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REVIEW

Dendroecology in the tropics: a review

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Abstract Over the last decade the field of tropical dendroecology has developed rapidly and major achievements have been made. We reviewed the advances in three main themes within the field. First, long chronologies for tropical tree species were constructed which allowed climate reconstructions, revealed sources of climatic variation and clarified climate–growth relations. Other studies combined tree-ring data and stable isotope (^{13}C and ^{18}O) measurements to evaluate the response of tropical trees to climatic variation and changes. A second set of studies assessed long-term growth patterns of individual trees throughout their life. These studies enhanced the understanding of growth trajectories to the canopy, quantified autocorrelated tree growth and yielded new estimates of tree ages. Such studies were also used to reconstruct the disturbance history of tropical forests. The last set of studies applied tree-ring data to growth models. Tree-ring data can replace diameter

measurements from research plots, provide additional information to construct population models, improve timber yield models and validate model output. Based on our review, we propose two main directions for future research. (1) An evaluation of the causes and consequences of growth variation within and among trees and their relation to environmental variation. Studies evaluating this directly contribute to improved understanding of tropical tree ecology. (2) The simultaneous measurement of widths and stable isotope fractions in tree rings offers the potential to study responses of trees to climatic change. Given the major role of tropical forests in the global carbon cycle, knowing these responses is of high priority.

Keywords Tree rings · Climate–growth relations · Tropical forest dynamics · Long-term growth patterns · Tree age · Growth modelling

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Introduction

The occurrence of annual growth rings in the tropics has been denied for a long time (e.g. Lieberman et al. 1985). The absence of annual growth rings was thought to be a consequence of a lack of clear seasonality in the humid tropics. Yet, as early as 1927 the existence of annual growth rings in tropical trees had been described (Coster 1927). Since then it has become clear that annual rings are formed when tropical trees experience cambial dormancy in one period of the year due to unfavourable environmental conditions. Such a period can be the dry season in areas with distinct seasonality (e.g. Worbes 1999) and flooding periods in floodplain forests (e.g. Schöngart et al. 2002) and fluctuations in salinity in mangrove forests due to seasonality in precipitation and temperature (Chowdhury

et al. 2008). As seasonally dry forests, floodplain forests, and mangroves cover large part of the total tropical forest area, there is a large potential for the application of tree-ring analysis in the tropics. Even in evergreen forests successful tree-ring studies have been conducted in areas where a short dry period triggers annual ring formation (e.g. Dünisch et al. 2003; Fichtler et al. 2003).

Tropical tree-ring boundaries are often anatomically less distinct and sometimes less reliable than those in temperate zones (Worbes 2002). Climatic fluctuations within the seasons can cause formation of false rings (Priya and Bhat 1998), wedging rings are common (Worbes 2002), and also non-annual ring formation has been shown (Dünisch et al. 2003; Wils et al. 2009). Hence, the annual nature of the rings needs to be proven before tree-ring studies can be conducted. Over the last decades, the annual character of tree rings has been established for a large number of species in many tropical areas (e.g. Worbes 2002; Dezzeo et al. 2003; Brienen and Zuidema 2005), thus providing a sound basis for applying tree-ring analysis to tackle ecological questions.

In temperate zones, tree-ring analysis has provided a major contribution to the understanding of tree ecology, forest dynamics and climate–growth relations of trees. In the tropics the potential contribution of dendroecological studies may likewise be large, because there is a clear need for reliable age estimates (Martínez-Ramos and Alvarez-Buylla 1998; Worbes 2002), long-term tree growth data (Ashton 1981) and information on tree recruitment patterns. Such data are needed to provide insights into tropical forest ecology, to guide forest management and conservation practices and to evaluate the impacts of climate change on these forests.

Over the last decade, the field of tropical dendroecology has developed rapidly. Interesting ecological insights have been obtained from studies in this field, and important methodological advances have been made. For instance, the combination of tree-ring analysis with determination of stable isotope fractions in wood tissue offers new ways to reconstruct historical growing conditions of trees and understand their physiological responses to changing conditions. Also, tropical tree-ring data have been used to construct and validate tree growth models and population models.

Since the review of tropical tree-ring research by Worbes (2002) a large number of new studies has been published, many of which have yielded new ecological insights. Thus, the rapid development of this field asks for a review of recent achievements. Here we discuss recent findings from tropical dendroecology studies and provide an outlook to future challenges in this field. First, we briefly refer to the methodology in tropical tree-ring research. Then, we discuss eight themes that are of relevance from an ecological viewpoint. For each of these

themes we discuss the new ecological insights that tropical tree-ring studies have contributed so far.

Periodicity in tree growth and detection of tropical tree rings

In most tropical areas seasonal changes in environmental conditions are less pronounced than in temperate forests. As a result, the periodicity in tree growth needs to be evaluated to prove annual ring formation and field sampling strategies need to be adjusted. Due to the presence of wedging rings, working with stem discs rather than increment cores is generally recommended (Worbes 2002). This implies that sampling may be confined to logged areas or to trees that died naturally. However, for some tree species measuring ring widths from increment cores has been successful.

Numerous techniques have been proposed and applied to evaluate the annual nature of tropical tree rings. While the aim of this review is not to extensively describe and discuss these techniques, we briefly mention them. A first technique to evaluate the annual character of ring formation involves measuring the periodicity of tree growth through dendrometer measurements (Bräuning et al. 2009; Krepkowski et al. 2010; Volland-Voigt et al. 2010). By measuring stem diameter increase and shrinkage over the seasons, insight in intra-annual growth dynamics can be obtained. Periodicity in tree growth can also be evaluated by looking at anatomical changes after cambial wounding, and counting the number of rings after pinning the cambium (e.g. Lisi et al. 2008). A second method is radio-carbon dating. Nuclear tests in the 1960s increased the level of ^{14}C in atmospheric CO_2 , allowing the possibility to rather precisely date trees of <50 years old (e.g. Worbes and Junk 1989; Hua et al. 1999). This method has been applied in various studies and may assist in the anatomical recognition of ring boundaries (Fichtler et al. 2003; Soliz-Gamboa et al. 2010). Third, ring widths of trees from a population can be cross-dated, to assess whether synchronous ring formation occurs, which allows relating tree growth to climatic variables (e.g. Wils et al. 2010). For various tree species annual ring formation has been shown through correlating growth with rainfall (e.g. Couralet et al. 2005; Baker et al. 2008). In mangroves in particular, evaluating annual periodicity in tree growth and relating growth to climatic variables can be challenging, as multiple factors have been shown to influence growth (Robert et al. [this issue](#)). For the mangrove species *Rhizophora mucronata* annual ring formation has been shown using cambial wounding (Verheyden et al. 2004).

