IAWA Journal, Vol. 16 (4), 1995: 337–351

HOW TO MEASURE GROWTH DYNAMICS IN TROPICAL TREES A REVIEW

by

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SUMMARY

Cambial dormancy and annual rings in tropical trees are induced by annually occurring dry periods or flooding. Growth periodicity is indicated by the leaf fall behaviour and is connected with an annual periodicity of shoot elongation. Changes in stem diameter are measured with a dendrometer or by measurable differences in the electrical resistance of the cambium. Dendrochronological methods applied to carefully prepared samples can serve as proof of the annual periodicity of growth zones. For this purpose the following methods have been used: cambial wounding, radiocarbon dating, pointer year detection and regression analyses of ring width and climate data. Although X-ray densitometry and the analysis of stable isotopes in rings of tropical trees promise to provide interesting climatological information, the use of these methods remains difficult.

Key words: Tropical trees, annual rings, dendrochronology, dendrometer measurements, radiocarbon datings, X-ray densitometry, phenology.

INTRODUCTION

The existence of annual rings in trees of the temperate and semi-arid zones has been a truism for centuries. Tree-ring analysis has been widely developed and is used for numerous purposes in forestry, botany, climatology, and the earth sciences. For tropical regions, however, there is still assumed to be a general absence of annual rings in trees (Whitmore 1990), despite several reports to the contrary since the beginning of our century (Worbes 1992; Killmann & Hong 1995). This disagreement can be traced back to uncertainties in the distribution of rainfall seasonality in tropical regions. The paper in hand gives an overview of the climatic conditions which effect tree-ring formation, particulary the formation of annual rings in tropical trees.

Bormann and Berlyn (1981) proposed different methods to solve the problem whether visible growth zones in tropical trees are annual in nature or not. Meanwhile these and more methods have been tested and applied by the author and others. In the following overview these methods will be briefly presented and discussed with examples from my own investigations on trees from Central Amazonian floodplain forests, from the Gran Sabana and from the Caparo Forest in the Western Llanos in Venezuela.

