbata shows that tree species are able to adapt to different growth conditions by varying the wood formation within a certain range (Akachuku 1984; Mio et al. 1984; cf. Wilkes 1988). This is expressed by the range of its specific gravity (from 0.5 to 0.9) corresponding with the fact that a fast growing tree produces a large amount of storage tissue (parenchyma) whereas the wood of slow growing individuals consists to a greater extent of fibres with thicker walls.
Conclusions

A survey of the literature and the present investigation show that the number of tropical tree species forming annual rings is much greater than is generally assumed. Dendrochronological studies on tropical trees require not only refined techniques but also much patience, and are certainly always more difficult than those on trees of the temperate zones. Nevertheless, despite all problems, tree ring analysis has a great potential to broaden our knowledge of the functioning of tropical forest ecosystems – a point of great importance in view of the worldwide deforestation in the tropics.

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References


