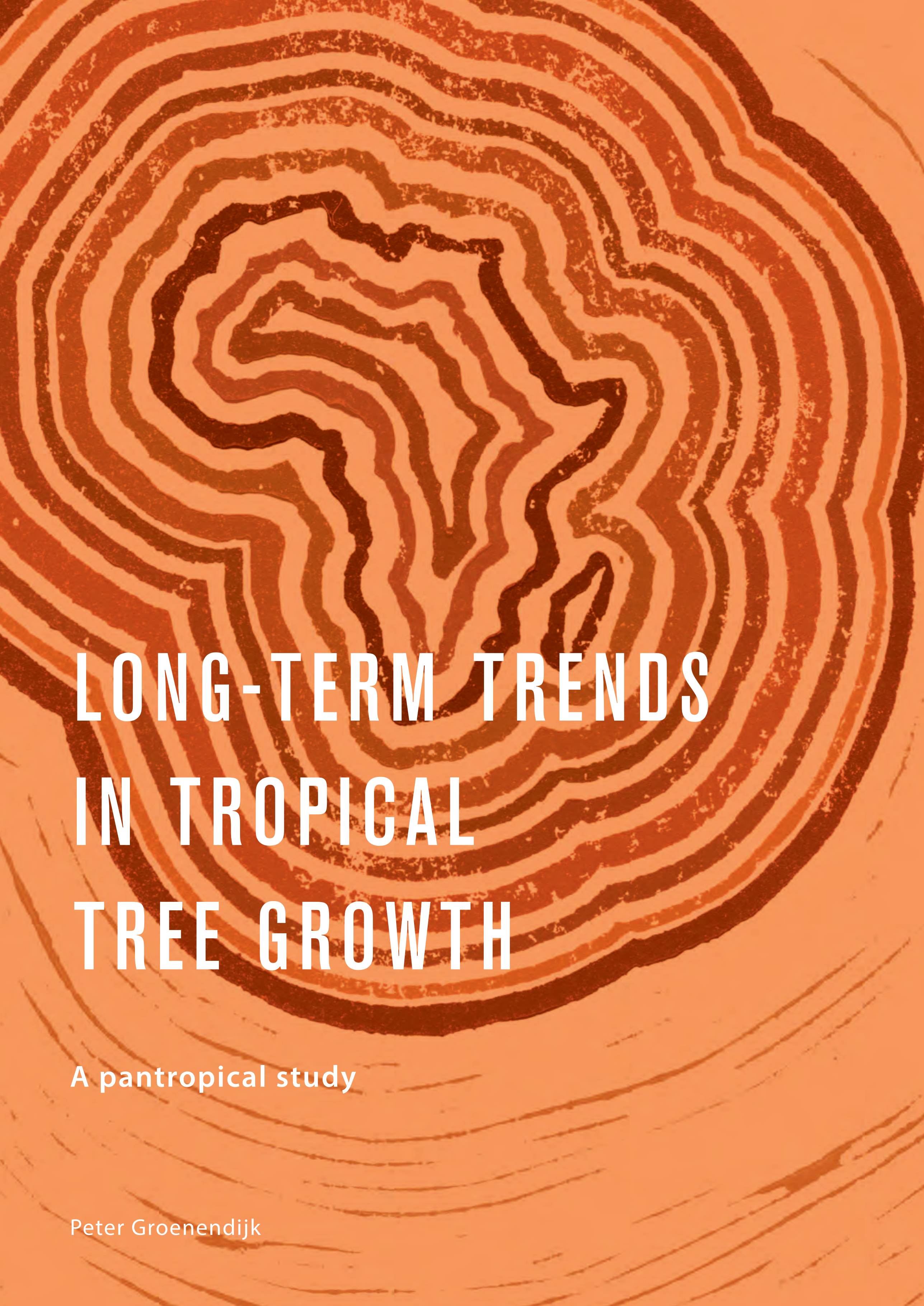

LONG-TERM TRENDS IN TROPICAL TREE GROWTH

A pantropical study

Peter Groenendijk

Long-term trends in tropical tree growth:

a pantropical study

Peter Groenendijk

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Long-term trends in tropical tree growth:

a pantropical study

Peter Groenendijk

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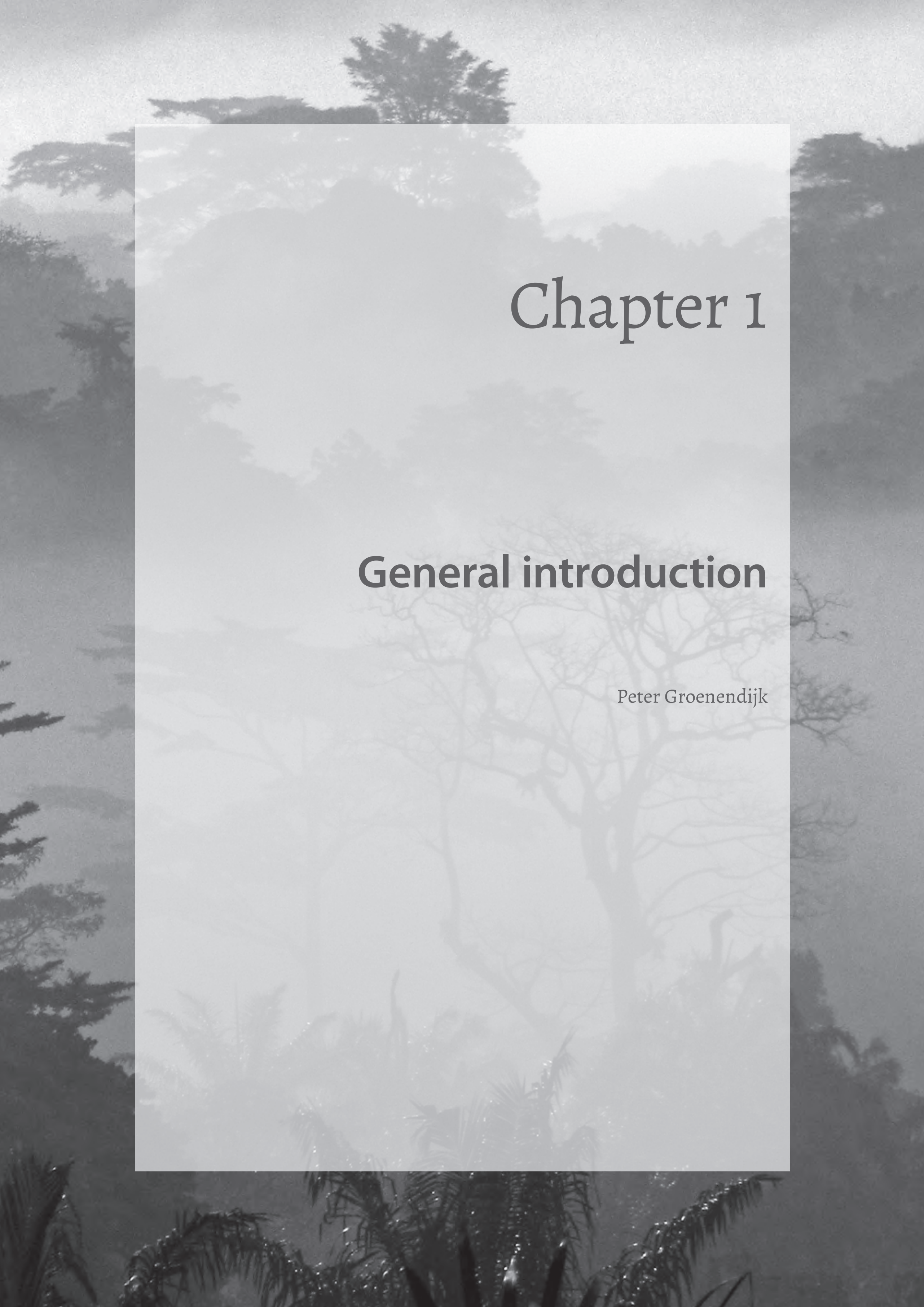


Chapter 1

General introduction

Peter Groenendijk

Tropical forests harbour a high biodiversity, provide many goods such as timber and non-timber forest products and are an important component of the terrestrial carbon cycle. Although covering only 7% of the earth's surface, tropical forests hold 25% of the world's terrestrial carbon pool (Pan *et al.*, 2011) and account for a third of the terrestrial net primary productivity (Bonan, 2008). Since tropical forests store and process so much carbon, net loss or uptake of carbon by tropical forests has major implications for the global carbon cycle (Achard *et al.*, 2002). Understanding these changes is crucial to predict tropical forests responses to climate changes (Wright, 2005) as forests can speed up climate change by acting as source of CO_2, or might mitigate it by sequestering carbon.

Currently, tropical forests are under large pressure of change due to deforestation, conversion to other land uses and logging (Lambin *et al.*, 2003). Deforestation is still high in tropical forests (Hansen *et al.*, 2013) having affected an estimated 50% of all tropical forests (Asner *et al.*, 2009).

Tropical forests are logged at rates 20 times higher than the rate at which they are cleared (Asner *et al.*, 2009) and the area of tropical forests assigned for logging is estimated to be 403 million hectares, or over a fifth of the total forest area (Blaser *et al.*, 2011). Also, several studies have found indications of changes in tree growth rates and in forest biomass and dynamics (Wright, 2005). As these changes were found throughout the tropics in apparently undisturbed forests, an external factor (such as climate change) has been suggested to be the driver of these changes. The main focus of this thesis is on changes in tropical forest tree growth using a long-term perspective.

1.1 Changing tropical forests in a changing world?

Worldwide, forest monitoring studies using permanent sample plots (PSP) have provided evidence for changes in growth, dynamics and biomass of tropical forests (e.g., Laurance *et al.*, 2004b; Lewis *et al.*, 2009a; Murphy *et al.*, 2013). Decadal scale increases in forest biomass have been found for forests in Africa (Lewis *et al.*, 2009b), Asia (Phillips *et al.*, 1998; Chave *et al.*, 2008), and South-America (Lewis *et al.*, 2004; Phillips *et al.*, 2008), suggesting a global and pervasive carbon sink in tropical forests. Additionally, increases in tree growth have also been reported (Laurance *et al.*, 2004b; Lewis *et al.*, 2009a). These biomass and growth increases have been interpreted to reflect a growth stimulation by increased atmospheric

CO_2 concentrations (e.g., Phillips *et al.*, 2008; Lewis *et al.*, 2009a). On the other hand, decreasing (Dong *et al.*, 2012) or fluctuating (Murphy *et al.*, 2013) forest biomass have also been observed, together with growth decreases (Feeley *et al.*, 2011; Nock *et al.*, 2011). These changes have in turn been interpreted to reflect the negative effect of higher temperatures on growth (Feeley *et al.*, 2011; Nock *et al.*, 2011).

Up to now, no consensus has been reached on whether tropical forests growth and biomass are indeed changing and little clarity exists on the drivers of these changes. Although forming the basis for detecting changes in tropical forests, monitoring plot studies have so far focussed more on describing forest-level changes, while being unable to assess their underlying mechanisms. These forest-level responses are the aggregate result of species-specific responses to climatic changes or to disturbances and assessing these species-level thus forms the basis to understand responses of whole communities. Yet, virtually nothing is known about species-level responses so far (Zuidema *et al.*, 2013).

The high biodiversity of tropical forests combined with the small size of monitoring plots (usually 1 hectare) has restrained analysis to the community level and species-level analysis are rare (Feeley *et al.*, 2011). Furthermore, the short duration of most plot studies (under 30 years) has limited assessing the drivers of changes. The detected changes may have resulted from decadal-scale growth fluctuations induced by climatic variability (Feeley *et al.*, 2011), and therefore not represent progressive long-term alterations in tropical forests, as expected under climate change. Additionally, changes reported in plots may also arise if forests are recovering from past disturbances (Fisher *et al.*, 2008; Chambers *et al.*, 2013; Vlam, 2014). Figure 1.1 provides a schematic overview of the suggested drivers of changes in tropical forests. For a more profound understanding of the responses of tropical forests to a changing world, a move from descriptive studies of decadal-scale changes on forest level, to more long-term studies on species level is clearly needed (Zuidema *et al.*, 2013).

1.2 Tropical tree-ring research

The scarcity of long-term growth data for tropical forest trees can be overcome using tree-ring analysis. Tree rings provide a window to the past and can be used to assess century-scale growth changes in tropical trees (Rozendaal *et al.*, 2010a; Zuidema *et al.*, 2013). However, it is crucial to prove that tree-rings are formed annually prior to applying tree-ring analysis to obtain long-term growth data, especially when working with tropical tree species for which this has not yet been done.

Tree-ring analysis has been performed for over a century in the tropics (Coster, 1927; Worbes, 2002). However, for long the formation of annual rings in tropical rainforests trees has been denied (Swaine, 1994; Kurokawa *et al.*, 2003). Researcher often believed that there is no clear seasonality in tropical rainforests, and that growth in these ecosystems is continuous throughout the year (i.e., no period of cambial dormancy). Additionally, many of the early publications on tropical tree rings were published in German (Coster, 1927; Coster, 1928) or in French (Mariaux, 1967), hampering a wider dissemination of the results. The belief of lacking annual tree-rings in tropical species has thus for long caused the potential for tree-ring analysis in the tropics to be neglected. More recently, however, the annual character of tree-rings has been proven for many tropical tree species growing in seasonally dry (Dünisch *et al.*, 2003; Vlam *et al.*, 2014b) or seasonally flooded tropical forests (Worbes *et al.*, 1995; Schöngart *et al.*, 2002). Extensive lists have been compiled of tree species with proven annual ring formation for different tropical biomes (Worbes, 1989; Alves & Angyalossy-Alfonso, 2000; Tarhule & Hughes, 2002; Worbes, 2002), including species from tropical rainforests (with 1800–4200 mm annual rainfall; Zuidema *et al.*, 2012). However, in tropical wet forests, i.e., with annual rainfall >4000 mm, the potential for tree-rings analysis has barely been assessed (Fichtler *et al.*, 2003).

Proving the annual character of tree-ring formation is not straightforward. First, the complex anatomy of tropical trees hampers tropical tree-ring research (Stahle *et al.*, 1999) as understanding this anatomy is required for the correct identification of ring-boundaries (Worbes & Fichtler, 2010). For instance, false and wedging rings are common in the wood of tropical tree species. False rings are anatomical structures in the wood that resemble a ring boundary, but that are formed due to intra-annual growth variation. Wedging rings occur when trees grow on only a limited part of the circumference of the stem, producing rings boundaries that 'wedge' together on the parts the tree did not grow. These problems are not exclusive to the tropics, but appear to be more prevalent in tropical species than in temperate (Worbes, 1995). The existence of these problems often requires working with entire stem discs, to be able to follow rings around the circumference of the stem. Second, climate-growth relations are often used to prove the annuality of tree-rings (e.g., Brienen & Zuidema, 2005). This entails building chronologies – an index for annual growth variation – for each species and relating these chronologies to local or regional climate data. However, building chronologies is not always possible in the tropics (Fichtler *et al.*, 2003) and the general low quality of climate records in the tropics (Clark & Clark, 2011) hampers the analysis of climate-growth variations. Finally, in the case chronologies cannot be built, radiocarbon dating can be used to confirm the dating of the marked rings (Worbes & Junk, 1989). Radiocarbon dating is based on measuring the decay of the radioactive carbon isotope ^{14}C in organic material. However, radiocarbon cannot be used to date samples between 350 years old and the 1960s due to the 'Suess effect' (Worbes & Junk, 1989). The high price of radiocarbon dating also limits its wider application (~US$ 400 per sample). In spite of these limitations, tree-ring analysis in the tropics provides a nearly unexplored and unique opportunity to assess long-term patterns in tropical tree growth.

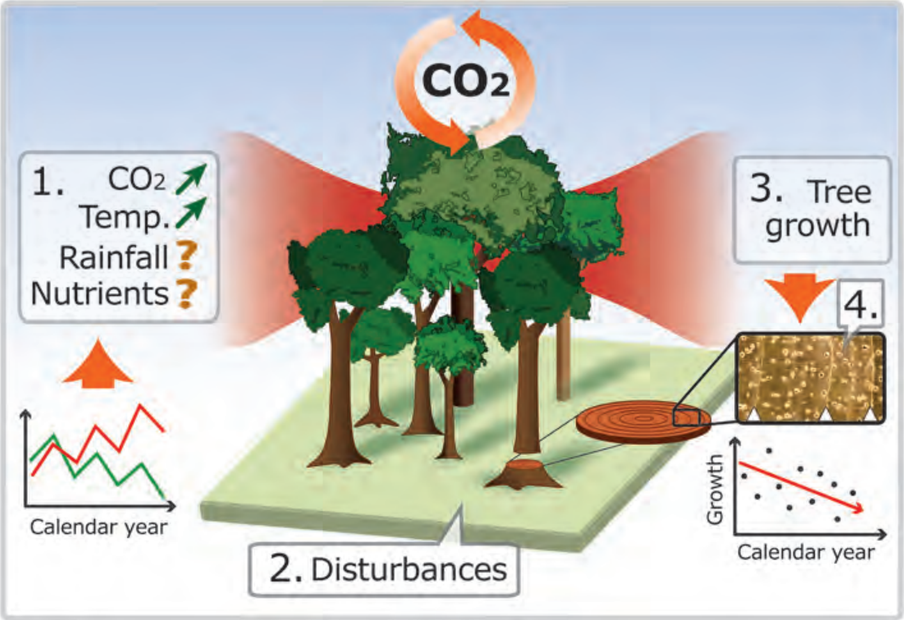


Figure 1.1 Schematic overview of drivers of long-term changes in tropical forests and the proposed methods to assess them. Several global change factors (1.) have been suggested to drive growth changes in tropical forest, e.g., rising ambient CO_2, increasing temperatures, and the unresolved (question marks) changes in rainfall and nutrient deposition. Factors related to forest history (2.) may also induce growth change, such as recovery from large-scale disturbances (e.g., forest fires and blowdown events). These changing factors affect tree growth (3.) over long timescales, and tree-ring analysis (4.) can be used to assess these long-term changes in tree growth.

1.3 Timber exploitation

Worldwide, more than 400 million hectares of tropical forests are destined for selective logging (Blaser *et al.*, 2011). Timber exploitation obviously disturbs these forests, but damage is limited in well-managed selectively logged forests (e.g., using reduced impact logging; Valle *et al.*, 2007) and these forests retain large carbon stocks after exploitation (Sist *et al.*, 2014). In Africa the area of certified production forests (e.g., FSC, PEFC, OLB, etc.) more than tripled between 2005 and 2010, from 1.48 to 4.63 million hectares (Blaser *et al.*, 2011). Under such certification schemes logging companies are required to evaluate whether species are exploited sustainably and if not the case, adapt their logging scheme. However, the data needed to assess this sustainability – growth, mortality and regeneration rates of trees – are scarce, and especially so for African species (Picard *et al.*, 2010). Tree-ring analysis provides lifetime species-specific growth data that can be used to improve the projections of how much timber will be available at the next logging cycles. Despite the relevance of such calculations for sustainable forest management, they have rarely been performed African timber species (Putz *et al.*, 2012; De Ridder *et al.*, 2013b). This is surprising, given the knowledge that many African timber species produce tree-rings (Mariaux, 1967; Détienne *et al.*, 1998). More studies that evaluate timber exploitation are thus urgently needed given the importance of sustainable management for conserving forested areas and maintaining biodiversity of tropical forests (Edwards *et al.*, 2011; Putz *et al.*, 2012).

1.4 Detecting long-term growth trends

Tree-ring analysis provides long-term growth data that cover the entire lifespan of trees. These lifetime growth data contain long-term trends in growth that reflects the ontogenetic development of an individual or a species, i.e., an age/size growth trend (Figure 1.2). To detect long-term trends in growth rates measured from tree rings it is essential to first account for this species' age/size trend. Multiple growth-trend detection methods (GDMs) exist to disentangle age/size trends in growth from long-term growth changes. Yet the trend-detection capacity of these methods has never been assessed and these methods strongly differ in approach and assumptions, with possible implications for their output. Given the large differences in approach between methods, it is pertinent to evaluate whether they yield consistent output when applied on a single dataset, and to assess the sensitivity, reliability and accuracy of these methods to detect growth trends. Although individual GDMs have been evaluated and weaknesses have been noted for several of them (e.g., Esper *et al.*, 2003; Biondi & Qeadan, 2008; Briffa & Melvin, 2011), only rarely have studies applied and compared multiple methods (e.g., Briffa *et al.*, 1992; Esper *et al.*, 2010; Andreu-Hayles *et al.*, 2011). A critical comparison and evaluation of the most commonly used trend-detection methods in tree-ring research is therefore needed.

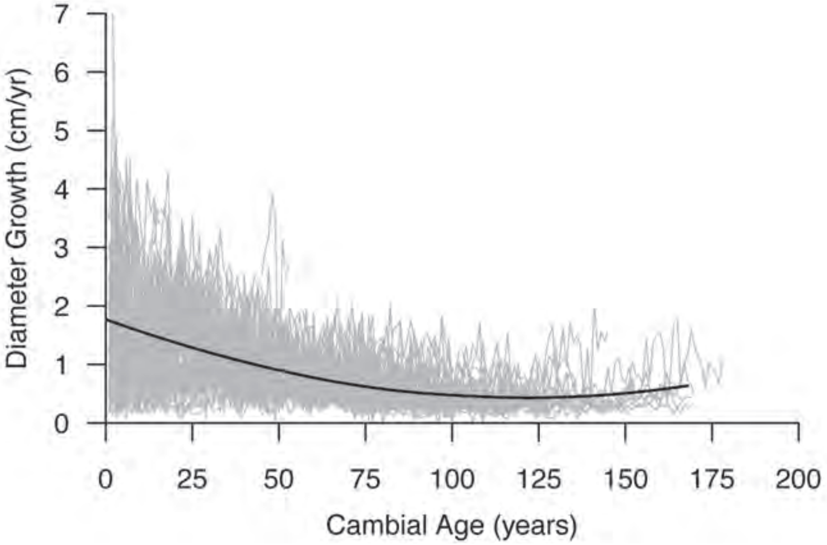


Figure 1.2 Lifetime growth trajectories measured from tree rings for the tropical tree species *Terminalia ivorensis*, from Southwest Cameroon. Each grey line represents the lifetime growth trajectory of an individual tree; black line shows the average age/size trend for the species (for >5 samples)

1.5 Main objectives of this study

In this thesis I apply a pantropical approach using tree-ring analysis to assess long-term changes in growth of tropical forest trees. Tree-ring analysis was used to measure long-term growth rates of ~1350 trees of different species coming from three sites across the tropics. Trends in growth over the last two centuries were then analysed using one established an one new trend-detection method. Additionally, I applied the long-term growth data from rings to improve the evaluation of forest management practices in Cameroon.

The main objectives of this thesis were: (1) to assess the potential for using tree-rings in a wet tropical forest in Central Africa; (2) to project timber yields in the next logging round for four Cameroonian tree species; (3) to evaluate the sensitivity and accuracy of four commonly used methods to detect long-term trends in tree-ring data; and (4) to detect whether growth rates of forest trees have changed over the past ~150 years for sites in Bolivia, Cameroon and Thailand.

1.6 A pantropical approach

This thesis was embedded in the TROFOCLIM project led by Pieter Zuidema. The goal of this project was to use tree-ring analysis to detect, explain and predict the long-term effects of climate change on tropical tree growth and dynamics. Trees were sampled in three forest sites across the tropics and also includes two other PhD theses. Sample collection was divided among the three PhD projects and the three sites: in Bolivia (samples collected by Peter van der Sleen), Cameroon (by me) and in Thailand (by Mart Vlam). At each site, around 500 trees of four to five species were collected as stem discs and increment cores. The main criteria for selecting these species were that they showed visually identifiable rings and were present in adequate abundance in the forest to allow the collection of approximately 100 trees per species. Together, this set of species represent various families, various leaf phenology characteristics and different ecological guilds: from shade-tolerant species to light demanding long-lived pioneers (Table 1.1). In all study sites, we sampled trees in old-growth forest using an identical sampling scheme, in which trees of all sizes were collected randomly inside a large area of forest (of 144-297 ha). This approach resulted in a large dataset that allows to assess a broad array of ecological questions at a pantropical scale. The three dissertations embedded in the project focussed on different themes: on long-term growth changes (this dissertation); on the effect of past disturbances on present-day forest dynamics (Vlam, 2014); and on the physiological and environmental drivers that may have affected tropical tree growth (van der Sleen, 2014).

Table 1.1 Characteristics of species studied in this thesis. Shown are family, shade-tolerance guild (cf. Poorter *et al.*, 2006), description of ring boundaries and leaf phenology. The 'Annual rings' column contains references to publications in which the annual nature of ring formation was described.

County	Species	Family	Guild[1]	Ring Boundary	Leaf phenology[2]	Annual rings	CHAPTER
Bolivia	*Ampelocera ruizii*	Ulmaceae	ST	Parenchyma band	E	Lopez *et al.* (2012)	5
	Cariniana ianeirensis	Lecythidaceae	PST	Compressed fibres	D	Lopez *et al.* (2012)	5
	Hura crepitans	Euphorbiaceae	PST	Compressed fibres	D	Lopez *et al.* (2012)	5
	Sweetia fruticosa	Fabaceae	LLP	Parenchyma band	BD	Brienen and Zuidema (2003)	5
Cameroon	*Brachystegia cynometroides*	Fabaceae	PST	Parenchyma band	BD	CHAPTER 2 this thesis	2;5
	Brachystegia eurycoma	Fabaceae	PST	Parenchyma band	BD	CHAPTER 2 this thesis	2;3;5
	Daniellia ogea	Fabaceae	LLP	Parenchyma band	BD	CHAPTER 2 this thesis	2;3;5
	Entandrophragma utile	Meliaceae	ST	Parenchyma band	D	CHAPTER 2 this thesis	2;3;5
	Terminalia ivorensis	Combretaceae	LLP	Density variations	D	Détienne *et al.* (1998)	2;3;5
Thailand	*Afzelia xylocarpa*	Fabaceae	LLP	Parenchyma band	D	Vlam *et al.* (2014b)	5
	Chukrasia tabularis	Meliaceae	PST	Parenchyma band	BD	Vlam *et al.* (2014b)	5
	Melia azedarach	Meliaceae	LLP	Density variations	D	Vlam *et al.* (2014b)	4;5
	Neolitsea obtusifolia	Lauraceae	ST	Ring porous	E	Vlam *et al.* (2014b)	5
	Toona ciliata	Meliaceae	LLP	Ring porous	D	Vlam *et al.* (2014b)	5

[1] Ecological guilds: Guilds: ST = shade-tolerant, PST = partial shade-tolerant, LLP = long-lived pioneer. Sources: Bolivia (Peña-Claros *et al.*, 2008), Cameroon (Hawthorne, 1995), Thailand (Baker *et al.*, 2005).

[2] Phenology: E = evergreen, D = deciduous, BD = brevi-deciduous. Sources: Bolivia (Mostacedo *et al.*, 2003), Cameroon (Hawthorne, 1995; Lemmens *et al.*, 2012), Thailand (Williams *et al.*, 2008)

[3] Ring boundary definition cf. Worbes (1995)

1.7 Study sites

We sampled trees from undisturbed tropical forests on three continents: South America (in Bolivia), Africa (in Cameroon) and Southeast Asia (in Thailand). In Bolivia, wood samples were collected in the 'La Chonta' logging concession, situated at 15.84° S, 62.85° W, ca. 300 km northeast of Santa Cruz de la Sierra (Figure 1.3). The forest at La Chonta is a semi-deciduous moist forest, on the transition between dry-forest (Chiquitano) and moist Amazonian forests (Peña-Claros *et al.*, 2008). Precipitation in the region is unimodal, with an annual average of 1580 mm and a four month dry season (with <100 mm rainfall) from May to September (Figure 1.3). Around 1992 the area was selectively logged for the commercially valuable broad-leaf mahogany – *Swietenia macrophylla* (Gould *et al.*, 2002)**.** That extraction was at a very low intensity (ca. 1 m^3/ha) and we have not found any signs of logging operations in our study area (e.g., old stumps or remains of logging roads).

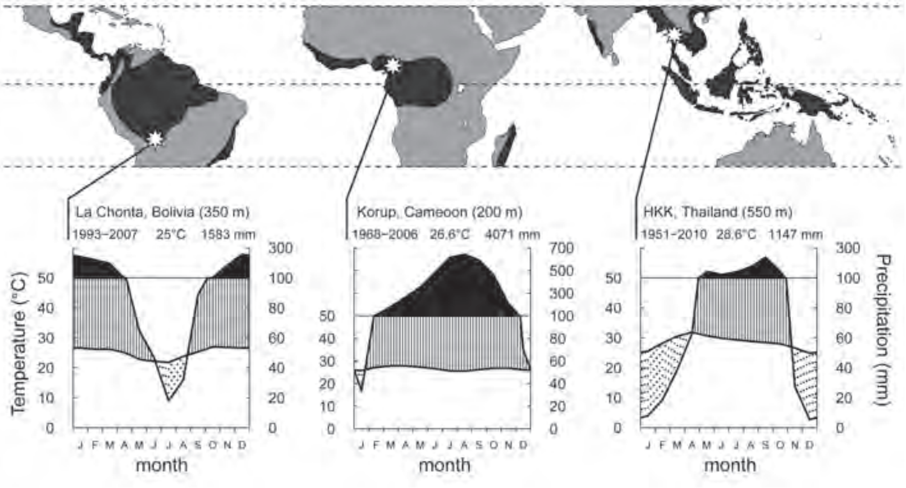


Figure 1.3 Locations of the study sites in Bolivia, Cameroon and Thailand and their climate diagrams. In Bolivia, samples were collected inside the La Chonta logging concession; in Cameroon inside the TRC 11.001 concession; and in Thailand inside the Huai Kha Khaeng Wildlife Sanctuary (HKK). Stars indicate the approximate location of the sites, which were all located inside wet tropical forests (>1500 mm rainfall $year^{-1}$; dark grey areas). Sources of climatic data were: in Bolivia, precipitation data from La Chonta sawmill weather station (30 km to the north of the study site; covering the period 1993-2007) and temperature from Ascención de Guarayos (60 km to the west; 1987-2006); for Cameroon the average precipitation and temperature data from the Bulu meteorological station (40 km to the south) and Mamfé Airport weather station (40 km to the north); and for Thailand, precipitation and temperature data from Nakhon Sawan weather station (100 km to the east). Climate diagrams cf. Walter and Lieth (1960), with dotted area indicating dry season (rainfall<temperature), and black area the rainy season (>100 mm $month^{-1}$).

In Cameroon, samples were collected inside the Forest Management Unit 11.001 of the logging company Transformation REEF Cameroon (TRC, 2008). The area is situated in the Southwest region, at 5.23° N, 9.10° E (Figure 1.3), and is adjacent to the Korup National park. Vegetation consists of semi-deciduous lowland rainforest of the Guineo-Congolian type (Kenfack *et al.*, 2006). Precipitation is unimodal, with an annual average around 4100mm (Nchanji & Plumptre, 2003) and a three-month dry season from December to February (Figure 1.3). Although the North-Western part of the concession was previously exploited in the 1980s, our study area consisted of primary forest (TRC, 2008) without signs of any previous exploitation.

The study site in Thailand was situated in the Huai Kha Khaeng Wildlife Sanctuary (HKK), at 15.60° N 99.20° E, around 250 km northwest of Bangkok. The vegetation at HKK consists of a mosaic of seasonal dry evergreen forest with mixed deciduous forest (Bunyavejchewin *et al.*, 2009). Precipitation is unimodal, with an annual average of 1473 mm and a 4-6 months dry season from November to April (Figure 1.3). There is almost no human interference in HKK and no logging activities are known to have taken place in the study area.

