

General discussion and summary

Tree rings in tropical trees

Many tropical ecologists have long believed that tropical rain forest trees do not form annual tree rings (cf. Lieberman et al. 1985, Whitmore 1998), due to a lack of seasonal climate in tropical regions. In this dissertation, I proved that all six tree species included in my study do form annual rings. Evidence of the annual nature of rings was obtained by correlating ring width and monthly rainfall data for four of the six species and for two other species by counting rings on trees of known age and by radiocarbon dating (chapter 2). The trigger of tree ring formation in the north of Bolivia is probably a growth cessation during the annual dry season of about 3 months (< 50 mm rain per month). During this dry season tree growth is periodically limited by shortness of water resulting in the formation of annual rings and the study species either completely lose their leaves for several weeks (deciduous) or replace their leaves in a short period (brevi-deciduous).

I used annual tree rings of six study species to reconstruct historical growth patterns and determine tree ages. Historical growth patterns were used to study rainfall-growth relations (chapter 2) and to analyze temporal patterns of growth of juvenile trees towards the canopy (chapter 3). I also used the lifetime growth data of four species to study autocorrelated growth and investigate its significance to the genesis of size/age variation among trees (chapter 4). Finally, ring data were used to estimate future timber yields and evaluate potential for sustained timber yields of four of our species, which are exploited for timber (chapter 5). This chapter summarizes the main results of the research and provides a generally discussion on the theme.

Tree growth and rainfall

Water availability influences tropical tree growth, not only as a result of seasonal water deficits during the year, but also because of variation in rainfall among years (chapter 2). In four of six study species, variation in diameter growth (i.e., ring widths) among years was partially determined by inter-annual variation in rainfall. There was a positive relation between diameter growth and the amount of rainfall during several months of the year indicating that rainfall can be limiting to tree growth even in moist tropical forests.

Rainfall influenced growth similarly in three of the four species, which all were sensitive to the amount of rain during the early rainy season. Thus, diameter growth was higher (i.e., wider rings) when those months were relatively wet and was lower when they were relatively dry, when compared to other years. These first months of the rainy season are probably most important to tree growth as this is the start of the growing season and water reserves in the soil are low after the prolonged dry season of three months. Hence, diameter growth in the early rainy season is strongly rain-dependent, while growth later is less limited by rainfall. Also, trees probably grow more in the early rainy season compared to the late rainy season when a higher proportion of carbohydrates is probably stored. In *Cedrela odorata*, we found a different pattern: its growth was most dependent on the amount of rain in the transitional months from the previous rainy season to the dry season. This pattern is probably explained through storage of reserves during this period, which are

used to enhance growth during the next growth season. These results showed that tree growth even in tropical rain forests can be limited by rainfall and that species might differ in their response to rainfall pattern.

Getting to the canopy

How do juvenile trees in the dark understorey of tropical rainforests reach the canopy? A large share of trees in the understorey of tropical rain forests is highly limited by light, and grows at a slow pace. At these low growth rates it would take very long to attain large stature unless these trees are released from low light by an opening in the canopy. Many non-pioneer tree species are thought to require such releases to reach the canopy (Denslow 1980; Brokaw 1985). This gap requirement is hard to quantify, as long periods of growth data are needed. Tree ring analysis provided a solution to this impediment by revealing historical growth patterns of the entire growth trajectory from seedling to adult tree (chapter 3).

Results on temporal growth patterns of four tree species showed that canopy trees did not reach the canopy by slow and steady growth, but rather by irregular patterns of growth releases and suppressions. The majority of the trees attained a position in the canopy after one or more growth spurts, which were probably caused by temporal variation in light availability, due to canopy openings. The temporal pattern of this replacement seemed to take place by frequent, small-scale disturbances caused by the death of individual trees (cf. Runkle 1982), rather than by large-scale catastrophic disturbances destroying large forest patches and resulting in single-aged cohorts of trees (cf. Zimmerman et al. 1994).

Tropical rain forest tree species vary in their degree of shade tolerance and in their responses to high-light conditions (Hartshorn 1978; Chazdon et al. 1996; Canham et al. 1999), resulting in interspecific differences in the growth trajectory towards the canopy. We looked for such differences for four tree species. To this end, we identified four different canopy accession patterns: (a) steady growth without major growth changes, (b) growth by one growth release event, (c) growth by one suppression event, or (d) growth by several release and suppression events. We also evaluated the length of consecutive periods of relatively slow growth and used this as an indicator of the ability of species to survive periods of suppressed growth (cf. Canham 1985; Orwig & Abrams 1994; Landis 1999).