Finally, there are a number of methods that have been proposed to detect rings for tree species that do not form

distinguishable ring boundaries. Many of these methods are still in a rather experimental phase, but often with promising results. For instance, periodicity in tree growth has been shown by evaluating the periodicity in vessel density for a mangrove species (Verheyden et al. 2005). Similarly, intra-annual fluctuations in stable isotope concentrations have been evaluated, which indicated periodicity in tree growth (Poussart et al. 2004; Anchukaitis et al. 2008; Ohashi et al. 2009; Pons and Helle [this issue](#)).

Climate–growth relations

For numerous species it has been shown that tree radial growth is influenced by climatic factors (Fig. 1). Through identifying the common, temporal growth pattern in a population of trees and relating this pattern to rainfall data, species-specific responses to rainfall can be determined. Seasonally dry forest species respond to rainfall in different ways (Fig. 1). Tree species have been shown to respond to total annual rainfall, total rainfall in the rainy season, rainfall in the dry season, rainfall in the transition and a relation between growth and rainfall in the previous year has been found (Fig. 1). These species-specific responses may reflect differences in growth strategies among species (cf. Enquist and Leffler 2001; Couralet et al. 2010). Also negative correlations between growth and rainfall have been reported (e.g. Buckley et al. 2007; Soliz-Gamboa et al. 2010), which may indicate a response to higher light levels due to low cloud cover. Most studies report correlations between growth and rainfall, as temperature shows in general little interannual variation in tropical areas. For some species, nevertheless, a correlation was found between both growth and temperature and growth and precipitation (e.g. Trouet et al. 2001; Buckley et al. 2007; López and Villalba 2010). In Amazonian floodplain forests tree growth was found to be correlated with the water level in the non-flooded period (Dezzeb et al. 2003), or with the length of the non-flooded phase (Schöngart et al. 2005).

Climatic conditions may not only be driving tree growth, but could also influence tropical forest dynamics. In tropical pine forests in northern Thailand, the relation between climatic variability and recruitment was evaluated using tree-ring analysis for two *Pinus* species (Zimmer and Baker 2009). Although recruitment was not directly related to climate, periods of several years of cool and wet conditions were associated with enhanced recruitment. These results indicate that climate may influence patterns of tree establishment (Zimmer and Baker 2009).

The existence of a relationship between growth and precipitation provides the possibility to reconstruct historical precipitation patterns. Because the meteorological records of precipitation in the tropics do rarely span more

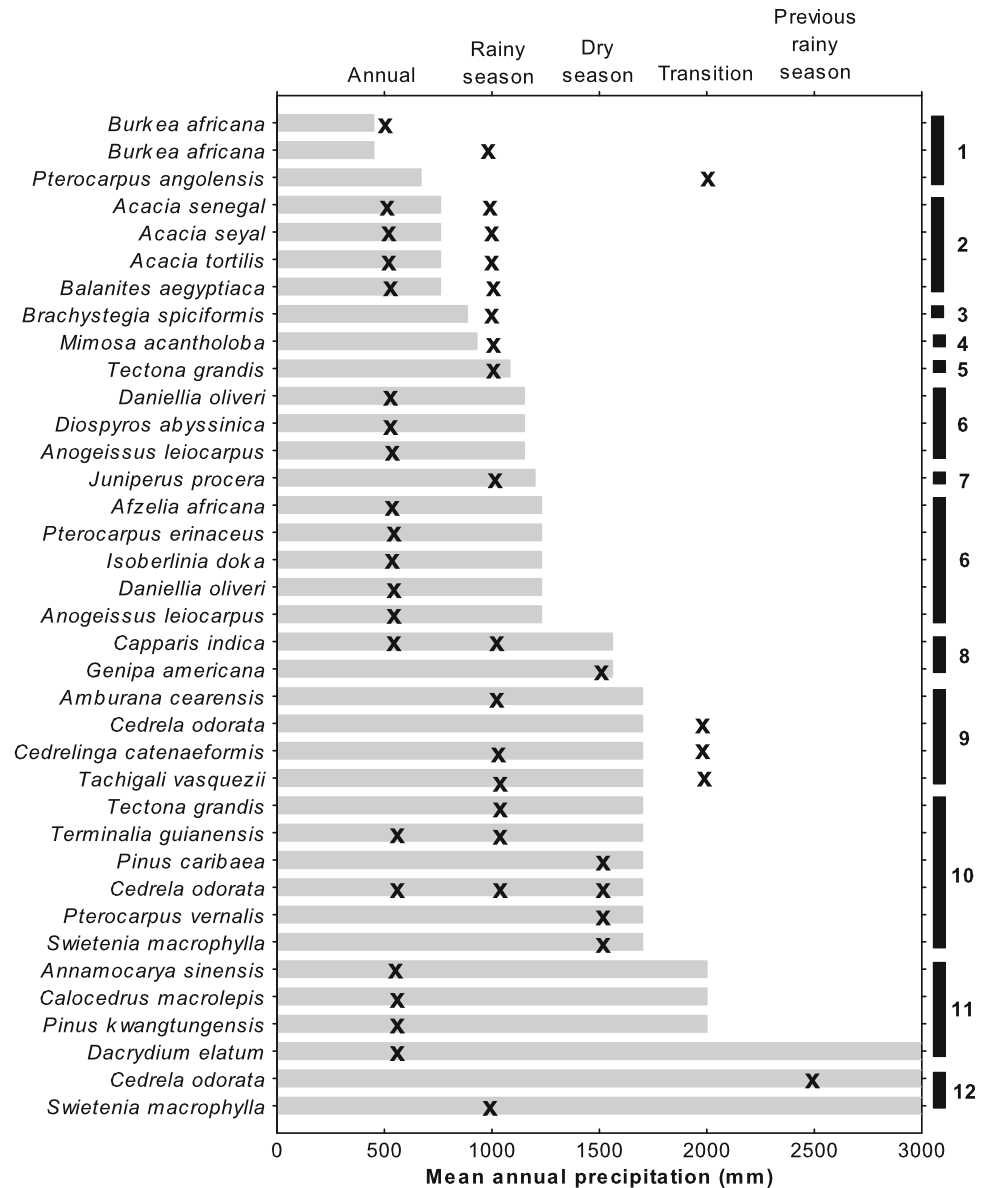
than a few decades, tree-ring based climate reconstructions may strongly enhance our insights about historical climate. By now, several long chronologies have been established, varying from a length of ~150–200 years for some species (Schöngart et al. 2006; Therrell et al. 2006; Sass-Klaassen et al. 2008), to almost 400 years for *Macrolobium acaciifolium* in an Amazonian black-water floodplain forest (Schöngart et al. 2005). Apart from responding to rainfall and temperature, trees also respond to larger-scale climatic fluctuations such as the El Niño Southern Oscillation (ENSO; e.g. Schöngart et al. 2004; Rodríguez et al. 2005; Therrell et al. 2006; Gebrekirstos et al. 2008). As climate reconstructions have been reported now for tropical Africa, South America, and Asia, large-scale climatic fluctuations can be identified. The reconstructed climatic fluctuations in the Central Amazon could be largely recognized in African forests as well (Schöngart et al. 2006). In general, a trend towards drier conditions in more recent times has been observed. Increasing aridity has been observed in West Africa over the last 160 years (Schöngart et al. 2006) and also in Amazonia the frequency of El Niño-induced droughts increased over the last two centuries (Schöngart et al. 2004).