1.8 Thesis outline

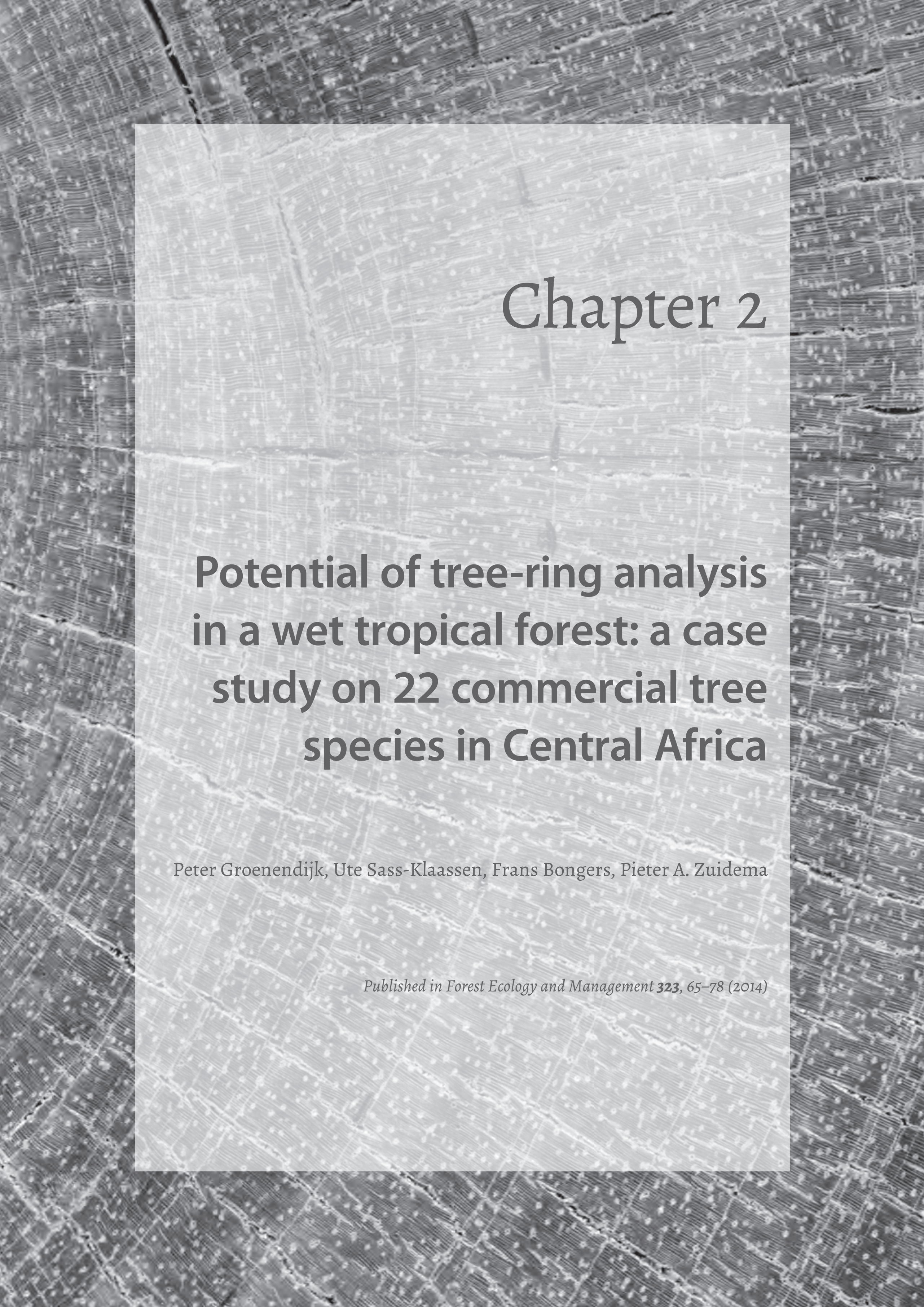
The main objective of this thesis is to use long-term growth data from tree-ring analysis to assess growth changes in tropical forest trees and improve the analysis of sustainability of timber exploitation. The first step when applying tree-ring analysis in the tropics is proving the annual character of the measured tree-rings. In CHAPTER 2 of this thesis, I therefore evaluate whether tree rings are formed annually by trees growing in a wet African tropical forest. For this purpose, I collected and prepared wood samples of 21 commercially exploited timber species and evaluate the presence of anatomical structures on the wood that indicate ring boundaries. On a subset of five species I analyse whether these ring boundaries are formed annually using radiocarbon bomb-peak dating.

In CHAPTER 3, I apply the growth data obtained from tree-ring analysis for four Cameroonian timber species to forecast future logging yields for these species The main goal of this chapter is to evaluate whether logged volumes can be sustained in the next logging round. Additionally, I assess the effect of changing the logging cycle length and of using species-specific logging intensities on these yield projections.

In CHAPTER 4, I use growth data from the Thai species *Melia azedarach*, combined with a modelling approach to assess the strengths and limitations of four commonly used trend-detection methods. For this purpose I first evaluate the consistency in the output of these methods by applying them to detect growth trends in the *M. azedarach* data set. Next, I simulated tree growth trajectories under different growth-trend scenarios, with imposed increasing and decreasing trends and a no-trend scenario. By applying the four trend-detection methods on these scenarios, I assess each method's sensitivity, accuracy and reliability to detect long-term trends.

In CHAPTER 5, growth trends in 13 tropical tree species from three study sites located across the tropics are assessed. Using nearly all the tree rings measured in this study – nearly 100.000 – and applying the two most suitable trend-detection methods, I assess whether long-term growth changes have occurred on for the study species. Alongside the species-level trend analysis, I assess trends aggregated per site and across all sites. These aggregated responses show whether growth changes are pervasive across species and sites and, if so, provide evidence for an external factor changing tree growth over the scale of centuries.

CHAPTER 6 provides a general discussion of the main findings. In this chapter I summarize the main findings of each chapter and discuss their consequences. Then I provide an overview of the main methods used to detect changes in tropical forests and provide recommendations on how to integrate them.



Chapter 2

Potential of tree-ring analysis in a wet tropical forest: a case study on 22 commercial tree species in Central Africa

Peter Groenendijk, Ute Sass-Klaassen, Frans Bongers, Pieter A. Zuidema

Published in Forest Ecology and Management ***323****, 65–78 (2014)*

Abstract

Implementing sustainable forest management requires basic information on growth, ages, reproduction and survival of exploited tree species. This information is generally derived from permanent sample plots in which individual trees are monitored. Accurately estimating growth rates and especially tree ages from plots is however challenging, as plots often contain only few individuals of the exploited species and monitoring periods cover only a fraction of the lifespan of most trees. Alternatively, tree-ring analysis is increasingly used to obtain accurate age estimates and growth rates for tropical tree species, especially in regions with seasonally harsh conditions. However, for species from wet tropical forests (>4000 mm yr^{-1} rainfall) few tree-ring studies exist. Under persistent high levels of rainfall, formation of distinct tree rings is uncertain due to the lack of strong seasonal variation in climate factors. Here we evaluated the potential of applying tree-ring analysis on commercial tree species in a wet tropical forest in Central-Africa. For this purpose we screened the wood anatomy of 22 tree species for the presence of tree-ring structures and, on a subset of five species, we assessed crossdating potential and evaluated the annual character of tree-ring formation by radiocarbon dating. A total of 14 of the 22 tree species showed distinct tree-ring boundaries. Radiocarbon proved annual tree-ring formation in four of the five tested species. Crossdating between trees was problematic for all species and prohibited to exactly date each detected ring and build tree-ring chronologies. We also show that diameter growth rates vary strongly between and among species, with important consequences for the calculation of future timber yields. Tree-ring analysis can thus be applied on tree species growing in wet tropical forests to obtain growth rates. We argue that tree-ring analysis should actually be applied on more tree species from different areas to obtain accurate, site specific growth data. This data is urgently required to design and improve sustainable forest management practices.

Keywords: Tree-ring analysis; tropical wet forest; timber species; forest management; radiocarbon dating; Cameroon

2.1 Introduction

While constituting the world´s second largest tropical forest belt, the West and Central African rain forests are relatively poorly studied. Over 44 million hectares of these forests have been designated for selective logging (Bayol *et al.*, 2012). Sustainable management of these forests is hence essential to ensure a continued supply of timber without affecting their services and functions (e.g., carbon retention). Planning sustainable forest management requires basic ecological information of the exploited species (e.g., age, growth trajectories, regeneration and survival). This information can for instance be used to calculate future timber yields in selective logging operations (e.g., Rozendaal *et al.*, 2010b). Despite the relevance for designing and evaluating forest management, such calculations have only been performed for a limited set of tropical tree species worldwide and are almost absent in Africa (Putz *et al.*, 2012; De Ridder *et al.*, 2013b). This paucity of studies is worrisome seen the importance of and great public attention given to sustainable management of (African) tropical forests.

In tropical forestry research, basic ecological information on exploited tree species – diameter growth rates and ages – is commonly obtained from measurements of trees in Permanent Sample Plots (PSPs). The contribution of PSPs to providing this information on African timber species has, however, remained very limited. PSPs are still scarce in tropical Africa (Verbeeck *et al.*, 2011) and the uneven geographical distribution of PSPs implies that information on commercially important forest areas is missing (Picard *et al.*, 2010). In addition, most PSPs are small, typically one hectare, and therefore contain only few individuals of commercial tree species, which typically occur at densities of <5 trees ha^{-1} (Poorter *et al.*, 1996; Hall *et al.*, 2003). And finally, the monitoring period of most PSPs spans just a fraction of the ages of trees, often resulting in biased tree-age estimations (Martínez-Ramos & Alvarez-Buylla, 1998) leading to a lack of accurate long-term data on ages and growth of commercial tree species.

An alternative and relatively fast approach to obtain tree ages and growth data is the use of tree-ring analysis (Brienen & Zuidema, 2006a; Schöngart *et al.*, 2006; Rozendaal *et al.*, 2010b). Data obtained from tree rings typically consider information on growth across the entire life-span of trees and can thus be used to calculate ages and growth trajectories of logged trees. These data can also be used to calculate ages of trees to reach the legally set logging diameters (minimum cutting diameter, MCD). For forest management, tree-ring analysis can thus be used to supplement data from PSPs. In Africa, tree-ring studies have mostly been performed in dry, sub-tropical areas outside important wood-producing areas (e.g., Dunwiddie & LaMarche, 1980; Till & Guiot, 1990; Gourlay, 1995; Stahle *et al.*, 1999; Tarhule & Hughes, 2002; Wils *et al.*, 2010; Wils *et al.*, 2011). Despite the knowledge that many commercial tree species in tropical Africa form annual rings (Mariaux, 1967; Détienne, 1989), tree-ring analysis has hardly been applied to aid forest management in West and Central Africa (De Ridder *et al.*, 2013b; Gebrekirstos *et al.*, 2014) and never so in wet forests of these regions.

Working with tree rings in tropical wet forests presents specific challenges. Under such persistently wet conditions, growth of trees has suggested to be continuous (Raven *et al.*, 1999) and distinct annual tree rings to be absent (Swaine, 1994; Kurokawa *et al.*, 2003). Although annual tree-rings formation has been proved for species growing in wet tropical forests (Fichtler *et al.*, 2003), the absence of strong growth-limiting environmental factors can result in only weak variation in cambium activity. This weaker cambium activity with increasing precipitation levels may thus lead to less variation in wood anatomy and hence in tree-ring visibility (Moya & Tomazelo-Filho, 2009). Lack of a growth-limiting factor that synchronises cambium activity in a given species also leads to varying growth patterns among individual trees, as local growing conditions are likely more influential than climate factors. This reduction of the 'common signal' in tree growth also affects crossdating and hampers chronology building for tree populations growing under very wet conditions (Fritts, 1976). Thus, for tree-ring studies in wet tropical forests, identifying ring boundaries and investigating their annual character is essential prior to obtaining growth data and tree ages.

Here we present results of a tree-ring study on commercial tree species in a wet (~4100 mm rainfall.year^{-1}) lowland tropical forest in the Southwest province of Cameroon. We first performed a screening for tree-ring boundaries in the wood of 22 commercial species. We expected to find distinct tree-ring boundaries in several species. The presence of a dry season and the seasonality in phenology (15 of the 22 species have a (brevi-)deciduous character) may induce periodic cambial dormancy, causing the formation of tree-ring boundaries. Next, we performed a more detailed analysis on a subset of five species showing clear tree-ring boundaries. We assessed the crossdating potential of these species and tested the annual character of tree-ring formation by radiocarbon dating. Finally, we described diameter-growth patterns and determined maximum tree ages and ages at minimum cutting diameters for this subset of species.

2.2 Materials and Methods

Study area

Samples were collected inside the Forest Management Unit (FMU) 11.001, of Transformation REEF Cameroon (TRC, 2008). This FMU is certified by the Forest Stewardship Council (FSC) and is located in the Southwest Region of Cameroon, between 5°23'N, 9°09'E and 5°23'N, 9°12'E, adjacent to Korup National Park (Figure 2.1). The vegetation of the region consists of semi-deciduous lowland rainforest (~200m a.s.l.) of the Guineo-Congolian type (cf. White, 1983), dominated by Leguminosae–Caesalpinioideae. Soils in the area are deep, skeletal (lithosols), with high sand content and a low pH (Gartlan *et al.*, 1986). Due to leaching by the high rainfall, soils are nutrient poor and only a thin organic layer is present (Newbery *et al.*, 1997). Regional climate is equatorial, with an unimodal rainfall distribution and a dry season from December to February (monthly rainfall <60mm, cf. Worbes, 1995). Rainfall amounts vary between nearby weather stations: at the Bulu station (40 km to the South of the study area) annual rainfall averaged 5220 mm, whereas at the Mamfé Airport station (40 km to the North) it averaged 2920 mm (Figure 2.1). Although total rainfall amounts vary between stations, both stations show an unimodal rainfall distribution. At our site, we expect annual rainfall to be intermediate, and similar to the 4082 mm measured at the Nguti weather station, located 27 km to the East (data not available; Nchanji & Plumptre, 2003). Temperature data was only available for the Mamfé station and shows little variation between months: maximum temperature averaged 30.2°C and minimum 23.7°C. A climate diagram for the Mamfé station is presented in Figure 2.1.

Study species, sample collection and preparation

Between June 2010 and May 2012, we collected samples of 601 individuals belonging to 22 tree species (Table 2.1). Nearly all 22 species belong to the top-35 most logged species in Central Africa (Ruiz-Pérez *et al.*, 2005) and commercial names, guild, distribution and uses are given in Table 2.1. We collected cross-sectional samples (discs) from 177 felled trees and three to four increment cores each from 424 standing trees using 5.15 mm increment borers (type Suunto and Haglof). Samples were taken at 1 m stem height or above anomalies or buttresses. Each sampled tree was geo-referenced (Garmin GPS60X) and we measured diameter at breast height (dbh) using a diameter tape.

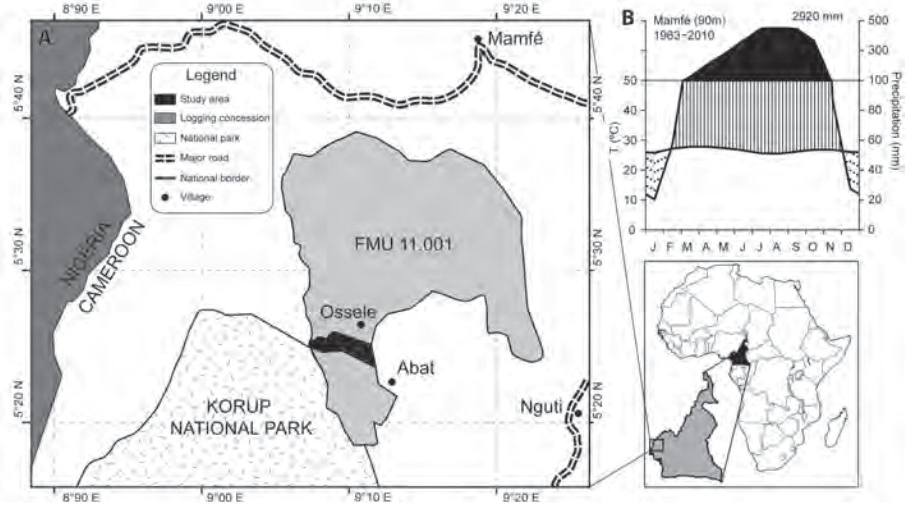


Figure 2.1 (A) Map of study site: 2012 cutting block (black) of the Forest Management Unit 11.001 (light grey). Korup National Park (hatched), Nigerian border (dark grey), major villages, and roads are also shown. Inlay shows the location of the study site in Cameroon. (B) Climate diagram for Mamfé Airport weather station (cf. Walter & Lieth, 1960; period 1968–2009) indicating dry season (rainfall<temperature, dotted area) and rainy season (>100 mm month^{-1}; black area).

About 90% of the samples were collected in a stratified random sampling design, inside an unlogged and seemingly undisturbed area of the FMU (TRC, 2008). For this purpose, we installed circular plots of c. 1 hectare at random coordinates inside 16 cells of 300 x 300m (located in a virtual grid of 4 x 4 cells). Inside these plots, all trees >5 cm dbh of our target species were sampled. The remaining samples were collected non-randomly, from large trees or from individuals of less abundant tree species. These samples were collected to increase the amount of species and the amount of large and presumably old trees in our analysis. For some rare species we collected only a few individuals or only increment cores, as rare species were spared from logging or because there was no commercial demand at the time (Table 2.2).

To allow inspection of tree-ring structures, all samples were air dried. Discs were polished with increasingly finer sandpaper, from grain 40 up to 1000, and increment cores were either polished or cut using a large sliding microtome (Gärtner & Nievergelt, 2010).

Tree-ring analysis

We investigated the potential for tree-ring analysis of the 22 commercial tree species (henceforth called 'screened species') by assessing the presence of distinct tree-ring boundaries. On a subset of five species, the 'subset species', we performed a detailed analysis to assess their cross-dating potential, test the annual character of tree-ring formation by radiocarbon dating, and assess their general growth patterns. The subset species were selected based on the presence of clear tree-ring structures, tree abundance in the forest (sample size >60 individuals), currently being logged in the study area, and the possibility of extracting increment cores, i.e. wood density neither too high nor too low. Four species fulfilled these criteria: *Brachystegia eurycoma* Harms, *Brachystegia cynometroides* Harms, *Daniellia ogea* (Harms) Rolfe ex Holl. and *Terminalia ivorensis* A. Chev. For these species we collected discs and cores of 62 to 128 individuals per species (Table 2.2). For a fifth species, *Entandrophragma utile* (Dawe & Sprague) Sprague, which was not very abundant but known to produce very clear tree-rings (Détienne *et al.*, 1998), we also sampled 10 discs.

Screening for tree-ring structures

After surface preparation, we evaluated, both macroscopically and under a stereo-microscope (magnification 16-40x, Leica) whether continuous tree rings could be identified around the stem circumference. We classified tree-ring structures and wood anatomical markers for ring boundaries in our species following Coster (1927) and Worbes and Fichtler (2010) in the following four types: (A) variations in wood density, (B) boundaries marked by a marginal parenchyma band, (C) repeated patterns of fibre and parenchyma bands, and (D) variation in vessel distribution and/or size. By following wood-anatomical markers around the circumference of discs, we evaluated their continuity and screened for the occurrence of phenomena that can obscure ring detection. Such phenomena include the presence of wedging rings and intra-annual growth variations. Wedging rings are distinct tree rings that merge (two or more rings join) on certain parts of the stem circumference, induced by local differences in cambial activity. Ring wedging often occur in slow growing species or on very eccentric stem disks (Wils *et al.*, 2009). Intra-annual growth variations are growth variations that can, in some species, resemble true ring boundaries and therefore lead to ring-misdetection. Characteristics of these intra-annual variations vary between species depending on their specific wood anatomy and may consist of bands of thick-walled fibres (density variations) or be characterised by the presence of (discontinuous) parenchyma bands. For all screened species we systematically identified possible problems and provided categories of the potential for tree-ring analysis using the following categories: high (++), good (+), possible (+-), low (-) and not possible (--). This potential is based on the presence and distinctness of tree-ring boundaries found in this study, but also in previous tree-ring studies on the same species or congeners (for more details, see Fact sheets in Appendix B).

Table 2.1. Characteristics of 22 commercial tree species from a wet tropical forest in Cameroon: commercial name, guild, Minimum Cutting Diameter (*MCD*) in Cameroon, distribution (*W Africa* = West Africa, *C Africa* = Central Africa, *CAM* = Cameroon, *NIG* = Nigeria), main applications of wood, and previous studies on the potential of tree-ring analysis.

Species	Family	Commercial name	Guild*	MCD (cm)	Distribution	Main uses wood	Previous tree-ring study?
Afzelia bipindensis	Fabaceae (C)	Doussie Rouge	PST	80	(W)+C Africa^{1,2}	Furniture, flooring^{2,5}	Yes^{7}
Afzelia pachyloba	Fabaceae (C)	Doussie Blanc	PST	80	(W)+C Africa^{1,2}	Furniture, flooring^{2,5}	Yes^{7}
Bikinia le-testui	Fabaceae (C)	Ekop Mayo	ST	60	C Africa^{3}	Plywood, interior^{2,6}	No
Brachystegia cynometroides	Fabaceae (C)	Ekop Nom Naga	PST	60	Cameroon^{2}	Plywood, interior^{2,5}	No
Brachystegia eurycoma	Fabaceae (C)	Ekop Naga	PST	60	CAM+NIG^{2}	Plywood, interior^{2,5}	No
Canarium schweinfurthii	Burseraceae	Aiele	LLP	60	W+C Africa^{1,2}	Plywood, interior^{2,5}	Yes^{7}
Daniellia ogea	Fabaceae (C)	Faro	ST	60	W+C Africa^{1,2}	Plywood^{2,5}	No
Didelotia letouzeyi	Fabaceae (C)	Gombé Mamel	ST	60	(W)+C Africa^{4}	Furniture, plywood^{6,5}	No
Entandrophragma angolense	Meliaceae	Tiama	LLP	80	W+C Africa^{1,2}	Veneer, furniture^{2,5}	Yes^{8}
Entandrophragma candollei	Meliaceae	Kosipo	LLP	90	W+C Africa^{1,2}	Veneer, furniture^{2,5}	Yes^{8}
Entandrophragma utile	Meliaceae	Sipo	LLP	80	W+C Africa^{1,2}	Veneer, furniture^{2,5}	Yes^{8}
Erythrophleum ivorense	Fabaceae (C)	Tali	LLP	50	W+C Africa^{1,2}	Furniture, hydraulic^{2,5}	Yes^{7,9}
Gilbertiodendron dewevrei	Fabaceae (C)	Limbali	ST	60	(W)+C Africa^{2}	Flooring, exterior^{2,6}	No
Guarea thompsonii	Meliaceae	Dark bosse	ST	80	(W)+C Africa^{2}	Flooring, interior^{2}	Yes^{7}
Khaya anthoteca	Meliaceae	Acajou d'Afrique	LLP	80	W+C Africa^{1,2}	Furniture, veneer^{2,5}	Yes^{8}
Lophira alata	Ochnaceae	Azobe	LLP	60	W+C Africa^{1,2}	Hydraulic, sleepers^{2,5}	No
Nauclea diderrichii	Rubiaceae	Bilinga	ST	80	W+C Africa^{1,2}	Furniture, sleepers^{2,6}	No
Pterocarpus soyauxii	Fabaceae (P)	Padouk rouge	PST	60	W+C Africa^{1,2}	Furniture, flooring^{2,5}	Yes^{7}
Pycnanthus angolensis	Myristicaceae	Ilomba	LLP	60	W+C Africa^{1,2}	Plywood, interior^{2,5}	No
Rhodognaphalon brevicuspe	Bombacaceae	Kondroti	LLP	60	W+C Africa^{1,2}	Plywood, interior^{2,5}	No
Staudtia kamerunensis	Myristicaceae	Niove	ST	50	Central Africa^{2}	Furniture, flooring^{2,5}	Yes^{10}
Terminalia ivorensis	Combretaceae	Framire	LLP	60	W Africa^{2}	Furniture, plywood^{2,5}	Yes^{7}

[1] Hawthorne and Jongkind (2006), [2] Lemmens *et al.* (2012), [3] Wieringa (1999), [4] Rietkerk *et al.* (1996), [5] CIRAD (2012), [6] ITTO (1990), [7] Détienne *et al.* (1998), [8] Détienne (1989), [9] Nzogang (2009), [10] Worbes *et al.* (2003)

*Guilds: *PST* = Partially shade tolerant, *ST* = Shade tolerant, *LLP* = Long-lived pioneer

Tree-ring measurements and crossdating potential

We measured ring widths on scanned images of each tree of our subset species using the software WinDendro Regular (version 2009b, Regent Instruments, Canada). For cores, we scanned and measured all cores extracted from individual trees; discs were scanned and rings were measured along four radii. For scanning we used a resolution of 1600 to2400 dpi, on a flatbed scanner (Epson Expression 10000XL). To increase tree-ring visibility samples were often wetted and/or scanned with a film of water on the scanner's glass plate. For sample sections with narrow rings, we marked rings under a microscope prior to scanning and on discs we interconnected every 10th to 15th clear ring to facilitate measuring and crossdating.

Crossdating consists of matching patterns of wide and narrow rings between radii measured from the same tree, or between mean ring-width patterns from different trees, to assign a calendar year to each detected ring (Douglass, 1941). We crossdated ring-width series within and among trees, both visually and statistically. Visual crossdating was performed while measuring, by matching ring-width patterns of different radii, and by ensuring that interconnected rings from different radii dated to the same year. Statistical crossdating was performed in WinDendro (version 2009b; Regent Instruments Canada Inc.), using the percentage of parallel run (ppr) between radii, and using the software COFECHA (Holmes, 1983; Grissino-Mayer, 2001). Successful crossdating among ring-width series of the same tree verifies concentric patterns in ring formation. Crossdating of ring-width series of different individuals of the same species becomes possible if radial growth of different individuals is limited or driven by the same external factor (Cook & Kairiukstis, 1990; Worbes, 1995). From these crossdated ring-width series, a site chronology can be calculated that reflects the common variance in growth of the tree species. Chronologies are usually calculated as annual averages of standardised ring-widths series. We standardized averaged diameter-growth series for each individual using 15-year cubic splines in COFECHA. Finding correlations between a chronology and annually/seasonally varying climate variables (e.g., precipitation in the rainy season) can be taken as strong evidence that tree-rings are formed annually, in response to these variable. Chronologies can then be used to calibrate the measurements of remaining trees, by synchronising their growth with the chronology and searching for mistakes in ring identification.

To build a chronology for each of the subset species, we first excluded all trees growing in the understorey (<50 cm dbh). Growth of these smaller trees is strongly influenced by competition for light and this competition signal may interfere with the climate-induced variation and thus hamper the detection of common climate-related growth-signals. From these larger trees, we selected the 10 individuals with the clearest tree-ring structures and highest within-tree crossdating as a basis to build the chronologies (i.e., mostly excluding juvenile trees and trees with phases of suppressed growth). We thus searched for the common growth-signal between trees, from a subset of trees assumed to be correctly crossdated and showing the strongest year-to-year variation in growth. We also included individuals for which tree-ring measurements were proven annual by radiocarbon dating (see below).

Radiocarbon dating

In the case of weak or absent common growth signals, the annual character of tree-ring formation can be tested by radiocarbon dating, a dating method independent of tree growth (Worbes & Junk, 1989). This method is based on the peak in ^{14}C in the atmosphere caused by above-ground atomic weapon tests (Nydal & Lövseth, 1983). To verify the annual character of tree-ring formation, we applied the ^{14}C bomb-peak dating method on our subset species except for *T. ivorensis*. Tree-ring formation for *T. ivorensis* had earlier been proven to be annual (Détienne, 1989) and we assumed rings to be formed annually due to its strong deciduous character in the study area.

Problematic tree-ring structures (e.g., vague or discontinuous rings) are common in the tropical species and may hinder ring identification (Worbes, 2002; Brienen & Zuidema, 2005). It is therefore important to identify whether these structures are actual tree-ring boundaries or structures formed by intra-annual growth variations. To identify these problematic structures, we selected three individuals per species based on the ease of measurements and the clarity of their tree-rings: one individual with 'very clear' rings and good internal crossdating (usually a disc); one individual with 'clear' rings and good internal crossdating but showing some problematic structures; and a third individual showing several problematic structures (i.e., vague rings or anomalous structures; usually cores). With this selection we expected to prove the annual character of ring formation in these species (on the 'very clear' samples), while also being able to verify our definition of tree-ring boundaries and to quantify possible dating errors on the ‘normal’ and ‘problematic’ samples.

For each individual, we sampled three to four tree-rings that were pre-dated by ring counting (and crossdating) and spaced eight to ten years apart. From each ring, we collected 35-50 mg of wood to determine radiocarbon age. By analysing samples from different years per individual, it is possible to identify if and where errors in measurements have taken place. If all dates coincide between pre-dated rings and ^{14}C measurements (margin of error ±1 year), rings are formed annually and no measurement errors took place. If a constant discrepancy in measurements is found between all samples in one individual, measurement errors occurred in the wood formed in more recent years (between the most recent ^{14}C-dated tree ring and the bark). If a discrepancy is found between samples, measurement errors occurred between the predated rings. By going back to the original wood samples after ^{14}C dating, it is possible to identify measurement mistakes and verify tree-ring boundary definitions. In the case of discrepancies that cannot be solved, tree-ring formation can still be annual, but measurement errors occur. Including the ‘problematic’ samples, with less clear rings, allows for an estimation of the frequency of these measurement errors. This estimation is calculated as the probability of ring misidentification by dividing the number of misidentified rings by the period under analysis provides (expressed in errors per 100 years, cf. Soliz-Gamboa *et al.*, 2011).

The fraction modern ^{14}C (F^{14}C) was determined on the holocellulose portion of the wood samples at the Center for Isotope Research at Groningen University, following their protocol for Accelerator Mass Spectometry analysis. We used the program CALIbomb (http://intcal.qub.ac.uk/CALIBomb) to determine the date for the each F^{14}C (±sd) value using the dataset corresponding to our study region (NH_Zone 3; Hua *et al.*, 2013). As a given radiocarbon concentration may yield several possible calendar dates, we determined the mostly likely date of each sample based on the dates of the other samples from the same tree, i.e., subsequent samples from bark to center in one tree should have subsequently older ages.

Growth patterns and ages to reach Minimum Cutting Diameters (MCD)

For each of the subset species we calculated annual diameter increments as the average growth of the different radii multiplied by two. Over- or underestimations in growth rates may arise from shrinkage of discs and cores or from measuring tree-ring widths on irregular parts of the stem i.e., in buttresses. Therefore, we applied a correction factor on the diameter increments, accounting for the difference in diameters measured from rings and the diameters measured in the field (cf. Brienen & Zuidema, 2006b). If information on the first formed rings was missing, due to rot in the stem centre or the fact that the pith was not hit when coring, we estimated the distance to the pith assuming a circular growth pattern. To estimate the number of missing years, this distance was divided by the average growth rate of the first five tree rings present in the sample. Furthermore, tree ages presented here are slightly underestimated as ages were calculated from samples obtained at approximately 1 m height. The time to reach this height can vary between fast growing, often light demanding species (e.g., *T. ivorensis*) and slower growing, often shade tolerant species (e.g., *D. ogea*).

The corrected diameter growth rates were used to describe life-time growth patterns of the subset species. First, we calculated for each species average diameter growth rates (in cm/year) per tree age. This allows for the comparison of patterns in growth rates, i.e., ontogenetic growth patterns between species. We also compared these average growth rates with the rates used in Cameroon for the calculation of future timber yields for these species (cf. MINEF, 2001). Finally, we calculated average cumulative diameters (in cm) per age for each species and used these diameter-age relationships to assess species-specific maximum (for the fastest growing individual), minimum (for the slowest grower), and average ages to reach MCD (as set by Cameroonian legislation for each species).

2.3 Results

Tree-ring structures and distinctness of ring boundaries

Here we discuss briefly the tree-ring structures of the screened species and provide more detailed descriptions for the subset species. In the Supplementary Material (Appendix B) we provide fact sheets for all screened species, with descriptions and images of tree-ring boundaries, as well as information on applicability for tree-ring analyses. Detailed anatomical descriptions of wood characteristics are also available for most of the screened species in Détienne *et al.* (1998), Richter and Dallwitz (2000) and on the InsideWood database (www.insidewood.lib.ncsu.edu; Wheeler, 2011).

Of the 22 screened species, 14 formed tree-ring boundaries of which eight species showed a ‘good’ or ‘high’ potential for tree-ring analysis (Table 2.2). All four types of tree-ring structures were observed in the screened species as well as combinations of structures. The most common tree-ring structure was type B (marginal parenchyma bands), as found in most Fabaceae and Meliaceae (Table 2.2). Two species - *Pycnanthus angolensis* and *Canarium schweinfurthii* - showed relatively clear structures on freshly sawn discs, but structures became unclear or disappeared after drying and polishing. Working with these species might require a different preparation approach (e.g., faster drying to avoid fungus infestations). Some individuals of *Staudtia kamerunensis* and *Gilbertiodendron dewevrei* showed clear anatomical structures. However, these structures were often discontinuous within the individual (disappearing on parts of the circumference), while other individuals completely lacked these structures. *S. kamerunensis* has been suggested to produce annual tree rings in a drier forest (Worbes *et al.*, 2003), but ring formation may not be annual, or could be suppressed, under the high levels of rainfall at our study site.

Of the five subset species, *E. utile* showed the most distinct tree-ring boundaries (Figure 2.2), consisting of parenchyma bands (growth zone type B), sometimes combined with repeated patterns of fibre and parenchyma bands (type C). Some individuals showed large differences in growth rates between radii (e.g., in trees with asymmetric centres, or with buttresses). In the shorter radii, clarity of ring boundaries decreased and many wedging rings occurred, often hindering ring identification.

T. ivorensis also showed very clear tree-ring boundaries that consisted of wood density variations (marked by thick-walled fibers; type A), and variations in vessels distribution and/or size (type D). Juvenile individuals were often fast growing (>1 cm year^{-1}) and showed the most distinct rings. Growth rates decreased with increasing diameter and rings became very narrow at large diameters. These narrow ring were more difficult to distinguish and measure.

Tree-ring boundaries of *D. ogea* were also clear and consisted of thin (2-3 cells wide) parenchyma bands with sometimes variation in vessel distribution. However, parenchyma bands were sometimes vague or disappeared on certain parts of stem. Vague bands that disappeared along the circumference of the disc or in one of the radii were considered to be intra-annual growth variations, and thus, no true ring boundaries.