There were clear differences between species: trees of *Cedrela* and *Peltogyne* grew into the canopy through three different patterns in nearly equal proportions, whereas *Cedrelinga* predominantly entered the canopy through one major growth release. *Amburana* had high growth rates as a juvenile, suggesting that it is often located in gaps in early life stages. Species also differed in the lengths of slow-growth periods they experienced. *Cedrela* and *Peltogyne* showed long periods of relatively slow growth (~40 y with < 2 mm/y), while the other species lacked such long periods. The absence of long periods of low growth are probably attributable to low survivorship in the shade, as juveniles that have experienced longer periods of suppression probably have died and are thus not present in our sample.

These differences are indicative for life-history differences among the four non-pioneers tree species and suggest differences in degree of gap-dependence (or shade-tolerance) and differences in growth responses to gaps. This study shows how ring analysis can be used to quantify gap dependence of rainforest trees, and thus further our understanding of life history differences which cannot be obtained from short-term data.

Autocorrelated tree growth

Tropical forest trees show high variation in growth rates both among and within trees. In demographic and population studies this variation is often neglected or considered to be random. We proved, however, that growth rates are not randomly distributed among trees and also not randomly distributed within individual trees over time (chapter 4). Instead, some trees are persistently better performers than others and growth rates tend to be similar between subsequent years.

Usually, autocorrelated growth is calculated over all individuals of the population by correlating growth during one time interval with growth during a subsequent interval. We refer to this type of autocorrelated growth using the term *total autocorrelated growth*, which is made up of two components: *within-tree autocorrelated growth* and *among-tree autocorrelated growth*. Within-tree autocorrelated growth concerns temporally correlated growth within an individual tree. Among-tree autocorrelated growth concerns the correlation of growth rates among different trees in a population, and differs from total autocorrelated growth, as it does not include the temporal correlation of growth of individual trees.

Among-tree autocorrelated growth was strong and long-lasting: fast-growing trees tend to maintain high growth rates for long periods. Total autocorrelated growth was high (Pearson's $r \sim 0.75$) between growth rates of subsequent years and decreased gradually at larger time lags. At time lags of 20 years growth rates were still positively autocorrelated in some species.

Taking apart the two components of total autocorrelated growth (within-tree and among-tree) provided important insights into the causes and processes that determine autocorrelated growth. In smaller trees within-tree autocorrelated growth was high and contributed strongly to total autocorrelated growth, whereas within-tree autocorrelated growth was low for larger trees. The higher within-tree autocorrelated growth in smaller trees was largely caused by periods of suppression and release. These were lacking in large trees (chapter 3). In figure 1, an example of temporally autocorrelated growth within one *Cedrela* tree is shown. The upper panel of the figure (Fig 1A) shows the growth trajectory and the lower panels show correlation of growth data of consecutive years. The distinct periods of high and low growth rates in the smaller trees (0-20 cm diameter) clearly led to higher positive temporal correlates in growth (cf. Fig 1B) compared to larger trees (40-60 cm diameter, Fig 1C). Temporal variation in growth rates of large trees was highly variable from year to year and for a substantial part determined by annual variation in rainfall (chapter 2). Annual variation in rainfall is temporally less correlated than variation in light experienced by juvenile trees growing in the understory. Factors that may cause temporal correlates in growth of large trees include recovery from physical damage and lag effects due to storage of carbon reserves. Knowing the importance of these factors for (persistent) growth variation among trees is useful to understand tree ecology and to develop more realistic growth models.

Implications of autocorrelated growth for age estimates and growth models

Persistent growth differences among trees should be included in growth models, as they have important consequences for calculating long-term growth, age (chapter 4) and timber yield (chapter 5). Such persistent differences can be incorporated by explicit simulation of