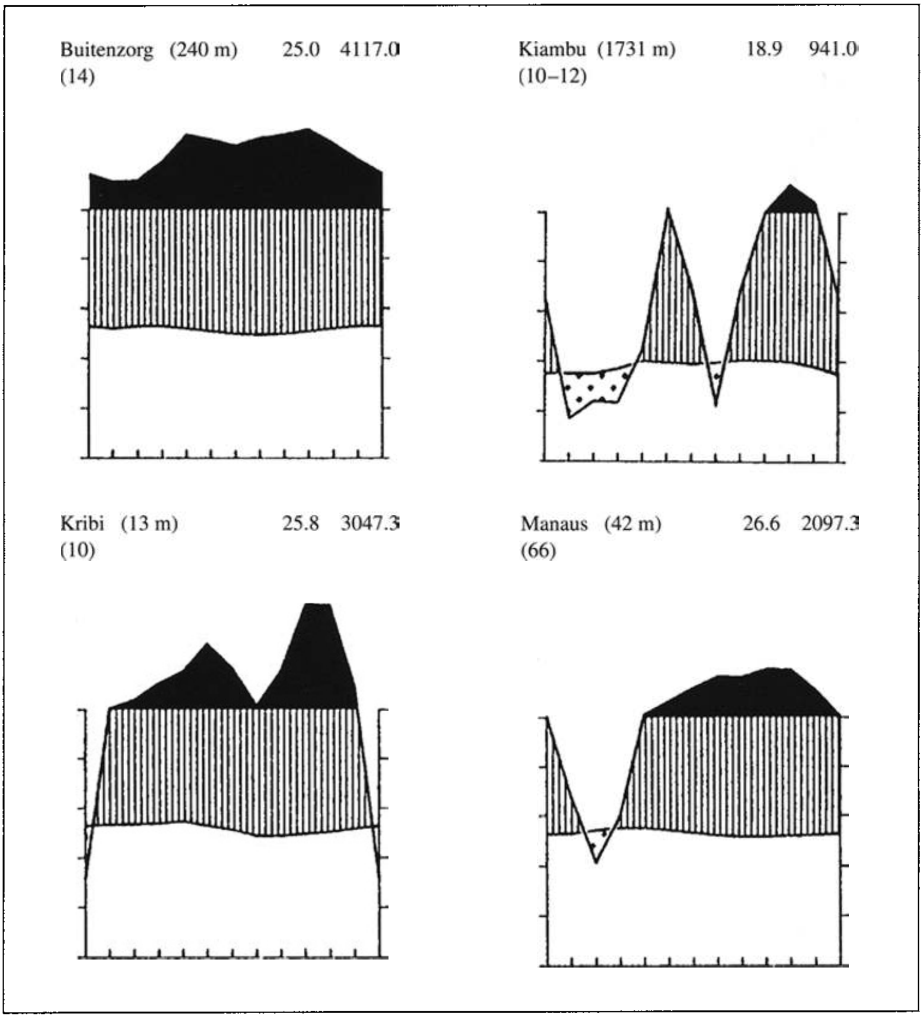

Fig. 1. Climate diagrams for Bogor (Buitenzorg) at 240 m at sea level, 14 years of observation for temperature and precipitation, 25°C mean annual temperature, 4117.0 mm mean annual precipitation, Java; Kiambu, Kenya; Kribi, Cameroon and Manaus, Brazil, from Walter & Lieth (1967). Black = perhumid season, striped = humid season, dotted = relatively dry season.

CLIMATICAL CONDITIONS FOR TREE-RING FORMATION

Tree rings in woody plants are generally induced by seasonally alternating favourable and unfavourable growth conditions. Stress factors which occur seasonally are low winter temperatures in the temperate zones and higher elevations everywhere as well as dry seasons and floodings in the tropics. These climatic stress factors induce a cambial dormancy in trees and, in consequence, growth zones in the wood.

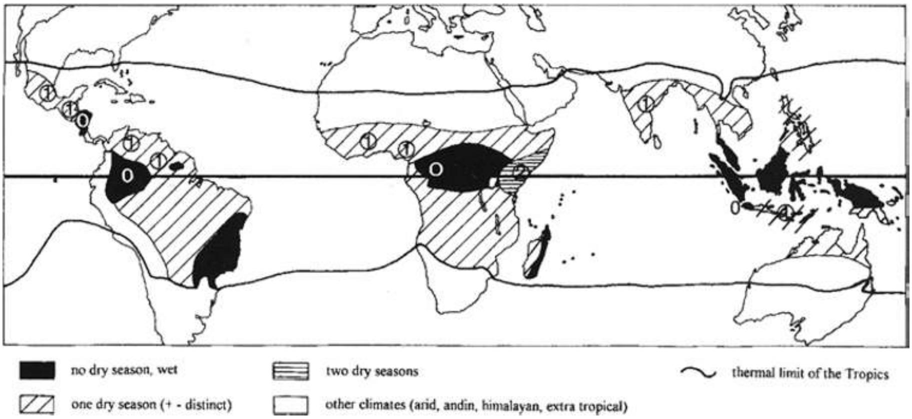

Fig. 2. Distribution of seasonality in the tropics based on climate diagrams from Walter & Lieth (1967). The numbers indicate investigations on growth periodicity of trees by different authors (Worbes 1992); 1 = formation of annual rings, 2 = two rings per year are formed, 0 = no distinct growth periodicity.

My own observations and investigations together with the results of many others (Worbes 1992) indicate that an annual dry season with a length of 2 to 3 months and less than 60 mm monthly precipitation induce annual rings in tropical trees. The existence of two rings per year has been documented by Jacoby (1989) and Gourlay (1995) for trees from East Africa in regions with two dry seasons. Investigations in regions with everwet conditions showed that growth zone patterns in trees could not be connected with corresponding changes in climate (Coster 1928; Wrobel 1977).

The three climate types which are relevant for dendrochronological investigations can be described by the climate diagrams of Walter and Lieth (1967) (Fig. 1). The regional distribution of these climate types is shown in Figure 2. Regions of desert climates or montane climates as well as local deviations have not been regarded. Everwet conditions are mainly restricted to regions close to the equator. Two distinct dry seasons occur, with the exception of smaller regions mainly in East Africa. Wide regions, however, are characterized by annual rainfall seasonality.

An exceptional case is the formation of annual rings caused by the annual floodings of great rivers in the tropics, such as the River Amazon and the Rio Negro (Worbes 1985, 1989). The long lasting and high rising inundations result in anoxic conditions in the root space. This leads to reduced root activity, water deficit in the crown and, in consequence, to cambial dormancy and the formation of tree rings (Worbes 1985, 1996).

METHODS TO INVESTIGATE GROWTH RHYTHMS IN TROPICAL TREES

It became clear that the climatic conditions in certain tropical areas enable the use of dendrochronological methods for various purposes. However, even rings from trees that grow under a seasonal climate are often relatively indistinct (Détienne 1989). To characterize tree rings an integrated concept of the investigation of growth rhythms is required that includes the observation of cambial acivity and phenological events. The discussion of non-destructive methods preceeds that of the classical dendrochronological tools.