For the two *Brachystegia* species, tree-ring boundaries consisted of a thin parenchyma bands with lens-shaped vessels attached to it (closed *triangles,* Figure 2.2). Both *Brachystegia* species also showed interconnected, eye-shaped vessels without the thin parenchyma band (*open triangles,* Figure 2.2). These interconnected vessels often occurred slightly before or after a tree-ring boundary and were often discontinuous on parts of the circumference of the stem. Due to their discontinuous character, we considered these structures to be intra-annual growth variations.

For all our subset species, identifying tree-ring boundaries and ring wedging was easier on discs, where individual rings could be followed, than on cores and also easier for species with parenchyma bands than for *T. ivorensis,* where ring boundaries are marked by thick-walled fibres. Furthermore, tree-ring boundary distinctiveness decreased in more narrow rings: i.e., towards the centre of trees (for the *Brachystegia's*, *D. ogea* and *E. utile*) and towards the bark (for *T. ivorensis*), or during periods of growth suppression. During these slow growing phases, wedging rings were also more common.

Crossdating potential

We first crossdated radii within trees and then among trees (on both single radii and on averages of radii per tree). Good internal crossdating was found for two species: 77% of *D. ogea* trees and 61% of *B. eurycoma* showed high levels of internal crossdating (i.e., a combination of well-matching long-term growth patterns and high ppr values; Table 2.3). The high levels of within-trees crossdating for these species, facilitated identifying intra-annual growth variations. However, on cores it was not always possible to ensure whether these anomalous structures were discontinuous over the entire circumference.

For the other species internal crossdating was less successful. Despite the clarity in tree-ring boundaries, all *E. utile* trees showed medium internal crossdating levels, i.e., matching growth patterns but low ppr rates. Growth rates often showed a low degree of synchronous year-to-year variation (complacent rings, cf. Stokes & Smiley, 1968) and crossdating was often only possible using the interconnected rings on discs, especially in trees with buttresses or asymmetric centres. For *T. ivorensis,* high levels of internal crossdating were found in only 34% of trees, while 52% showed 'medium' levels of crossdating. Juvenile individuals often exhibited complacent and wide rings (>1 cm year^{-1}), but ring-width decreased with age, resulting in very narrow tree rings in large, old trees. Larger *T. ivorensis* individuals also showed more buttresses. Rings were usually very clear in radii following buttresses, but wedging rings occurred in the slow growing parts between buttresses. The wide and complacent rings in juvenile wood and the slow growth with wedging rings in adult wood, often hampered crossdating between radii. Again, crossdating was often only possible using the interconnected rings on discs, or by matching the strong ontogenetic growth trends in radii. The lowest levels of crossdating were found in *B. cynometroides*: only 40% of the trees showed high within-tree crossdating levels, whereas for 37% crossdating levels were low (poorly matching growth patterns and low ppr). As most samples for *B. cynometroides* consisted of cores, it was not possible - as in disc - to interconnect rings to solve crossdating problems.

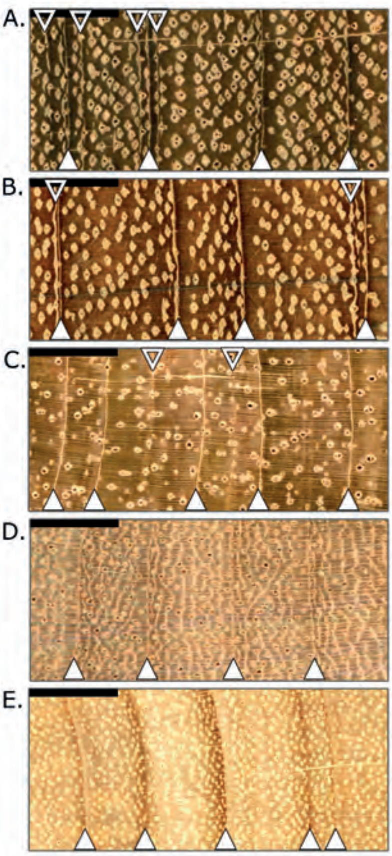


Figure 2.2 Tree-ring boundaries of five tree species from a wet tropical forest in Cameroon: A. *Brachystegia cynometroides*, B. *Brachystegia eurycoma*, C. *Daniellia ogea*, D. *Entandrophragma utile*, and E. *Terminalia ivorensis.* Growth direction from left to right; black bar = 5 mm scale, filled white triangles = annual tree-ring boundaries, open white triangles = intra-annual growth variations.

Crossdating among trees, i.e., finding a common growth signal, proved difficult for all species (Figure 2.3). The only species showing some degree of synchronicity in growth was *E. utile*. Two individuals, for which tree-ring formation was proven annual by radiocarbon dating (see section 3.2. below), showed synchronous growth patterns between ca. 1974 and 1992 (Figure 2.3, *black lines*). Remarkably, these trees showed a low-frequency synchronicity in growth (~5-10 years) but no synchronicity in annual growth variation (Figure 2.3). *B. eurycoma*, *D. ogea,* and *T. ivorensis* individuals showed no synchronicity in growth at all and we did not search for common growth patterns in *B. cynometroides* due to the uncertainties in measurement and low internal crossdating. Without a common growth signal, it was impossible to crossdate samples and ascertain dating of our rings was absolute. We were therefore not able to build chronologies for any of the species.

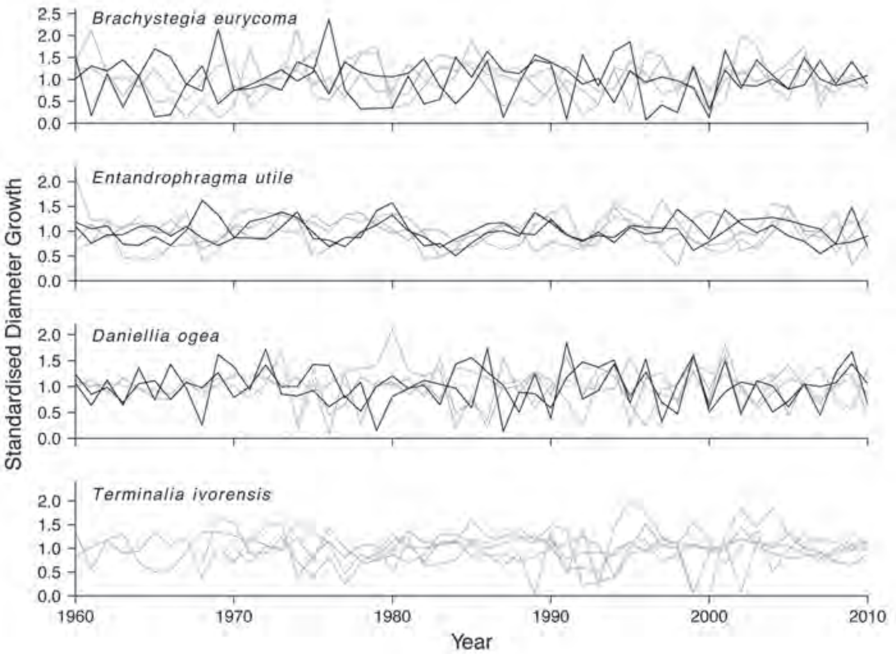


Figure 2.3 Standardized (residual) diameter growth rates of five individuals with clear rings for *Brachystegia eurycoma, Daniellia ogea, Entandrophragma utile,* and *Terminalia ivorensis* in a wet tropical forest in Cameroon. Black lines represent individual trees correctly dated using radiocarbon dating (not applied on *T. ivorensis*); grey lines represent other individuals showing clear rings (i.e., no doubtful structures and good internal crossdating). Standardization performed with a 15-year cubic spline.

Table 2.2. Growth-ring characteristics of 22 commercial tree species from a wet tropical forest in Cameroon. Ring boundary codes: (A) wood density variation, (B) marginal parenchyma band, (C) patterns of alternating fibre and parenchyma bands, (D) variations in vessels distribution and/or size, and (-) no ring boundary. Total number of individual trees collected (and number of discs), leaf phenology, difficulties and overall potential are also given. The five selected species for which further analyses were done are **in bold.**

Species	Tree-ring boundary	# trees (as discs)	Leaf phenology*	Difficulties**	Potential
Afzelia bipindensis	B	2 (2)	Deciduous	W	+
Afzelia pachyloba	B	2 (1)	Deciduous	W	+
Bikinia le-testui	B	10 (10)	Evergreen	C+D+S+W	+-
Brachystegia cynometroides	B	124 (4)	Brevi-Deciduous	D+M+S+W	+-
Brachystegia eurycoma	B	128 (32)	Brevi-Deciduous	D+M+S+W	+
Canarium schweinfurthii	-/A	5 (3)	Deciduous	n/a	+-
Daniellia ogea	B	105 (18)	Deciduous	D+S+W	++
Didelotia letouzeyi	-/B	2 (0)	Evergreen	n/a	-
Entandrophragma angolense	B	1 (0)	Deciduous	n/a	++
Entandrophragma candollei	B	1 (0)	Deciduous	n/a	++
Entandrophragma utile	B	10 (10)	Deciduous	W+S	++
Erythrophleum ivorense	D	15 (10)	Deciduous	W	+-
Gilbertiodendron dewevrei	B	10 (4)	Evergreen	n/a	+-
Guarea thompsonii	A	1 (1)	Evergreen	n/a	+-
Khaya anthoteca	-	3 (1)	Evergreen	n/a	-
Lophira alata	-	2 (2)	Brevi-Deciduous	n/a	--
Nauclea diderrichii	-	5 (0)	Evergreen	n/a	--
Pterocarpus soyauxii	C+B	5 (1)	Brevi-Deciduous	n/a	+-
Pycnanthus angolensis	-/B	30 (12)	Brevi-Deciduous	n/a	+-
Rhodognaphalon brevicuspe	-/A	5 (1)	Deciduous	n/a	+-
Staudtia kamerunensis	-/B	73 (13)	Evergreen	n/a	+-
Terminalia ivorensis	A+D	62 (52)	Deciduous	W+S	+

* Phenology: deciduous: tree leafless for >4 weeks; brevi-deciduous: tree briefly or only partially leafless; evergreen = trees without leafless periods.

** Difficulties: C = coring (wood too hard or to bristle), D = doubtful / vague ring-boundaries, M = rings missed (^{14}C analysis), S = periods of slow growth, W = wedging rings, n/a = not assessable

Radiocarbon dating

The ^{14}C bomb-peak dating yielded variable results for the four tested species (Figure 2.4). In *E. utile,* pre-dated ring measurements matched radiocarbon ages in all cases and within the 1-year margin of error of radiocarbon dating. This confirms annual ring formation for this species and shows that it also produces reliable annual tree rings under very wet conditions. Close matches between tree-ring and ^{14}C dates were also found for most measurements in *D. ogea*, again confirming annual tree-ring formation. However, in the *D. ogea* tree with problematic rings, a discrepancy of two years was found (points above the diagonal; Figure 2.3), indicating that some of the marked structured were not true ring-boundaries.

In most measurements for *B. eurycoma* we also found close matches between the tree-ring dates and radiocarbon dates. We did, however, also find discrepancies for *B. eurycoma,* with a maximum error of seven years (negative sign indicates rings were missed). These discrepancies were present in the tree with 'difficult' rings (measurements were shifted 3-5 years) and for the tree with 'very clear' rings. In the latter, discrepancies were present in the inner-most rings, i.e., the juvenile wood), in a difficult part of the disc with slow growth. Except for these rings in juvenile wood, the division into ring clarity was thus reflected in the radiocarbon dating results.

Discrepancies between tree-ring dating and ^{14}C dating were found for all three individuals of *B. cynometroides*. In this species, rings were missed during measurements (points below the diagonal line, Figure 2.3) and the maximum measurement error was 10 years. The division into ring clarity classes was not reflected in the radiocarbon dating results for *B. cynometroides:* rings were missed in all three individuals, but surprisingly dating was most accurate in the individuals considered to have problematic rings.

We also calculated the probability of ring misidentification, to quantify the frequency of measurement errors (errors per 100 years, cf. Soliz-Gamboa *et al.*, 2011). This probability was highest for *B. cynometroides*: -12.3% (i.e., there is a chance of missing a ring every ~8 years). For *B. eurycoma* the mean misidentification probability was -3.1%, and for *D. ogea* +1.9% (Table 2.3). Results of the radiocarbon dating and detailed figures per dated tree are given in the Supplementary Materials (Appendix A).

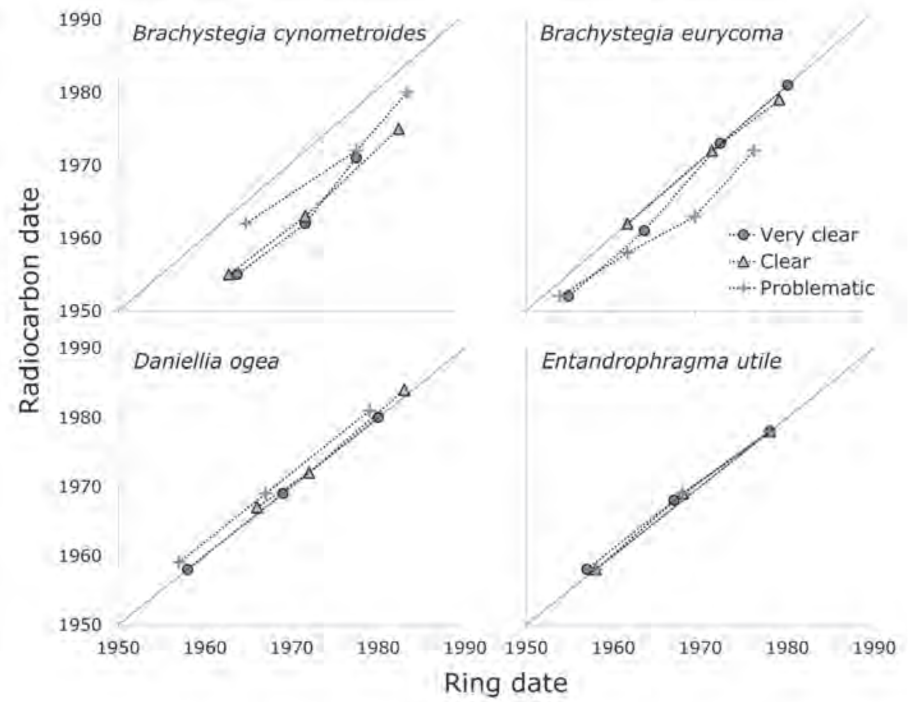


Figure 2.4 Comparison of dates from tree-ring measurements and ^{14}C bomb-peak derived dates for four species in a wet tropical forest in Cameroon. Rings are formed annually when symbols are on the diagonal Y=X line. Connected symbols represent measurements on the same individual. Three categories of tree-ring clarity were distinguished: very clear - tree-ring boundaries were very clear with good internal crossdating; clear - some doubtful structures but good internal crossdating; problematic – tree showing typical problems for the species (e.g., vague or discontinuous rings). Detailed results provided in Supplementary Materials Appendix A.

Growth patterns and ages at MCD

The five subset species showed large differences in ages, growth rates and lifetime growth trajectories. *D. ogea* and *E. utile* had the longest lifespans (>275 years old), while the other three species reached maximum ages of 180 to 200 years (Table 2.3). Average growth rates (± standard deviations) ranged between 0.43±0.35 cm yr^{-1} for *D. ogea* and 0.96±0.71 cm yr^{-1} for *T. ivorensis* (Table 2.3). Lifetime growth patterns also varied between species, with *B. cynometroides* showing rather constant growth rates over time, while *B. eurycoma*, *E. utile*, and *D. ogea* presented low juvenile growth rates that increased at intermediate ages, decreasing again slightly for older trees. *T. ivorensis* trees exhibited an ontogenetic growth pattern typical for light-demanding species, with high growth rates (>1 cm yr^{-1}) for juvenile trees that strongly decreased with age (Figure 2.5). The presented growth rates of *B. cynometroides* likely overestimate actual growth rates because of the high frequency of rings missed.

Growth rates also varied strongly within species, inducing large variation in ages to reach MCD (Figure 2.6). For instance, *T. ivorensis* trees reached MCD on average after 45 years, but ages varied more than fourfold, ranging from 21 to 91 years. In the slowest growing species, *D. ogea*, MCD was reached after 148 years on average, but this ranged from 77 to 214 years (for all species, see Table 2.3).

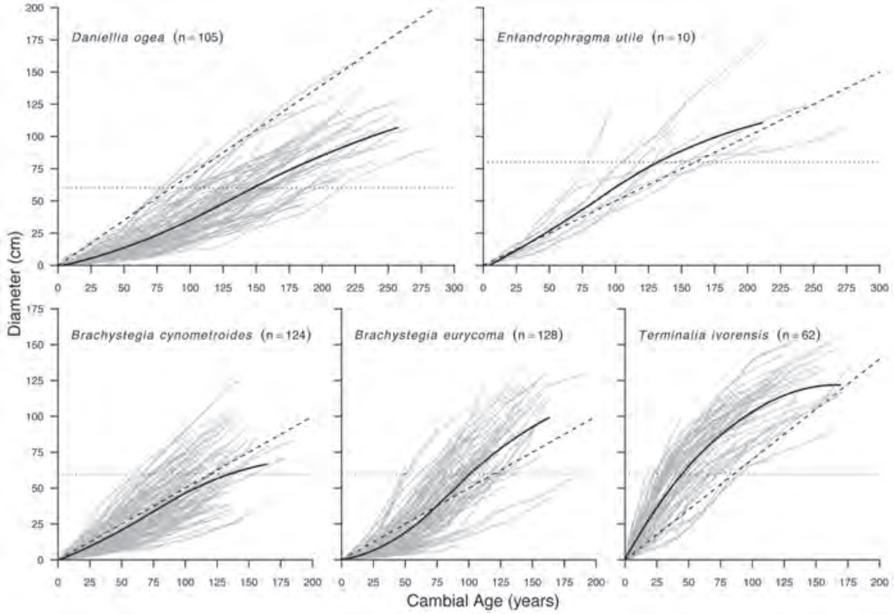


Figure 2.5 Diameter growth rates vs. cambial age of five tree species from a wet tropical forest in Cameroon. Each grey line represents diameter growth values of an individual tree; black lines show average growth rates if >5 samples were available. Dashed lines show the growth rates for each species in Cameroon used for timber yield calculations (cf. MINEF, 1999).

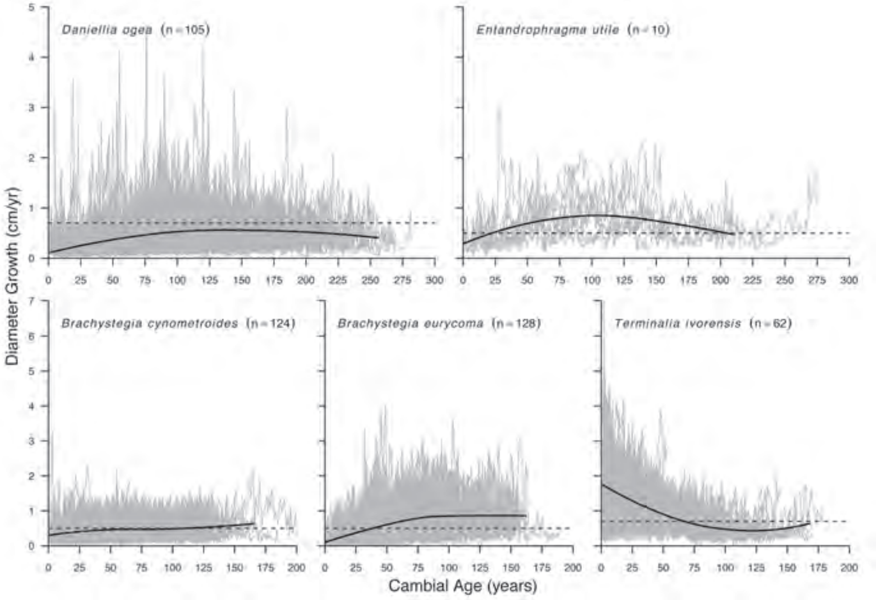


Figure 2.6: Lifetime growth trajectories for five tree species in a wet tropical forest in Cameroon. Each grey line represents the lifetime growth trajectory of an individual tree; black lines show the average growth pattern if >5 samples were available; dashed horizontal lines indicate minimum cutting diameters (MCD) and diagonal lines show the growth rates for each species in Cameroon used for timber yield calculations (cf. MINEF, 1999).

Table 2.3. Growth and age characteristics of five selected commercial tree species from a wet tropical forest in Cameroon. Number of trees collected, number of trees cored (3 to 4 cores per tree) and discs. Diameter growth and age at Minimum Cutting Diameter (MCD) refers to the population average. Crossdating level: high (well-matching growth patterns and high ppr), medium (matching growth patterns, intermediate ppr), and low (poorly matching growth patterns and low ppr). Percentage of ring misidentification (RMI): based on radiocarbon dating, is the average amount of misidentified rings divided by the period of measurement (cf. Soliz-Gamboa *et al.*, 2011). Positive values indicate that anatomical structures were erroneously identified as tree-ring boundaries; negative values indicate that rings were missed.

Species	**# trees**	**cores / discs**	**Diameter growth (cm/yr, ±SD)**	**Age at MCD (y, range)**	**Crossdating level (high/medium/low)**	**RMI (in %)**
Brachystegia cynometroides	124	120 / 4	0.45±0.29	126 (58-154)	40% / 23% / 37%	-12.3
Brachystegia eurycoma	128	96 / 32	0.56±0.48	100 (48-135)	61% / 33% / 6%	-3.1
Daniellia ogea	105	87 / 18	0.43±0.35	148 (77-214)	77% / 23% / 0%	1.9
Entandrophragma utile	10	0 / 10	0.72±0.40	126 (79-203)*	0% / 100% / 0%	<1
Terminalia ivorensis	62	10 / 52	0.96±0.71	45 (21-91)	34% / 52% / 14%	n.a.

*MCD = 60 cm, except for *E. utile* = 80cm

2.4 Discussion

We evaluated the potential to apply tree-ring analysis in a wet Central-African lowland tropical forest. Even under wet tropical conditions, 14 of the 22 tree species produced visible tree-ring boundaries. The annual character of tree-ring formation was proven using radiocarbon dating for three species, while a fourth species showed rings were frequently missed. Although clear and annually formed rings were present in four species, we were unable to build chronologies. Growth rates varied strongly between and within species, implying that different species reach MCDs at different ages and that ages also vary strongly within species.

Tree-ring boundaries and annual ring formation in wet tropical forests

This study is one of the very few tree-ring studies performed in wet tropical forests (>3000 mm yr-1; Zuidema *et al.*, 2012) and the first one conducted in wet African forests. Even under these wet conditions, tree-ring structures were formed in 14 of the 22 commercial tree species. Overall, most tree species forming tree-ring boundaries were (brevi)deciduous, whereas evergreen species (e.g., *K. anthoteca, D. letouzeyi*) and species with a very short leafless period (e.g., *L. alata, P. angolensis*) mostly showed no or vague tree-ring boundaries. In about 36% of the screened species (8 out of 22), the potential for tree ring analysis is good or high (+ or ++, Table 2.2). This proportion is in accordance with studies from dry (Tarhule & Hughes, 2002; Brienen *et al.*, 2009) and humid forests (Beltrán Gutiérrez & Valencia Ramos, 2013), suggesting that the potential of tree-ring analysis for wet forest is similar to that of drier environments. Anatomical wood descriptions exist for most of the 22 tree species (Richter & Dallwitz, 2000) and annuality of ring formation had been studied for several of them, albeit in drier sites (Détienne & Mariaux, 1977; Détienne *et al.*, 1998; Worbes *et al.*, 2003). For 10 of the screened species this is the first time the potential for tree-ring analysis is evaluated (Table 2.1) and for three species - *B. eurycoma, D. ogea* and *B. cynometroides* - this is the first time the annual nature of ring formation is evaluated.

Radiocarbon dating confirmed annuality of tree-ring formation but also showed measurement mistakes or occasional absence of (distinguishable) tree-ring boundaries occurred (Figure 2.4). This independent dating allows for correcting tree-ring boundary markings on samples. However, in both

Brachystegia species, we were unable to locate all rings missed. Growth rates for these species are thus somewhat overestimated, especially for *B. cynometroides* (Table 2.3). The typical slow growth rates of this species, combined with the low rates of internal crossdating further hampered detection of mistakes and probably increased ring misidentification. On the other hand, points within individuals were mostly parallel to the x=y line in Figure 2.3, indicating that the number of rings between (radiocarbon dated) samples within a tree was estimated quite accurately. Although ring misidentification is thus common, we believe that ring measurements in *B. cynometroides* can still provide valuable basic information on the growth rates of this species. It is important to work with discs instead of cores to reduce measurement errors. Alternatively, a correction factor to account for ring misidentifications could be applied (e.g., by decreasing growth rates of *B. cynometroides* with 12.6%), but establishing a reliable correction factor would require (costly) radiocarbon analyses on many more individuals.

In *D. ogea*, intra-annual growth variations were present and not always identified. Identifying these structures was often difficult, especially on cores or during periods of slow growth (e.g., juvenile rings). Growth rates could thus be slightly underestimated (as indicated by the radiocarbon dating), however we expect the high levels of internal crossdating to have limited the amount of misidentified rings.

For all subset species we found problems common to tropical dendrochronology: small, wedging or vague rings and intra-annual structures resembling tree-ring boundaries. These problems have been reported in several studies and have led previous researchers to recommend to perform ring measurements on discs rather than cores (Worbes, 2002; Brienen & Zuidema, 2005), which we reiterate here.

Chronology building and asynchronous growth under wet conditions

Despite the high levels of internal crossdating and the proven annual ring formation for several species, we were unable to crossdate measurements among trees. Chronologies of *E. utile* have been successfully built in drier forest areas (Nzogang, 2009). However, in this study crossdating among individuals was weak and we only observed synchronicity at 5-10 year cycles for individuals standing close to each other. Growth variation might thus be driven by other factors: local factors (e.g., soil depth, water table), internal cycles (e.g., reproduction) or canopy dynamics (Fritts & Swetnam, 1989).

The strong ontogenetic growth trend in *T. ivorensis* and the difficult identification of rings near the bark made crossdating in this species harder. Difficulties to build chronologies using a few discs of young (~30 years) trees were also reported for the congener *T. superba* (Couralet, 2010), but chronologies have been built recently for that species (De Ridder *et al.*, 2013a). In the Congolese Mayombe forest, *T. superba* produced clear rings and growth correlated to local precipitation, whereas in the wetter forests in Ivory Coast, ring clarity was lower and growth showed no correlations to local climatic variables (De Ridder *et al.*, 2013a). A similar decrease in ring clarity with increasing precipitation was also reported for *Gmelina arborea* in Costa Rica (Moya & Tomazelo-Filho, 2009). *T. ivorensis* is most commonly found in dryer forests (1250–3000 mm; Lemmens *et al.*, 2012) and may thus be growing on the wetter edge of its distribution in our study site. Precipitation thus may not limit growth, thwarting the common growth signal (Cook & Kairiukstis, 1990). The combination of complacent rings, irregular growth and lower ring clarity may thus have hampered detecting common growth signals.

Despite the many discs and the good internal crossdating of *D. ogea* and *B. eurycoma*, we were unable to crossdate measurements among individuals. Growth was not even synchronous between trees growing near one another: two fast growing *B. eurycoma* individuals (Be169 and Be170) of similar size (~60 cm diameter), showing very clear rings, high levels of internal crossdating and growing ~30m apart did not show synchronous growth patterns. Chronologies have been built for congeners from drier forests (D. oliveri, Schöngart *et al.*, 2006) or savannah (B. spiciformis, Trouet *et al.*, 2006), suggesting – again – that the high amounts of rainfall in our study site reduce the synchronicity in growth.

Are there other factors that could explain this apparent lack in a common growth signal? We believe that not only the high levels of rainfall, for some species the wetter edge of their distribution could obscure the common growth-signal (cf. Cook & Kairiukstis, 1990), but also (observed) asynchronous leaf-fall. During the dry season, individuals of *B. eurycoma*, *B. cynometroides*, *D. ogea*, and *T. ivorensis*, growing near each other could be simultaneously in different stages of leaf change (i.e., with old leaves, without leaves and with new leaves). This could cause cambial activity - and thus growth - to be asynchronous between trees, especially at the beginning of the growing season.

Building chronologies for tree species in the wet tropics is thus challenging, even if those species possess clear rings that are formed annually. The cycles of (inter)annual cambial activity and wood formation are poorly understood, while forming the basis for tree-ring studies. Filling this knowledge gap requires a more intensive evaluation (than we have done) of tree-ring formation. This evaluation should go further than descriptions of tree-ring boundaries (cf. Alves & Angyalossy-Alfonso, 2000; Richter & Dallwitz, 2000; Beltrán Gutiérrez & Valencia Ramos, 2013) and should include periodic dendrometric measurements, like summarized for South American woody species by (Callado *et al.*, 2013). This can be done either by periodic cambial wounding (e.g., Mariaux, 1967; Trouet *et al.*, 2012; Tolera *et al.*, 2013) or successive micro-sampling for evaluations of cambium activity throughout a given period (cf. Amobi, 1973; Krepkowski *et al.*, 2011; Volland-Voigt *et al.*, 2011). This would be especially insightful when combined with phenological observations (i.e., leave flushing, fruiting; e.g., Borchert, 1999) and high-resolution meteorological data. Further techniques that show promising results for tropical tree-ring studies should also be explored. For instance, X-ray densitometry can be applied to aid in recognizing tree-ring boundaries (Worbes, 1995) and the analysis of stable isotope ratios (e.g., carbon and oxygen) has shown promising results in tropical species as a proxy to reconstruct climate (cf. Brienen *et al.*, 2012b).

Application for forest management studies

Tree-ring analysis can be applied in wet tropical forests to obtain local and species-specific growth data and tree ages that can be used to plan and evaluate forest management. In Cameroon, management decisions (e.g., MCD and logging intensities) are based on timber yield calculations using the software TIAMA (MINEF, 1999). These calculations are done using legally set average growth rates for each species, established by the Ministry of Forestry and Wildlife in Cameroon. We argue that three potential problems arise when using set growth rates to calculate future timber yields: (1) set rates may be incorrect (i.e., too high or too low), potentially leading to incorrect regulations on logging intensity or length of cutting cycle; (2) ontogenetic growth patterns are ignored when using a single life-time average growth rate for a given species; and (3) persistent differences in growth between individuals are ignored if one species-average value is used.

First, we found discrepancies between the set growth rates and the actual (measured) values for the subset species. The legally set rates in Cameroon for these species are: 0.5 cm yr^{-1} for *B. eurycoma*, *B. cynometroides*, and *E. utile* and at 0.7 cm yr^{-1} for *T. ivorensis* and *D. ogea* (MINEF, 2001). *B. eurycoma, B. cynometroides* and *E. utile* showed similar growth rates to the set rates. On the other hand, *D. ogea* showed rates that were 39% lower than the set rates and *T. ivorensis* 47% higher. These discrepancies between legally set and actual growth rates may lead species to be under- or overexploited. If growth rates used in yield simulations are higher than actual rates, future timber yields for a species will be overestimated. This may lead to the species being exploited at higher intensities than it is able to regrow. The discrepancies found here highlight the importance of measuring accurate growth rates for each managed species. Preferably, these rates should be measured locally, as rates vary within species for trees growing in different areas (Therrell *et al.*, 2007). Growth rates found here were, however, comparable with those reported for the same species at other sites (cf. Nzogang, 2009), for congeneric species (Worbes *et al.*, 2003; Schöngart *et al.*, 2006; Trouet *et al.*, 2006; De Ridder *et al.*, 2013b) and for other tropical wet forest tree species (e.g., Fichtler *et al.*, 2003; Brienen & Zuidema, 2006a).

Second, ignoring the ontogenetic growth trend found for many species may also lead to incorrect management decisions. For instance in a light-demanding species as *T. ivorensis*, growth rates decrease strongly with age. Until an age of ca. 65 years, the average growth rate for *T. ivorensis* trees is higher than the set rates (Figure 2.5). At this age though, most trees have already reached the MCD (Figure 2.6). Growth in young years is thus relatively more important for wood production than at higher ages. This is the opposite for more shade tolerant species as *B. cynomtroides* and *D. ogea*, that show increasing growth rates with age.

And finally, the fan-shaped growth trajectories found here (Figure 2.6) indicate that persistent differences in growth rates are present in our species. These differences strongly influence size–age variations within a species (Bullock *et al.*, 2004) and may lead to underestimations of estimated future timber yields (Brienen & Zuidema, 2007). Calculation of timber yields should thus include this variation and not be calculated using only average growth rates. Growth data presented here contain this variation and can thus be used to produce more accurate and species-specific estimations of future timber yields.

Outlook and recommendations

Here we show for the first time the potential for tree-ring studies in an African wet tropical forest. Annual ring formation in wet tropical forests has been shown before (Dünisch *et al.*, 2003; Fichtler *et al.*, 2003), but studies in (non-flooded) wet tropical forests are an exception (Zuidema *et al.*, 2012). Although possible, there are some limitations and difficulties of working with tree-rings in such wet climates. Not finding a common growth-signal (i.e., not being able to build chronologies) implies that annuality has to be proven using (expensive) radiocarbon dating analyses. Furthermore, the lack of a chronology also limits the options for quality checking as ring measurements cannot be compared across samples, potentially reducing accuracy. It is therefore essential to assess cycles of wood formation (see section 4.2) in combination with (traditional) tree-ring analysis.