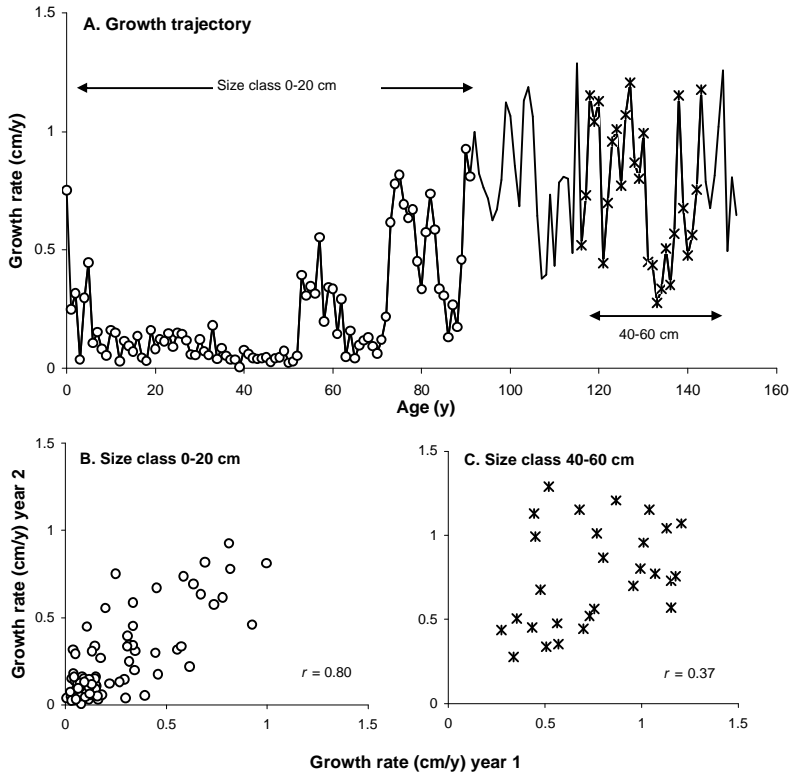


Figure 1

Temporal autocorrelated growth within a single tree of *Cedrela odorata*. Upper panel (A) shows the growth trajectory and the lower panels (B,C) show the correlation between growth in one year and growth in subsequent year for the size class 0-20 cm in diameter (left figure, B) and 40-60 cm in diameter (right figure, C). Note that the higher correlation in the smaller size class is caused by the alternating periods of slow and fast growth at these sizes.

the underlying processes, but this requires detailed understanding of mechanisms by which environmental factors influence tree growth. Such information is often lacking in tropical trees and therefore simple growth models with low data requirements are usually applied. Incorporation of autocorrelation in those models could be a useful tool leading to persistent variation among trees and more realistic predictions of tree age variation (chapter 4).

One of the most important consequences of autocorrelated growth is that persistently slow-growing trees have a higher accumulated risk to die before reaching large sizes compared to fast-growing individuals (chapter 4). For example, the accumulated total mortality chance for a slow growing *Cedrela* tree taking 120 years to grow to 30 cm in diameter is 91%, while a tree that takes only 30 years to reach 30 cm in diameter has a much lower mortality chance of 45% (assuming annual mortality rate of 2%). Hence, fast growing trees are more likely to reach mature sizes and above average-growth rates should be used to estimate tree ages and to calculate timber yields.

To the extent that trees which successfully have reached the canopy had above-average growth rates, ages obtained by tree ring analysis are expected to be lower than those based

on average growth rates. The ages calculated for our study species are indeed lower than most tree ages projected for tropical trees, but direct comparisons of observed and projected ages for the same species and for the same area are required. I compared the mean growth rates from permanent sample plots with those derived from ages of large trees using tree ring analysis or radiocarbon dating (Fig 2). As expected, for most species, growth predicted by ring or radiocarbon dating on large trees was higher than that of extant trees in permanent plots. This suggests that large trees indeed have had above-average growth rates. Similarly, other studies found that indirect age estimates were higher than those inferred from tree rings (Baker 2003; Baker et al. 2005) or by other methods (Terborgh et al. 1997; Martinez-Ramos & Alvarez-Buylla 1998). These results suggest that median or mean growth rates tend to overestimate tree ages. Many authors recognize this and therefore used above-average growth rates (cf. Clark & Clark 1992; Condit et al. 1993; O'Brien et al. 1995; Terborgh et al. 1997; Laurance et al. 2004). However, a basis for the degree of age adjustment is missing. Inclusion of realistic levels of autocorrelated growth may help improving age predictions and growth models. Validation of these models with independent age determinations is required to assess the accuracy of model output.