The recent development of the Monsoon Asia Drought Atlas (MADA) by Cook et al. (2010) is a major step forward in the application of tree rings to the reconstruction of tropical climates. Their reconstruction of monsoon variability across Asia is based on >300 tree-ring chronologies from temperate, sub-tropical, and tropical Asian sites and provides an annually resolved, spatially explicit record of drought intensity over the past 1,000 years. The MADA provides a unique record of climate variability that can be compared to long-term records of sea surface temperature, ENSO, and other major drivers of regional climate variability. One of the key features of the monsoon variability that the MADA has identified is the occurrence of several intense, multi-decade droughts over the past millennium. Through reconstructing climate fluctuations in the past, it is possible to predict the response of tropical trees to future climatic change. For a Mexican dry forest tree species, for example, a growth decline ranging from 12 to 21% was predicted for the end of this century (Brienen et al. 2010a).

Pathways to the canopy

How do tropical trees grow to the canopy? Growth trajectories of canopy trees have been reconstructed with tree-ring analysis to tackle this question, and have revealed large variation in the way in which trees attain the canopy both among and within species (Baker and Bunyavejchewin 2006; Brienen and Zuidema 2006a). Many researchers have hypothesized that juvenile trees of canopy species

Fig. 1 Overview of observed climate–growth relations for some tropical tree species in seasonally dry tropical forests with different mean annual precipitation. x indicates a significant, positive correlation (Pearson's r , $P < 0.05$) with precipitation: either total annual precipitation, the precipitation in the rainy season, precipitation in the dry season, precipitation in a transition between the seasons or total precipitation in the rainy season of the previous year. Numbers at the right part indicate the source: 1 Fichtler et al. (2004), 2 Gebrekirstos et al. (2008), 3 Trouet et al. (2006), 4 Brien et al. (2010a), 5 Pumijumnong et al. (1995), 6 Schöngart et al. (2006), 7 Sass-Klaassen et al. (2008), 8 Enquist and Leffler (2001), 9 Brien et al. (2010), 10 Worbes (1999), 11 Zuidema et al. (2003)



would require at least one gap event to reach the canopy (e.g. Turner 2001). Brien and Zuidema (2006a) indeed found that trees of four non-pioneer species experienced on average 0.8–1.4 releases before attaining the canopy. Species differed in growth patterns towards the canopy, which suggests that the four non-pioneer species differ in shade tolerance (Brien and Zuidema 2006a). Similarly, Baker and Bunyavejchewin (2006) found large differences in canopy accession patterns among species in a seasonal tropical forest in Thailand. The most shade-intolerant species, *Melia azedarach*, reached the canopy with constant fast growth, whereas the shade-tolerant *Neolitsea obtusifolia* established mostly in low-light conditions and required at least one release to reach the canopy (Baker and Bunyavejchewin 2006). Importantly, they showed that almost none of the >100 individuals studied reached the

canopy by establishing in the understorey and growing into the canopy without the presence of a gap. A third study compared canopy accession patterns in a tropical dry and moist forest for the same tree species, *Cedrela odorata* (Brien et al. 2010c). In the moist forest more and stronger releases were found and a larger proportion of the juvenile trees showed suppressed growth. Thus, in the moist forest light availability may be governing canopy accession, while in dry forest, most likely, water availability is more important in determining growth patterns (Brien et al. 2010c).

Which trees are able to attain the canopy? Most juvenile tropical trees grow slowly, as light availability in the understorey is low (Chazdon and Fetcher 1984). Because slow-growing juveniles experience higher mortality rates (Wyckoff and Clark 2002), they may have a considerably