Non-destructive methods

Phenological investigations

Phenological observations give a first indication of the growth rhythm of a tree, a tree species or a forest type. This tool is mainly used to differentiate between vegetation types such as evergreen, semi-deciduous and deciduous forests connected with large-scale climate zones (Holdrige 1947). On the species level it provides information on different growth strategies of evergreen and deciduous species growing together in one stand (Franco 1979). The observation of single trees over a period of several years shows that leaf fall behaviour in the tropics is correlated with the occurrence of dry seasons, even if periods of low precipitation may appear unpredictably throughout the year (Medway 1972).

The use of litter samplers offers the possibility to quantify phenological observations. Results integrate the leaf fall behaviour of a forest stand and also show its dependence on external growth factors (Klinge 1977). In floodplain forests, for example, maximum leaf fall occurs within the flood period; a second peak occurs during the dry season in the flood-free period (Fig. 3).

Dendrometer bands

Dendrometer bands enable the continuous measurement of diameter growth and thus of the cambial activity of a tree. The comparison of these results with climate data provides information on growth rhythms dependent on climatic events (Kätsch et al. 1992). Dendrometer measurements of different tree species from a site in the Caparo forest in the Western Llanos, Venezuela

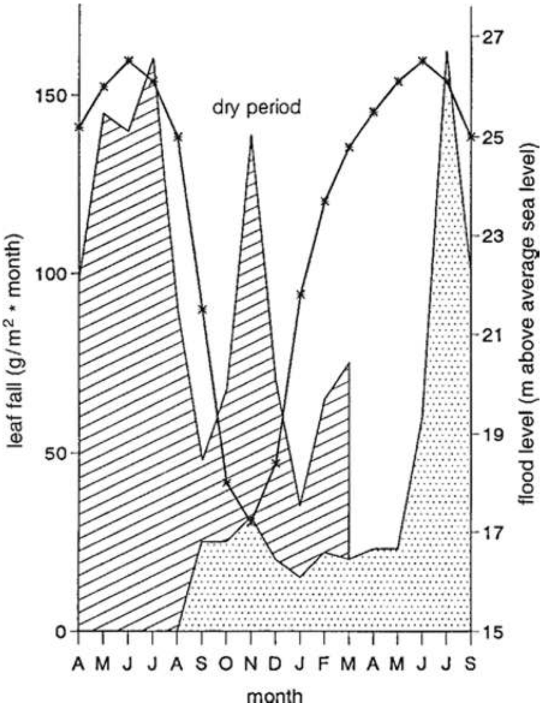

Fig. 3. Monthly leaf fall in g per m^2 in two stands of Central Amazonian floodplain forests, together with the mean monthly flood level at the harbour of Manaus, Brazil. — Dotted = leaf fall stand I; striped = leaf fall stand II; ✳ = flood level.

(Fig. 4), show that deciduous tree species, such as *Cedrela odorata*, Meliaceae, have a long period of cambial dormancy during the dry period, whereas evergreen species, such as *Cordia alliodora*, Boraginaceae, tend to have more constant growth with a short interruption (Mariaux 1969, 1970).

Measuring cambial activity with a Shigometer

Measurements of the electrical resistance of the cambial zone with a Shigometer (Shigo & Shortle 1985) have occasionally been used to describe cambial activity (e.g. Böttcher 1987; Torelli et al. 1990). Measurements that have been conducted throughout a one-year period on trees growing in the Amazonian floodplain forests show less cambial activity (= higher electrical resistance) during the flood period than during the flood-free period (Fig. 5). However, the cambial activity seems to increase at the end of the inundation at high water levels. During this period trees flower and

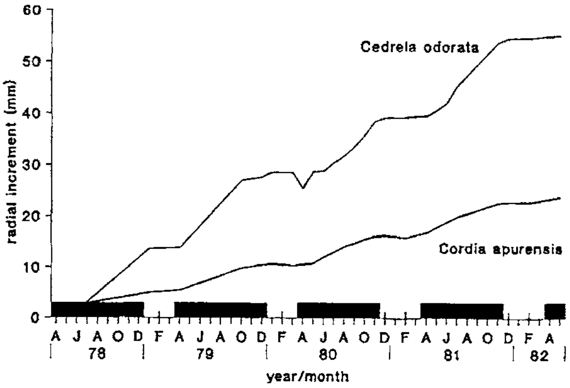

Fig. 4. Mean cumulative radial increment from dendrometer measurements of *Cedrela odorata*, Meliaceae, and *Cordia apurensis*, Boraginaceae, (mean of 4 individuals each) between April 1978 and June 1982 in the Caparo Forest in Venezuela. The black bars indicate the duration of the rainy season.