Incorporation of autocorrelated growth also has important consequences for estimates of timber volume growth. First, tree growth will be higher, resulting in higher timber volume estimates, as explained above. Second, when allowing for realistic variation in long-term growth rates among trees, also higher estimates are obtained compared to a situation when deterministic growth rate are used (chapter 5). This difference is due to the small proportion of fast-growing trees, which contribute disproportionately to timber volume growth when allowing for variation in the simulations.

Autocorrelated growth also plays an important role in population models. Often, the demography of tropical forest tree species is analyzed using matrix projection models (Zagt 1997; Zuidema 2000b; Caswell 2001). Positive autocorrelations that lead to markedly different growth trajectories violate the assumption of matrix model projections that implicitly assume that the performance of individuals is not influenced by their history (i.e., assumption of a one-step Markov process, Ehrlen 2000; Caswell 2001). A study by Pfister and Stevens (2003) showed that strong autocorrelated growth in combination with size-dependent growth and survival strongly affects the output of matrix models, leading to underestimated abundance of large individuals compared to individual-based models (Pfister & Stevens 2003). This asks for a cautious approach of matrix models or for

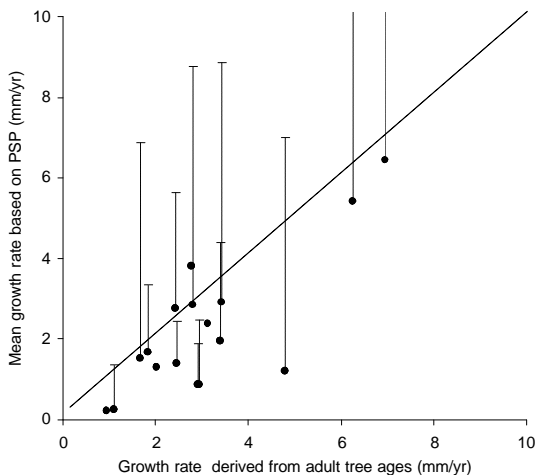


Figure 2

Comparison of mean growth rates of 19 species in the same region as derived by age determinations of adult trees from radiocarbon dating or from tree ring analysis (X-axis), and growth rates measured directly on all extant trees in permanent sample plots (Y-axis). The top of the error bars indicate the maximum growth rates (not for all species). Each point represents a different species, comparing studies of Laurance et al. (2004) vs. Chambers et al. (2001), Fichtler et al. (2003) vs. Clark & Clark (1992) and Condit et al. (1993), and comparisons in Ogden (1981) and in Zagt (1997). Nearly all points lie below the X=Y line, which shows that growth of successful trees has been faster than the mean growth of all individuals based on permanent sample plot measurements (extant trees).

adaptations of these models to account for autocorrelated growth. Individual-based models are probably more useful, as these are more suitable for dealing with autocorrelated growth (DeAngelis et al. 1993; Fox et al. 2001; Pfister & Stevens 2002; Bullock et al. 2004; Arets 2005).

How old are tropical rainforest trees?

This particular question has occupied scientists since long and has been the focus of several international workshops (e.g., Bormann & Berlyn 1981; Baas & Vetter 1989). Since the publication of findings of millenarian trees in the Amazon (Chambers et al. 1998) the debate about the likelihood of the occurrence of such very old trees increased and the accuracy of different ageing methods have been discussed (cf. Worbes & Junk 1999; Chambers & Trumore 1999; Williamson et al. 1999; Martinez-Ramos & Alvarez-Buylla 1999, 1998). In this paragraph, I will try to shed some light on this discussion by comparison of estimates of tree ages found in literature with results of this study and other tree ring studies.

Tree ages can be obtained by direct or indirect methods. Direct methods involve counting of annual tree rings or radiocarbon dating (the latter is only accurate for ages > 350 years, cf. Stuiver & Becker 1986), while indirect methods estimate tree longevity by projecting short-term growth rates over long time spans in a deterministic (Clark & Clark 1992; Condit et al. 1993) or stochastic fashion (Lieberman & Lieberman 1985, chapter 4), or by inferring longevity estimates from mortality rates (Condit et al. 1995b). Longevity estimates are generally obtained by determination of the ages of the largest trees in the population, assuming that these are also the oldest.