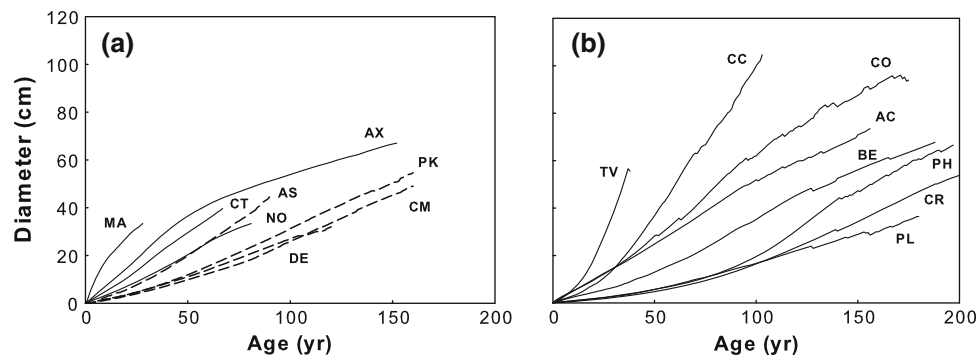


Fig. 2 Average growth-trajectories of tropical tree species from Thailand, Vietnam and Bolivia. Averages at a certain tree age were shown only if at least ten trees of a species which reached that age were included. **a** Tree species from Thailand (continuous lines) and Vietnam (dashed lines). Data for *Melia azedarach* (MA), *Azelia xylocarpa* (AX), *Chukrasia tabularis* (CT) and *Neolitsea obtusifolia* (NO) are adapted from Baker et al. (2005). Data for the Vietnamese species *Annamocarya sinensis* (AS), *Pinus kwangtungensis* (PK), *Calocedrus macrolepis* (CM), and *Dacrydium elatum* (DE) are

adapted from Zuidema et al. (2010). **b** Bolivian tree species. *Tachigali vasquezii* (TV); *Cedrelinga catenaeformis* (CC); *Cedrela odorata* (CO); *Amburana cearensis* (AC); *Bertholletia excelsa* (BE); *Peltogyne cf. heterophylla* (PH); *Clarisia racemosa* (CR); *Pseudolmedia laevis* (PL). Data for TV, CC, CO, AC and BE are adapted from Brienen and Zuidema (2006a), data for PH and CR are adapted from Rozendaal et al. (2010c), and data for PL are from Rozendaal (2010)

lower chance to attain the canopy compared to the fast-growing individuals (e.g. Enright and Hartshorn 1981). This would mean that successful trees have grown faster as juveniles, compared to juvenile trees at this moment in the forest ('juvenile selection effect'). Rozendaal et al. (2010a) compared growth rates of extant juvenile trees with growth rates of trees that made it to the canopy at the time they were young and of the same size. For three out of five species juvenile growth rates increased with extant tree size, implying that for these three species fast juvenile growth may be essential to reach the canopy.

As the number of studies reconstructing lifetime growth patterns is very limited, general patterns in growth strategies towards the canopy cannot be derived yet. However, the few studies that have been performed do show that long-term growth patterns differ strongly across the studied species (cf. Fig. 2; Baker and Bunyavejchewin 2006; Brienen and Zuidema 2006a; Zuidema et al. 2010) and across forest types (Brienen et al. 2010c). Tree-ring studies can play an important role in revealing these growth patterns.

Ages of tropical trees: an age-old debate

The report that millennia-old trees are present in the Amazon (Chambers et al. 1998), led to an intensive debate about the accuracy of different age estimation methods and the actual occurrence of such old trees (cf. Martínez-Ramos and Alvarez-Buylla 1998; Worbes and Junk 1999). Probably, the importance of very old trees for carbon cycling has been overestimated, as those trees will occur at very low densities in the forest (Martínez-Ramos and Alvarez-Buylla 1998; Williamson et al. 1999). Nevertheless, also in

other studies some very old trees were found using ^{14}C -dating (e.g. Kurokawa et al. 2003). The primary limitation of ^{14}C -dating is that the atmospheric ^{14}C values for the period from 1650 to 1940 have multiple peaks with similar values making it difficult to age wood samples correctly (cf. Martínez-Ramos and Alvarez-Buylla 1998). Most canopy trees of today are likely 70–350 years old; therefore ^{14}C -dating has not been widely applied in tropical ecology.

A second approach to obtain tree ages—the use of growth data from permanent sample plots—similarly resulted in very high estimates (Martínez-Ramos and Alvarez-Buylla 1998). This is likely caused by the use of average growth rates in the calculations, which implicitly assumes that both slow-growing and fast-growing trees eventually reach the canopy (cf. Laurance et al. 2004). The application of age estimation methods that use above-average growth rates is justified by the recent finding of a 'juvenile selection effect' in tropical forest trees (Rozendaal et al. 2010a). Such a juvenile selection effect implies that fast-growing juveniles have higher chance of reaching the canopy compared to slow-growing juveniles in these species. Age estimations from growth models can be much improved by comparing outcomes with observed ages from tree-ring data for the same trees or tree species (Baker 2003; Brienen et al. 2006; Chien 2006). Baker (2003) developed age estimation methods for tropical trees based on such comparisons by testing them for temperate species with a varying degree of shade tolerance. Results of age projections can be improved by accounting for auto-correlated growth, which results in higher, more realistic, variation in tree ages (Brienen et al. 2006). A recent approach using plot data accounts for variation in growth