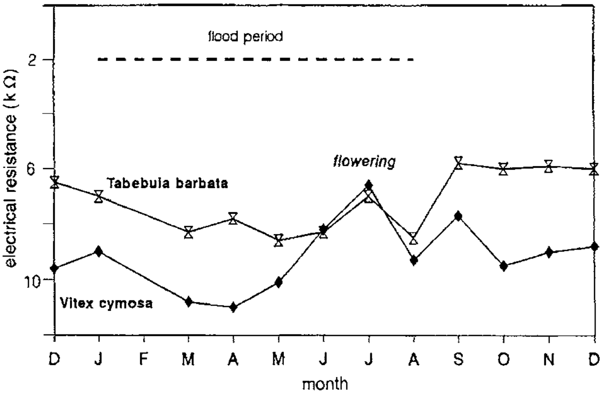

Fig. 5. Electrical resistance of the cambial zone measured monthly with a Shigometer in two tree species from the Amazonian floodplain forests; both species flower at the end of the flood period.

fruit. Values of low electrical resistance possibly reflect the mobilization of carbohydrates from the storage tissues in the wood. Although Shigometry provides a good indication of cambial activity more basic research is necessary for a proper interpretation of the results.

Destructive methods

Sample collection and preparation

The above mentioned methods give first indications of the growth rhythms of trees. For further information on growth rates and for the interpretation of growth behaviour in connection with ecological growth factors, it is necessary to investigate the tree-ring structure using dendrochronological methods. The often discussed problems with partially indistinct growth zones and wedging rings (Coster 1927, 1928; Worbes 1985; Norton et al. 1987; Détienne 1989) usually require the investigation of stem discs. The analysis of increment cores is only possible in tree species with very distinct rings and concentric ring formation, such as, e.g., *Cedrela odorata*, Meliaceae, *Tectona grandis*, Verbenaceae (Pumijumnong et al. 1995) or some coniferous species (Buckley et al. 1995). In all cases the surface of the samples must be prepared with great care in order to increase the visibility of the growth zones as much as possible. The best results have been achieved with sanding methods using a grit size of up to 400–600 µm. Careful moistening with water during the observation often improves the contrasts at the growth boundaries.

The conservation of samples with organic fungicides must be avoided if the isotopic contents are planned for later analysis. This would result in a contamination of the wood and lead to misinterpretations, e.g. of the results of radiocarbon datings.

Wood anatomy

Growth zone analysis requires above all investigations of the anatomical wood structure and the definition of the ring boundaries. Much information is available on this topic from trees of all tropical regions (Coster 1927, 1928; Fahn et al. 1981; Worbes 1989; Vetter & Botosso 1989; Détienne 1989).

Ring counting in trees of known age

The comparison of the number of rings with the known age of the tree readily proves the periodical nature of tree rings. Information on the age, however, is usually only available from plantation trees (Tschinkel 1966), trees from botanical gardens, and sometimes from natural grown trees if local people give reliable information (Gourlay 1995).

Cambial woundings (Windows of Mariaux)

The cambial wounding developed by Mariaux (1967) provides exact information on the growth rhythm. The cambium is injured in a small ‘window’ of some square centimetres either mechanically by incision or chemically by injection. The optimal advantages of different cambial marking methods are discussed by Sass et al. (1995). The wounds are covered by callus tissue in the consecutive years and remain as an

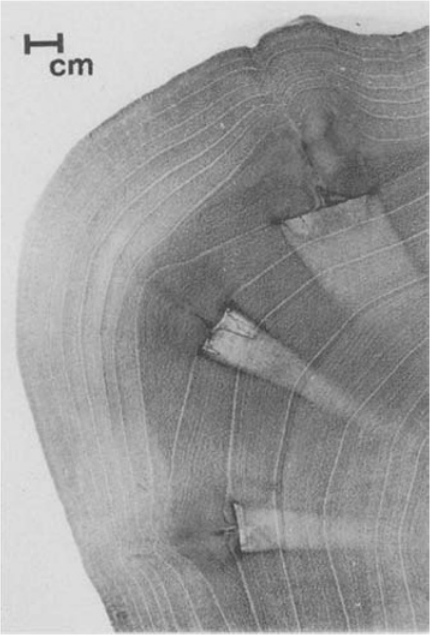

Fig. 6. Segment of a disc of *Cedrela odorata*, Meliaceae, from the Caparo forest in Venezuela with first cambial mark in 1980 and in two consecutive years.

artificial and exactly datable scar in the wood. After several years the trees can be cut and the number of rings on the stem disc can be compared with the time difference between different cambium marks (Fig. 6). Moreover incisions made in different seasons throughout the year can give information on the formation of different tissues which depend on corresponding seasonal climatic conditions (Sass et al. 1995). In the example of *Cedrela odorata*, Meliaceae (Fig. 6) a band of parenchyma tissue is formed shortly after the wounding at the beginning of the dry period.