Comparison of published tree ages and estimated longevity reveal a remarkably large variation among ageing methods, areas and species (Table 1). Some of the longevity estimates in Table 1 seem unrealistic as they are extremely high in comparison to other ages or use dubious methods (e.g., Condit et al. 1995b). The projected age of nearly 4000 years old trees of 80 cm diameter in the rainforest of Queensland (Nicholson in Ogden, 1981) is the most extreme example. Radiocarbon dating of a smaller tree of the same species did not confirm these high ages (~620 years at 58 cm DBH).

Other extremely high age estimates are presented by Condit et al. (1995b) based on mortality rates of species. The use of such mathematical calculations assumes an equal mortality rate for all individuals in the population regardless of their age or diameter and assumes that trees do not grow senescent and may become infinitely old. Such assumptions are probably unrealistic as longevity of trees is dependent on investments in defenses and the rate of wood decay (Loehle 1988).

Omitting these unrealistic ages, we still observe a remarkably large variation in estimated tree longevity: average estimated longevity vary from 22 years for pioneer species (Martinez-Ramos & Alvarez-Buylla 1998) to ~1000 years for some non-pioneer canopy species (Laurance et al. 2004). Variation of longevity estimates within the broad group of non-pioneers (i.e., understory, subcanopy, canopy and emergent species) is high, and may differ 10 to 20-fold among species (cf. Lieberman et al. 1985a; Korning & Balsev 1994; Laurance et al. 2004). Our own results showed a somewhat lower, but still considerable variation in the maximum ages of species (70-430 years). These results demonstrate that maximum longevity vary greatly among different tree species, reflecting the high diversity of life histories of tropical rain forest tree species.

Table 1

Review of age-estimates of large broad-leaved tropical rain forest trees: mean observed and predicted ages for trees at particular diameter or at their maximum observed diameter (*Max*), and the maximum observed ages or maximum projected life-spans. The italic values are ages-projections based on above average growth rates (see subscript references).

Dating method	Mean ages (observed/projected)			Maximum ages (observed/projected)				
	Area	Age(s) (y)	Diameter (cm)	# species	Age(s) (y)	Diameter (cm)	Species	Source
<u>Radiocarbon dating (only >350 yr)</u>								
Central Amazon	370-750	80-180	8	1370 ± 80	180	<i>Cariniana micrantha</i>	Chambers et al (2001)	
Sarawak	625	60-126	1	>> 838 ¹	121	<i>Eusideroxylon zwageri</i>	Kurokawa et al. (2003)	
Brasil	-	-	1	440 ± 60	233	<i>Bertholletia excelsa</i>	Camargo et al. (1994)	
Eastern Australia	620-630	58-155	2	620 ± 100	58	<i>Xanthophyllum octandrum</i>	Ogden (1981) ²	
Guyana	-	-	1	350	110	<i>Chlorocardium rodiei</i>	Zagt (1997)	
<u>Ring analysis</u>								
Costa Rica	70-416	38-128	5	650 ³	156	<i>Hymenolobium mesoamericanum</i>	Fichtler et al. (2003)	
Cameroon			21	220	-	<i>Celtis zenkeri</i>	Worbes et al. (2002)	
<i>emergents</i>	85-124	> 10	2	124	-			
<i>canopy species</i>	42-91	> 10	12	220	-			
<i>understory sp</i>	41-70	> 10	7	146	-			
Zimbabwe	90,120	~35	1	>200	-	<i>Pterocarpus angolensis</i>	Stahle et al. (1999)	
Thailand	42-257	-	12	257	-	<i>Azelia xylocarpa</i>	Baker, pers comm..	
Bolivia	50-170	60	6	427	180	<i>Bertholletia excelsa</i>	This study	
<u>Projections</u>								
Costa Rica	284-608 92-125 ⁵	100	6	608	100	<i>Lecythis ampla</i>	Clark & Clark (1992)	
Costa Rica	-		45	52-442 ³	<i>Max</i>		Lieberman et al. (1985)	
Ecuador	-		22	54-529 ³	<i>Max</i>		Korning&Balsev (1994)	
Central Amazon	-		93	981 ⁴	<i>Max</i>	<i>Pouteria manaosensis</i>	Laurance et al. (2004)	
<i>Pioneers</i>	-			104±118 ⁴	<i>Max</i>			
<i>Subcanopy sp.</i>	-			326±118 ⁴	<i>Max</i>			
<i>Canopy species</i>	-			320±200 ⁴	<i>Max</i>			
<i>Emergents</i>	-			438±175 ⁴	<i>Max</i>			
<u>Panama</u>								
<i>Fastest growers</i>	32-111 19-69 ⁶	60	15	-			Condit et al. (1993)	
<i>Timber species</i>	140-250; 75-120 ⁶	60	7	-			Condit et al. (1995a)	
Panama	88-205 ⁷	30 m H.	8	-			O'Brien et al (1995)	
Australia	500-3955 253-2594 ⁵	20-140	11	3955	80	<i>Xanthophyllum octandrum</i>	Ogden (1981)	
Guyana	-		2	450-575	<i>Max</i>		Zagt (1997)	
Mexico	-		7	22-1030 ~600 ⁶	<i>Max</i>	<i>Brosium alicastrum</i>	Martinez-Ramos & Alvarez Buylla (1998)	
<u>Projections based on mortality rate</u>								
Panama	-			>35-2000	<i>Max</i>	<i>Swartzia simplex</i>	Condit et al (1995b)	