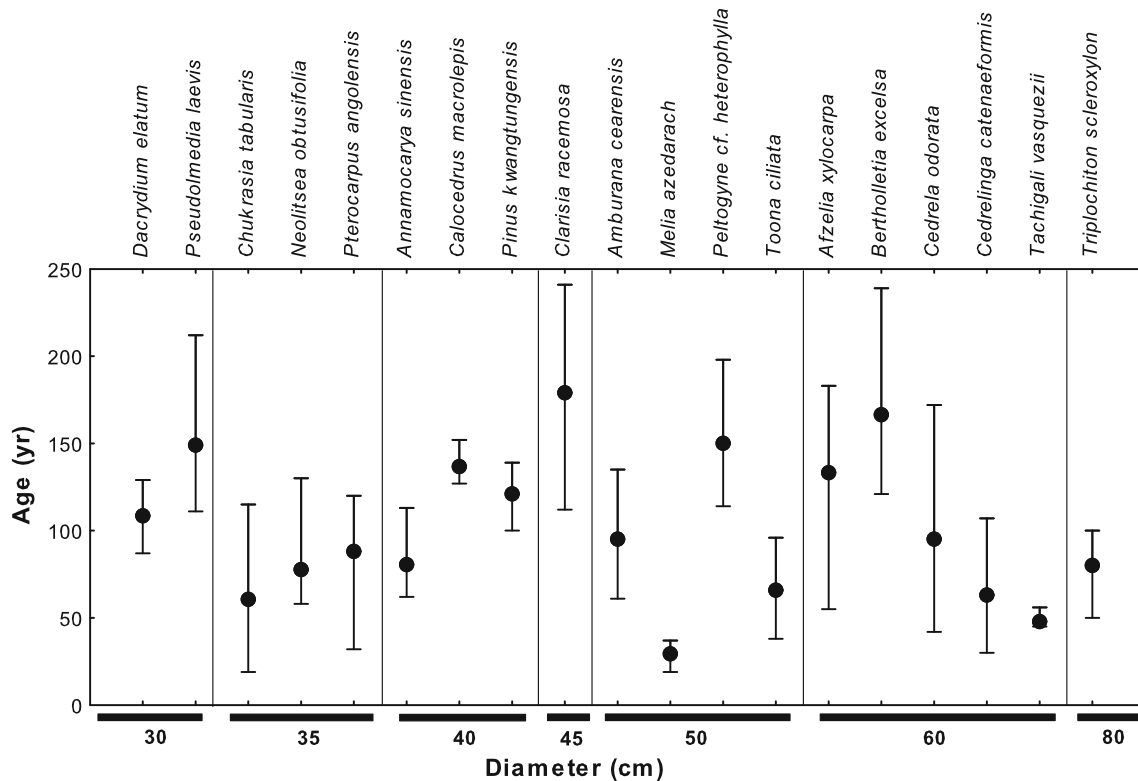


Fig. 3 Average and range in ages determined through tree-ring counts at a certain tree diameter for various tropical tree species from South America, Asia and Africa. Ages for *Annamocarya*, *Calocedrus*, *Dacrydium* and *Pinus* are obtained from Zuidema et al. (2010); for *Pseudolmedia* from Rozendaal (2010); for *Chukrasia*, *Melia* and *Toona* from C.A. Nock (unpublished data); for *Neolitsea* and *Afzelia*

from Baker et al. (2005); for *Pterocarpus* from Stahle et al. (1999); for *Clarisia*, *Cedrelinga* and *Peltogyne* from Rozendaal et al. (2010c); for *Amburana* and *Cedrela* from Brien and Zuidema (2006b); for *Bertholletia* and *Tachigali* from Brien and Zuidema (2006a); and for *Triplochiton* from Worbes et al. (2003)

by allowing autocorrelation in light levels and linking that directly to growth rates (Metcalf et al. 2009), but without an independent check of ages.

Tree-ring analysis provides a direct method for age determination and is likely the most accurate method to determine tree age (Martínez-Ramos and Alvarez-Buylla 1998). We summarized ages obtained from tree-ring counts for 19 tropical tree species (Fig. 3). Average age of the species included was 101 years, while maximum ages varied between 37 and 241 years. Although these ages were not obtained at maximum tree size, still the values are much lower than some of the estimates based on ^{14}C bomb peak dating and do probably not include trees that would reach the age of 1,000 years.

Variation among trees: autocorrelation, persistent growth differences and implications

Large variation in growth exists among individual trees of a given species in a given piece of forest. Such variation has been observed in permanent plot studies (Clark and Clark 1992) and is probably caused by differences in

growth conditions among trees, in combination with temporal changes in those conditions. Altogether, this may lead to autocorrelated growth, implying that growth of a tree during one year is related to its growth in the next year, or the following, and/or that growth differences among trees are maintained over time (Brien et al. 2006). Strong temporal autocorrelation in tree growth has been observed in permanent sample plot studies (e.g. Kammerheid et al. 2003; Grogan and Landis 2009). Using tree-ring analysis, it is possible to detect autocorrelated growth over much longer periods than available from permanent plots.

So far, dendroecological studies have evaluated persistence of growth differences among trees for eight tropical tree species (Brien et al. 2006, 2010c; Zuidema et al. 2010). For all species, growth differences among trees were found to persist over one to several size categories for larger trees (Table 1). Thus, fast-growing trees keep growing fast over prolonged time periods, and slow-growing trees continue to do so over long timespans as well. Overall, these growth differences seemed to be most persistent for trees that have already grown out of the dark understorey (10–15 cm diameter; Table 1). Smaller trees in the understorey experience more switches between periods

of suppression and release, which probably leads to lower persistence in growth differences among trees over time (Brienen et al. 2006). However, in tropical dry forest even for small trees among-tree growth differences were strongly persistent over time (Table 1; Brienen et al. 2010c). In tropical dry forest, among-tree differences in growth reflect, most likely, spatial variety in water availability. Thus, factors driving long-term growth patterns may vary among forest types (Brienen et al. 2010c).

This finding has several important implications. First, the strongly persistent differences in growth rates lead to large variation in age at a certain tree size (Fig. 3; Brienen et al. 2006). Accounting for persistent growth differences in tree growth projections leads to more realistic estimates of average and variance in tree age (Brienen et al. 2006). A second consequence of persistent growth differences is the disproportional importance of the persistent fast growers for the growth of populations. Persistently fast growing trees may boost population growth by reaching reproductive size at a young age. This has important implications not only for insights in tree demography (Zuidema et al. 2009), but also for estimating the regrowth of timber after selective logging (Brienen and Zuidema 2007).

Tree growth responses to increasing atmospheric CO₂

The importance of tropical forests in the global carbon cycle has prompted considerable interest in the changes in carbon stocks in these forests. Data from permanent sample plots have shown that over the past decades aboveground biomass, tree growth and stem turnover increased (Lewis et al. 2009). Causes of these changes are strongly debated (e.g. Lewis et al. 2004; Wright 2005; Chave et al. 2008), but may be due to the increase of atmospheric CO₂ (cf. Lewis et al. 2009). In temperate forest, tree-ring analysis has been widely applied to show the response of trees to, most likely, increasing atmospheric CO₂ (e.g. Voelker et al. 2006; Wang et al. 2006; Cole et al. 2010). In tropical regions, similar approaches can be applied. So far, two tropical studies have evaluated evidence for increased growth rates, using different approaches. The first study by Rozendaal et al. (2010a) compared diameter growth rates of trees of varying extant diameter for five Bolivian tropical tree species. This approach allowed evaluating whether growth rates of large extant trees further back in time were higher than the recent growth rates of small extant trees in the same diameter class. For four of the five species a historical growth increase was found. Nevertheless, these results need to be interpreted cautiously as they may have been partially caused by sampling biases

(Rozendaal et al. 2010a). Although one cannot rule out some influence of sampling biases in the results, these results are consistent with the expected response to increased atmospheric CO₂ (Lloyd and Farquhar 2008) and with the finding in temperate regions that small trees showed stronger growth increases over time than larger trees (Voelker et al. 2006; Wang et al. 2006). The second study by Nock et al. (2010) took a different approach: tree-ring measurements were combined with stable isotope concentrations in the rings. For three tropical tree species from tropical dry forest in Thailand, basal area growth was related to the calendar year using a mixed modelling approach. In this study the opposite pattern was found, as for all species basal area growth decreased in recent years. This growth decline may have been caused by increased water stress from, amongst others, the rise in temperature and a higher frequency of El Niño events (Nock et al. 2010).