We reiterate the importance of working with discs instead of cores, especially when studying wet forest species. Working with discs allows for a higher accuracy in tree-ring identification and we argue that obtaining discs directly at sawmills would greatly facilitate fieldwork. On the other hand, working solely with discs also limits sample collection to trees above the MCS and to (the small group of) commercial species. Increment cores can be used to expand sampling to smaller trees or to species not being logged and successful tropical tree-ring studies exists based (almost) solely on increment cores (e.g., Schöngart *et al.*, 2006) or on a combination of discs and cores (e.g., De Ridder *et al.*, 2013a; De Ridder *et al.*, 2013b). Therefore, we recommend working with discs as the basis to identify (problems in) ring-boundaries and using cores to expand sample sizes and species.

Obtaining discs at the sawmills facilitates fieldwork, without reducing the applicability of the measured tree-ring data. Many of the meta-data relevant for tree-ring analysis and necessary to calculate future timber yields (e.g., tree location, densities per hectare, dbh, bole height, etc.) can nowadays be obtained from logging inventories. Although these data may be less accurate than actual measurements in the field (e.g., tree locations are usually roughly estimated), time gained probably outweighs possible losses in accuracy. Furthermore, trees being logged are usually above MCD, thus representing a subset of successful, surviving trees. Growth rates of these (successful) trees may be more representative for the growth of trees to be logged in the future and thus provide more accurate yield estimations (Rozendaal *et al.*, 2010b). We also recommend working with sample sizes >35-50 (large) trees per species, as done in this study, to obtain accurate growth rates and quantification of persistent growth differences. Setting up national or regional (multi-country) tree-ring laboratories should be encouraged, to measure growth rates for more species, locally and in different forest areas per country or region.

Finally, from a forest management perspective in (Central) Africa, we recommend focusing tree-ring analysis on the 15 most exploited tree species. These species comprise ~92.5% of the total volume logged in tropical Africa (Ruiz-Pérez *et al.*, 2005) and most of these species (12 out of 15) produce tree-ring boundaries (Richter & Dallwitz, 2000). Four of these species were included in this study (*C. schweinfurthii, E. utile, E. ivorense, and P. soyauxii*). We also express the importance of reporting and publishing both the successful studies (i.e., species with annual rings, chronologies and climate-growth correlations) and the failures (i.e., no annual rings, no chronologies). Publications are probably biased to the successes, whereas knowledge on which species do not form rings is equally important.

There is a great potential to use tree-ring analysis, even in wet tropical forests, to provide essential ecological data that can be used for forest management. Tree-ring analysis obviously only provides growth rates of surviving trees. Combining growth rates from rings with survival and regeneration data from PSP in the same forests would allow for realistic simulations of population growth (cf. Couralet *et al.*, 2005). This would be especially interesting when combined with (long-term) monitoring studies on the effects of logging and silvicultural treatments on the development of exploited forests (cf. Peña-Claros *et al.*, 2008; Gourlet-Fleury *et al.*, 2013). Such an analysis would allow for a more accurate evaluation of the consequences of forest exploitation. We hope that this study (and the supplemented fact sheets) may form the beginning of a better information basis for sustainable forest management in (Central) Africa.

Acknowledgements

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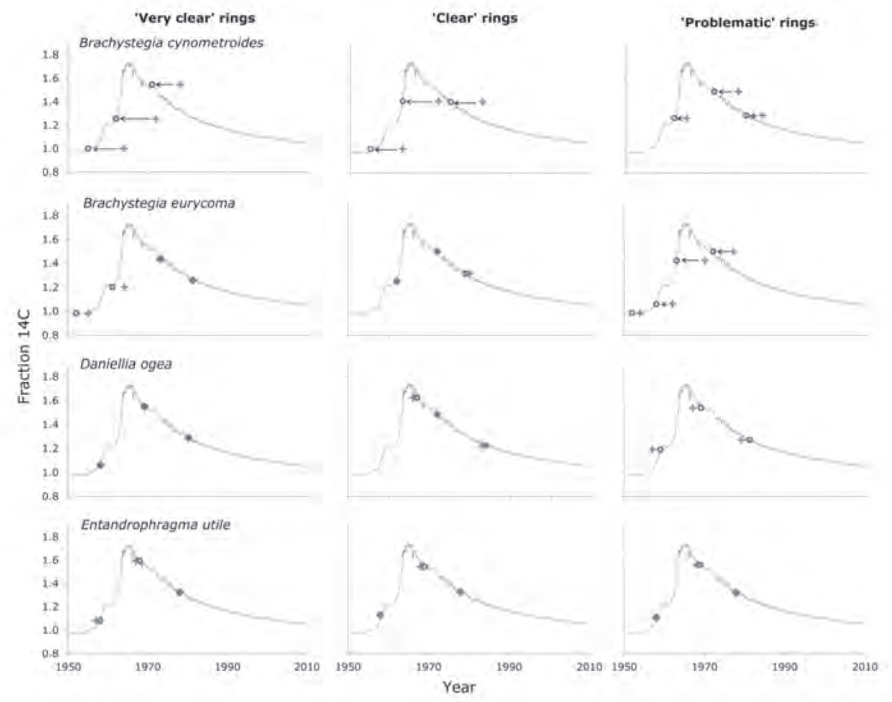
Supplementary Materials Chapter 2

Appendix A – Radiocarbon dating



Supplementary Figure S2.1 ^{14}C fraction in wood of pre-dated rings (red crosses) and the corresponding radiocarbon dates (green circles) for four species from a wet tropical forest in Cameroon. When pre-dated rings and radiocarbon dates correspond, ring dating was correct. Discrepancies (indicated by arrows) indicate measurement mistakes. Grey lines are the reconstructed northern hemisphere zone 3 radiocarbon values (NH_Zone3, cf. Hua & Barbetti 2013)

Supplementary Table 2.1 Ring dates and radiocarbon (^{14}C) dates for four tree species from a wet tropical forest in Cameroon. For each of the species 3-4 samples were analysed. Ring dates were determined by counting rings back in time from the bark. Radiocarbon dates were determined with the program CALIbomb (http://intcal.qub.ac.uk/CALIBomb), using the fraction of ^{14}C (±sd) in the wood (measured by Accelerator Mass Spectometry on holocellulose) using the NH_Zone3 (Hua & Barbetti 2013). Positive differences indicates that ring dates were overestimated (i.e. false rings) and negative differences indicate and underestimation of the date (i.e. missing rings). Percentages of rings missed was calculated as the amount of rings missed per measurement and the period over which these rings were missed (average percentages calculated over all measurements per species). *For *E. utile* amount of rings missed was within the measurement accuracy of radiocabon dating and percentages were not calculated.

Species	Ring clarity	Tree-ring date	Radiocarbon date	^{14}C fraction (in %)	Sigma ^{14}C fraction	Amount missed rings	Period over missed rings	Amount/Period missed rings	Average missed rings (in%)
Brachystegia cynometroides	Very clear	1964	1955	100.22	0.37	1	8	12.5%	
Brachystegia cynometroides	Very clear	1972	1962	125.46	0.46	-3	6	-50.0%	
Brachystegia cynometroides	Very clear	1978	1971	154.66	0.56	-7	33	-21.2%	
Brachystegia cynometroides	Clear	1963	1955	100.35	0.38	1	9	11.1%	
Brachystegia cynometroides	Clear	1972	1963	140.55	0.48	-1	11	-9.1%	
Brachystegia cynometroides	Clear	1983	1975	139.73	0.47	-8	28	-28.6%	
Brachystegia cynometroides	Problematic	1965	1962	126.22	0.45	3	13	23.1%	
Brachystegia cynometroides	Problematic	1978	1972	148.54	0.53	-2	6	-33.3%	
Brachystegia cynometroides	Problematic	1984	1980	128.43	0.46	-4	27	-14.8%	**-12.3%**
Brachystegia eurycoma	Very clear	1955	1952	98.38	0.33	0	9	0.0%	
Brachystegia eurycoma	Very clear	1964	1961	120.20	0.39	-3	9	-33.3%	
Brachystegia eurycoma	Very clear	1973	1973	143.56	0.47	0	8	0.0%	
Brachystegia eurycoma	Very clear	1981	1981	125.88	0.43	0	30	0.0%	
Brachystegia eurycoma	Clear	1962	1962	124.83	0.42	0	10	0.0%	
Brachystegia eurycoma	Clear	1972	1972	149.60	0.47	1	8	12.5%	
Brachystegia eurycoma	Clear	1980	1979	131.07	0.42	-1	31	-3.8%	
Brachystegia eurycoma	Problematic	1954	1952	98.40	0.34	2	8	-3.5%	

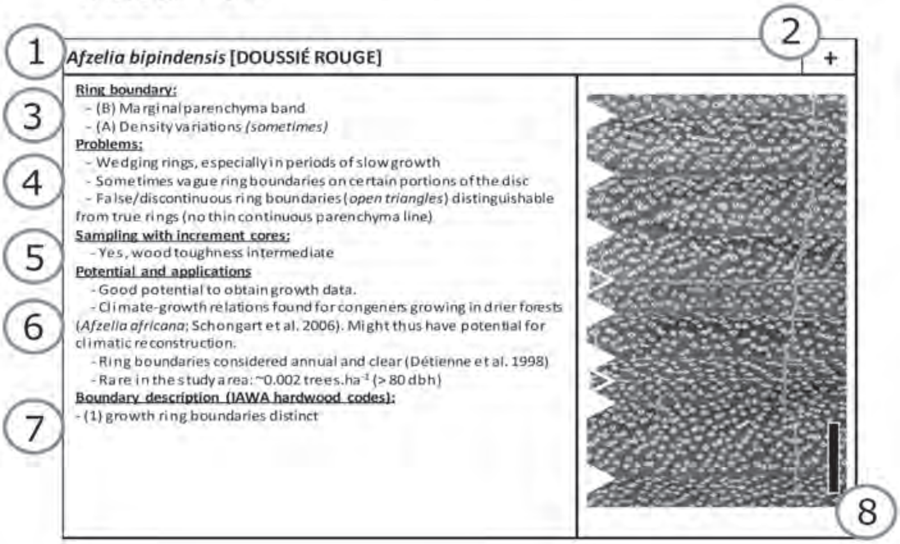
Supplementary Table 2.1 Continued

Species	Ring clarity	Tree-ring date	Radiocarbon date	^{14}C fraction (in %)	Sigma ^{14}C fraction	Amount missed rings	Period over missed rings	Amount/Period missed rings	Average missed rings (in%)
Brachystegia eurycoma	Problematic	1962	1958	105.83	0.36	3	8	37.5%	
Brachystegia eurycoma	Problematic	1970	1963	141.99	0.47	-2	7	-28.6%	
Brachystegia eurycoma	Problematic	1977	1972	149.49	0.48	-5	34	-14.7%	**-3.1%**
Daniellia ogea	Very clear	1958	1958	105.91	0.39	0	11	0.0%	
Daniellia ogea	Very clear	1969	1969	154.89	0.52	0	11	0.0%	
Daniellia ogea	Very clear	1980	1980	128.61	0.45	0	31	0.0%	
Daniellia ogea	Clear	1966	1967	162.02	0.51	1	6	16.7%	
Daniellia ogea	Clear	1972	1972	147.83	0.49	-1	11	-9.1%	
Daniellia ogea	Clear	1983	1984	122.26	0.42	1	28	3.6%	
Daniellia ogea	Problematic	1957	1959	118.83	0.41	0	10	0.0%	
Daniellia ogea	Problematic	1967	1969	153.51	0.50	0	12	0.0%	
Daniellia ogea	Problematic	1979	1981	126.86	0.44	2	32	6.3%	**1.9%**
Entandrophragma utile	Very clear	1957	1958	107.94	0.40	0	10	*	
Entandrophragma utile	Very clear	1967	1968	159.29	0.55	1	11	*	
Entandrophragma utile	Very clear	1978	1978	132.17	0.47	0	33	*	
Entandrophragma utile	Clear	1958	1958	112.44	0.41	-1	10	*	
Entandrophragma utile	Clear	1968	1969	153.86	0.55	1	10	*	
Entandrophragma utile	Clear	1978	1978	132.10	0.47	0	33	*	
Entandrophragma utile	Problematic	1958	1958	110.48	0.41	0	20	*	
Entandrophragma utile	Problematic	1978	1978	131.60	0.47	-1	-10	*	
Entandrophragma utile	Problematic	1968	1969	155.44	0.52	1	43	*	*

Appendix B – Fact sheets

Each fact sheet comprises of:

1. Species name [COMMERCIAL NAME]
2. Indicative potential for tree-ring analysis:
   - ring analysis has high potential (++)
   - ring analysis has good potential (+)
   - ring analysis might be possible (+-)
   - ring analysis has low potential (-)
   - ring analysis not possible (--)
3. The tree-ring boundaries found in this study
4. Problems encountered in this study or mentioned in the literature
5. The possibility of sampling with increment cores
   - i.e. wood neither too tough or too bristle to be cored
6. Potential and applications to apply tree-ring analysis on this species
   - Based on findings of this study and on literature
   - Also includes the tree densisties for the study area (based on own observations and from inventory of 3200 ha (TRC 2011-2012)
7. A description of the ring boundary as given in the InsideWood database
8. Scale bar = ~ 5mm



Afzelia bipindensis [DOUSSIÉ ROUGE] +

Ring boundary:
- (B) Marginal parenchyma band
- (A) Density variations *(sometimes)*

Problems:
- Wedging rings, especially in periods of slow growth
- Sometimes vague ring boundaries on certain portions of the disc
- False/discontinuous ring boundaries (*open triangles*) distinguishable from true rings (no thin continuous parenchyma line)

Sampling with increment cores:
- Yes, wood toughness intermediate

Potential and applications
- Good potential to obtain growth data.
- Climate-growth relations found for congeners growing in drier forests (*Afzelia africana*; Schongart et al. 2006). Might thus have potential for climatic reconstruction.
- Ring boundaries considered annual and clear (Détienne et al. 1998)
- Rare in the study area: ~0.002 trees.ha^{-1} (> 80 dbh)

Boundary description (IAWA hardwood codes):
- (1) growth ring boundaries distinct

Afzelia bipindensis Harms [DOUSSIÉ ROUGE]

+

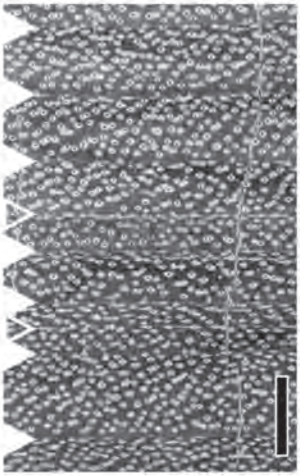
Ring boundary:
- (B) Marginal parenchyma band
- (A) Density variations *(sometimes)*

Problems:
- Wedging rings, especially in periods of slow growth
- Sometimes vague ring boundaries on certain portions of the disc
- Discontinuous ring boundaries lacking parenchyma bands (*open triangles*), needs to be evaluated

Sampling with increment cores:
- Yes, wood toughness intermediate

Potential and applications
- Good potential to obtain growth data. Needs proof on the annual character of ring formation.
- Climate-growth relations found for congeners growing in drier forests (*Afzelia africana*; Schongart et al. 2006). Might thus have potential for climatic reconstruction.
- Ring boundaries considered annual and clear (Détienne et al. 1998)
- Rare in the study area: ~0.002 trees.ha^{-1} (> 80 dbh)

Boundary description (IAWA hardwood codes):
- (1) growth ring boundaries distinct



Afzelia pachyloba Harms [DOUSSIÉ BLANC]

+

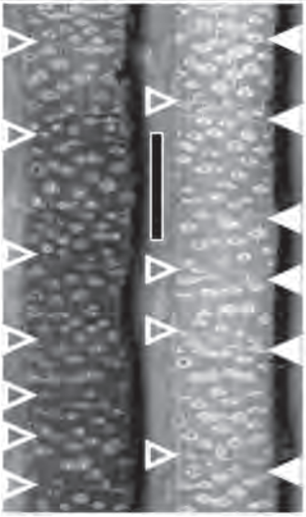
Ring boundary:
- (B) Marginal parenchyma band
- (A) Density variations *(sometimes)*

Problems:
- Wedging rings, especially in periods of slow growth
- Sometimes vague ring boundaries on certain portions of the disc
- Discontinuous ring boundaries lacking parenchyma bands (*open triangles*), needs to be evaluated

Sampling with increment cores:
- Yes, wood toughness intermediate

Potential and applications
- Good potential to obtain growth data. Needs proof on the annual character of ring formation.
- Climate-growth relations found for congeners growing in drier forests (*Afzelia africana*; Schongart et al. 2006). Might thus have potential for climatic reconstruction.
- Ring boundaries considered annual and clear (Détienne et al. 1998)
- Rare in the study area: ~0.01 trees.ha^{-1} (> 80 dbh)

Boundary description (IAWA hardwood codes):
- (1) growth ring boundaries distinct



***Bikinia le-testui* (Pellegr.) Wieringa [EKOP MAYO]** **+/-**

Ring boundary:

- (B) Marginal parenchyma band
- (A) Density variations *(sometimes)*

Problems:

- Wedging rings, especially in periods of slow growth
- Discontinuous ring boundaries / parenchyma (*open triangles*)
- Rings can be very narrow in juvenile wood.

Sampling with increment cores:

- No, wood very tough (fibrous)

Potential and applications

- Crossdates well internally.
- Annuality needs to be proven
- Trees can have buttresses (up to ~2.0m height)
- Useful to obtain growth data.
- Work with discs. Coring is difficult and presence of wedging rings.
- Clustered distribution, rare: ~0.16 trees.ha^{-1} (>60cm dbh)

Boundary description (IAWA hardwood codes):

- (1) growth ring boundaries distinct
- (2) growth ring boundaries indistinct or absent

***Brachystegia cynometroides* Harms [EKOP NOM NAGA]** **+/-**

Ring boundary:

- (B) Marginal parenchyma band (*closed triangles*)

Problems:

- Wedging rings, especially in periods of slow growth
- Discontinuous boundaries / intra-annual growth variations present. Often near tree-ring boundaries (*open triangles*)
- Rings can be very narrow (in juvenile wood).

Sampling with increment cores:

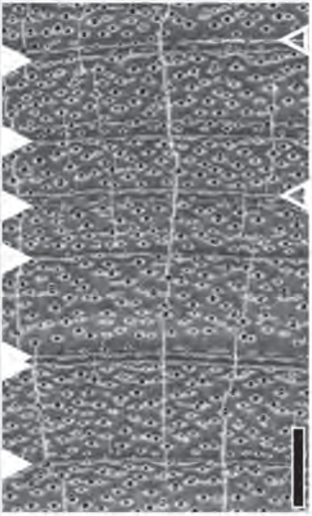
- Yes, wood intermediate toughness

Potential and applications

- Useful to obtain growth data (but measurement mistakes occur).
- Ideally work with discs, due to false and wedging rings.
- Clustered distribution, locally abundant: ~7 trees.ha^{-1} (>5cm dbh)

Boundary description (IAWA hardwood codes):

- (1) growth ring boundaries distinct
- (2) growth ring boundaries indistinct or absent



Brachystegia eurycoma Harms [EKOP NAGA] +

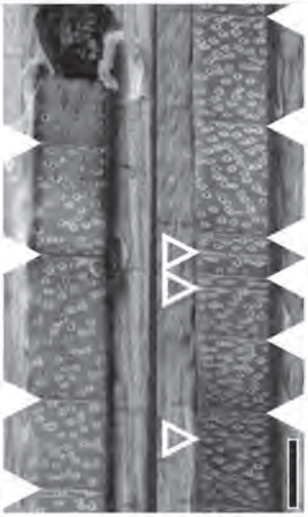
Ring boundary:
- (B) Marginal parenchyma band
- (A) Density variations *(sometimes)*

Problems:
- Wedging rings, especially in periods of slow growth
- Discontinuous boundareis / intra-annual growth variations present. Often near tree-ring boundaries (*open triangles*)
- Rings can be very narrow (in juvenile wood).

Sampling with increment cores:
- Yes, wood intermediate toughness

Potential and applications
- Crossdates well internally. No buttresses.
- Useful to obtain good quality growth data.
- Ideally work with discs, due to discontinuous and wedging rings
- Clustered distribution, locally abundant: ~8 trees.ha^{-1} (>5cm dbh)

Boundary description (IAWA hardwood codes):
- (1) growth ring boundaries distinct
- (2) growth ring boundaries indistinct or absent



Canarium schweinfurthii Engl. [AIELE] +/-

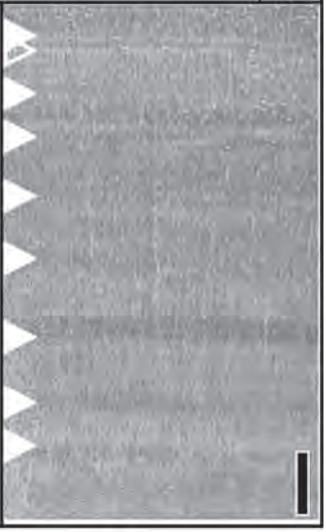
Ring boundary:
- No ring boundaries
- (A) Density variations

Problems:
- Wedging rings, especially in periods of slow growth
- Rings are vague, little difference late vs. early wood
- Presents discontinuous structures (*open triangles*)
- Juvenile wood with unclear/vague structures

Sampling with increment cores:
- Yes, wood is soft

Potential and applications
- Strong deciduous character => rings possibly annual
- Potential to obtain growth data (important spp).
- Work with discs, due to vague rings
- However, no ring boundaries cf. Detienne et al. (1998)
- Requires pinning / cambial wounding experiments to determine annual character of ring structures
- Rare in the study area: ~0.02 trees.ha^{-1} (> 60 dbh)

Boundary description (IAWA hardwood codes):
- (2) growth ring boundaries indistinct or absent



Daniellia ogea (Harms) Rolfe ex Holl. [FARO]

++

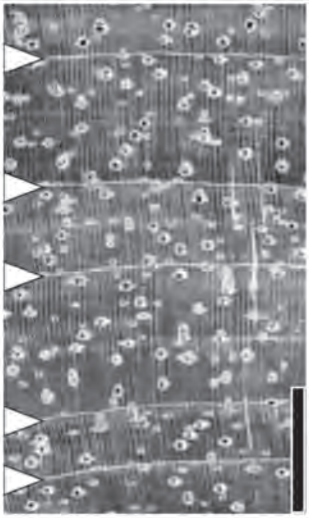
Ring boundary:
- (B) Marginal parenchyma band
- (A) Density variations *(sometimes)*

Problems:
- Wedging rings, especially in periods of slow growth
- Rings can be vague and presents discontinuous structures resembling true rings (more often in juvenile wood)
- Slow growth of juvenile trees, tree ages may be underestimated

Sampling with increment cores:
- Yes, wood intermediate toughness

Potential and applications
- Crossdates well internally. No buttresses
- Good potential to obtain high quality growth data.
- Climate-growth relations found for congeners growing in drier forests (*D. oliveri*; Schongart et al. 2006).
- Ideally work with discs, due to discontinuous and wedging rings.
- Clustered distribution, rare: ~0.05 trees.ha^{-1} (>60cm dbh)

Boundary description (IAWA hardwood codes):
- (1) growth ring boundaries distinct
- (2) growth ring boundaries indistinct or absent



Didelotia letouzeyi Pellegr. [GOMBÉ MAMEL]

-

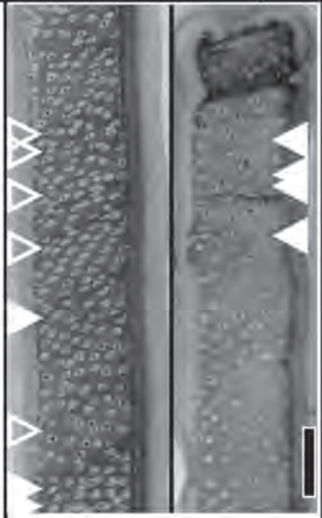
Ring boundary:
- No ring boundaries
- (B) Parenchyma bands (*sometimes, closed triangles*)
- (A) Density variations *(sometimes, open triangles)*

Problems:
- Sometimes shows very thin parenchyma bands and some density variations are present. Also large parts without any visible structures (*right image*)

Sampling with increment cores:
- Yes, wood intermediate toughness

Potential and applications
- Presence of some ring boundaries. May form rings during drier years
- Perhaps rings in drier forests
- Ideally work with discs
- Requires pinning / cambial wounding experiments
- Rare: ~0.04 trees.ha^{-1} (>60cm dbh)

Boundary description (IAWA hardwood codes):
- (2) growth ring boundaries indistinct or absent



Entandrophragma angolense **(Welw.) C.DC. [TIAMA]** ++

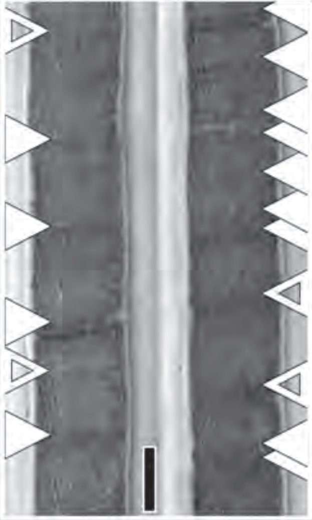
Ring boundary:
- (B) Marginal parenchyma band
- (C) Alternating fibre and parenchyma bands *(sometimes)*
- (A) Density variations *(sometimes)*

Problems:
- Wedging rings
- Rings may be narrow or unclear (*open triangles*)
- Rings less clear than in other *Entandrophragma* spp (Détienne et al. 1998)

Sampling with increment cores:
- Yes, wood intermediate toughness

Potential and applications
- Widespread species with high commercial value
- Good potential to obtain growth data
- Climate-growth relations found for congeners growing in drier forests (Nzongang 2009)
- Rare in the study area: ~0.004 trees.ha^{-1} (> 80 dbh)
- Ideally work with discs, due to butresses

Boundary description (IAWA hardwood codes):
- (1) growth ring boundaries distinct
- (2) growth ring boundaries indistinct or absent



Entandrophragma candollei **Harms [KOSIPO]** ++

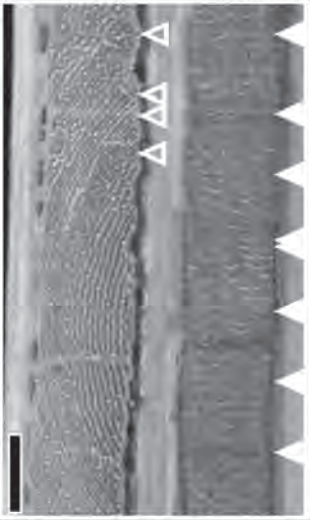
Ring boundary:
- (B) Marginal parenchyma band
- (C) Alternating fibre and parenchyma bands (*sometimes*)
- (A) Density variations *(sometimes)*

Problems:
- Wedging rings
- Rings may be narrow or unclear (*open triangles*)
- Slow grower

Sampling with increment cores:
- Yes, wood intermediate toughness

Potential and applications
- Good potential to obtain growth data
- Has wedging rings but no false rings (cf. Détienne et al. 1998)
- Slow growth / shade tolerant => ages may be underestimated
- Climate-growth analysis possible in drier forests (Nzongang 2009)
- Rare in the study area: ~0.003 trees.ha^{-1} (> 80 dbh)
- Ideally work with discs, due to slow growth rates

Boundary description (IAWA hardwood codes):
- (2) growth ring boundaries indistinct or absent



Entandrophragma utile (Dawe & Sprague) Sprague [SIPO] ++

Ring boundary:
- (B) Marginal parenchyma band
- (C) Alternating fibre and parenchyma bands *(sometimes)*
- (A) Density variations *(sometimes)*

Problems:
- Wedging rings, especially in areas between buttresses
- Weak crossdating between radii (in this study)
- Sometimes vague ring boundaries on certain portions of the disc
- Slow growth of juvenile trees, age may be underestimated

Sampling with increment cores:
- Yes, wood intermediate toughness

Potential and applications
- Good potential to obtain growth data (important sp.)
- Climate-growth relations found in drier forests (Nzongang 2009)
- Rare in the study area: ~0.009 trees.ha^{-1} (> 80 dbh)
- Ideally work with discs, due to weak (internal) crossdating.

Boundary description (IAWA hardwood codes):
- (1) growth ring boundaries distinct
- (2) growth ring boundaries indistinct or absent

Erythrophleum ivorense A.Chev. [TALI] +/-

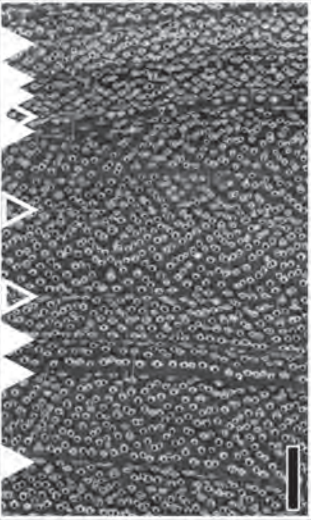
Ring boundary:
- (A) Density variations (*closed triangles*)
- (B) Marginal parenchyma band *(sometimes)*

Problems:
- Wedging rings, especially in periods of slow growth and between buttresses
- Ring boundaries can be vague (*open triangles*) on certain portions of the disc

Sampling with increment cores:
- No, wood tough

Potential and applications
- Good potential to obtain growth data (important species)
- Climate-growth relations found in drier forests (Nzongang 2009)
- Might thus have potential for climatic reconstruction.
- Common in the study area: ~0.3 trees.ha^{-1} (>70 dbh)
- Ideally work with discs, due to wedging rings in buttresses

Boundary description (IAWA hardwood codes):
- (1) growth ring boundaries distinct
- (2) growth ring boundaries indistinct or absent



Gilbertiodendron dewevrei (De Wild.) J.Léonard [LIMBALI] +/-

Ring boundary:
- (B) Marginal parenchyma bands (*closed triangles*)

Problems:
- Rings can be vague, discontinuous parenchyma bands (*open triangles*)
- Wedging and more vague rings in juvenile wood

Sampling with increment cores:
- No, wood very tough (fibrous)

Potential and applications
- Potential to obtain growth data
- Widespread in Africa
- Gregarious species: forms monodominant stands
- Locally very abundant: ~80 trees.ha^{-1} (>5cm dbh)

Boundary description (IAWA hardwood codes):
- (1) growth ring boundaries distinct

Guarea thompsonii Sprague & Hutch. [DARK BOSSÉ / BOSSÉ FONSÉ] +/-

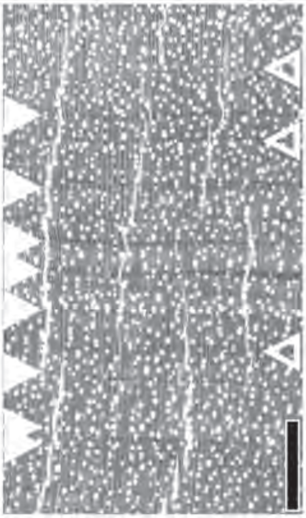
Ring boundary:
- (A) Density variations (*closed triangles*)
- (B) Marginal parenchyma band (*sometimes*)

Problems:
- Slow growth
- Vague or discontinuous ring boundaries on portions of the disc (*open triangles*)

Sampling with increment cores:
- Yes, wood toughness intermediate

Potential and applications
- Congener suggested to produce annual rings (*G. cedrata*; Détienne et al. 1998)
- Imporatant commercial species
- Potential to obtain growth data but requires thorough evaluation of annuality ring formation (pinning / cambial wounding)
- Rare in the study area: ~0.003 trees.ha^{-1} (> 80 dbh)

Boundary description (IAWA hardwood codes):
- (1) growth ring boundaries distinct
- (2) growth ring boundaries indistinct or absent



Khaya anthoteca C. DC. [ACAJOU DE BASSAM] -

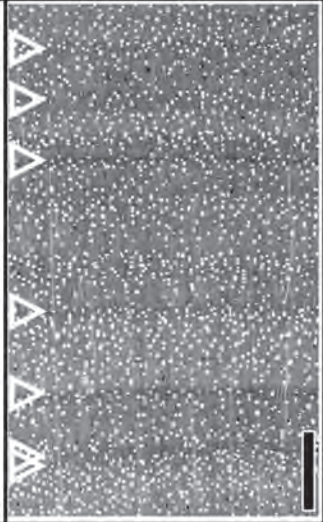
<u>**Ring boundary:**</u>
- No ring boundaries
- (A) Density variations *(open triangles)*

<u>**Problems:**</u>
- Some density variations present, but unclear (difficult to distinguish)

<u>**Sampling with increment cores:**</u>
- Yes, wood toughness intermediate

<u>**Potential and applications**</u>
- From cambial marking experiment: ring analysis not possible (Détienne et al. 1998)
- Evergreen species: might have continuous growth in wet tropical forests. It however, shows density variations.
- Commercially important species, interesting to apply screening and cambial wounding (in drier forests) to assess ring formation.
- Rare in the study area: ~0.04 trees.ha^{-1} (> 80 dbh)

<u>**Boundary description (IAWA hardwood codes):**</u>
- (2) growth ring boundaries indistinct or absent