¹ Predicted life span is 1207 year; ² Data were presented by Ogden in this paper, but originated from data and projections executed by D.I.Nicholson; ³ Based on a combination of tree ring analysis and projections; ⁴ life-spans calculated from 10 cm diameter to the max observed diameter; Based on ⁴ above average growth; ⁵ on maximum growth rates; ⁶ on growth +SD; ⁷ at 30 meter height.

Comparison of different age estimation methods shows seemingly higher maximum ages by radiocarbon dating than the ages obtained by tree ring analysis. One reason for this difference is that radiocarbon dating is only reliable for trees older than 350 years (Stuiver & Becker 1986). Nevertheless, the highest ages obtained by tree ring analysis in this study

(430 years) and in Costa Rica (416 year; Fichtler et al. 2003) are clearly lower than the ages of ~1400 years in the Central Amazon (Chambers et al. 1998) that have been questioned by others (cf. Worbes & Junk 1999; Williamson et al. 1999; Martinez-Ramos & Alvarez-Buylla 1999). Two other high radiocarbon ages of tropical trees were found (cf. 838 years; Kurokawa et al. 2003 and 620 years; Ogden 1981), but these are not as high as the ages found by Chambers et al. (1998). Clearly, the findings of high age of more than 1000 years need to be confirmed by other methods. Laurance et al. (2004a) predicted that some trees in the central Amazon might indeed reach ~1000 years relying on indirect age estimates. Direct methods such as tree ring analysis, which can be applied to large sample sizes of trees, should give conclusive answers as to the existence and abundance of millennial trees in tropical rain forests.

Based on the reviewed ages, most species probably do not grow much older than 500 years, which is in concordance with maximum longevities of most broad-leaved temperate trees (cf. Loehle 1988). Those occasional species that do grow older are probably of very high wood density and extremely slow growth (eg. *Eusideroxylon*; Kurokawa et al. 2003) or occur in areas with low turn-over rates (eg. Chambers & Trumore 1999), such as the central Amazon (cf. Vieira et al. 2004; Malhi et al. 2004).

Use of tree rings to estimate timber yields

Tree ring analysis can be a good alternative to the use of short-term growth rate measurements in permanent sample plots and complex growth models for predicting timber volume growth. In chapter 5, we illustrated how historical growth data provide useful measures to evaluate whether sustained timber yields can be obtained. Ages of harvested trees give rough estimates on the times required to replace the harvested trees. Recuperation times to reach pre-harvest volumes after the first logging operation were calculated based on the densities of trees below the minimum cutting diameter. The obtained growth trajectories also provided measures on the size distribution of potential crop trees for the next harvest.

Timber yields after one cutting cycle were estimated in two ways: based on predicted ingrowth of trees from below the minimum cutting diameter ('prospective analysis'), and based on the historical ingrowth of trees that are currently above the minimum cutting diameter ('retrospective analysis'). Retrospective analysis has not been used before, to our knowledge. The two methods gave similar results for two of the four species, but somewhat different predictions for the other two species. These differences were probably due to the population size distributions of these species; higher densities of trees below the minimum cutting diameter give higher estimates using the prospective analysis, while higher adult tree densities give higher estimates with the retrospective analysis. The retrospective analyses can only be used in undisturbed populations for species that have continuous regeneration and do not depend on infrequent, large-scale disturbances. One of the most important assumptions of the retrospective analysis is that historical ingrowth is identical to future ingrowth, regardless of the available trees below the minimum cutting diameter. Nonetheless, this method might be a convenient tool for forest managers as it has low data requirements: no data on mortality rates are needed and tree densities are only needed for trees above the minimum cutting diameter, which are often available from forestry censuses.