Fluctuations in growing conditions and physiological responses: stable isotope levels in tree rings

Apart from ring width, measurements on the fraction of stable isotopes (¹³C and ¹⁸O) in tree rings may help reconstructing the physiological responses of tropical trees to climatic variables (McCarroll and Loader 2004). The fraction of ¹³C in tree rings ($\delta^{13}\text{C}$) is determined by discrimination against the heavy ¹³C isotope in the diffusion and carboxylation of CO₂. As drought, light availability and atmospheric CO₂ pressure all influence these two physiological processes, the $\delta^{13}\text{C}$ fraction in wood cellulose varies with changes in growing conditions. Information on $\delta^{13}\text{C}$ fractions can be used to estimate changes in water use efficiency or long-term changes in internal CO₂ concentration (C_i). For ten tropical tree species long-term trends in stable isotope levels have now been obtained (Hietz et al. 2005; Gebrekirstos et al. 2009; Nock et al. 2010; Brienen et al. 2010b; Gebrekirstos et al. 2010). A decrease in $\delta^{13}\text{C}$ over time was reported, which led to an increase in intrinsic water use efficiency (iWUE) for six species (Hietz et al. 2005; Nock et al. 2010; Brienen et al. 2010b). *Cedrela odorata* and *Swietenia macrophylla* from Brazil showed an increase in C_i over time, which led to an increase in iWUE of 34 and 52%, respectively, from 1850 to 1990 (Hietz et al. 2005). *Mimosa acantholoba*, a Mexican dry forest species, showed a 40% increase in iWUE over the past 40 years. However, no increase in C_i was observed for this species (Brienen et al. 2010b). Nock et al. (2010) showed, similarly, an increase in iWUE for three tropical tree species from Thailand. In contrast, growth rates for these species decreased over time (Nock et al. 2010). These studies show that tree species seem to

Table 1 Persistent differences in growth among trees over subsequent diameter classes

	Diameter (cm)	+5	+10	+15	+20	+25	+30	+35
<i>Amburana cearensis</i> ^a	0–10	–		–			–	
<i>Cedrelinga catenaeformis</i> ^a	0–10		–		■		–	
<i>Peltogyne cf. heterophylla</i> ^a	0–10		■		–		–	
<i>Cedrela odorata</i> (moist forest) ^b	0–5	■	–	–	–	–	–	–
<i>Cedrela odorata</i> (dry forest) ^b	0–5	■	■	■	■	■	■	■
<i>Annamocarya sinensis</i> ^c	0–5	–	–	–	–	–	–	–
<i>Calocedrus macrolepis</i> ^c	0–5	■	–	–	–	–	–	–
<i>Dacrydium elatum</i> ^c	0–5	–	–	–	–	–	–	■
<i>Pinus kwangtungensis</i> ^c	0–5	■	–	–	–	–	–	–
<i>Amburana cearensis</i> ^a	10–20		■		■		■	
<i>Cedrelinga catenaeformis</i> ^a	10–20		■		–		–	
<i>Peltogyne cf. heterophylla</i> ^a	10–20		■		–		–	
<i>Cedrela odorata</i> (moist forest) ^b	10–15	■	■	■	–	–	–	–
<i>Cedrela odorata</i> (dry forest) ^b	10–15	■	■	■	■	■	■	■
<i>Annamocarya sinensis</i> ^c	10–15		■		■		–	–
<i>Calocedrus macrolepis</i> ^c	10–15		■	■	■	■	■	■
<i>Dacrydium elatum</i> ^c	10–15		■	■	■	■	■	■
<i>Pinus kwangtungensis</i> ^c	10–15		■	■	■	■	■	■

Grey areas indicate a significant rank correlation (Spearman's ρ , $P < 0.05$) between the indicated diameter class and the subsequent diameter class. – indicates a non-significant correlation (Spearman's ρ , $P > 0.05$). +5 to +35 indicate the distance (in cm) to the lower limit of the larger diameter class. For *Amburana cearensis*, *Cedrelinga catenaeformis* and *Peltogyne cf. heterophylla* diameter classes of 10 cm width were applied, while for the other species classes of 5 cm width were applied

^a Brienen et al. (2006)

^b Brienen et al. (2010c)

^c Zuidema et al. (2010)

respond physiologically to increased atmospheric CO₂ levels, but that this does not necessarily lead to elevated diameter growth.

Although $\delta^{13}\text{C}$ fractions do respond to water availability (cf. Gebrekirstos et al. 2009; Fichtler et al. 2010), a better approach to detect historical variation in rainfall is the determination of $\delta^{18}\text{O}$. As $\delta^{18}\text{O}$ is not altered by photosynthetic activity, it provides a more direct account of the growing conditions in terms of water availability, although the interpretation of $\delta^{18}\text{O}$ values is not straightforward due to strong interannual and intra-annual fluctuations in $\delta^{18}\text{O}$ in rainfall (cf. McCarroll and Loader 2004). The stronger

climatic signal was clearly illustrated in the study of Pons and Helle (this issue) for two tropical tree species. The simultaneous use of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ fractions probably represents a powerful approach to use stable isotopes as a tool to understand tree responses to climatic variation and changes (cf. Nock et al. 2010). Such combined measurements allow detecting historical droughts and quantifying their frequency from simultaneous signals of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$. The longer-term variation (at decadal scale) in $\delta^{13}\text{C}$ and the long-term trends in this isotope can then be interpreted as physiological responses to other drivers (light, CO₂ level).