Lophira alata Banks ex P.Gaertn. [AZOBE] --

<u>**Ring boundary:**</u>
- No ring boundaries

<u>**Problems:**</u>
- Shows broad wavy bands of parenchyma in a homogeneous structure only occasionally showing some patterns of density variation

<u>**Sampling with increment cores:**</u>
- No, wood is too tough

<u>**Potential and applications**</u>
- Tree ring analysis is not possible with standard techniques.
- Relatively common in the study area: ~0.65 trees.ha^{-1} (> 80 dbh)

<u>**Boundary description (IAWA hardwood codes):**</u>
- (2) growth ring boundaries indistinct or absent

Nauclea diderrichii Merr. [BILINGA] --

Ring boundary:
- No ring boundaries

Problems:
- Wood difuse-porous without apparent growth-ring patterns

Sampling with increment cores:
- Yes, but wood is tough

Potential and applications
- Tree ring analysis is not possible with standard techniques.
- Rare in the study area: ~0.01 trees.ha^{-1} (> 80 dbh)

Boundary description (IAWA hardwood codes):
- (2) growth ring boundaries indistinct or absent

Pterocarpus soyauxii Taub. [PADOUK ROUGE] +/-

Ring boundary:
- (C) Alternating fibre and parenchyma bands *(sometimes)*
- (B) Marginal parenchyma band

Problems:
- Rings are not very clear and working with cores is not possible
- Wedging rings occur in juvenile wood and between buttresses

Sampling with increment cores:
- Yes, wood is tough but corable

Potential and applications
- May be used for estimation of growth rates
- Annual rings and climate-growth relations found for congeners growing in drier forests (*P. angolensis*; Fichtler et al. 2004).
- Deciduous character might not be annual, therefore, ring formation should be studied together with phenological observations.
- Commercially important species, interesting to apply screening and cambial wounding to assess ring formation
- Rare in the study area: ~0.14 trees.ha^{-1} (> 70 dbh)

Boundary description (IAWA hardwood codes):
- (2) growth ring boundaries indistinct or absent

Pycnanthus angolensis (Welw.) Warb. [ILOMBA] +/-

Ring boundary:
- No ring boundaries
- (A) Density variations *(sometimes)*

Problems:
- Structures clear on certain parts of the disc (*closed triangles*)
- Sometimes vague structures on portions of disc (open *triangles*)
- Large parts (>6cm) radii without ring structures (*top of the image*) and (clear) structures dissapear

Sampling with increment cores:
- Yes, but wood is rather bristle and breaks easily

Potential and applications
- On freshly sawns discs ring structures can be seen (*below*)
- Deciduous species, perhaps annual rings (in drier forests)
- Rare in the study area: ~0.3 trees.ha^{-1} (> 60 dbh)

Boundary description (IAWA hardwood codes):
- (2) growth ring boundaries indistinct or absent

Rhodognaphalon brevicuspe (Sprague) Roberty [KONDROTI] +/-

Ring boundary:
- No ring boundaries
- (A) Density variations *(sometimes)*

Problems:
- Ring boundaries can be vague on certain portions of the disc

Sampling with increment cores:
- Yes, but wood is rather bristle and breaks easily

Potential and applications

- Rings very similar to other Bombacaceae (e.g. *Ceiba pentandra*), similarly, rings are probably annual but working with discs is required to be able to destinguish rings and problems (Worbes et al. 2003).
- Rare in the study area: ~0.07 trees.ha^{-1} (> 60 dbh)

Boundary description (IAWA hardwood codes):
- (1) growth ring boundaries distinct
- (2) growth ring boundaries indistinct or absent

No image available

***Staudtia kamerunensis* Warb. [NIOVÉ]** +/-

Ring boundary:

- (B) Marginal parenchyma band

Problems:

- Parenchyma bands very thin (*closed triangles*)
- Ring boundaries disappear on certain parts of discs (*open triangles*)
- Slow grower (1 to 4 mm yr^{-1}, PROTA 2012)
- Large sections of radii (>4 cm) without ring structures

Sampling with increment cores:

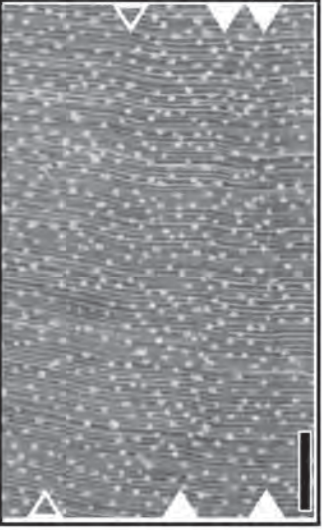
- Yes, wood tough but corable

Potential and applications

- Rings not formed annually, maybe only in dry years
- Suggested to form annual rings in drier forest (Worbes et al. 2003) but annuality was not tested
- Important commercial species
- Abundant in study area: ~12 $trees.ha^{-1}$ (>5 cm dbh)

Boundary description (IAWA hardwood codes):

- (2) growth ring boundaries indistinct or absent



***Terminalia ivorensis* A.Chev. [FRAMIRÉ]** +

Ring boundary:

- (A) Density variations *(sometimes)*
- (D) variations in vessels distribution and/or size

Problems:

- Wedging rings, especially on large trees (between buttresses)
- Ring boundaries vague on outer parts of disc

Sampling with increment cores:

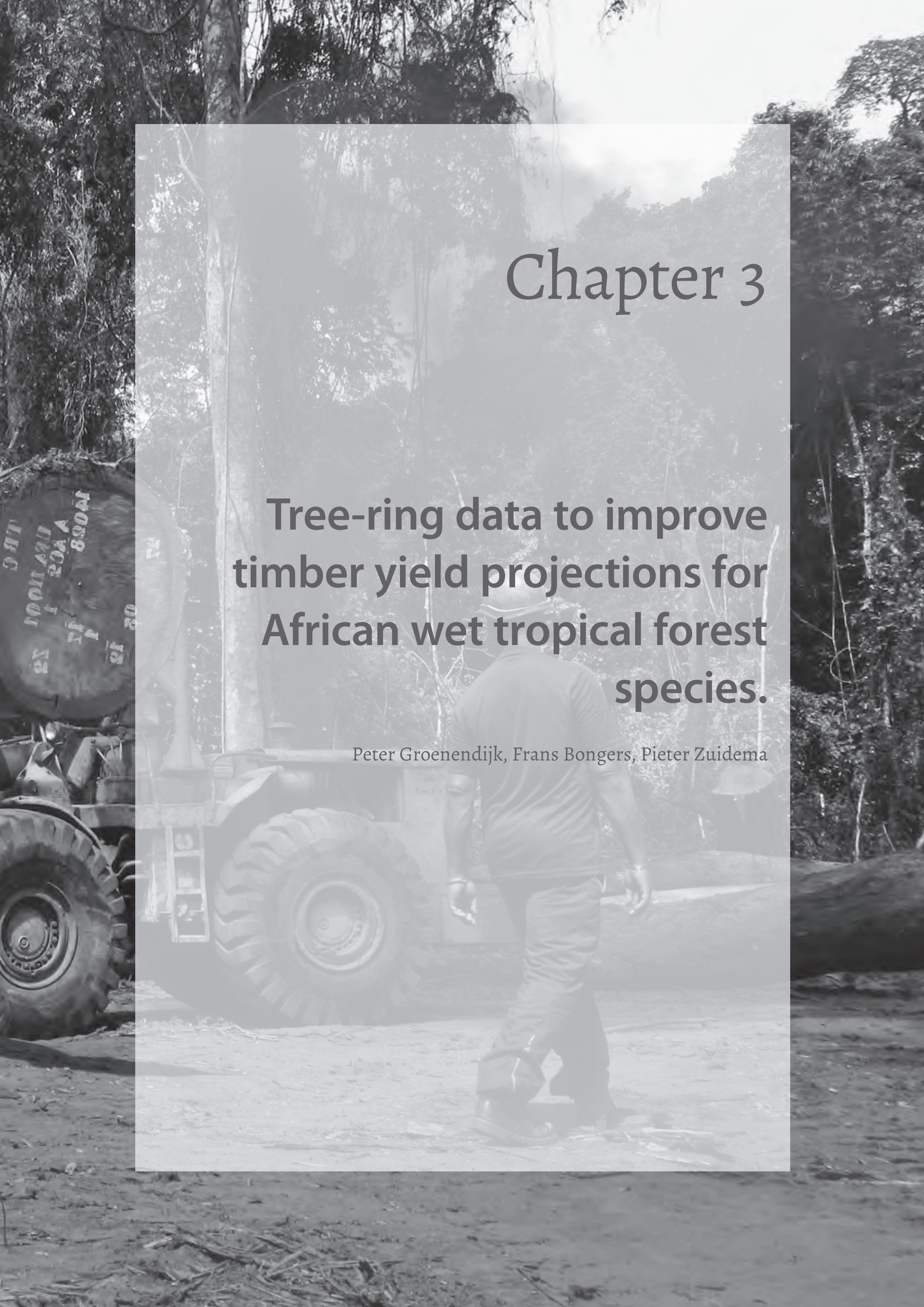
- Yes, wood toughness intermediate

Potential and applications

- Good potential to obtain growth data.
- Climate-growth relations found for congeners growing in drier forests (*T. superba*; de Ridder et al. 2013). Might thus have potential for climatic reconstruction (in drier forersts).
- Rare in the study area: ~0.2 $trees.ha^{-1}$ (> 60 dbh) but common around villages and in secondary forests

Boundary description (IAWA hardwood codes):

- (1) growth ring boundaries distinct
- (2) growth ring boundaries indistinct or absent



Chapter 3

Tree-ring data to improve timber yield projections for African wet tropical forest species.

Peter Groenendijk, Frans Bongers, Pieter Zuidema

Abstract

Worldwide, over 400 million hectares of tropical forests are set aside for timber production. Several certification schemes exist to ensure more sustainable exploitation (e.g., FSC, PEFC, OLB, etc.) and large areas of production forests are currently certified. Under such schemes, logging companies are required to evaluate whether species are not overexploited and, if necessary, adapt their logging activities. However, the data needed to project exploitation intensities – growth, mortality and regeneration rates of trees – are scarce. Tree-ring analysis provides lifetime species-specific growth data that can be used to improve the projections of how much timber will be available at the next logging cycles. In this study, we integrated growth data from tree-rings with logging inventory data to forecast timber yields in the next harvest round for four timber species in Cameroon. We compared projections using tree-ring growth data with projections using fixed growth rates, as set by law and applied in Cameroon. Additionally, we assessed the effect of increasing logging cycle and of using filed-based species-specific logging intensities on the next cycle's yield projections. Under current logging practices, future logging yields are projected to reduce for all species to 21-36% of the volumes exploited at first harvest. Simulations using fixed rates often resulted in lower yields with lower volume ingrowth from trees that were below minimum cutting diameters in the first harvest. Increasing the length of the logging cycle increased yield predictions but did not result in yields being sustained over time (remaining between 26-48%). Using species-specific logging intensities resulted in the largest increases in predicted yields: with projected yields of up to 73% of the initial harvested. That overall yields were low is worrisome for forest conservation, as loss of economic value may lead to conversion of forests to other land uses. Thus, declining species-level yields seems to be inevitable. Ultimately, finding a balance between economic gain and the (ecological) sustainability of logging operations is crucial to ensure that, on a forest level, exploitation is ecologically and economically sustainable and that forests are not converted to other land-use.

3.1 Introduction

Tropical forests harbour a rich biodiversity and hold almost half of the world's terrestrial biomass (Pan *et al.*, 2011). Simultaneously, these forests are an important source of timber and large tracts of tropical forest – 403 million hectares – are being logged or have been assigned for logging in the near future (Blaser *et al.*, 2011). The area of forest destined for logging has increased mostly in tropical Africa, with a tripling of the area as signed for logging between 2005 and 2010 (Blaser *et al.*, 2011). Sustainably exploiting these forests is essential to ensure a continued supply of timber with limited disturbance of their ecosystem services and functions (e.g., biodiversity, carbon retention). Furthermore, ensuring exploitation is sustainable is important as logged forests are often classified as "degraded" and are therefore more susceptible to conversion to other (non-forest) land uses (e.g., Giam *et al.*, 2011).

In many tropical countries, forestry legislations have been developed that aim to ensure logging operations do not affect economic, societal and ecological forest functions on the long term (Estève, 2001). Often, national legislation requires that management plans are developed prior to exploitation (Nasi *et al.*, 2006). Furthermore, several international certification schemes have been set up to evaluate the sustainability of logging, guarantee socio-economic benefits and safe-guard the future of forest areas. Currently, the area of logging concessions with some form of certification (e.g., FSC, PEFC, OLB, etc.) accounts for only 8% of the world's forests, with only a small worldwide increase in area between 2005 and 2010 (Blaser *et al.*, 2011). On the other hand, the area of certified forests in Africa has more than tripled in the same period, from 1.48 to 4.63 million hectares (Blaser *et al.*, 2011). Under such certification schemes, logging is usually performed in polycyclic logging systems, in which the largest individuals in a forest parcel are selectively logged and the parcel is allowed to regrow for several years, i.e., for the length of the logging cycle. Logging cycle length may be either fixed by national legislation (typically 20-40 years) or adjusted per forest type. Additionally, only part of all potentially exploitable trees is allowed to be logged (i.e., there is a maximum logging intensity) and a species specific minimum diameter threshold to log trees (Minimum Cutting Diameter, MCD) is usually fixed by law or by the certification body (Nasi *et al.*, 2006). Logging companies are then required to evaluate whether the combination of logging cycle length, intensity, and MCD results in the sustainable exploitation of a species.

In many countries in the Congo Basin in Central Africa, sustainability of exploitation is assessed using stock recovery rate calculations (Picard *et al.*, 2009). Stock recovery rate is the tree stock available for harvest (i.e., above MCD) after one logging cycle, compared to the stock harvested at the first logging round (Durrieu de Madron *et al.*, 1998). These calculations use the current population structure and vital rates of a species (i.e., growth and mortality) to forecast its population in the next harvest round. Regeneration is often not included in these projections, which is unrealistic but an acceptable assumption when using short-term projections (i.e., one logging cycle; Picard *et al.*, 2009). Ideally, the recovery rate should equal 100%. If necessary to attain sustainable stocks, the MCD of a species is usually adjusted, as cycle length and maximum logging intensity are often fixed by law (e.g., in Cameroon at 30 years and 80%, respectively). Alternatively, these projections can be performed including estimates of logged volume, instead of solely working with number of trees. Such timber yield projections provide an indication whether exploited volumes can be sustained in the next harvest round (Brienen & Zuidema, 2006b) and thus provide a more complete picture of timber exploitation. Despite their relevance, such calculation only exist for a limited set of tropical tree species worldwide (Putz *et al.*, 2012) and are nearly absent for African species (De Ridder *et al.*, 2013b). This shortage of studies is worrisome, given the importance of sustainable management for conserving forested areas and maintaining biodiversity of tropical forests (Edwards *et al.*, 2011; Putz *et al.*, 2012).

Irrespective of the methods used, it is evident that calculations of the sustainability of timber exploitation depend strongly on the logging cycle length, logging intensities and MCDs. However, the basis for calculating timber yields is ultimately the ecological information on the vital rates for each exploited species (e.g., growth rates, regeneration and survival). This basic ecological information is commonly obtained from monitoring trees in Permanent Sample Plots (PSPs). Plot data is, however, often limited when used to estimate growth rates and tree ages for single species, especially for canopy and commercial tree species (Picard *et al.*, 2010). Given that commercial species usually occur in low densities per hectare (Poorter *et al.*, 1996; Hall *et al.*, 2003) and that plot studies sample a small area (typically one hectare) and over short monitoring periods (typically a few years to a few decades), only little vital rate data is being collected for commercially exploited species. For these species accurate long-term data on survival, ages and growth is thus still lacking.

Tree-ring analysis can be used to obtain long-term data on the ages and growth rates of trees. It offers a reliable and relatively fast tool to assess tree ages (at logging) and to measure growth rates throughout the entire life-span of trees. These data can be used to improve calculations of future timber yields (Brienen & Zuidema, 2006b; Schöngart, 2008). Additionally, tree-ring growth data and ages provide an information basis for management decisions such as determining the size range of trees that may attain harvestable sizes in one logging round (i.e., future crop trees) and that need to be protected or tended. In the last decades, tree-ring analysis on tropical tree species has increasingly been applied (Worbes, 2002; Zuidema *et al.*, 2012) and growth data derived from tree rings has been used in assessments of exploitation sustainability for several species in South-America (Brienen & Zuidema, 2006b; Schöngart, 2008). Despite the long-known potential for tree-ring analysis in Africa (Mariaux, 1967) such calculations exist for only one African species (i.e., Terminalia superba; De Ridder *et al.*, 2013b). Given the strong increase in demand for timber from Africa and the increase in certified African forests (Blaser *et al.*, 2011), it is eminent that such calculations are needed for many more species.

Another advantage of tree-ring derived growth data is that it inherently contains persistent growth-differences between individuals (i.e., fast growing trees remain fast growing and vice-versa). These growth differences among trees within a species lead to large variation in the time needed to reach harvestable sizes and thus in the tree ages at harvest size. Persistently fast-growing individuals have been shown to strongly drive population dynamics (Bullock *et al.*, 2004) and thereby disproportionally contribute to future timber yields (Brienen & Zuidema, 2007; Rozendaal *et al.*, 2010b). This has large consequences for the forecasting of future population structures and thus on the estimates of future timber yields. Including persistent growth-differences in timber yield predictions provides more realistic estimates of future yields compared to calculations using fixed growth rates (Brienen & Zuidema, 2007), thus improving the assessment of logging sustainability.

In this study we used tree-ring data for four Cameroonian timber species to project future timber yields for these species. For each of these species we predicted future yields under different logging scenarios, using their size distribution in the field combined with growth data. The scenarios were based on current Cameroonian national logging legislation, but varied in the growth data being used (legally fixed or tree-ring based), the length of the cutting cycles (the current 30 year cycle used in Cameroon and cycles of 40 and 60 years), and in the logging intensities (maximum allowed or field-based intensities). We assessed the following research questions: (1) what proportion of timber extracted at first harvest will be available in the next standard harvest round for four timber species in Cameroon? (2) do these proportions change when using legally fixed or tree-ring based growth rates? (3) how do these proportions change for the different species when increasing logging-cycle lengths to 40 and 60 years? (4) what is the effect of changing the logging intensities on future timber yields?

We collected life-time growth data for four timber species in Cameroon using tree-ring analysis. We then used legally fixed by Cameroonian legislation (MINEF, 2001) and tree-ring based growth data to project future timber yields under different logging scenarios. First we assessed yields using the standard logging cycle length of 30 years, and the maximum logging intensity. Next, we projected yields under longer logging cycles of 40 and 60 years. Finally, we assessed how yield projections change when using the actual intensities at which each of the species was logged in the field. Finally, we used the tree-ring data to determine the range of diameters of future crop trees and to assess the amount of years trees have grown between reaching MCD and being logged. This age gives an indication of how long wood volume has ‘accumulated’ after trees have passed MCD. If this age is similar or lower than the logging cycle, this suggests yields may be sustained in the next logging cycles.

3.2 Methods

Study area

Samples were collected inside the adjacent 2011 and 2012 cutting blocks of the FSC-certified (Forest Stewardship Council) logging concession 11.001, of Transformation REEF Cameroon (TRC, 2008). This concession lies in the Southwest Region of Cameroon, adjacent to Korup National Park (Figure 3.1), at approximately 5°23’N, 9°10’E. Although a large area in the North-west of the concession was previously exploited in the 1980s, our sampling area consisted of primary forest without signs of major disturbances or previous exploitation. The vegetation consists of semi-deciduous Guineo-Congolian lowland rainforest (~200m a.s.l.; cf. White, 1983) dominated by Leguminosae–Caesalpinioideae tree species, with a canopy height of ca. 40 m (and emergent trees up to 53m).

Regional climate is equatorial, with an unimodal rainfall distribution and a dry season from December to February (monthly rainfall <100mm). Total annual precipitation averages ~4000 mm (Nchanji & Plumptre, 2001) and mean annual temperature averages 26.7°C (range: 25.7-29°C). See the climatic diagram (Mamfé weather station; cf. Walter & Lieth, 1960) in Figure 3.1.

Study species, sample collection and ring measurements

In the period of June 2010 to May 2012 we collected samples of four timber species known to produce annual growth rings (Groenendijk *et al.*, 2014) and that were being commercially exploited (Table 3.1). These species vary in their use, commercial value and abundances in the forest. For two species, we collected ~100 individuals: *Brachystegia eurycoma* Harms, and *Daniellia ogea* (Harms) Rolfe ex Holl. For *Terminalia ivorensis* A.Chev. we collected 63 samples and for *Entandrophragma utile* (Dawe & Sprague) Sprague 10 individuals (Table 3.1). These later two species were not abundant in the area, but have high commercial value (Lemmens *et al.*, 2012). Each sampled tree was georeferenced (Garmin GPS60X) and its diameter at breast height (dbh) was measured.

We collected most samples (~90%) in previously unlogged parts of the FMU (TRC, 2008) not showing apparent signs of past disturbances (e.g., from logging, agriculture, fire). For trees that were logged, we collected cross-sectional discs (ca. 30% of the samples), as working with discs allows identifying the presence of wedging (rings that merge on certain parts of the circumference of the tree) or discontinuous rings (intra-annual growth variations). For trees not being logged and for smaller trees (below MCD) we collected cores (in three to four directions) using 5.15mm increment borers (Suunto and Haglof). Samples were usually taken at 1m height or above anomalies or buttresses and we sampled all trees >5 cm dbh. All samples were air dried and surfaces prepared to allow for growth-ring identification by polishing them (with increasingly finer sandpaper; grain 40 to 1000) or using a large sliding microtome (Gärtner & Nievergelt, 2010). Ring boundaries were assessed and marked by naked eye or under a stereo microscope (magnification 16-40x) and ring-widths measured on scanned images (using an Epson Expression 10000XL flatbed scanner) at a resolution of 1600-2400 dpi. Samples were often wetted and/or scanned laying on a film of water on the scanner plate to increase ring visibility. Ring widths were measured using the software WinDendro Regular (Regent Soft, Canada) in three to four radii per tree (for more details of the ring measurements see Groenendijk *et al.* (2014). Growth rates were averaged for all radii and converted to diameter growth rates.

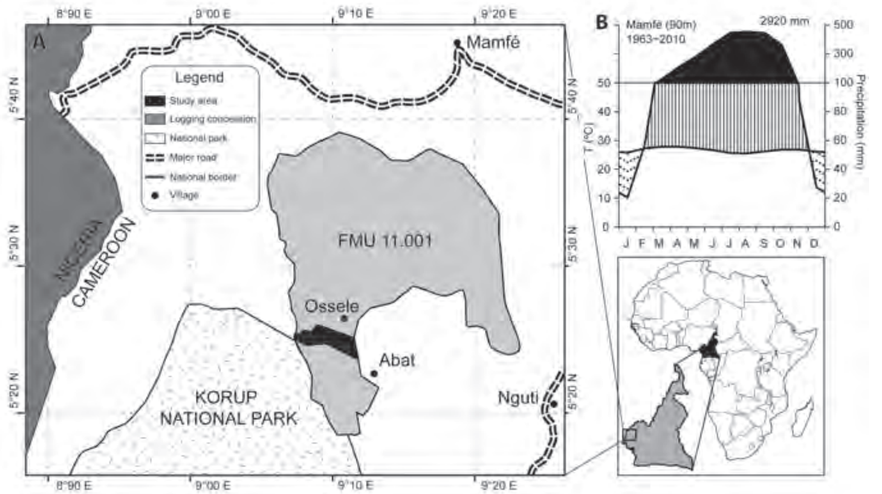


Figure 3.1 (A) Location of study site: Forest Management Unit 11.001 (light grey) and the sampling area (black). Inlay shows the location of the study site in Cameroon. Roads, national borders and national parks are also shown. (B) Climate diagram (cf. Walter & Lieth, 1960; period 1968–2009) for the Mamfé Airport weather station, indicating the rainy (>100 mm month-1; black area) and dry seasons (rainfall<temperature, dotted area).

The quality and accuracy of the tree-ring measurements were assessed by crossdating. Crossdating consists of matching patterns of variation in ring-widths between different ring-width series and can be performed within trees (i.e. among different radii) and between different trees. Within-tree crossdating helps identifying wedging and 'false' rings and ensures the same (amount of) rings are measured between different radii. Internal crossdating proved successful for most samples (i.e. good visual and statistical match). Crossdating among trees proved challenging for all species, and building species chronologies was impossible (Groenendijk et al. 2014). Radiocarbon dating confirmed annual nature of ring formation for the three species: *B. eurycoma, D. ogea* and *E. utile* (Groenendijk *et al.*, 2014). For *T. ivorensis* (and for *E. utile*) the annual nature of ring formation had been previously demonstrated by Détienne *et al.* (1998) in Cameroon. Note that tree ages used here are slightly underestimated as we do not include a correction for the time trees require to growth to sample height (about 1 m above the ground).

Projecting population structures

To predict future timber yields we first used growth and mortality rates of trees to project the population structure of a species after one logging cycle (e.g., after 30 years) and then calculated future timber volumes based on the future size distributions. For this purpose, we first determined current population structures for our species. Next, we predicted the development of these populations over time using two types of growth data: fixed growth data per species, as set by the Cameroonian administration (MINEF, 2001), and tree-ring based growth data. We then used the projected amount and sizes of trees to calculate future timber volumes. We performed these projections under different scenarios, to simulate the effect of changing the length of the cutting cycle and the intensity of logging on future timber yields.

Population structures, i.e., the number of individuals per diameter class, were derived from the logging company and from our own measurements in 16 circular plots of ~1 ha (see Groenendijk *et al.*, 2014). The primary sources for diameter distributions of trees >20 cm were two inventories carried out by the logging company: one systematic inventory of all trees >MCD in the two annual cutting blocks, and another stratified throughout the entire logging concession (for trees >20 cm) using 946 plots of ~0.5 hectare (TRC, 2008). In both inventories, the diameter of trees was estimated by inventory crews within 10-cm diameter windows. We corroborated these distributions, and completed them for trees smaller than 20 cm, using the size distributions measured in our sampling plots (Groenendijk *et al.*, 2014). For the projections of future diameter distributions we generated a 'current population' of 500 individuals according to the species' size distributions in the field, and every individuals was assigned a random diameter within the size class (e.g., between 20.0 and 29.9 cm for trees in class 20 cm). We performed the yield calculations based on a fixed amount of individuals and not on a fixed area (cf. Rozendaal *et al.*, 2010b), to account for the large differences in abundances of trees per hectare among species (Figure 3.2 and Table 3.2).

Table 3.1 Growth and age characteristics of five commercial tree species from Southwest Cameroon. Provided are species name, number of trees collected, average diameter growth rates measured from tree rings, legally fixed growth rates used for timber projections in Cameroon, ages to reach Minimum Cutting Diameter (MCD), guild (cf. Poorter *et al.*, 2006) and the main uses of wood.

Species	Family	Commercial name	# samples (as discs)	Growth tree-rings (cm yr^{-1}, ±SD)	Growth fixed (cm yr^{-1})	Age at MCD (range)	Guild**	Main uses wood
Brachystegia eurycoma	Fabaceae (C)	Ekop Naga	128 (32)	0.56±0.48	0.5	100 (48-135)	PST	Plywood, interior[1,2]
Daniellia ogea	Fabaceae (C)	Faro	105 (18)	0.43±0.35	0.7	148 (77-214)	ST	Plywood[1,2]
Entandrophragma utile	Meliaceae	Sipo	10 (10)	0.72±0.40	0.5	126 (79-203)	LLP	Veneer, furniture[1,2]
Terminalia ivorensis	Combretaceae	Framire	62 (52)	0.96±0.71	0.7	45 (21-91)	LLP	Furniture, plywood[1,2]

*Minimum Cutting Diameter (MCD) is 60 cm, except for *E. utile* = 80 cm
**Guilds: PST = Partially shade tolerant, ST = Shade tolerant, LLP = Long-lived pioneer}
[1]Lemmens *et al.* (2012), [2]CIRAD (2012)

Table 3.2 Number of stems and logging intensities for four species inventoried and logged in the 11.001 concession of TRC Cameroon. Not-exploitable are trees growing on steep slopes, within 25m of rivers, or that have crooked or rotten stems. Logging intensity is defined as the percentage of exploitable trees that were logged. Numbers correspond to trees above minimum cutting diameter (MCD) in the cutting block of 2011 (~1630 hectares).

Species	Inventoried (all trees >MCD)	Not-exploitable	Exploitable (in % of all)	Exploited (in % of exploitable)	Exploited volume (in m^3)
Brachystegia eurycoma	2356	625	1731 (73%)	933 (54%)	12741
Daniellia ogea	113	27	86 (76%)	33 (38%)	456
Entandrophragma utile	10	3	7 (70%)	6 (86%)	117
Terminalia ivorensis	137	25	112 (82%)	52 (46%)	798
All species*	8542	2305	6237 (73%)	3187 (51%)	40654

*Including all 70 species being exploited in the concession

Fixed and tree-ring based growth rates

To assess the effect of using different types of growth data on projected timber yields, we used fixed and tree-ring based data to forecast future population structures. The fixed data were based on growth rates set by Cameroonian law (MINEF, 2001) to be used for timber yield predictions. These growth rates are fixed – irrespective of tree size – at 0.5 cm yr^{-1} for *B. eurycoma* and *E. utile* and at 0.7 cm yr^{-1} for *D. ogea* and *T. ivorensis*. The tree-ring based data were obtain through tree-ring analysis for our species (Groenendijk *et al.*, 2014). The amount of trees measured varied among species (Table 3.1) and was rather low for *E. utile,* with only ten trees measured. To ensure a similar amount of growth data for all species and to increase the number of growth trajectories, we performed bootstrap simulations using the tree-ring data and generated 1000 growth trajectories for each species, following the approach by Brienen and Zuidema (2006b). These growth trajectories reflect the age/size variation in growth and we explicitly incorporated variation in growth among individual trees (i.e., growth autocorrelation) in these simulations. Incorporating this growth variation in the simulated trajectories leads to realistic growth variation in the simulated data and to reliable estimates of timber yield recuperation (Brienen & Zuidema, 2007; Rozendaal *et al.*, 2010b). We incorporated growth autocorrelation by randomly choosing a growth rate for the current year from trees that were in the same 'growth rate class' in the previous year (i.e., using a 1-year time interval) from a diameter window of 10 cm around (5 cm above and below) the current tree diameter.

Next, we projected the sizes of trees after one logging round by assigning one of the bootstrapped growth trajectories to each of the 500 trees in our 'current population'. For the final population structure, we applied an annual mortality chance of 1% randomly on all trees, e.g., the fraction of trees that survived in the 30-year logging cycle scenario was $(0.99)^{30}$. This mortality chance also fixed by the Cameroonian administration (MINEF, 2001) and in range with rates found in the adjacent Korup National Park (Figure 3.1) for trees >50 cm dbh: between 0.0 and 6.3% yr^{-1} (average 1.4%, n = 1651; Newbery *et al.*, 2013). Mortality of juvenile trees is usually higher than that of adult trees, but may be in the same range (e.g., 1.1% per year; Newbery *et al.*, 2013), but we do not account for this difference in our simulations. For a schematic overview of the population projections, se figure 3.2.

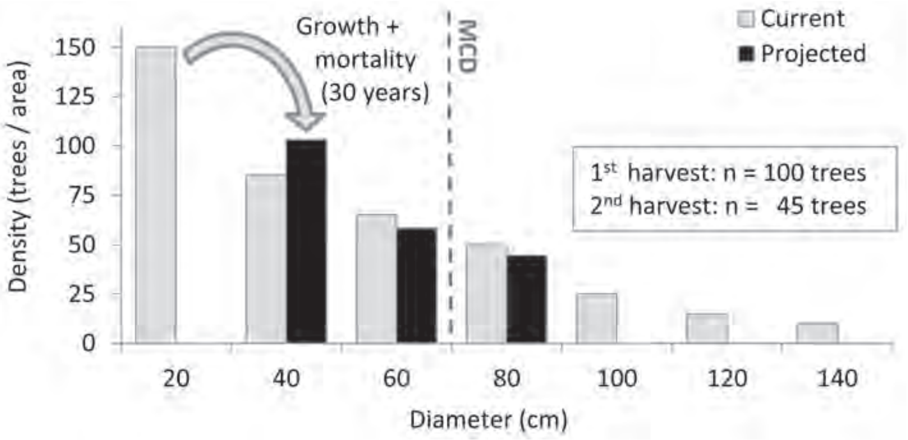


Figure 3.2 Schematic overview of the population structure projections under a logging cycle of 30 years. Grey bars show the 'current' population density per size classes and black bars the projected population structure after 30 years, using a growth rate of 0.75 cm yr^{-1} and a 1% mortality rate. All trees above Minimum cutting diameter (MCD, dashed line) of 80 cm are considered exploitable. Timber stock recovery is 45%: stock at second harvest (45 trees) divided by the first harvest of 100 trees.