Radiocarbon dating

Another artificial marker is the content of radiocarbon in individual growth zones. This method uses the atomic weapon effect (Nydal & Lövseth 1983). As a result of atomic bomb explosions, the concentration of atmospheric ^{14}C almost doubled between 1950 and 1965 and subsequently decreased until today. The ‘bomb peak’ of the mid 60s is detectable by radiocarbon measurements in any tree on earth which was growing at that time. Analogous to the cambial wounding method, growth periodicity can be proven by counting the number of rings between the radiocarbon-dated growth zone and the youngest growth zone under the bark. In the example given (Fig. 7) the radiocarbon concentration of growth zones of unknown age from different tree species growing in the Gran Sabana, Venezuela, was analyzed. Rings were taken at definite distances from each other (one ring between sample number one and two, three rings between sample number two and three and so on). The differences in the radiocarbon concentration of the samples in comparison with the curve of the radiocarbon level in the atmosphere allows the dating of the samples and provides the proof that rings are annual in nature. The methodical background and the results of investigations on Amazonian floodplain trees have already been presented in Worbes and Junk (1989) and Worbes (1989). The radiocarbon method is one of the safest tools for the dating of growth zones and, in consequence, growth dynamics if the use of cambial woundings is impossible.

Fire scars and pointer years

Natural scars in the wood are the result of cambial injuries caused by, e.g., fires. Investigations in forests in the Gran Sabana, Venezuela, which have often been af-

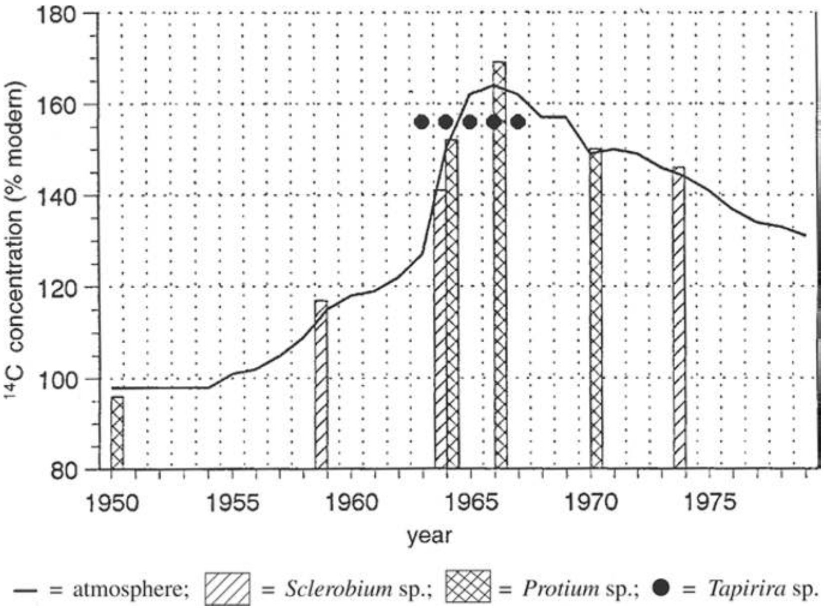

Fig. 7. Radiocarbon content in growth zones of trees from the Gran Sabana, Venezuela, and in the atmosphere (Worbes & Junk 1989). The bars represent the ^{14}C content of individual growth zones; only from *Tapirira guianensis*, Meliaceae, five very narrow rings of the assumed growing period around 1965 were analyzed together in one sample.

fected by intensive fires, show numerous fire scars in trees from different forest stands (Worbes 1996). Fire scars occur principally in physically damaged trees, where mechanical injuries have been overgrown (Fig. 8). Other trees can react by the formation of traumatic parenchyma bands, probably induced by crown damage (Fig. 9). Together with existing reports of the fire the scars serve to date the adjacent growth zones.

Pointer rings are growth zones with notable properties that differentiate them from adjacent rings. Conspicuous small or wide rings as well as rings with

Fig. 8. Cross section of Sapotaceae sp. from the Gran Sabana, Venezuela with an overgrown fire scar from 1946.

density fluctuations can be classified as pointer years (Schweingruber et al. 1990). Samples of *Pinus caribaea*, Pinaceae, from the Caparo forest in Venezuela show two small false rings at the beginning of the ring from 1977. Climate data from this region show two occasions of precipitation during the dry season in March 1977 with 50 mm rainfall in one or two days followed by dry periods of 2 to 3 weeks. During these alternating periods of rainfall and drought cambial activity started and stopped within short periods, resulting in two small rings of dense wood (Fig. 10). The occurrence of pointer years enables the crossdating of different samples because they are formed in response to an extreme external event that affected all trees in the same way.