Forest dynamics: towards a reconstruction of disturbance history

“Where are all the large trees, if this is a virgin tropical forest?”. This question was posed by Hartshorn (1978) in a publication on forest turnover in Costa Rica. The study showed that forest turnover was rather fast, ranging from 80 to 138 years in the La Selva area, Costa Rica (Hartshorn 1978). Similar findings were obtained in a tropical forest in French Guiana where 0.64–1.33% of the canopy was opened through gap formation per year (van der Meer and Bongers 1996). Thus, we may consider tropical forests to be rather dynamic. In temperate forests, tree-ring analysis has been widely applied to reconstruct the disturbance history and historical stand dynamics (e.g. Lorimer and Frelich 1989; Oliver and Larson 1996; Lusk and Smith 1998). By studying growth patterns, in terms of releases, suppressions, and establishment dates of all trees in a certain area, the history of a forest stand can be revealed. Now, as tree-ring analysis starts to be applied also in tropical forests, similar approaches can be used to reconstruct historical stand dynamics. Nevertheless, usually not all species are suitable for tree-ring analysis; thus some adjustments in the methods may be required.

Some tree-ring studies have evaluated historical forest dynamics. Worbes et al. (2003) reconstructed the historical dynamics of a seasonally dry tropical forest in Cameroon in an area of 1 ha, by determining growth rates and ages of trees of nearly all species. The largest trees belonged to long-lived pioneer species, which were usually older than the trees of mature forest species and almost no recruitment of these species was present in the understorey. Mature forest species, in contrast, showed abundant regeneration. In all, the forest was classified as a late secondary forest (Worbes et al. 2003). Similarly, the disturbance history of a seasonal tropical forest in western Thailand was reconstructed by Baker et al. (2005), using a combination of tree-ring analysis and age estimations from growth projections (cf. Baker 2003). The stand structure data of the Huai Kha Khaeng Wildlife Sanctuary showed a single cohort of canopy trees and the simulated age distributions showed that the cohort of canopy trees established in the 1800s and showed that there was a pulse in establishment for the shade-intolerant species in the mid-1900s. Tree-ring analysis provided a more detailed picture: there were peaks in recruitment and growth in the 1910–1920s, 1940–1950s and minor peaks in the late 1800s and 1970s. Tree-ring series of the oldest trees (mostly *Afzelia xylocarpa*) showed elevated growth in the 1850s. Together, these results indicate that around 1850 a large, widespread disturbance occurred, followed by a few minor disturbances more recently (Baker et al. 2005). A third study on forest dynamics was conducted by Rozendaal et al. (2010b) to

assess the frequency of growth releases in a Bolivian moist forest. No trend in release frequency was found over the past 200–300 years. A second method that could reveal changes in forest dynamics—changes in the degree of temporal autocorrelation over time—also did not reveal clear changes over the same period (Rozendaal et al. 2010b). These results show that the occurrence of disturbances at different spatial scales may be important in shaping tropical forest structure and dynamics. Although these are a few isolated studies, the implications of their findings may be far reaching, as they show that current species composition and forest structure can be the result of transient dynamics and past (major) disturbances such as windstorms, droughts or fires. One needs to realize that the current ‘state’ of tropical forests, in terms of structure and dynamics, may depend strongly on their history (Clark 2007). Tree-ring studies may provide an important contribution to enhance insights into the history of tropical forests, although the interpretation of growth releases in tree-ring series needs to be done cautiously (Soliz-Gamboa 2010), and the sampling design of such studies should probably be adjusted for this aim (Rozendaal et al. 2010b).

Tree-ring analysis may also be useful in enhancing the understanding about secondary forest succession. Secondary forest succession is usually studied in chronosequences, a ‘space-for-time’ substitution, through comparison of secondary forest stands of different, but known age (e.g. Selaya et al. 2008). Worbes et al. (1992) determined the ages of successional stands in floodplain forests by ring counts of the largest trees, but growth patterns were hardly presented. Similarly, an approach was presented to determine ages of secondary forest stands in Mexico, using tree-ring analysis (Brienen et al. 2009). Annual periodicity of the growth rings could be validated through comparison of ring counts with known stand ages. In the Mexican study, ring counts closely matched stand ages, although pioneer species in older stands may already have disappeared, leading to errors in the reconstruction of stand dynamics (Brienen et al. 2009).

Forest management: how tree rings can help improving timber yield models

Sustainable forest management requires reliable data to calculate the consequences of various logging regimes for tree populations and future timber availability. Ideally, these growth data should represent the ‘lifetime’ growth trajectory of a tree, i.e. its growth patterns up to reaching harvestable size. Most growth data from permanent sample plots, however, cover short timespans relative to the lifespan of a tropical tree (cf. Condit 1995). Tree-ring analysis provides a means to do so, and the large advantage of this

method is that growth rates of the ‘successful’ trees can be obtained (cf. Rozendaal et al. 2010a).

For a number of commercial tree species, tree-ring analysis has been applied to find that ages of trees at reaching the minimum cutting diameter were high. For example, *Pterocarpus angolensis* needed on average more than 100 years to reach the minimum cutting diameter of 35 cm in various sites in deciduous woodlands in tropical southern Africa (Stahle et al. 1999; Therrell et al. 2007). In Cameroon, *Triplochiton scleroxylon* needed on average 80 years to reach 80 cm (Worbes et al. 2003). In Central Amazonian white-water floodplain forests large variation in ages at the minimum cutting diameter was observed among commercial tree species: low-wood density species reached the minimum cutting diameter of 50 cm in an average of 15–67 years, while high-wood density species needed on average 106–151 years (Schöngart 2008). Also in moist forests in the Bolivian Amazon, the timespan needed to reach the minimum cutting diameter was long. Average ages at the minimum cutting diameter for five commercial tree species ranged from 61 to 179 years (Brienen and Zuidema 2006b; Rozendaal et al. 2010c). However, one should take into account that within species ages at the minimum cutting diameter may differ strongly across forest types (da Fonseca et al. 2009). *Tabebuia barbata* attained the minimum cutting diameter of 50 cm on average in 117 years in nutrient-rich Amazonian white-water floodplain forest (várzea), while it took on average 270 years in nutrient-poor black-water floodplain forest (igapó). Similar variation was found for *Vatairea guianensis*, 70 and 162 years to reach the minimum cutting diameter in the várzea and the igapó, respectively (da Fonseca et al. 2009). Thus, management criteria should not be defined only per species, but the forest type should also be taken into account.