Calculations of timber volume

Based on the current and projected population structures, we calculated the available volume of timber >MCD for each species. To calculate stem volumes we established the relationship between dbh and the volume for trees logged in the 2011 cutting block using third-degree polynomial functions. We calculated species specific relationships for the two species most logged in the cutting block: *B. eurycoma* (n = 933 trees) and *T. ivorensis* (n = 52 trees). For the two other species – *E. utile* (n = 6) and *D. ogea* (n = 35) – the amount of trees logged was deemed too low to calculate strong relationships and the average relationship between dbh and volume for all trees logged that year was used (n = 3186). These volumes represent bole volumes in the forest (i.e., round wood) and incorporate the dbh-stem height relationship and the taper of the stem. These calculations, however, do not account for the amount of sapwood in a stem (sapwood is usually discarded) nor for losses during the transformation of boles at the sawmill (i.e., sawn wood volume). We do not account for the sapwood and transformation factors, as we assume that the relative changes in round wood yields will be reflected on changes in sawn-wood yields.

Logging scenarios

We created different scenarios to assess the effect of data type, logging cycle length and logging intensity on timber volume recuperation. To simulate the current logging conditions in Cameroon, our 'standard' scenario had a cycle length of 30 years and we applied the maximum allowed logging intensity of 80%. We use this standard scenario as a basis to assess the effect of using fixed and tree-ring based growth rates. To assess how future timber volumes change under longer logging cycles we simulated two scenarios with longer cycle lengths of 40 and 60 years, using the maximum logging intensity. Finally, to assess the effect of changing logging intensities on future yields, we applied a standard 30-year cycle but used species-specific logging intensities based on field measurements. For the simulations using longer logging cycles and species-specific logging intensities we used the tree-ring data only, as these data provide accurate and realistic growth rates.

To determine the species specific logging intensities, we determined the intensities for each species based on the inventory of the logging company and on the data on which trees were logged. Depending on factors such as commercial demand for a timber species, stem quality, etc. the actual intensities of logging may vary between species or between years. We calculated these species specific intensities based on the amount of trees inventoried and logged in the 2012 cutting block. Inventory usually takes place in the year prior to exploitation and, during inventory, all trees above MCD are tagged, their diameter is estimated and each tree is classified as exploitable or non-exploitable. A tree is classified as non-exploitable when logging it is not viable, e.g., trees with rotting or strongly crooked stems, trees growing on steep slopes, or growing 25 m from rivers. Additionally, not all of the trees considered exploitable are harvested during logging operations: certain species have varying commercial demands over time, larger trees are preferentially logged (TRC unpublished data; Van Rheenen, 2005), and trees may be sparred if heavily covered by lianas (for safety reasons) or if rotting is noted prior to logging (that was not recorded during inventory). Any tree that is cut down is considered exploited, including trees discarded for having rotten stems (noted after logging) and trees used for bridges. It is thus possible to calculate intensities relative to the total amount of trees inventoried or to the total amount of trees considered exploitable. We calculated the species specific logging intensities as the proportion of exploitable trees that are actually exploited, assuming that trees considered non-exploitable in the inventory, will fall in the same category for the following logging cycles, as these trees will still be crooked, rotten or growing near a river. Thus, the intensities we use, although higher than if calculated using all trees, provide a much more realistic estimate of the proportion of exploited over exploitable trees in the forest.

Timber yield calculations

For each of logging scenarios we simulated an initial logging round on the 'population' of 500 individuals by randomly choosing trees from >MCD according to the logging intensities applied. For instance, in the scenarios with the maximum logging intensity of 80%, 20% of trees >MCD were not exploited. We then simulated a second logging round incorporating the growth of all trees remaining after the first round: those below MCD and the trees above MCD remaining after the first round. Next, we calculated future timber yields by dividing the exploitable volumes projected in the second logging rounds with the volumes exploited in the first round. As timber yields were calculated for virtual populations, our results provide estimates of second harvest volumes relative to the first round's volume (see Table 3.2). We also calculated what proportion of the volume at second harvest was determined by the ingrowth of trees <MCD (i.e., the 'commercial ingrowth') or by the trees that remained from the first harvest (i.e., those that were not logged). For each scenario, we repeated these calculations 10 times (i.e., for 10 'populations' of 500 trees), to calculate average projected timber yields and avoid that results were affected by the (random) choice of trees to be logged.

Future crop trees and accumulated growth years

Finally, we used the growth data from tree-rings to determine the size range of future crop trees and to assess the amount of years trees have grown after reaching MCD. The size range of future crop trees can be used as an information basis for forest managers to determining the size ranges of trees that need to be protected or tended during current logging activities. These trees may attain harvestable sizes in one logging round (here 30 years) and it is thus important to conserve them. We determined this diameter range by calculating the size of trees 30 years before reaching MCD, based on the tree-ring data. We also calculated how many years trees have grown between reaching MCD and being logged, as an indication of how long wood volume has 'accumulated' after trees have passed MCD. If this age is much larger than the logging cycle, this suggests yields may not be sustained in the next logging cycles. These ages were again calculated using the tree-ring data, simply as the difference between the total age of a tree when logged, and its age when reaching MCD.

3.3 Results

Stem densities over the diameter classes

Stem densities varied strongly among species. For instance in the 2011 cutting block, *Brachystegia eurycoma* showed ~235 more trees above MCD than and *Entandrophragma utile* (Table 3.2). Population structures also varied between species: *B. eurycoma* was the only species showing regeneration (i.e. with individuals in the smaller diameter categories), while the other three species showed hump-shaped diameter distributions (Figure 3.2). Additionally, the population structure of *E. utile* lacked individuals in the diameter classes of 60 and 70 cm, just below MCD.

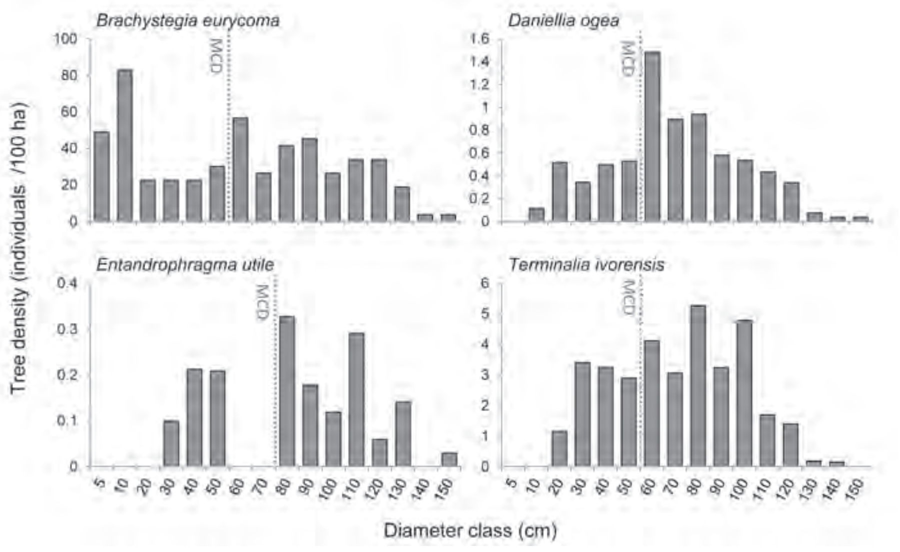


Figure 3.3 Density of trees per 10-cm diameter classes for four Cameroonian timber species. Densities of trees were obtained from forest inventories in two annual cutting blocks (~3260 ha) for above their minimum cutting diameters (MCD, dotted vertical lines); in 946 inventory plots of ~0.5 ha across the logging concession for trees >20cm diameter; and using 16 plots of ~ 1 ha for smaller diameters.

Growth rates and ages at logging

Growth rates and ages to reach minimum cutting diameters (MCD) varied within and among species. Average growth rates ranged between 0.43 cm yr^{-1} for *Daniellia ogea* and 0.96 cm yr^{-1} for *Terminalia ivorensis* (Table 3.1). Lifetime growth patterns also varied among species. *T. ivorensis* trees show a growth pattern typical for light-demanding species, with high growth rates (>1 cm yr^{-1}) in the juvenile phase but that decrease with age (Figure 3.3). *B. eurycoma*, *E. utile*, and *D. ogea* presented growth patterns characteristic of more shade-tolerant species, with growth that is slow for juveniles but increased at intermediate diameters (Figure 3.3). Growth rates also varied across trees within species, inducing large variation in tree ages to reach MCD (Figure 3.4). For instance, for *T. ivorensis* ages of trees to reach MCD varied more than fourfold: from 21 to 91 years (average of 45 years). For *D. ogea*, the slowest growing species, the average tree age to reach MCD was 148 years, ranging from 77 to 214 years (Table 3.1). Growth rates measured from tree-rings also differed from the fixed rates used by the Cameroonian administration to calculate timber yields. For *B. eurycoma* and *E. utile* measured growth rates were higher than the fixed rate of 0.5 cm yr^{-1} (grey lines, Figure 3.3), while *D. ogea* growth rates were consistently below the fixed rate of 0.7 cm yr^{-1} (black lines, Figure 3.3). For *T. ivorensis*, measured growth was above the set rate for trees < 80 cm dbh and fluctuated around it for larger trees (black lines, Figure 3.3). Simulated growth trajectories showed similar average growth rates and variation as the tree-ring data. However, for *B. eurycoma* simulated growth showed less variation than the original tree-ring data, i.e., the spread in measured data (grey lines) was somewhat higher than for the simulated data (red lines; Figure 3.4).

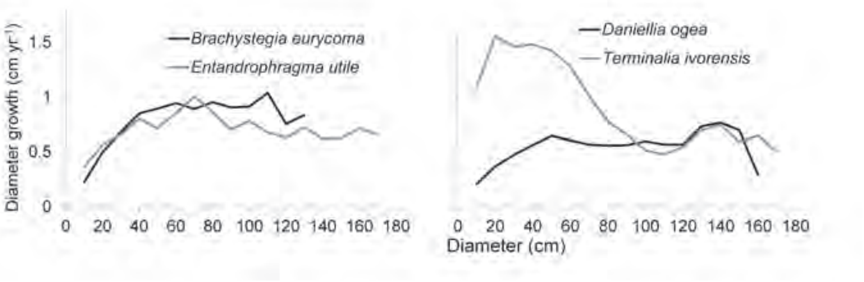


Figure 3.4 Diameter growth rates calculated from tree-ring measurements for four timber species in Cameroon. Dotted lines indicate the fixed growth rates used for yield simulations in Cameroon: 0.5 cm yr^{-1} for *B. eurycoma* and *E. utile*; and 0.7 cm yr^{-1} for *D. ogea* and *T. ivorensis*.

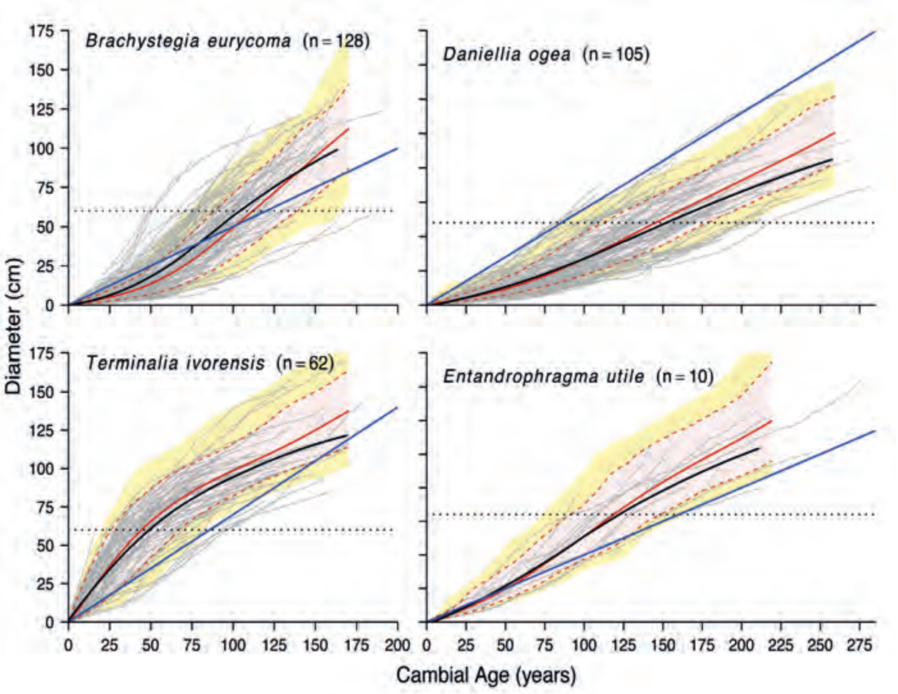


Figure 3.5 Measured and simulated tree-growth trajectories. Grey lines: growth trajectories measured with tree-ring analyses; black lines: mean growth trajectory from tree-rings; continuous red lines: mean of simulated trajectories; dashed red lines and pink areas: the 95% confidence interval of simulated trajectories; and yellow shading: highest and lowest simulated diameters per age. Horizontal dotted lines indicate minimum cutting diameters (80 cm for *E. utile* and 60 cm for the other species) and blue lines the fixed growth rates used for yield simulations as set by the Cameroonian administration.

Timber yield projections

We combined diameter distributions with growth data to project future timber yields for four species in Cameroon under different scenarios: using different input growth data, logging cycle length, and logging intensities. First, we assessed the effect of using simulated growth data versus fixed growth rates on future yields. Under the standard logging scenario – with a cycle of 30 years and maximum logging intensity of 80% – yields at second harvest were rather low irrespective of using fixed or tree-ring based growth data (Figure 3.6). For all species, projected yields in the second harvest round were between 21% and 36% of the volumes at first harvest (Figure 3.6). Commercial ingrowth (i.e., volume ingrowth from trees <MCD at the first harvest that grew above MCD in the second) was quite low and the largest proportion of the future yields originated from the 20% of trees not logged in first harvest (black bars; Figure 3.5). For *E. utile*, projections using fixed growth rates did not show any new ingrowth, i.e., none of the trees below MCD attained exploitable diameters within the 30-year logging cycle. For *D. ogea*, total yield projections were higher when using fixed growth rates but commercial ingrowth was nearly identical to the projections using tree-ring data.

Second, we assessed the effect of increasing the logging cycle length on future yields by predicting future yields under varying cycle length of 30, 40 and 60 years. These predictions were performed using the tree-ring based growth data and a logging intensity of 80%. Increasing logging cycle length usually resulted in increased timber yields. However, these increases were not very strong and yields remained under 48% for all species, even for the longest cycle of 60 years (Figure 3.6). Under longer cycles, the share of the future yields originating from the commercial ingrowth changed, becoming larger with increasing cycle length (grey bars, Figure 3.6). The share arising from trees not logged in the first round varied per species (black bars, Figure 3.6): it remained rather stable for *E. utile*, irrespective of cycle length, it decreased for *B. eurycoma*, and for *D. ogea* and *T. ivorensis* remained rather constant.

Finally, we assessed future timber yields using species-specific logging intensities measured in the field. We calculated and applied the following species-specific intensities: 54% for *B. eurycoma*; 38% for *D. ogea*; 86% for *E. utile*; and 46% for *T. ivorensis*. These percentages are calculated relative to the amount of exploitable trees in the forest and thus not to the total amount of trees inventoried. Using the field-based intensities and the standard logging cycle of

30 years, timber yields predictions increased remarkably for *B. eurycoma*, *D. ogea* and *T. ivorensis*, increasing from 24%-36% to 52-73% (Figure 3.6). On the other hand, yield decreased slightly for *E. utile*, from 25% to 21%, as the intensity of logging increased from 80% to 86%. Commercial ingrowth was similarly low for both intensity scenarios: on average ~7.5% of the volume logged at first harvest (grey bars, Figure 3.6). The increase in yields were thus solely resulted from a larger amount of trees that remained after first harvest. The share of future yields from remaining trees increased from on average 20% of the volume logged at first harvest to 45% (black bars, Figure 3.6).

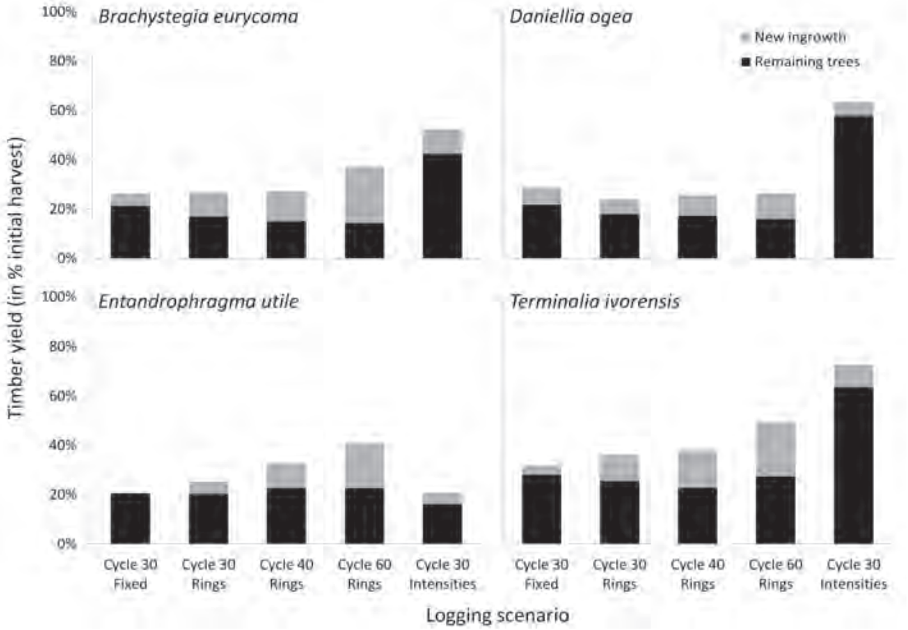


Figure 3.6 Predicted timber yields for four commercial tree species from Southwest Cameroon. Results presented for five different logging scenarios: two scenarios under the standard logging cycle of 30 years and maximum allowed logging intensities of 80% used in Cameroon, but using fixed growth rates (Cycle 30 Fixed) or rates measured from tree-rings (Cycle 30 Rings); two scenarios applying longer logging cycle lengths of 40 and 60 years (using tree-ring data and 80% logging intensity); and one scenario with a standard cycle length and species-specific logging intensities based on intensities observed in the field (Cycle 30 Intensities). Species logging intensities: *B. eurycoma* = 54%; *D. ogea* = 38%; *E. utile* = 86%; and *T. ivorensis* = 46%. Grey bars represent new volume ingrowth from trees below minimum cutting diameter (MCD) in the first harvest; and black bars the ingrowth from trees not cut at initial harvest (i.e., the remaining trees).

Using the tree-ring data, we also assessed the diameter range of future crop trees under the standard 30-year logging cycle and measured the amount of years trees have grown between reaching MCD and being logged. The diameter range from which individuals have the potential to reach MCD differed strongly between species: for *E. utile* future crop trees range from ~40 to 80 cm in diameter whereas for *T. ivorensis*, this range was from 0 to 60 cm, indicating that *T. ivorensis* trees that establish at the first logging cycle may be logged during the following cycle. The amount of years trees have grown between passing MCD and being logged also varied between the species: for *B. eurycoma* on average ~30 years, while for *E. utile* on average ~75 years (with a maximum of >175 years).

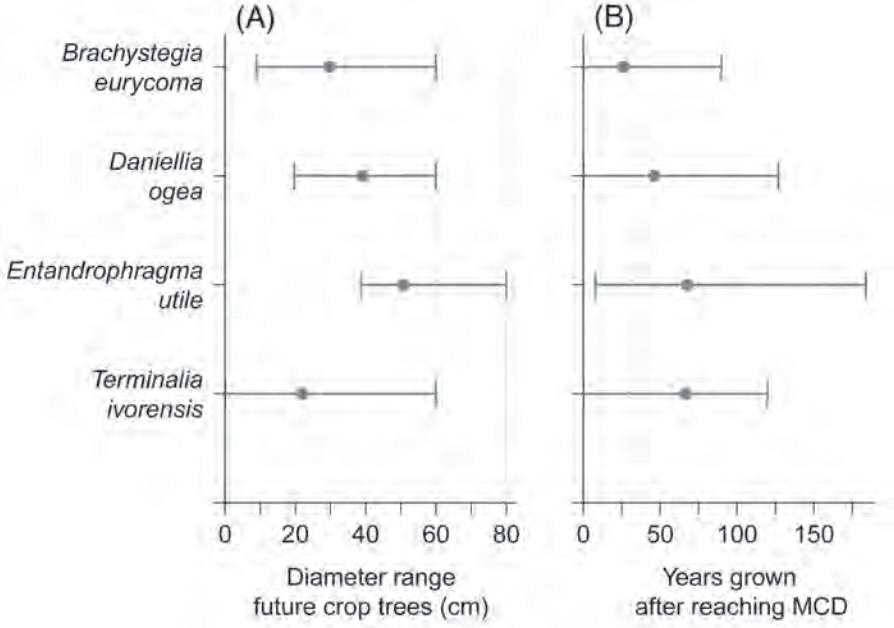


Figure 3.7 (A) Diameter range of future crop trees for four timber species from Southwest Cameroon, based on tree-ring analysis. Shown are the ranges and average (dot) diameters of trees 30 years before reaching the Minimum Cutting Diameter (MCD), dashed lines indicate MCDs (80 cm for *E. utile* and 60 cm for other species) (B) Amount of years trees have grown between reaching MCD and being logged, dashed line indicate the standard 30-year logging cycle length used in Cameroon.

3.4 Discussion

In this study we used tree-ring data for four Cameroonian timber species to project timber yield development in the next harvest round in a polycyclic logging system. Predictions using standard logging scenarios resulted in low volume recuperation (of 21-36% of the volumes at first harvest), both for simulations using fixed and tree-ring based growth rates. Simulation using fixed rates often resulted in lower yields with lower volume ingrowth from trees that were below minimum cutting diameters in the first harvest. Additionally, increasing the length of the logging cycle increased yield predictions but did not result in yields being sustained over time (remaining between 26-48%) . Changing logging intensities – to intensities registered in the field – resulted in the largest increases in predicted yields: with yields of up to 73% of the initial harvest volume projected for the next harvest round.

Growth simulations and robustness of yield predictions

The simulated growth trajectories used in this study to estimate future timber yield showed average growth rates that resembled the tree-ring based growth rates. However, for *Brachystegia eurycoma* the simulated age to reach minimum cutting diameters (MCD) was slightly higher than the measured age and the variation in growth rates was also lower. For this species, the projected yields may thus be somewhat conservative, due to the slightly lower growth rates in the simulations compared to actual growth rates but also due to the lower growth variation. This variation is known to increase future yield projections (Brienen & Zuidema, 2007).

We used logging intensities based on field data of trees inventoried and actually exploited. However, these field data did not allow to assess what proportion of trees considered exploitable was not logged for commercial reasons (e.g., for being relatively small or because of no demand for a species' timber) or for being rotten or malformed. The amount of trees marked for exploitation but that are eventually considered not-exploitable can be quite significant: in the Amazon 28% of trees (Holmes *et al.*, 2002). As our data did not allow for these quantifications, we included only those trees that were considered as not-exploitable during the inventory. Our timber yield predictions may thus overestimate the actual yields in the future. It is also important to note that the field-based logging intensities used in this study correspond to the intensities in a specific year (of 2012). These intensities may, however, vary depending on several factors such as (species specific) commercial timber demand, species availability in the forest, etc. More accurate inventories of species specific proportions of exploitable trees and logging intensities, covering several years and large areas (i.e., different logging concessions) would greatly increase the accuracy of yield predictions.

For the species *E. utile*, its low abundances in the forest means that diameter distributions of this species need to be interpreted with care. For rare species, diameter distributions are very sensitive for the presence/absence of single trees in the sampling plots and extrapolating distributions to large areas thus need to be done with care. Additionally, due to the low abundance we only sampled 10 trees. Timber yield projections for this species thus need to be interpreted with care, as they are based on a small number of trees. Nonetheless, due to the commercial valued of *E. utile* (and of the genus) and its presence throughout African tropical forests, we deemed it relevant to also calculate yields for this species. Contrastingly, *B. eurycoma* occurred at very high densities in the 2012-2013 cutting blocks. This species was, however, nearly absent in other parts of the logging concession (P. Groenendijk, *personal observations*), probably growing gregariously in a similar way as its close Central-African congener *Brachystegia laurentii* (Germain & Evrard, 1956). Our predictions may also underestimate future yields as we do not account for the increase in growth rates that is often reported to occur after logging caused by the opening of the canopy (Peña-Claros *et al.*, 2008; Gourlet-Fleury *et al.*, 2013). Additionally, disturbances caused by logging could induce a regeneration wave for light-demanding species, such as *Terminalia ivorensis,* that have the potential to reach MCD within one logging cycle and thus boost timber yields.

In spite of these limitations, we believe that the yield predictions in this study are still accurate, as they were based on growth data from tree-rings, which provide accurate lifetime growth data of trees and incorporate within-species growth variation. As well as being based on realistic growth data, our predictions also better reflect the actual situation in the field by incorporating realistic and species-specific logging intensities instead of a general maximum allowed intensity for all species.

Fixed versus tree-ring based growth rates

We compared the effect of simulating logging yields using two types of data: legally fixed and tree-ring based growth rates. The fixed rates used for yield simulations in Cameroon differed from averaged of measured growth rates of all species but *B. eurycoma*. These differences were strongest for *T. ivorensis* and *Daniellia ogea*. Individuals of *T. ivorensis* showed growth rates consistently higher that the fixed rates (Figure 3.3), especially in for trees < 80 cm dbh (Figure 3.3). On the other hand, *D. ogea* trees grow consistently slower than the fixed rates (Figure 3.3). Using rates that differ from the actual growth of a species, may potentially lead to incorrect decisions on the logging intensity or cutting cycle lengths. Furthermore, knowledge on growth rates and its variation, and the lifetime growth pattern of a species can provide crucial guidelines for managers, such as, size-ranges of trees to be protected during logging and whether liberation of these future crop trees (e.g., by girdling competing non-commercial trees) may be a valuable silvicultural intervention (De Ridder *et al.*, 2013b). Our results show that the size range of future crop trees varies strongly between species: *T. ivorensis* individuals that recruit at first logging may already reach harvestable sizes within one cutting cycle, whereas for the other species these trees 'originated' from ranges starting at ~10-40 cm. Focussing on the protection on relevant future crop trees can thus be used to more efficiently apply such measures in the field and may help to increase future yields.

Ages to reach minimum logging diameter

Average ages for trees to reach MCD varied strongly among species: from 45 years for *T. ivorensis* to 148 years for *E. utile*. These ages already provide an indication of the yield recuperation potential of a tree species: if ages at MCD far exceed the logging cycle length, volume regrowth may not be sufficient to replenish timber stocks. For *T. ivorensis*, trees reached MCD on average in ~45 years, with the fastest-growing individual reaching it in 21 years. Such relatively low ages to reach MCD, and the corresponding fast growth rates, have also been found for other African light-demanding timber species: ~75 years to reach 80 cm for *Triplochiton scleroxylon* (1.1 cm yr^{-1}; Detienne et al. 1998), 60 years to reach 60 cm dbh for the congener *Terminalia superba* (De Ridder *et al.*, 2013b). Similar ages have also been found for several species growing in white-water floodplains in the Amazon: between 17 and 82 years to reach 50 cm (low wood density species; Schöngart (2008). These low ages to reach MCD for the fast growing *T. ivorensis,* suggest that timber yields may be sustained in the future (Schöngart, 2008), assuming that recruitment of young individuals is ensured. Sustained yields were also suggested for the fast-growing congener *Terminalia superba,* from forests in Ivory Coast and the Democratic Republic of the Congo (De Ridder *et al.*, 2013b). Ultimately, this may lead exploitation to shift to fast growing species in the long run (Valle *et al.*, 2007), as the stock of slow-growing species is exhausted. Such shifts in species may have important financial consequences, as fast-growing species tend to have lower wood densities and lower market value (e.g., Schöngart, 2008).

For the other three species – *B. eurycoma, D. ogea* and *E. utile* – ages to reach MCD exceeded the cycle length by a factor of three to five (ages of ~100-150 years, Table 3.1), suggesting low yield recuperation for these species. For the two Caesalpinioideae, growth rates and ages at MCD, measured from tree-rings, do not exist in wet African forests and are even sparse for other Caesalpinioideae: in the adjacent Korup National Park (Figure 3.1), diameter growth rates of 0.48-0.50 cm yr^{-1} were reported for *Microberlinia bisulcata* (Newbery *et al.*, 2013); in Southwest Cameroon, under a rainfall of ~1600 mm yr^{-1}, average growth rates of 0.53 cm yr^{-1} were found for *Erytrophleum ivorense* (Nzogang, 2009), with ages to reach the 50 cm MCD between 61-128 years; in the Democratic Republic of Congo, with ~1200 mm yr^{-1} annual rainfall, diameter growth rates of 0.46 cm yr^{-1} have been reported for *Prioria balsamifera* (Couralet, 2010), but all trees were below 60 cm. The ages to reach MCD of *E. utile* compare to the ages of 126-172 found for three *Entandrophragma* species (including *E. utile*) in Southwest Cameroon with rainfall ~1600 mm yr^{-1} (Nzogang, 2009). These ages are, however, lower than the ages of ~250 years reported for *Entandrophragma cyllindricum* from Central African Republic (Détienne *et al.*, 1998). These high ages suggest that under current logging cycle lengths, timber recuperation for these slow-growing species will be low.

Timber yield projections

We simulated timber yields at the next harvest round varying three aspects: the input data (using fixed growth rates or simulated rates with variation), the logging cycle lengths (cycles of 30, 40 and 60 years), and the variations in intensity of logging (maximum allowed or actual species-specific intensities. The simulations using legally fixed growth rates usually showed lower yield predictions than the simulations using bootstrapped growth trajectories based on tree-ring data (Figure 3.5). Only for *D. ogea* did using legally fixed growth rates give higher predictions of future timber yields. These higher predictions arise from the fact that fixed rates for *D. ogea* were also consistently higher than the actual measured rates for all size classes (Figure 3.3). The most striking difference between the simulations with fixed versus simulated growth rates is the consistently higher commercial ingrowth (volume growth from trees <MCD) when using the simulated growth data (i.e., 'new ingrowth' grey bars; Figure 3.5). These results illustrate the importance of incorporating persistent differences in growth between individuals in yield predictions (Brienen & Zuidema, 2007; Rozendaal *et al.*, 2010b) as fast-growing trees contribute disproportionally to timber ingrowth in future cycles (Brienen & Zuidema, 2007).

Increasing logging cycle lengths resulted in increased future yield projections, but did not result in sustained yields. Commercial ingrowth increased under longer logging cycles as trees below MCD had more time to grow to harvestable sizes. Except for *E. utile*, these longer cycles reduced the contributions of the trees remaining after logging, probably due to the accumulated mortality over time. For *E. utile*, the share of future timber volume from the remaining trees increased over time, probably due to the size distribution of *E. utile* (Figure 3.2), which showed relatively high amounts of individuals in the size classes 80 and 110 cm. Volume growth for these large trees is fast, due to the third degree relationship between stem diameter and volume, and under longer logging cycles, these trees thus had more time to accumulate stem volume. At longer logging cycles, the role of mortality and regeneration become more important and our predictions do not incorporate these aspects well: mortality is fixed for all species and sizes and regeneration is not accounted for. This limits our simulations for longer logging cycles, especially for *T. ivorensis*, as recruiting individuals of this species have the potential to reach harvestable sizes within one logging cycle. Not accounting for regeneration caused an increasingly underestimation of future yields with increasing logging cycle lengths.

The most striking changes in yields from changing logging intensities. Our results suggest that up to 73% of the initial volume logged can be recuperated in the next harvest round. These yields are twice the yields predicted under maximum intensities. Reducing logged volumes at first harvest obviously increases future yields, as second harvest volumes are divided by a lower number. Additionally, these simulations assume that trees not logged in the first harvest round will be available in the following round, which is not always the case. Trees that may be available in the next round are those (above MCD) that were not logged for being rather small (larger trees are preferentially logged), for a lack of commercial demand, or for safety reasons (e.g., crowns covered with lianas). However, trees with rotten stems, for which rotting was discovered only at logging, will still present rotten stems in the next round and not be available. Although we used the most realistic estimates of logging intensities, our simulations thus overestimate the available trees in future logging cycles and thus also overestimates future yields. Although yields increase when applying realistic field-based intensities with realistic growth trajectories from tree-rings, our results still suggest moderate to strong declines in available timber in the future.

Outlook and recommendations

The low predicted yields clearly suggest that the volumes exploited at the first logging round will not be sustained in the following cycle. Declining yields are in line with other studies (summarized in Putz *et al.*, 2012), and are considered almost inevitable, as the remaining trees cannot grow back the volume accumulated over many years – for our species often over more than 50 years (Figure 3.7) – within current (or reasonable) logging cycle length. This amount of accumulated volume over the years is also called the 'primary forests premium' (cf. Keller *et al.*, 2007). Although species-specific yield declines may be inevitable, it is essential to avoid forest level overexploitation of timber resources. Unsustained species-level yields should thus not lead to unsustainable forest use, i.e., to the conversion of forests to other land-uses. Increasing logging cycle lengths or minimum cutting diameters (MCD), or decreasing logging intensities, are measures that can ensure a more sustainable forest use. However, increasing logging cycle length requires long-term investments, which are hampered by the unstable politico-economical environments in many tropical countries. Increasing the MCD or reducing logging intensities – while maintaining logging cycle length – are then more viable options. That actual intensities in the field for three of the species are lower than the maximum allowed, is hopeful, and future yields increased remarkably under field-based intensities for these species (up to 73% of initial volume was recuperated). The lower field-based intensities imply that the primary forest premium is 'spread' over subsequent logging cycles, increasing the long-term financial viability of timber exploitation. However, for *E. utile* – the species with the highest commercial value – actual intensities were similar to the maximum allowed and predicted yields were low. For species with high value but low abundances, increasing MCD is then crucial to not overexploit them, and the high MCDs for *Entandrophragma* spp. in Cameroon (80-100cm; TRC 2009) is hopeful. Nonetheless, timber exploitation usually focusses on only a handful of these high-value species (Holmes *et al.*, 2002; Ruiz-Pérez *et al.*, 2005), and we expect that for most of them logging intensities are consistently high. Shifting exploitation to include more species – in our study area 72 species were inventoried for exploitation – is fundamental to maintain forest-level timber yields (Putz *et al.*, 2012). Any measures to stimulate the use of these 'lesser known species' are highly encouraged (e.g., ITTO, 1990), and current exploitation should ideally already broaden the focus of exploitation to include a higher number of species.