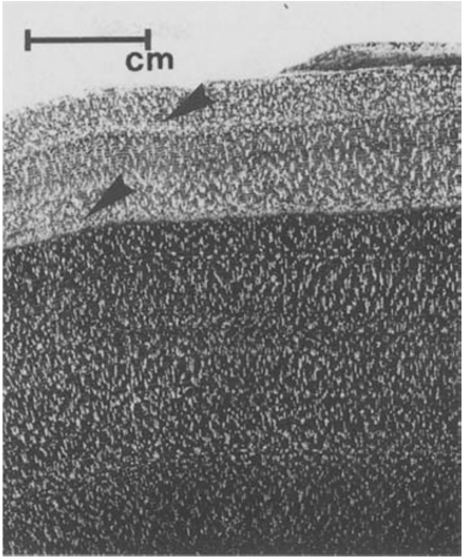

Fig. 9. Cross section of *Manilkara* sp., Sapotaceae, with traumatic parenchyma (arrows) induced by fires in the Gran Sabana, Venezuela.

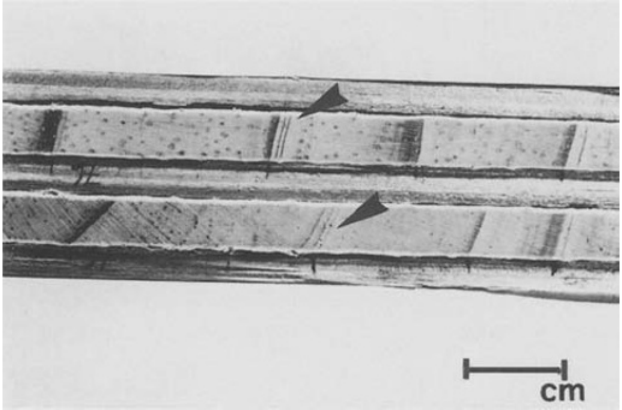

Fig. 10. Core samples of *Pinus caribaea*, Pinaceae, from the Caparo forest in Venezuela. At the beginning of the ring from 1977 two density variations were caused by rainfall in the dry period.

Ring-width analysis

Ring-width measurements can be made with a hand lens (Berlage 1931) or with tree-ring measurement devices (descriptions in Pilcher 1990). Successful crossdating of ring-width curves (Eckstein et al. 1981) gives a first indication of an oscillating external triggering factor of the growth rhythm. Crossdating means, in this case, the comparison of different tree-ring curves in order to recognize unique patterns of wide and narrow rings (Pilcher 1990). Crossdated ring-width curves can be summarized to a mean curve either for one species (Berlage 1931; Pumijumnong et al. 1995) or, in cases where different species have the same growth pattern (Fig. 11), even for different

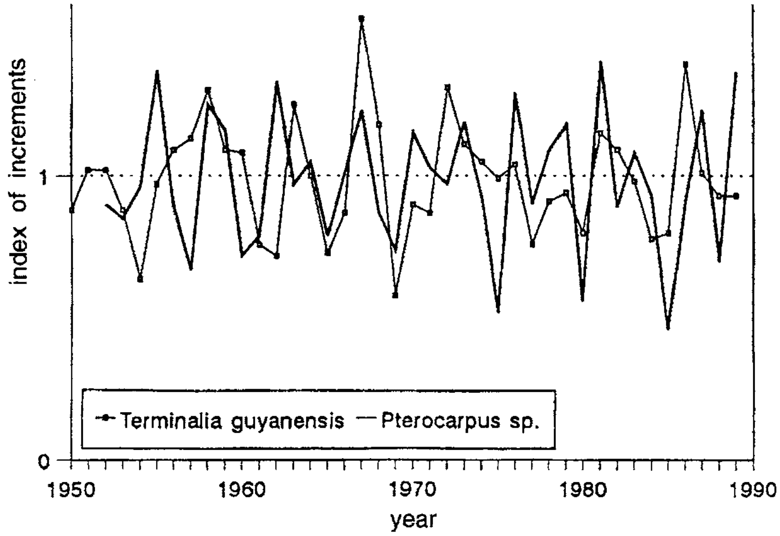

Fig. 11. Index ring-width curves of two species (mean of 6 individuals each) from the Caparo forests in Venezuela.

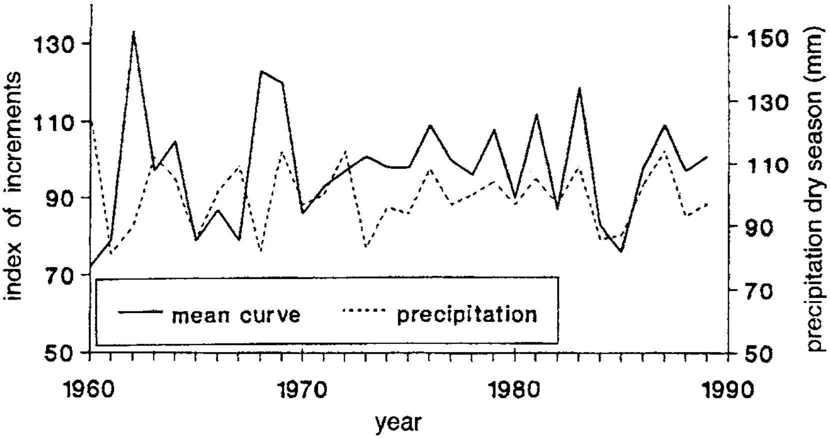

Fig. 12. Index ring-width curves of seven species (n total = 31) from the Caparo forests (line) in Venezuela and the time series of precipitation in the extended dry season (December–April) (dotted line).