Although ages at the minimum cutting diameter give some idea about long-term growth rates and, thus, the time needed for volume recuperation, growth projections are required. To determine the appropriate minimum cutting diameter and length of the cutting cycle to sustain timber yields, growth trajectories of the individual trees were averaged to derive species-specific long-term growth patterns (Schöngart et al. 2007; Schöngart 2008). In várzea floodplains, the estimated minimum cutting diameter ranged from 47 to 70 cm for a total of 13 species of different successional status and the estimated cutting cycle varied from 3 to 32 years (Schöngart 2008; da Fonseca et al. 2009). These results illustrate that species-specific management criteria are needed.

However, these studies did not take variation in growth among individual trees into account. Within a species ages at the minimum cutting diameter varied strongly among individuals (e.g. Brienen and Zuidema 2006b; Therrell

et al. 2007; Rozendaal et al. 2010c). The incorporation of growth variation among and within individual trees strongly influenced the projected timber volume. Brienen and Zuidema (2006b) applied tree-ring analysis to reconstruct growth rates over the entire lifespan of trees to determine the variation in ages among trees at the moment of attaining the minimum cutting diameter. The observed strength of autocorrelation was incorporated in growth simulation models to be able to simulate tree growth with the same degree of growth variation (cf. Brienen et al. 2006). Harvestable volume for a second cycle in 20 years was much higher, 36–50% of the harvestable volume at initial harvest, when realistic variation in growth was included for four commercial tree species. Nevertheless, recuperated timber volume at second harvest was low, 18–24% of initial harvestable volume (Brienen and Zuidema 2007).

Hence, the use of long-term growth data from ‘successful’ trees, in combination with realistic levels of growth variation included probably provides the most accurate estimations of future timber yield (Rozendaal et al. 2010c). As most slow-growing trees will not make it to the canopy (Landis and Peart 2005; Rozendaal et al. 2010a), average growth rates obtained from trees of all sizes in permanent sample plots likely underestimate long-term growth of trees that eventually reach harvestable size (cf. Sheil 1995; Condit et al. 1995).

Outlook

Over the past few years, the number of studies in tropical dendroecology has rapidly increased. Significant progress has been made in each of the themes included in this review. Yet, in many of these themes the number of studies is very limited and research has just started to develop. While the few case studies in those themes are valuable in their own right, their limited number does not allow evaluating general patterns. Only for two of the included themes—climate–growth relations and tree ages—quite a number of studies is now available. Climate–growth relations have been published for a large number of tropical tree species as establishing those relations is an often used step in determining the annual character of tree rings. As the annual character of tree rings in the tropics cannot be assumed, many studies evaluate this. Tree ages also have received quite some attention in tropical dendroecology, probably as tree ages are easily obtained and as new data on tree ages provide interesting input in an ongoing discussion about typical tree ages, mortality rates and tree turnover.

What can tree-ring studies contribute to tropical forest ecology? We see two main avenues for further research.

The first deals with improving our understanding of causes and consequences of growth variation in tropical trees. Tree-ring series show strong temporal variation in growth rates with clear year-to-year variation but also ‘plateaus’ of lower and higher growth rates. The former can often be related to climatic fluctuations while the latter are thought to be a result of canopy dynamics (gap formation and closure) and stand development patterns. Periods of higher and lower growth (releases and suppressions) are thought to be related to gap formation and closure, but causal relations have not been found. There is a dire need to find out to what extent the decadal-scale variation in growth is indeed related to canopy dynamics. Species-specific relations between light levels and growth rates need to be established to find threshold values for the detection of suppressions and releases in tree-ring data (cf. Baker and Bunyavejchewin 2006). This requires methodological approaches in which light-growth relations are assessed for trees in permanent plots allowing for the interpretation of historical growth variation obtained from tree-ring analysis.

The consequences of growth variation—both temporal, spatial and among individuals—also deserve attention in dendroecological work. Strong temporal growth variation influences year-to-year fluctuations in carbon sequestration of tropical forest trees and causes temporal fluctuations in population dynamics. The occurrence of persistent growth variation among individuals has important consequences for age calculations, tree population dynamics and the calculation of timber volume recuperation. Such consequences are poorly understood at this moment, although their implications may be large.

Studying causes and consequences of growth variation requires a different sampling strategy than often adopted in dendrochronological studies. Traditionally, tree-ring studies included small samples of preferably adult trees, from which only those ring series with high interseries correlations are selected, often without dealing with juvenile growth rings. For ecological studies often much larger sample sizes are required (minimally 50–80 trees per species) in which juvenile trees are also represented, as well as individuals of which temporal growth variation does not (strongly) correlate to that of the others.

A second avenue of dendroecological research that we consider to be important deals with the detection of climate change impacts on tree growth. Given the important role of tropical forests in the global carbon cycle, it is evident that the responses of tropical trees to atmospheric changes need to be unravelled (Baker 2010). Physiological, dendroecological and dendroclimatological studies can assist in providing much-needed insights into the physiological responses of trees to climatic variation. Although climate-growth relations have now been established for quite a number of species, the mechanisms by which multiple

atmospheric changes affect tree growth are poorly understood. The combination of tree-ring analysis with determination of stable isotopes (^{13}C and ^{18}O) is a promising approach to unravel the drivers of climate-growth relations (cf. Nock et al. 2010). In addition, novel wood anatomical approaches may provide a way forward in understanding and predicting responses of trees to climatic changes (cf. Fonti et al. 2010).

Tree-ring analysis in the tropics provides the much-needed long-term data on tree growth and tree recruitment. More widespread application of rigorous dendroecological studies will yield important insights into the mechanisms that govern tree growth and forest dynamics in tropical forests. Such knowledge is highly valuable in assessing how tropical forests will respond to the predicted climatic changes.

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