Silvicultural measures may be taken to enhance the growth of future crop trees, such as liberating them from lianas (Peña-Claros *et al.*, 2008) and thinning of the forest after logging (Gourlet-Fleury *et al.*, 2013). Additionally, measures such as enrichment planting or tending of natural regeneration may be needed to guarantee future timber stocks (Doucet *et al.*, 2009; Schwartz *et al.*, 2013), as the sustainability of logging will ultimately depend on the successful establishment the exploited species. However, depending on their intensities, these silvicultural measures may be expensive (Mostacedo & Fredericksen, 1999) and long-term monitoring is required to evaluate their effectiveness and economic viability (e.g., Peña-Claros *et al.*, 2008; Gourlet-Fleury *et al.*, 2013). Ideally, such evaluations should also include the demographic consequences of logging (e.g., Verwer *et al.*, 2008; Free *et al.*, 2014; Grogan *et al.*, 2014), using population models that incorporate the effects of logging on the regeneration, mortality and growth rates of a tree species. Population models should also be used to project future timber yields, as these models result in more realistic projections of population growth by explicitly incorporating the variation in vital rates (e.g., growth, reproduction, survivor) for a species (e.g., Zuidema *et al.*, 2010).

Future yield predictions were also low for the fast growing *T. ivorensis*, suggesting that yields do not depend solely on the ages of trees to reach MCD. Many factors drive future yields, including management factors such as the length of the cutting cycle, MCD, and logging intensities. Also, species (and area) specific factors, such as, diameter distributions, growth rates of trees (below and above MCD), local abundances, and mortality rates are important drivers of future yields. Accurate simulations of future yields obviously depend on accurate input data: growth data (from rings), inventory data and estimations of mortality rates. There is thus a pressing need for high-quality and long-term monitoring of the consequences of logging on tropical forests(e.g., Peña-Claros *et al.*, 2008; Gourlet-Fleury *et al.*, 2013). Only with such long-term data can yields simulations be expanded further than one or two logging cycles. The varying logging intensities, clustered abundances of trees in the field, and varying commercial demand also mean that yield predictions strongly vary from year to year. This complexity of factors ultimately requires a flexible and adaptive forest management, ideally one that bases decisions of logging intensities and MCDs on species-specific vital rates.

Finally, strict protection of forest areas will continue to be essential to conserve the biodiversity of tropical forests (Gibson *et al.*, 2011). However, selectively logged forests retain important environmental values, such as high-levels of biodiversity (Berry *et al.*, 2010) and the storage of carbon (Sist *et al.*, 2014). The large area of forests designated for production – more than 403 million hectares (Blaser *et al.*, 2011) – combined with the environmental value they retain, implies that sustainably using these forests is key to conserving tropical forests in the future (Edwards *et al.*, 2011). Measuring sustainability using timber yields may provide a bleak picture. However, emphasis should lay on sustainable forest use: extracting goods and services while maintaining forests standing in the best condition possible. Ensuring long-term financial viability of forest use is essential to avoiding conversion to non-forest land uses and timber yield projections can be used as an indicator of this viability. Increasing the number of species exploited while lowering logging intensities on the most exploited species is a promising way forward to avoid overexploitation of these species, therewith enhancing the ecological sustainability of forest exploitation. Additionally, ensuring higher prices for 'sustainably' logged timber may lead to shifts to better forest management practices (Meijaard *et al.*, 2005). Combined with payments for ecosystem services, e.g., carbon-offset schemes (e.g., under REDD+; Loarie *et al.*, 2009) sustainable forest use may be achievable, both financially and ecologically.

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Chapter 4

Detecting long-term growth trends using tree-rings: A critical evaluation of methods

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Abstract

Tree-ring analysis is often used to assess long-term changes in tree growth. A variety of growth-trend detection methods (GDMs) exist to disentangle age/size trends in growth from long-term growth trends. However, these methods strongly differ in approach, with possible implications for their output. Here we critically evaluate the consistency, sensitivity and reliability of four most widely used GDMs: Conservative Detrending applies mathematical functions to correct for decreasing ring-widths with age; Basal Area Correction transforms diameter into basal-area growth; Regional Curve Standardization detrends individual tree-ring series using average age/size trends; and Size Class Isolation calculates growth trends within separate size classes. First, we evaluated whether these GDMs produce consistent results applied to an empirical tree-ring dataset of *Melia azedarach*, a tropical tree species from Thailand. Three GDMs yielded similar results – a growth decline over time – but the widely used Conservative Detrending method did not detect any trend. Second, we assessed the sensitivity (probability of correct growth trend detection), reliability (1- probability of detecting false trends), and accuracy (whether the strength of imposed trends is correctly detected) of these GDMs, by applying them to simulated growth trajectories with different imposed trends: no trend, strong trends (-6% and +6% change per decade), and weak trends (-2%, +2%). All methods except Conservative Detrending, showed high sensitivity, reliability and accuracy to detect strong imposed trends. However, these were considerably lower in the weak or no-trend scenarios. Basal Area Correction showed good sensitivity and accuracy, but low reliability, indicating uncertainty of trend-detection using this method.Our study reveals that the choice of GDM influences results of growth-trend studies. We recommend applying multiple methods when analysing trends and encourage performing sensitivity and reliability analysis. Finally, we recommend Size Class Isolation and Regional Curve Standardization, as these methods showed highest reliability to detect long-term growth trends.

4.1 Introduction

Worldwide, forests store and process large quantities of carbon (Pan *et al.*, 2011). Changes in the growth rates of forest trees affect their net uptake or loss of carbon and may therefore have large consequences for the global carbon cycle (Bonan, 2008). Tree-ring analysis yields long-term growth data – covering centuries (Koutavas, 2013) to millennia (Salzer *et al.*, 2009; Esper *et al.*, 2012) – that can be used to detect such growth trends. Tree-ring analysis has been widely applied for this purpose on boreal and temperate tree species (e.g., Briffa *et al.*, 1998; Esper *et al.*, 2010; Villalba *et al.*, 2012) and more recently there is increasing attention to use this tool for assessing long-term growth trends in tropical tree species (Rozendaal *et al.*, 2010a; Bowman *et al.*, 2013; Zuidema *et al.*, 2013).

Tree-ring series contain information on tree-growth responses to different drivers that vary on different time scales (e.g., from years to centuries). Year-to-year variations in growth rates are often driven by inter-annual fluctuations in precipitation and temperature (Schöngart *et al.*, 2006; Subedi & Sharma, 2013), while decadal-scale variations are mostly responses to changes in light availability due to canopy dynamics (Brown & Wu, 2005; Baker & Bunyavejchewin, 2006). Long-term variations – spanning several decades to centuries – may reflect responses of trees to gradual environmental changes (e.g., in precipitation, temperature, or CO_2 concentration), but may also reflect age/size dependent trends in growth (i.e., caused by the ontogenetic development; cf. Briffa & Melvin, 2011). Detecting long-term growth trends using tree-rings requires disentangling these ontogenetic and short-term environmental signals from trends driven by gradually shifting environmental conditions.

Over the past decades, various growth-trend detection methods (henceforth referred to as GDMs) have been developed to detect environmental growth trends in tree-ring series and correct for the inherent age/size trends in growth (cf. Briffa *et al.*, 1998; Esper *et al.*, 2002; Biondi & Qeadan, 2008). While having similar aims – correcting for the age/size trend to reveal externally forced growth responses – GDMs differ largely in their approach; as illustrated in Figure 4.1 for the four most widely applied GDMs. GDMs correct for the age/size trends in quite different ways: by detrending growth of trees using curves that describe the age/size trend (Conservative Detrending or Regional Curve Standardization), by expressing growth rate in basal area instead of diameter (Basal Area Correction), or by comparing growth rates inside fixed age or size classes (Size Class Isolation). Trend analyses is then performed on the detrended data, on the corrected growth rates or on raw growth rates. Given the large differences in approach between GDMs, it is pertinent to (1) evaluate whether GDMs yield consistent output when applied on a single dataset, (2) assess the sensitivity and accuracy of GDMs to detect growth trends, i.e., the probability and strength of correct trend detection, and (3) quantify their reliability, i.e., one minus the probability that erroneous growth trends are detected. While individual GDMs have been evaluated and weaknesses have been noted for several GDMs (e.g., Esper *et al.*, 2003; Biondi & Qeadan, 2008; Briffa & Melvin, 2011), only in rare cases have studies applied and compared multiple GDMs (e.g., Briffa *et al.*, 1992; Esper *et al.*, 2010; Andreu-Hayles *et al.*, 2011). A comparative analysis and critical evaluation of the most commonly used GDMs in tree-ring research is therefore needed.

Here we critically evaluate the performance of the four most widely applied GDMs (shown in Figure 4.1). We first reviewed the available literature on the application of these GDMs in temperate, boreal, sub-tropical and tropical tree-ring studies. Then, we assessed their consistency, sensitivity and reliability using a combination of measured and simulated growth data. To evaluate the consistency in results across GDMs, we applied the four GDMs on tree-ring series from a tropical species from Thailand. Next, we applied these GDMs on simulated growth data with imposed growth trends to assess their sensitivity, accuracy and reliability. We simulated five growth-trend scenarios: two with strong positive and negative growth trends, two with weak trends, and one with no growth trend. Finally, we discuss differences in sensitivity, accuracy, consistency and reliability of GDMs and provide recommendations for GDM choice in tree-ring studies.

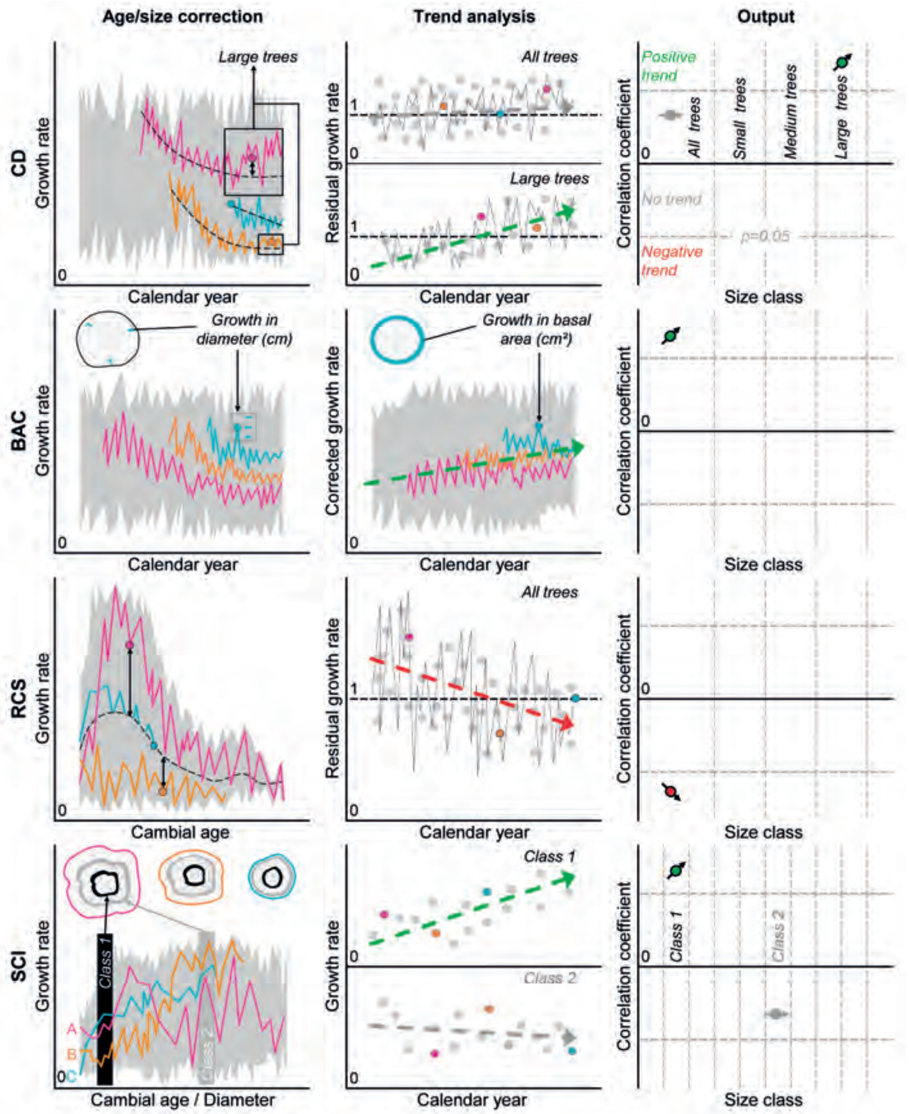

Figure 4.1. Schematic representation of the four Growth-trend Detection Methods (GDM) most commonly used to analyse long-term growth trends using tree-rings: Conservative Detrending (CD), Basal Area Correction (BAC), Regional Curve Standardization (RCS) and Size Class Isolation (SCI). The first column indicates how GDMs disentangle the age/size trend (i.e., the ontogenetic signal) from long-term growth trends. See the Methods section for more detailed explanation of the methods. The second column shows how trends are computed: either on raw or on residual growth rates over time, using Spearman's rank correlations. The third column represents how we present detected trends in this study: grey dot = no growth trend; green = temporal growth increase; and red = growth decrease. Results are presented for All trees (i.e., for all measured tree-rings) or per size category: Small trees = trees 0-27 cm diameter; Medium = 27-54 cm; and Large = trees > 54 cm diameter.

4.2 Materials and methods

Growth-trend Detection Methods (GDMs)

We performed a literature review to document which GDMs are most commonly used in tree-ring studies. Published papers were collected using Scopus and Google Scholar with one, or a combination, of the following search terms: tree-rings; dendrochronology; dendroecology; long-term growth trend; climate change; CO_2 fertilization; tree growth; climate-growth responses; basal area increment; regional curve standardization; age classes; and conservative detrending. We then selected publications in which GDMs were used and for each publication in this selection we noted the GDM(s) used, the period covered by growth trend analysis, study species and site, and growth trend(s) detected.

Below, we describe the methods and assumptions of the four most widely used GDMs: Conservative Detrending, Basal Area Correction, Regional Curve Standardization and Size Class Isolation. Figure 4.1 provides a schematic overview of the crucial steps within the application of each GDM: 'Age/size correction' shows how the ontogenetic trend is accounted for in the raw data; 'Trend analysis' indicates the chronology construction and regression analysis; and 'Output' how we present results of the trend analyses. Over time, several variations and new methods have been developed to cope with the (supposed) limitations of each GDM: signal-free standardization (Melvin & Briffa, 2008), age-band decomposition (Briffa *et al.*, 2001)2001, C-method standardization (Biondi & Qeadan, 2008), or the integration of different methods into mixed-effect models (e.g., Girardin *et al.*, 2008; Nock *et al.*, 2011). Although these variations exist, in this study we focus on the four most widely applied GDMs in their most basal form.

In Conservative Detrending (henceforth CD), mathematical function are fitted to individual ring-series (Figure 4.1; see 'Age/size correction') to account for the decrease in ring-width with tree age (i.e., the ontogeny) and residual growth is calculated around these functions. The fitted functions can be (rigid) splines (e.g., Kienast & Luxmoore, 1988; Andreu-Hayles *et al.*, 2011) or 'conservative curves' (i.e., negative exponential, linear regression, or horizontal lines; cf. Wang *et al.*, 2006; Koutavas, 2013). Residuals are calculated by dividing measured ring-widths by the fitted function. This method assumes that the fitted functions describe the decrease in ring-width with age of each individual, while fully or partially maintaining the long-term growth trends. Long-term growth trends are then calculated over the residual chronology (the average residual per year) and related to calendar year (Figure 4.1, see 'Trend analysis').

In the Basal Area Correction (BAC), the age/size trend is removed by converting diameter growth (in cm yr^{-1}) to basal area increment (BAI, in cm^{2} yr^{-1}; Figure 4.1). This method assumes that growth in BAI shows no trend in mature trees, contrary to diameter growth that often shows decreases with increasing tree size (Martínez-Vilalta *et al.*, 2008; Silva *et al.*, 2010). For each tree, BAI is calculated and growth trends in time are computed over the BAI chronology (Figure 4.1).

In the Regional Curve Standardization (RCS), an average age/size trend is calculated to describe the ontogeny, i.e., the 'regional curve', and individual tree-ring series are then divided by this average curve (cf. Esper *et al.*, 2003; Cole *et al.*, 2010). To establish the regional curve, ring widths of all individuals are first aligned to cambial age (years from the pith; Figure 4.1, see Age/size correction) and average growth rates are calculated for each age. A mathematical smoothing function is fitted through these averages per age to describe the relationship between growth and age (i.e., the regional curve). Ring-widths of individual trees are then divided by the expected growth for each cambial age. This process assumes that the age/size trend of the species is realistically described by the tree-ring series and that the regional curve is independent from long-term growth trends induced by environmental changes. Temporal trends in growth are calculated over the residual chronology, related to calendar year (Figure 4.1, see 'Trend analysis').

In the Size Class Isolation (SCI), the age/size trend in growth is not accounted for by curve fitting or data transformations. Instead, growth trends are analysed directly within an ontogenetic stage, i.e., within the same age or size classes for extant large/old trees and extant small/young trees (Landis & Peart, 2005; Rozendaal *et al.*, 2010a). Growth of small trees are thus compared with growth of large trees when they were small (Figure 4.1, see 'Age/size correction'). For instance, growth rates at a diameter of 12 cm can be compared between extant small and extant large trees and related to their corresponding calendar years to evaluate growth trends over time (e.g., Rozendaal *et al.*, 2010a; Zuidema *et al.*, 2011; Figure 4.1, see 'Trend analysis'). This method assumes that trees within a size class present similar growth rates and comparing growth within a size class thus removes the effect of the age/size trend. Trends are calculated over the raw growth data, in diameter growth or BAI, related to calendar year (Figure 4.1, see 'Trend analysis').

Empirical tree-ring series: Melia azedarach

We applied the four GDMs on tree-ring series for *Melia azedarach* A. Juss (Meliaceae, henceforth called *Melia*) in order to evaluate the consistency of results between methods. *Melia* is a deciduous, long-lived pioneer (up to 120 years) known to form high-quality annual rings (Vlam *et al.*, 2014b). We collected increment cores of 90 *Melia* trees (three to four cores per tree) in the Huai Kha Khaeng Wildlife Sanctuary, west-central Thailand (between 15°50' to 16°00' N and 99°00' to 99°28'E), in an undisturbed and unlogged area of the forest. Core surfaces were prepared, scanned at 1600 dpi with a flatbed scanner (Epson Expression 10000 XL) and ring-widths were measured using WinDENDRO (Regent Instruments Canada Inc. 2004). Average ring-widths for the different radii were converted to diameter increment prior to trend analysis. More detailed descriptions of the study site, sampling methods and ring measurement procedures are given in Vlam *et al.* (2014b) and in the Supplementary Materials (Appendix A).

Simulated tree-ring series

We simulated virtual growth trajectories that mimicked the growth characteristics of *Melia*, to allow for comparison of GDM outputs between measured and simulated data. Individual tree-ring series were simulated based on the following variables for *Melia*: the age trend in BAI, response to annual climatic variation, and the temporal autocorrelation of tree-growth. In addition, we included stochastic variation in the tree-growth simulations. A constant annual mortality chance of 1% was applied randomly for all simulated trees, independent of size class. Virtual tree-ring series were simulated for a period of 108 years (from 1901-2009). Every year, 300 new individuals were 'recruited' (at 1 cm diameter), thus creating a large amount of surviving series (>10,000) in the year of 'sampling' (i.e., in 2009). A full description of the tree-growth model is included in Appendix B.

We ran five different simulations, applying a gradient of imposed growth trends per decade: strong (-6%) and weak (-2%) growth decreases, no growth trends, and weak (+2%) to strong (+6%) growth increases. In the weak trend simulations, we imposed linear growth trends of 0.002 per year in both directions (i.e., a 2% change per decade) and in the strong trends, we imposed growth trends of 0.006 per year (6% change per decade). These growth changes were chosen as they resemble changes reported for permanent sample plots in tropical forests (cf. Lewis *et al.*, 2009a). The no-trend simulations contained no growth trends, as none of the input values showed trends over time. All simulations were performed in Matlab v8.1 (The Mathworks).

From the >10,000 surviving simulated tree-ring series, we created a database of 100 series randomly selected to be analysed for trends using the four GDMs. We chose this sample size as it is approximately the size of the empirical *Melia* dataset and similar to that of many (tropical) tree-ring studies. For every growth-trend scenario we created a fixed random selection of trees and applied all GDMs to detect trends on this selection. By repeating this random selection 100 times, we were able to assess the sensitivity of each method, i.e., the percentage of correct trend detections.

We also assessed the reliability, accuracy and consistency in trend detection for each GDMs under the different scenarios. The reliability of a GDM is defined as 100% minus the percentage of cases that erroneous growth trends were detected. We define the accuracy of a method as how well the strength of the imposed trends is reflected in the detected trend, i.e., is an imposed growth trend of 6% per decade translated to a detected trend of 6% per decade. For this purpose, we calculated the (relative) slope of the detected trends by the different GDMs and whether they coincided with the imposed trends. Finally, we used the simulated data to assess the consistency in trend detection between GDMs by analysing whether GDMs detected trends similarly when applied on the same random datasets (as also performed for *Melia*). To exclude any effect of the random selection of trees on the sensitivity, reliability, accuracy and consistency calculations, we repeated these analysis ten times, using ten different 'fixed' random datasets.

Implementation of Growth Detection Methods (GDMs)

GDMs were applied to both empirical and simulated tree-ring series. We applied CD using conservative curves (negative exponential curve, linear regression, or horizontal line), fitted to the diameter increments of each measured and virtual tree-ring series, using the dplR package in R (Bunn, 2008). Residuals ring-width series were calculated by dividing measured ring-widths by the fitted function and trends were calculated over average residuals per calendar year (i.e., the chronology). BAI conversion was performed using standard formulas (cf. Phipps & Whiton, 1988; Silva *et al.*, 2010; Gómez-Guerrero *et al.*, 2013). BAI of all individual series was then aligned to calendar year and trends were calculated over average BAI values per year. We applied RCS following Esper *et al.* (2003), determining the regional curve (i.e., the average age/size trend) for *Melia* by aligning all individual growth-rate series to cambial age. To obtain a regional curve not driven by annual variations in growth, we smoothened the curve using a 15-year spline function. Residuals were calculated by dividing the tree-ring series by the regional curve and trends calculated over average residuals per calendar year. For SCI, we applied classes of 4 cm diameter, i.e., every ring falling in a cumulative diameter class of subsequently 4 cm (e.g., at 4cm, 8cm, etc.) was marked as a central ring (Figure 4.1). To obtain growth values not driven by annual variations, growth rates per class were calculated as an average BAI of five rings: that of the central ring plus the two previous and two subsequent rings. In the case of missing rings (e.g., at the start or end of series) averages were calculated for at least four rings.

For each GDM, growth data (i.e., in either BAI or residuals) were related to calendar year to analyse long-term growth trends. For the sensitivity and reliability analysis, we tested for the presence of significant trends using Spearman's rank correlation coefficients (significance level $p < 0.05$; Figure 4.1 see 'Output'), as most data were not normally distributed. For the accuracy and consistency calculations, we assessed the magnitude of the trend detected by fitting linear regression models to each dataset. We then determined how strongly the imposed trends were reflected in the GDM results and whether the detected slopes corresponded to the imposed trends. For these analysis, we included all correlations, including non-significant ones. The strength of the detected trend was expressed in relative change per decade, i.e., expressed in percentages. To calculate relative slopes for SCI and BAC, we divided each detected slope by the average growth rate. For RCS and CD, we used slopes directly as these already reflect relative growth changes. For the consistency analysis, we used the RCS as a reference method and computed the correlation between the slopes detected by the other methods and the RCS' (see Appendix C).

In the SCI, trends were calculated for each size class containing at least 10 individuals. For CD, BAC and RCS, we excluded all calendar years with less than five individuals prior to trend analysis. Furthermore, for CD, BAC and RCS we analysed correlations for all series (all trees), but also for tree diameter at breast height (DBH) size classes separately: 0-27 cm (understory trees), 27-54 cm (small canopy trees) and >54 cm (large canopy trees). For ease of comparison we calculated the sensitivity and reliability for the SCI as an average of all the size classes. All statistical analyses were performed using the R software for statistical computing, version 3.2.00 (R development core team 2013).

4.3 Results

The use of GDMs in literature

We found a total of 46 studies on 77 species in which GDMs were used to detect growth trends. In total, 99 datasets of unique species × location × GDM combinations were evaluated (Figure 4.2 and Appendix D). In a few cases, two or more GDMs were used on the same dataset (e.g., Piovesan *et al.*, 2008; Esper *et al.*, 2010; Andreu-Hayles *et al.*, 2011). The studies were unevenly distributed over temperate, boreal, and tropical regions, with just four studies conducted in the tropics (13 datasets).

CD was the most widely applied GDM in all studies, with 20 studies on in total 46 datasets. In 26 of these 46 datasets positive long-term growth trends were reported, whereas 15 datasets showed no growth trends. SCI was the most applied method for tropical species, with two studies on nine datasets.

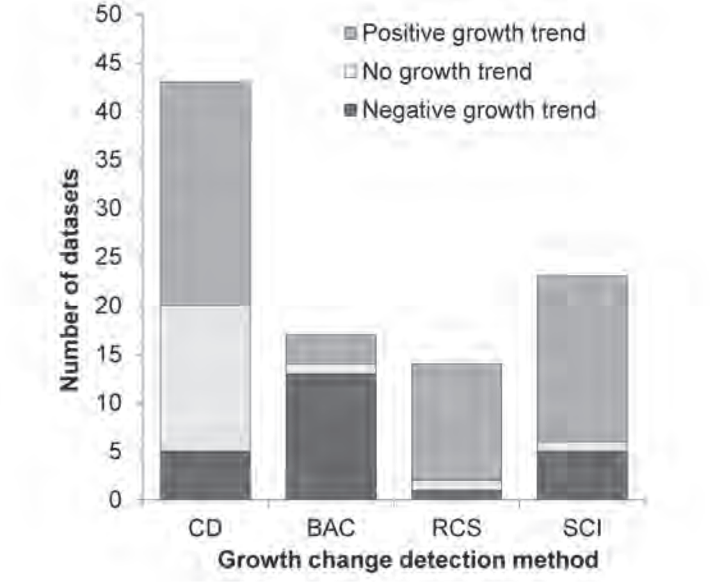

Figure 4.2. Results of a literature review of the most commonly used Growth-trend Detection Methods (GDM). A total of 46 studies on 77 species are presented, comprising of 99 datasets of unique species × location × GDM combinations. Bar colour indicates whether positive trends (green), no trend (grey) or negative trends (red) were detected. GDM abbreviations: Conservative Detrending (CD), Basal Area Correction (BAC), Regional Curve Standardization (RCS) and Size Class Isolation (SCI).

Detecting long-term growth trends in Melia *tree-ring series*

We analysed growth trends in the *Melia* tree-ring series using the four GDMs to assess differences in their output. Results for CD, BAC and RCS are presented for four size categories: all trees, small (0-27 cm DBH), medium (27-54 cm) and large trees (>54 cm). For SCI, results are presented per 4-cm size class (Figure 4.3) and we include a clarification on how trends were computed in SCI in a manner analogous to Figure 4.1.

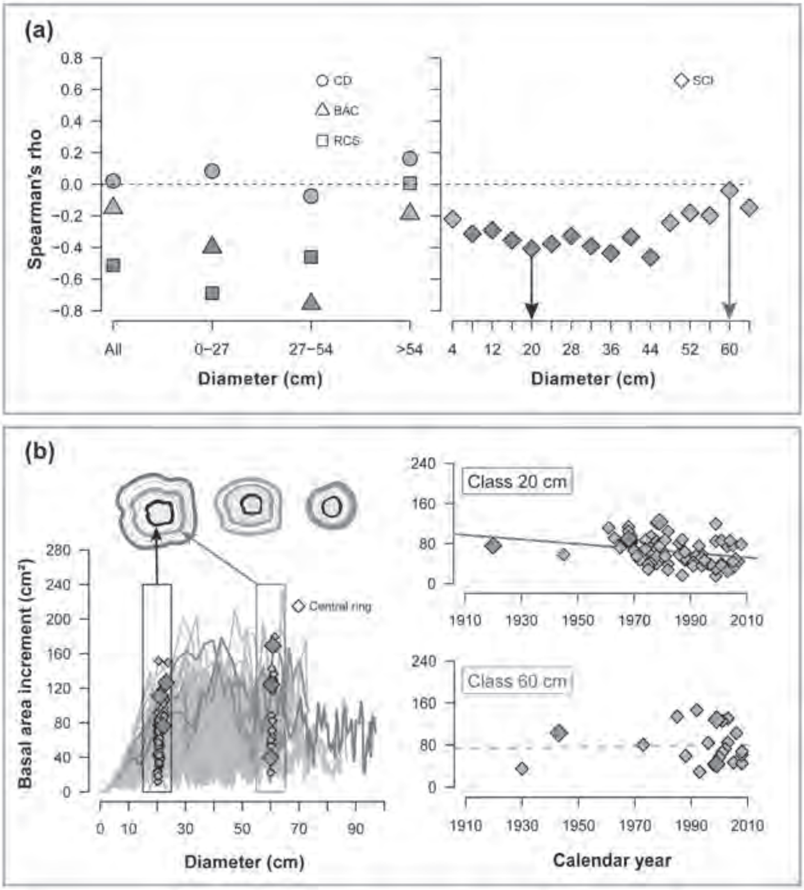

Figure 4.3. Results of the analyses of long-term growth trends on the tree-ring series of *Melia azedarach*. **(a)** Trends detected by each Growth-trend Detection Methods (GDM): Conservative Detrending (CD), Basal Area Correction (BAC), Regional Curve Standardization (RCS) and Size Class Isolation (SCI). Negative trends (red) and non-significant trends (grey) are presented for different diameter categories (in Spearman's rho, significance level $p < 0.05$). **(b)** Procedure and results of the SCI method: tree growth of all – small and large – individual trees is arranged to tree size (left panel) and average growth rates (of five years) are calculated within specific diameter classes, e.g., Class 20 and Class 60 cm. For each diameter class, growth rates are then arranged to calendar year (right panel) and trends computed over time, e.g., in the Class 20 cm, a negative trend was detected (red dot at 20 cm (in **a**)).

The trends detected for the *Melia* tree-ring series varied between specific methods. Three GDMs detected consistent negative growth trends over time: BAC, RCS and SCI. These trends were found for small and medium sized trees (BAC and RCS) and for 8-44 cm diameter trees (SCI). RCS was the only method detecting trends in the category all trees. Trends detected by BAC, RCS and SCI were highly significant (mostly $p < 0.001$). The non-significant results for CD in all size categories ($p > 0.05$) clearly contrasted with the highly significant results obtained by the other GDMs.

In short, three out of four methods (BAC, RCS and SCI) yielded evidence for declining growth rates over time in small and medium-sized *Melia* trees.

Detecting imposed long-term growth trends on virtual growth trajectories

We generated virtual growth trajectories mimicking the growth of *Melia*, to assess the sensitivity, reliability, accuracy and consistency of the four GDMs. The input of the model consisted of factors for the age/size trend, climate-growth relationship, growth autocorrelation (of 15 years) and stochastic variation. The modelled data mimicked the growth of *Melia* very well: modelled growth showed a similar age/size trend (and variation around it; Figure 4.4A) and similar year-to-year variation (Figure 4.4B) to the *Melia* data. This year-to-year variation was induced by the input factor for climate-growth relationship. We built a chronology for the modelled data – on the same way as for *Melia* (see Appendix A) – that was highly similar to this input climate-growth factor ($R^2 = 0.956$, data not shown). Analysis *a posteriori* on the no-trend scenario dataset showed that the age/size trend explained 18.8% of the variation in all growth data while climate explained 8.4% of the variation remaining after removal of the age/size trend (by dividing individual series by the input formula for the age/size trend). The remaining variation, not explained by the age/size trend or climate, can be attributed to the factor for stochastic variation and to the autocorrelation in growth. Growth in the simulated growth curves data was on average significantly autocorrelated for up to six years (data not shown). The simulation of positive and negative trends also clearly affected the modelled growth data (and its average variation), as shown in the mean basal-area chronology for each scenario (Figure 4.4C).