Tree ring analysis has several advantages over the use of permanent sample plot data. First, the age estimates are calculated directly without involvement of complex growth models with many assumptions, and are therefore more accurate. Second, the growth rates obtained

from ring data are representative for trees that successfully reached the canopy and do not include the probably slower growing individuals that are less likely to reach the canopy. They also represent the commercially interesting part of the population and are therefore the data that should be used in calculations of timber estimates. Third, the lifetime growth rates of large numbers of trees allow accurate assessment of individual variation among trees in long-term growth and incorporating this intra-specific long-term growth variation resulted in higher and more accurate estimates of timber yield (chapter 5).

We believe that the use of tree ring analysis deserves to be included in the portfolio of approaches to evaluate tropical forest management as a complementary tool to permanent sample plot measurements. To forest managers one of the advantages of tree ring analysis is the short time period in which long-term growth data can be gathered by direct counting and measuring of tree ring on discs of harvested trees.

Our results indicate that it will be difficult to sustain timber yields for the study species. The mean ages of the harvested trees were between 90 and 166 years and the oldest harvested trees were even ~300 years, which is disturbingly high from a forestry perspective. Calculated recuperation times to replace initial volumes after the first harvest were long (40 to 80 years), and strongly depended on the abundance of trees below the minimum cutting diameter. Predicted timber yields at the next harvest were small compared to those in the first cut (20-30%) and sustained timber yields for these species under the current management regimes are not feasible unless cutting cycles are much longer than 20 years and/or silvicultural treatments are applied.

Strengths and limitations of tree ring analysis

In this dissertation, I showed for six tropical tree species the value of tree ring analysis as a tool to enhance our understanding of tropical forest ecology and I showed the applications to forest management purposes. The power of tree ring analysis will increase as reliable annual tree rings are found in more species and in more different areas. Estimates on the number of species in the study region in the north of Bolivia are about 50% of the species (Brienen & Zuidema 2003), and I expect rings of most of these to be formed annually.

For most species the collection of entire stem discs will be required for reliable dating of tree rings, due to the occurrence of vague or irregular rings (chapter 2). This imposes limitations to the use of tree ring analysis: in protected areas such discs can only be obtained from dead trees, and collection of large sample sizes is only feasible for timber species.

Tree ring analysis allows reconstructions of historical growth patterns, but no accompanying data on the exact growth conditions at those times. For example, we used historical growth patterns to detect growth changes indicative for canopy dynamics (chapter 4), but the detected growth changes might have had a variety of causes other than canopy dynamics, such as physical damage to trees, lianas, herbivory or diseases. The degree to which each of these factors contributed to the observed growth variation cannot be measured by tree ring analysis and clearly requires field observations. These field observations are required to determine the frequency and sizes of gaps needed for successful regeneration for each species. The combination of field observations and historical growth patterns will provide a new tool for the tropics to evaluate species requirements for regeneration into the canopy and differences in shade tolerance. Such methods could reveal important insights in differences in life history among species, which cannot be detected by using short-term growth data.

Outlook

In the tropics, tree rings have hardly been used to study forest dynamics, although it has great potential to fill some of the gaps in our understanding on tropical forests. Recently, tree rings have been used to reconstruct the disturbance history of a tropical rain forest in Thailand, revealing important information on the influence of such disturbances to maintaining species diversity (Baker et al. 2005). Clearly, such information is highly valuable to gain a better understanding of forest dynamics and deserves to be more widely applied in tropical forests.

Tree rings of tropical forest trees may also prove useful to study responses of tropical trees to climate change. There has been a intensive debate about the question whether increased tree growth and forest dynamism during the last three decades are caused by climate change (cf. Baker et al. 2004; Phillips et al. 2004; Lewis et al. 2004) or by other factors (i.e., recovering from some kind of disturbance, decadal scale oscillations in solar radiation, etc). Permanent sample plot measurements cover too short periods to provide conclusive evidence, but long-term historical growth data from ring analysis are likely to provide answers.

The relatively unexplored field of tropical tree ring research will likely prove more useful than hitherto expected and contribute significantly to disciplines ranging from forest ecology to climatology. There is still a multitude of questions open to which the past may hold the answer.

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