species (Fig. 12). For the comparison with climatic events ring-width curves must be transformed into index curves (Cook & Briffa 1990). Precipitation data are usually documented as the monthly sum of precipitation. Time series of monthly data can be compared with tree-ring time series by regression analysis to show the influence of a single month's precipitation on ring width (Jacoby & D'Arrigo 1990). Berlage (1931) showed good correlations between the length of the dry seasons and ring-width variation in *Tectona grandis* trees from Java. The length of the dry seasons can be estimated indirectly from the sum of precipitation during the dry season and the precipitation of the transition months between the dry season and the rainy season. For trees from a forest on the Rio Caparo in Venezuela tree-ring series and time series of precipitation in the extended dry season correlate with a regression coefficient of 0.72 (Fig. 12).

X-ray densitometry

X-ray densitometry was originally applied to tropical species to identify ring boundaries due to differences in density between earlywood and latewood, if they are hardly visible macroscopically. However, in contrast to softwoods, the complex wood structure of hardwoods with zones of dense fibres alternating with parenchyma and vessels causes rapidly oscillating intra-annual density variations, which are often not distinguishable from the density variations at the ring boundaries (Mariaux 1967; Vetter & Botosso 1989). However, from numerous investigations in the temperate zones it is known that annual time series of wood density variations contain a strong climatic signal (Schweingruber et al. 1988). Therefore we constructed equipment for density measurements which allows the direct observation of X-ray photographs and the interactive marking of the ring boundaries in the data field during the density measurement (Worbes et al. 1995). We investigated trees from the Amazonian floodplains with distinct ring boundaries. From the resulting density measurements we calculated annual time series of minimum, maximum, mean, earlywood, and latewood densities. The time series of maximum density showed the best correlation with the time series of the length of the flood-free period (Fig. 13).

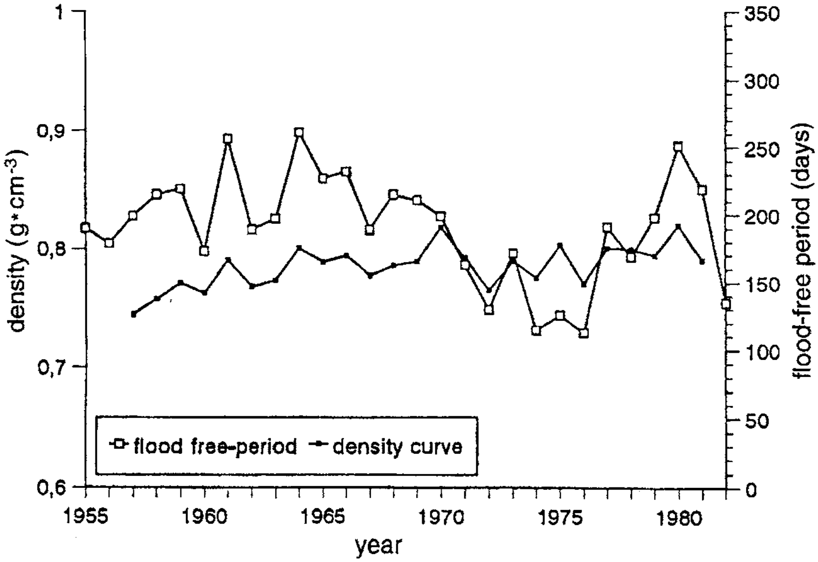

Fig. 13. Time series of maximum wood density in rings of *Swartzia polyphylla*, Caesalpiniaceae, from the Amazonian floodplain forest and flood-free period in days (adopted from Worbes et al. 1995).

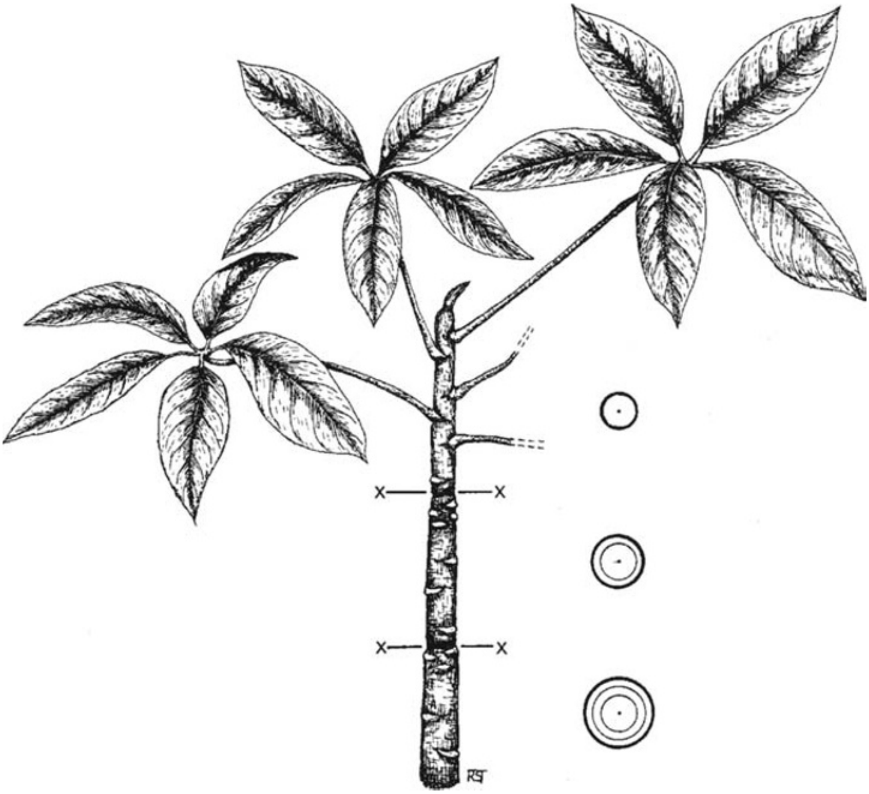

Fig. 14. Three-year-old seedling of *Pseudobombax munguba*, Bombacaceae, Amazonian floodplain forest with leaf bud scars between annual shoot sections (x–x); on the right side cross sections of the shoot are symbolized.

Stable isotopes

The variation of stable isotope concentrations in tree rings of the temperate zones was traced back to variations in climate (Long 1982; White 1983). The investigation of the annual variation of deuterium (D) and ^{13}C in the rings of *Swartzia laevicarpa* from the Amazonian floodplains showed no correlation with the inundation patterns. A weak correlation was found between the fluctuation of D in the latewood and the latewood density. The measurement of the stable isotope content in wood is very expensive and time consuming. More basic research on the influence of climate on the uptake of isotopes in the plants is necessary before the technique can be efficiently used for climatological investigations in the tropics.

Periodical shoot extension

From the existence of rhythmic radial growth it is likely to conclude that shoot extension is likewise periodical. This fact is well known for the temperate zones (Rauh 1939) but has only been proven in two cases for woody species in the tropics (Hallé &

Martin 1968; Gil 1989). The triggering factor and the time period of the growth rhythm in the tropical examples remained unclear. Periodically formed shoot segments can be identified by leaf bud scars (Fig. 14) or branching patterns. In species with annual rings, ring counts at cross sections easily prove the existence of annual shoot extension. Species from the Amazonian floodplains as well as species from non-flooded forests in Venezuela (*Cordia apurensis,* Boraginaceae, *Cecropia* sp., Moraceae, *Terminalia guianensis*, Combretaceae) show an annual periodicity of shoot elongation. This enables the easy and non-destructive age determination of seedlings and regeneration in tropical forests with a seasonal climate.

CONCLUSIONS

Most of the methods presented here serve to prove the existence of annual rings in the wood of tropical trees. For tropical regions with annual floodings or predictable dry seasons the proof has meanwhile been presented many times. In regions with short dry seasons (less than two months) or indistinct dry seasons (monthly precipitation > 60 mm) dendrochronological investigations still require the exact proof of the nature of growth periodicity. In cases of doubt different methods should be combined.

The methods described are well developed and it seems that there is no urgent need for more methodological research at the moment. There is, however, a great need for these methods to be applied in investigations in tropical forests. Dendrochronology in the tropics can cover a wide span of applications from climatology (Berlage 1931; Buckley et al. 1995), estimation of wood increment (Worbes 1994), and the analysis of the dynamic development of tropical forests (Worbes et al. 1992).

ACKNOWLEDGEMENTS

The investigations were carried out in cooperation with the Working Group Tropical Ecology of the Max-Planck Institute for Limnology, Plön, Germany, the Instituto Nacional de Pesquisas da Amazônia, and the Universidad de los Andes, Merida, Venezuela. They were financially supported by the Deutsche Forschungsgemeinschaft (DFG) and the Stiftung Volkswagenwerk. I am in debt to D. Eckstein for his assistance concerning the contents, language, and layout of the manuscript.

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