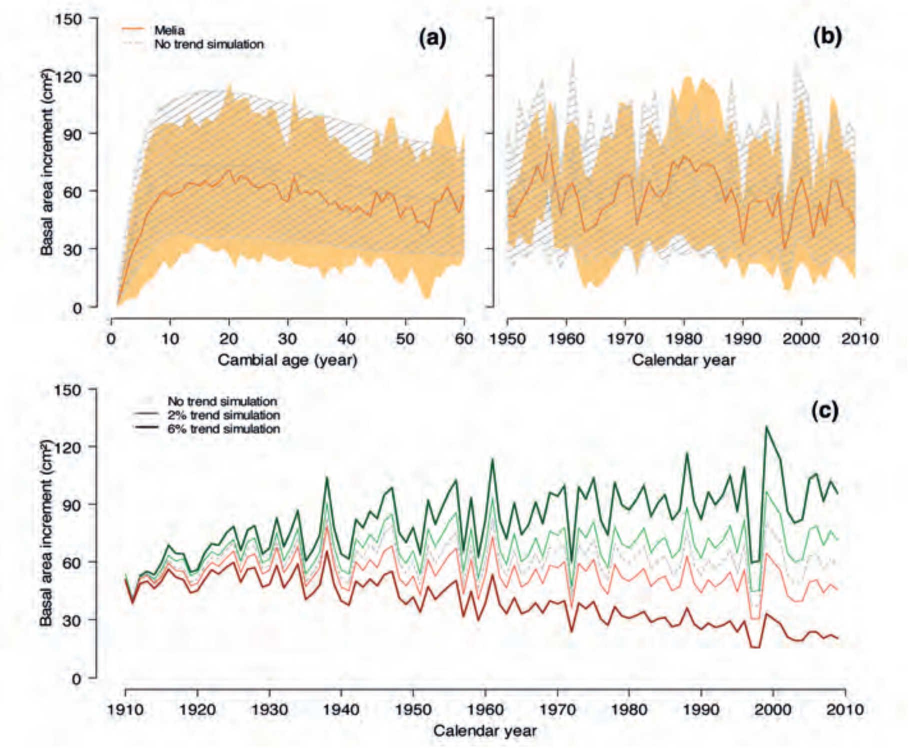

Figure 4.4. Simulated growth trajectories based on *Melia azedarach* and examples of the imposed growth trends. **(a)** Relationship of basal area increment (BAI) per cambial age for the simulated data (in the no-trend scenario; grey) and the measured growth rates for *M. azedarach* (orange). **(b)** Relationship of BAI per calendar year between modelled (grey) and measured data (orange). Lines represent average BAI for all measured or simulated series and shading their standard deviations. **(c)** Relationship of average BAI per calendar year for the five imposed growth trend scenarios: strong increases (i.e., 6% growth trend per decade; dark green line), weak increases (2% trend, light green), no trend (grey line); weak decreases (light red) and strong decreases (dark red).

Next, we assessed how well GDMs detected growth trends imposed on the virtual growth trajectories. Sensitivity (i.e., percentage of imposed growth trends correctly detected) varied considerably among GDMs (Figure 4.5, Table 4.1). On the datasets with the strongest imposed growth trends (i.e., 6% increase and decrease), BAC, RCS and SCI often correctly detected the direction of the imposed trends (Table 4.1). For these three GDMs, sensitivity was higher with imposed strong negative growth trends (93-100% of cases) than with positive trends (30-99%) and this difference was most evident in the SCI. CD had the lowest sensitivity, detecting almost none of the strong imposed positive trends and only 36% of the strong negative trends.

Table 4.1. Sensitivity and reliability of four growth-detection methods (GDM)* applied to a range of growth trends imposed to simulated tree-ring series. Sensitivity refers to the percentage of correct detection of the imposed growth trend. Reliability is 100% minus the percentage of erroneous growth-trend detections. Values are presented as an average of 10 analyses ± standard deviations. For SCI the results are presented as the average of all size classes and for the other methods, for the 'All trees' size category.

GDM*		**Imposed growth trend (per decade)**					**Mean**
	-6%	-2%	0	2%	6%		
CD	Sensitivity	36.4 ±6.4	5.5 ±2.9	95.9 ±1.8	1.5 ±1.2	0.8 ±1.2	28
	Reliability	98.6 ±1.1	98.7 ±1.2	95.9 ±1.8	97.9 ±1.1	99.4 ±0.7	98.1
BAC	Sensitivity	100.0 ±0.0	66.9 ±4.6	66.7 ±4.3	56.5 ±3.6	98.9 ±1.0	77.8
	Reliability	100.0 ±0.0	98.9 ±0.9	66.7 ±4.3	97.4 ±1.4	100.0 ±0.0	92.6
RCS	Sensitivity	100.0 ±0.0	37.6 ±3.7	85.3 ±4.0	35.6 ±3.7	86.3 ±4.0	69
	Reliability	100.0 ±0.0	99.2 ±1.0	85.3 ±4.0	99.7 ±0.5	100.0 ±0.0	96.8
SCI	Sensitivity	93.2 ±0.6	23.4 ±1.8	93.9 ±0.5	7.1 ±0.9	30.5 ±1.3	49.6
	Reliability	100.0 ±0.0	99.9 ±0.1	93.9 ±0.5	98.5 ±0.2	99.6 ±0.2	98.5

* CD = conservative detrending; BAC = basal area correction; RCS = regional curve standardization; SCI = size class isolation

Sensitivity decreased for all GDMs when detecting weak imposed growth trends of 2% increase or decrease, compared to the strongest (6%) simulated trends. For BAC and RCS, sensitivity was intermediate, with trends correctly detected in 36-67% of the simulations, whereas SCI had a lower sensitivity of 7-23%. Again, CD had the lowest sensitivity, varying between 2-6%.

In the no-trend simulations, reliability was high for CD, RCS, and SCI – varying between 85-96% of correctly detected 'no trends' – and was lower for BAC (67%; Table 4.1). Erroneous trend detection also occurred in the 2% increase and decrease scenarios (Figure 4.5), but overall, reliability was high in all simulations with imposed growth trends (Table 4.1). For BAC the lower reliability in the no-trend scenarios, compared to the other methods, was not reflected in the scenarios with imposed trends: reliability was high, with > 97% of trends correctly detected.

The accuracy of trend detection (i.e., correctly detecting the strength of the imposed trends) also varied between GDMs. CD showed nearly no differences in the strength of detected trends between increasing, decreasing and no-trend scenarios: detected slopes varied between 0.0% to 1.0% growth trend per decade (Figure 4.6, Supplementary Table 4.4 Appendix C). The other

GDMs appear to underestimate the detection of positive trends: in the scenarios with 2% growth increases growth trends were detected varying between 0.4% and 1.1% per decade and in the 6% increase scenarios between 1.7 and 3.5%. In the scenarios with growth decreases, on the other hand, BAC and SCI overestimated the imposed trends, e.g., in the 6% decrease scenario, growth decreases of >11% were detected (Figure 4.6, Supplementary Table 4.4 Appendix C). It is also clear that both BAC and SCI show a higher spread of detected trends, i.e., wider distribution of detected slopes, compared to the RCS (Figure 4.6).

Consistency in detecting trends was high between BAC and RCS: the detected trends showed high correlations for all different scenarios (average $R^2 = 0.678$; Supplementary Table 4.5 in Appendix C). The slopes detected by SCI correlated less strongly with the RCS' ($R^2 = 0.192$), while for CD, the detected slopes did not correlate at all ($R^2 = 0.022$). For more detailed results on the consistency, see Appendix C in the Supplementary materials.

In short, sensitivity varied between methods: detection of trends was good when 6% trends were imposed but lower with the 2% trends. Reliability was high on the simulations with imposed growth trends but erroneous trends were detected in the no-trend simulations, with results varying between GDMs. Accuracy also varied between GDMs: in CD nearly none of the imposed trends were detected and the remaining methods tended to underestimate the imposed positive trends, while overestimating the negative trends. Finally, methods are rather consistent in detecting trends when applied on the same datasets.

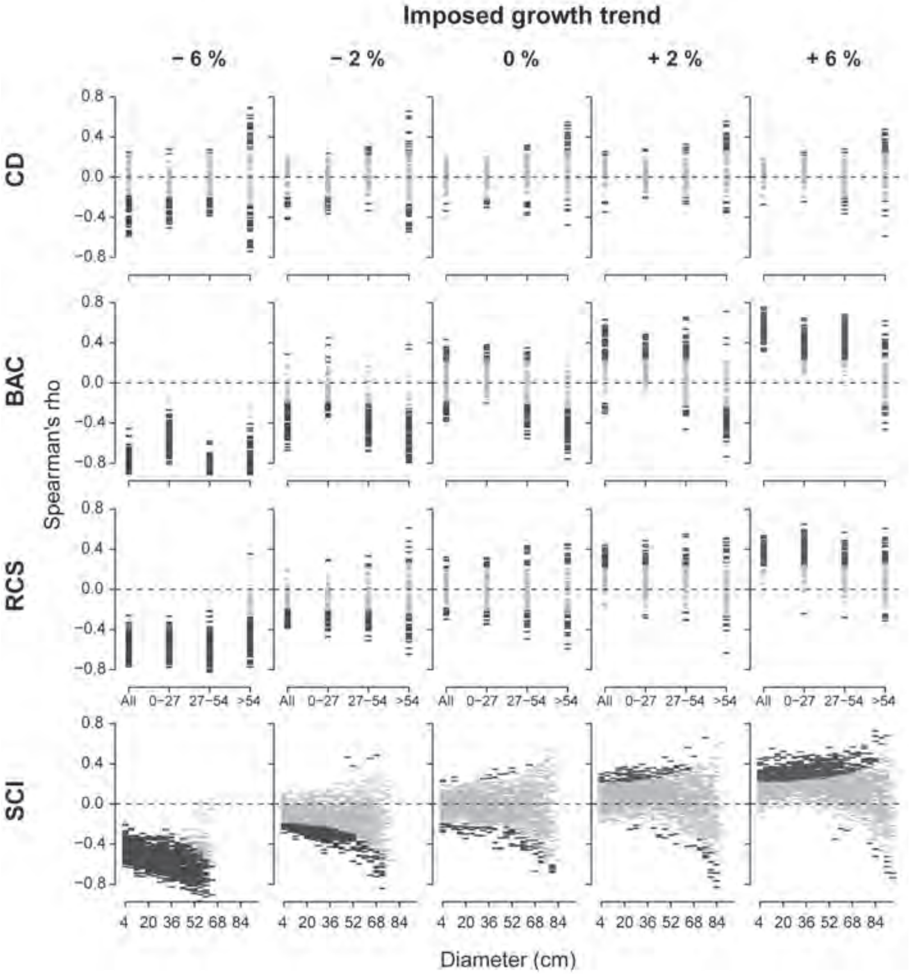

Figure 4.5. Results of the analyses with simulated growth trajectories for four Growth-trend Detection Methods (GDM). Significant negative (red) and positive trends (green), and non-significant trends (grey) are presented per GDM (in Spearman's rho, significance level $p < 0.05$) for different diameter categories. Results are presented for one subset of 100 times 100 trees per imposed trend. GDM abbreviations: Conservative Detrending (CD), Basal Area Correction (BAC), Regional Curve Standardization (RCS) and Size Class Isolation (SCI).

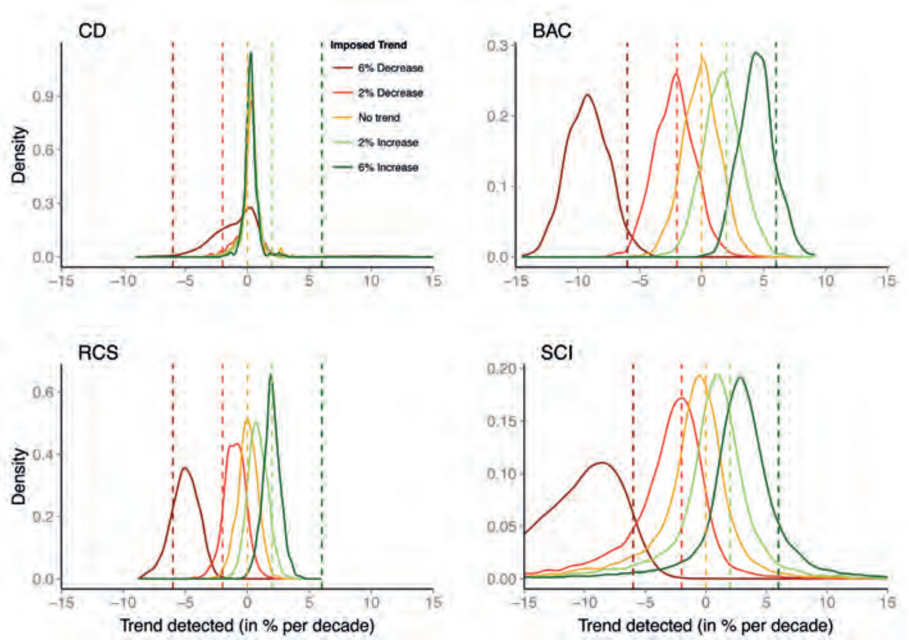

Figure 4.6. Comparison of slopes detected by the Growth-trend Detection Methods (GDMs; density plots) for each of the imposed growth-trend scenarios and runs. Coloured lines show the distribution of all slopes detected by the GDMs (as a Kernel density plots) and the vertical dotted lines the corresponding imposed growth trends. GDM abbreviation: Conservative Detrending (CD), Basal Area Correction (BAC), Regional Curve Standardization (RCS) and Size Class Isolation (SCI).

4.4. Discussion

Long-term growth trends for Melia azedarach

Three out of four growth-trend detection methods (GDMs) yielded similar results: long-term decreases in growth for the *Melia* tree-ring series for similar ranges of tree size (Figure 4.3). Application of Conservative Detrending did not yield trends over time at all. The negative growth trends are consistent with findings from Nock *et al.* (2011) who studied the same tree species at the same site. They calculated trends in BAI over different size classes, with a method that combines BAC and SCI, using a mixed effect model.

Identifying the causal drivers of decreasing growth rates is difficult (Clark & Clark, 2011) and multiple factors have been suggested: increased drought periods, increasing temperatures, closing of the canopy after disturbances (e.g., Nock *et al.*, 2011; Middendorp *et al.*, 2013). In addition, biases due to sampling methods (Nehrbass-Ahles *et al.*, 2014) or related to the nature of tree-ring data (Brienen *et al.*, 2012a) could also lead to the detection of (apparent) trends. For instance, the "juvenile selection effect" (cf. Landis & Peart, 2005; Rozendaal *et al.*, 2010a) could create negative growth trends in a light-demanding species such as *Melia*, where adult trees are probably the successful, fast-growing individuals from the past. In addition to these methodological issues, we show here that the choice of growth-detection method also influences the probability of detecting trends.

Applying Conservative Detrending (CD) did not yield significant trends for *Melia* in any of the size classes. This lack in trend detection is to be expected for CD (Briffa *et al.*, 1992) as the functions fitted to individual ring-series may not differentiate between age/size trends and trends induced by climatic influence (Cook *et al.*, 1995). Furthermore, this lack in trend detection may have been reinforced by the relatively short length of our ring-series (i.e., life-span of *Melia* ~100 years). On long series, function fit is mostly determined by the age/size dependent growth trend in the series, whereas on short series function fit is relatively more influenced by values at the end or beginning of a series, hampering the detection of trends. This pattern of lower trend detections on short series also emerged from the literature review: trends were detected by CD in 90% (19 out of 22) of studies working with long series, i.e., lifespans >130 years, while in just 43% (9 out of 21) of studies with short series (Appendix D).

The results on the *Melia* ring-series indicate that method choice influences the detection of long-term trends. This influence was also suggested by Esper *et al.* (2010) using multiple detrending methods on boreal trees. These differences in trend detection between methods suggests that results of studies using a single method should be interpreted with care.

Sensitivity, reliability, accuracy and consistency of growth-trend detection methods (GDMs)

If different GDMs yield similar results, this may be reassuring, indicating that the detected trend is likely. Yet, this does not imply that growth trends were correctly detected or that they were present in the tree-ring series in the first place. We addressed these issues by applying the four GDMs on simulated growth trajectories that had imposed growth trends. These growth trend scenarios, with either negative, no or positive trends as input, demonstrated that GDMs vary in their sensitivity (i.e., power to detect imposed trends), accuracy (i.e., how well the strength of trends are detected), and reliability (i.e., 1- the probability of detecting erroneous trends). Sensitivity was reasonably high when strong growth trends (of 6%) were imposed, but decreased when imposed trends were weaker (2%; Table 4.1). The accuracy of trend detection also differed between methods, with a higher tendency to detect (or overestimate) imposed negative trends than for positive trends (Figure 4.6). Similarly, the reliability of trend detection was high in the scenarios with strong trends, but was lower for the weak or no-trends scenarios (Table 4.1). In the following section, we discuss specific results for each of the GDMs.

Conservative Detrending is assumed to sufficiently remove the (negative) age/size trend in diameter growth, while maintaining long-term trends. However, several weaknesses of CD have already been noted (Briffa & Melvin, 2011) and detrending series individually has been suggested to inevitably also removes long-term trends in growth (Briffa *et al.*, 1992; Cook *et al.*, 1995). Our results confirm these suggestions, as CD showed the lowest sensitivity and accuracy of the four methods (Table 4.1; Figures 5 and 6), implying that imposed growth trends were completely removed from most simulated growth trajectories (Table 4.1). Additionally, CD was the least consistent method in detecting trends, i.e., slopes detected by CD showed nearly no correlation with slopes detected by the RCS (Appendix C). Although these weaknesses have been noted, CD is still widely applied (e.g., Wang *et al.*, 2006; see Appendix D; Villalba *et al.*, 2012). This low sensitivity is also reflected by the relatively high proportion of studies detecting no growth trends when applying CD (15 of the 43 reviewed datasets; Appendix D), which is considerably higher than for other GDMs (Figure 4.2). Similar to the *Melia* data, the complete removal of trends from the modelled data may have been reinforced by the relative short length of the simulated growth trajectories. Furthermore, the negative (exponential/linear) curves fitted in CD may also not be suitable for describing the initial growing phases of trees, when young growth years or young individuals are included. CD may thus be better suited for detecting trends on long-lived species.

Basal Area Correction (BAC) showed high sensitivity and good accuracy in detecting growth trends (Table 4.1; Figures 5 and 6) and trends detected using BAC were consistent with those detected with RCS (Appendix C). However, the reliability of BAC was the lowest of all methods, especially in the no-trend simulations (Tables 1 and 2). The frequent detection of erroneous trends by only expressing growth in basal area is worrisome, as BAC is still applied this way (e.g., Martínez-Vilalta *et al.*, 2008; Silva *et al.*, 2010) and this unreliability may lead to incorrect conclusions about growth trends. Our results suggest that BAC may not effectively disentangle age/size from long-term growth trends. Indeed, growth of *Melia* (and the simulations derived from *Melia* data) still show a clear age trend in basal area increment (Figure 4.4A). If the age/size trend is not correctly accounted for, trends may be induced by, for instance, changes in the relative abundances of small (slow growing) and large (fast growing) trees over time.

Simply expressing growth as basal area has the advantage of avoiding curve fitting procedures (as done in CD and RCS; Table 4.2). However, this conversion may thus not suffice to remove the age/size trends and additional steps are necessary to account for the remaining age/size trend when using BAC. These steps may include: analysing trends inside specific size classes (e.g., only for mature trees; cf. Jump *et al.*, 2006); detrending the BAI series by an estimated BAI growth trend (the C-Method, cf. Biondi & Qeadan, 2008); or incorporating tree-size explicitly (e.g., in mixed-effect models) when analysing trends (e.g., Martínez-Vilalta *et al.*, 2008; Nock *et al.*, 2011). Analysing trends inside specific size classes may indeed provide additional information, as illustrated in the trend analysis for *Melia*. When analysing trends in specific size classes, trends were detected for the small and medium size categories but not for all trees (Figure 4.3). Note that with small size classes, BAC effectively becomes analogous to SCI. We also applied the C-method (cf. Biondi & Qeadan, 2008) to the simulated data. Surprisingly, this method detected solely negative trends, irrespective of the imposed trends (see for more details Appendix E). We believe that C-method might not be suitable for short series, i.e., the small trees in our dataset, as it cannot account well for the ontogenetic growth trends in these small/juvenile trees (Biondi & Qeadan, 2008). We have not analysed trends using mixed-effect models, as this was beyond our scope of comparing existing and widely used methods. However, we believe that mixed-effect models, including generalized additive mixed models (GAMM), have great potential to disentangle age/size trends from long-term growth trends, as these models can simultaneously account for linear (i.e., growth trends) and non-linear (i.e., age/size) trends in a dataset (Wood, 2006; Polansky & Robbins, 2013). Such approaches are, however, rare in tree-ring studies (e.g., Martínez-Vilalta *et al.*, 2008; Nock *et al.*, 2011) and should receive more attention. Finally, the detection of trends using BAC may be hampered as growth (in basal area) may continually increase over a tree's life (Stephenson *et al.*, 2014). If a species shows a continually increasing trend in basal area growth over its life, BAC is hampered in disentangling age/size from long-term growth trends. However, such increasing growth trend poses less of a problem for the other methods, as the age-trend (or size-trend) will be accounted for by the fitted conservative curves, incorporated in the regional curve or, for the SCI, trees will be selected from within a particular size class (with its corresponding 'average' growth rate).

Table 4.2. Strengths and limitations of four different Growth-trend Detection Methods (GDM). Symbols indicate whether strength or limitation is applicable: check mark = applicable; crosses = not applicable; and question marks = still unclear / not assessed. Criteria are either assessed in this study or derived from literature (as indicated). Sensitivity refers to the percentage of correct detection of imposed growth trend and reliability = 100% minus the percentage of erroneous growth-trend detections. GDMs assessed: CD = conservative detrending; BAC = basal area correction; RCS = regional curve standardization; SCI = size class isolation.

Strength	**CD**	**BAC**	**RCS**	**SCI**
High sensitivity (Table 4.1)	✗	✓	✓	✗
High reliability (Table 4.1)	✗	✗	✓	✓
Can be applied on untransformed growth data (Figure 4.1)	✗	✓	✗	✓
Can be combined with climate-growth analysis (Figure 4.1)	✓	✓	✓	✗
Limitation				
Timespan ring-series should extend span of the trend assessed[1]	✓	?	✓	?
Low detection power for larger diameter classes[2]	✗	✗	✗	✓
Affected by sampling biases[3]	✓	✓	✓	✓

[1] To avoid the trend-in-signal bias (cf. Briffa & Melvin, 2011).

[2] Sample size decreases with increasing diameter (e.g., for *Melia*, n= 17 at 63 cm diameter).

[3] Slow-grower survivorship bias and big-tree selection bias (cf. Brienen *et al.*, 2012).

Overall, Regional Curve Standardization (RCS) showed high sensitivity, accuracy and reliability (Table 4.2). However, sensitivity was below 50% in the scenarios with weak growth trends (2%; Table 4.1) and RCS underestimated the strength of imposed positive trends (Figure 4.6). Weak (positive) growth trends over time are thus not easily detected using this method. Applying RCS requires large sample sizes (Briffa *et al.*, 1992; Esper *et al.*, 2002) and ideally species showing a 'strong' age-size relationship, to enable the calculation of a representative and 'strong' regional curve. Our light-demanding study species – and the simulated series – showed such strong age/size relationship. RCS may be less suitable for shade-tolerant species, as these species often exhibit rather weak age-size relationships (due to periods of slow or suppressed growth). Finally, in RCS, the period covered by the tree-rings series should ideally be longer than the period over which trends in environmental signals are assessed (Table 4.2; e.g., Esper *et al.*, 2002)2002, to avoid that externally driven growth trends are incorporated into the regional curve (the 'trend in signal bias'; cf. Briffa & Melvin, 2011). In boreal and temperate regions, fossil and sub-fossil wood are often incorporated to extend the timespan of long-term growth reconstructions (e.g., Esper *et al.*, 2012). In regions lacking fossil wood (e.g., in the tropics, due to the high decomposition rates) it is necessary to work with long-lived species when using RCS when analysing climate-change effects on tree growth. For tropical studies, the combined requirements of long life-spans and strong age/size relationships implies the RCS may be better suited for long-lived pioneer species.

The Size-Class Isolation (SCI) method was not very sensitive but showed high reliability (i.e., detecting few trends erroneously; Table 4.1 and Figure 4.5), detected the imposed trends rather accurately (Figure 4.6) and rather consistent with the RCS (Appendix C). Splitting the data into diameter classes reduces sample size, as trends are calculated on average growth values per tree and not on individual ring measurements. Sample size may be particularly low in smaller diameter classes, due to missing piths when coring, and in large diameter classes, if only a small portion of trees are large. The low sensitivity of SCI may be explained by these reduced sample sizes and working with SCI thus requires sampling relatively large numbers of trees (Table 4.2). Furthermore, SCI requires including both large and small trees, which is not always possible as many (tropical) species show periodic absence of recruitment (e.g., Vlam *et al.*, 2014a). Another limitation of SCI is that determining size classes is a subjective process that may lead to analyses of trends over a variety of size class for different species (e.g., Rozendaal *et al.*, 2010a), making comparisons between these analyses more difficult. Additionally, the output of SCI is less suitable for establishing climate-growth relationships (Table 4.2), which hampers assessing which environmental factors may explain growth trends. Despite its limitations, SCI showed low detection of erroneous trends, i.e., SCI is a reliable method. We argue that the reliability of a method is important, as a conservative method is preferred over an unreliable method. Finally, another advantage of SCI is that it directly evaluates growth trends on raw measurements, and therefore is not influenced by (subjective) decisions on curve fitting that are necessary for CD and RCS (Table 4.2).

Overall, the four tested GDMs differed in their sensitivity, reliability, accuracy and consistency. These results show that detection of long-term trends is affected by method choice and suggest that the age/size trend may not be completely removed in some methods. GDM sensitivity and accuracy varied, with CD not detecting trends while the other methods underestimate positive trends while overestimating negative trends. This stronger detection of negative trends can in part be explained by the fact that growth cannot be negative in our modelled data, or in real tree-ring data. Growth reductions over time force growth data nearer to zero, reducing variation in growth data over time. The contrary is true for the growth increase scenarios (see Figure 4.4C), in which growth variation increases. We believe that the lower variation in growth in the decrease scenarios implies trends are more easily detected, thus leading to the higher sensitivity and accuracy.

In our modelling approach, we attempted to assess how the variation present in tree growth affects the detection of trends (i.e., an improved power test) and determined each factor in the model using simple correlations. This approach only accounts for the stochastic variation in growth and is of course a simplification of all physiological and mechanistic factors affecting tree growth. A modelling approach based on mechanistic or physiological processes could greatly enhance the understanding of the effects climate change on tree growth and how to detect them. Furthermore, our finding should be interpreted with some care, as the growth characteristics of a specific species from the tropics do not necessarily apply to other species from other regions. Despite the limitations of our approach, we believe that it suffices when assessing the detection power of the different GDMs and that it forms an important first step in disentangling the effects of method choice on the detection of long-term growth trends.

Recommendations for growth trend detection

Tree-ring analysis has been widely applied to detect growth trends in boreal and temperate tree species and there is growing interest in using tree-rings for the same purpose for tropical tree species (Bowman *et al.*, 2013). In this paper we focused on the four methods most widely used in tree-ring research to disentangle age/size trends from long-term growth trends. Below we provide recommendations for tree-ring studies analysing trends in growth.

Our results suggest that, to detect long-term growth trends, Conservative Detrending (CD) is not very suitable, that Basal Area Correction (BAC) is not always reliable and that the Regional Curve Standardization (RCS) and Size Class Isolation (SCI) show good potential. Using CD, no trends were detected in the *Melia* tree-ring data and in nearly all simulated growth data. We recommend not using CD to evaluate trends, especially when working with short-lived species, and CD may be better suited when analysing climate-growth relationships. Basal Area Correction showed high sensitivity and accuracy, but showed the lowest reliability (i.e., it also detected trends erroneously). This low reliability is problematic, as determining when a trend is correctly or erroneously detected in measured ring data is difficult. Great care should thus be taken if only expressing growth in basal area. Several additional steps can be taken to improve analysis with BAC, as discussed above. The high sensitivity of BAC merits assessing which of these steps effectively increase BAC's reliability.

For future tree-ring studies analysing growth trends, we recommend the use of several trend-detection methods. We believe that combining the sensitive RCS with the reliable but somewhat conservative SCI would yield robust results. RCS showed high sensitivity and reliability and the SCI, despite its low sensitivity, was the most reliable method (i.e., the lowest erroneous detection of trends). These two methods are complementary in three aspects. First, SCI is independent of the age/size trend, whereas RCS depends on a 'strong' ontogenetic signal and may be less reliable when this signal is lacking. Second, the sensitivity of SCI depends of large sample sizes, as individuals (and not growth measurements) are the units of analysis. On the other hand, sensitivity of RCS is generally high as the individual ring measurements are the units of analysis. Thus, RCS is more suitable to detect weak growth trends and more suitable when sample sizes are relatively small. Third, the higher reliability is an important asset of SCI and – combined with its somewhat lower sensitivity – it makes SCI a high-quality, conservative method that can be used to verify the robustness of trends detected using RCS.

Detecting trends in tree-growth is challenging, whether one deals with growth data derived from permanent plot studies or from tree-ring analysis (Bowman *et al.*, 2013). For tree-ring data, both from temperate, boreal and tropical regions, specific limitations exist that need to be taken into account. First, many tree species show persistent temporal growth differences, i.e., fast growing individuals stay fast growers in time (e.g., Brienen *et al.*, 2006)2006. We believe that especially the RCS is sensitive to these growth differences. These differences lead to strong variation in diameter-age relationships that disproportionally affect the regional curve and therefore influence trend detection. Similarly, shade-tolerant species and species showing periods of growth suppression (e.g., slow growth due to overshadowing) show periods of low or high growth over multiple years. To minimize the effect of these persistent growth differences on the regional curve, we recommend calculating RCS using small cumulative diameter classes (e.g., 1 cm) instead of age (cf. Bontemps & Esper, 2011).

Second, biases due to sampling strategies can potentially induce growth trends over time (Brienen *et al.*, 2012a; Nehrbass-Ahles *et al.*, 2014). For instance, growth increases may be detected if slow-growing individuals within a population live longer, i.e., the 'slow-grower survivorship' bias (cf. Brienen *et al.*, 2012a; Table 4.2); but see Ireland *et al.* (2014). These slow-growing individuals will then be overrepresented in the more ancient portion of the dataset, leading to apparent growth increases over time. Irrespective of the GDM used, tree-ring series should be collected according to the population structure to avoid such sampling biases as much as possible (e.g., Vlam *et al.*, 2014a). Furthermore, we stress the importance of sampling near permanent sample plots and weather stations with long-term, high quality data (cf. Wang *et al.*, 2006; Clark & Clark, 2011), to provide critical contextual information on the sample site and conditions (Bowman *et al.*, 2013).

Finally, detecting trends using tree-ring analysis requires working with large sample sizes (~100 trees or more per species). Large samples are needed to increase trend detection power and to obtain 'representative' subsets of the population (e.g., for a 'representative' regional curve in RCS). Also, to avoid local or regional effects on trends, sampling should preferably occur over large geographical scales (e.g., Esper *et al.*, 2012; Villalba *et al.*, 2012). In the tropics, however, acquiring and measuring large number of trees is challenging, due to low species abundance of individuals and the difficulties of working with tropical tree rings (Groenendijk *et al.*, 2014). Collecting multiple species and simultaneously analysing their growth trends (e.g., with mixed effects models) can be applied to increase the statistical power of the analysis (e.g., Kint *et al.*, 2012; Lara *et al.*, 2013). Such combined analyses are particularly powerful if sampling follows a standardized strategy (cf. Nehrbass-Ahles *et al.*, 2014). A standardized sampling and analysis protocol would allow for a meta-analysis of tree-ring studies worldwide, which is critical to assess the effects of global environmental changes on tree growth and forest dynamics.

To accurately identify long-term growth trends when trends using tree-ring analysis, the best approach is probably to apply several methods simultaneously. This approach would be especially strong if combined with simulated tree-ring series that take sample sizes into account and that mimic the variance in tree-growth. Such integrative approaches are essential to determine whether detected growth trends really occur and should be extended to include more species, from boreal, temperate and tropical regions.

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Supporting information Chapter 4

Appendix A – Climate-growth relations

We examined climate-growth relations between the chronology constructed for *Melia azedarach* and station or modelled climate data, using standard correlation analysis (cf. Vlam *et al.* 2014). We first correlated tree-ring indices to monthly variation in climatic data of the phenological year: beginning at the start of rainy season (pervious calendar year May) until the end of the rainy season (current year October). Additionally, we correlated ring indices to averages of climatic variables subdivided in different 'climatic' periods according to rainfall patterns. These periods consisted of the entire phenological year (November until October), rainy season (May until October) and dry season (November until April; Bunyavejchewin *et al.* 2009), transition periods between previous rainy to current dry season (October until December previous year), the centre of the current dry season (January until March), current dry to rainy season (April until June) and the centre of the rainy season (July until September). We used linear regression modelling to determine the Pearson correlation between the yearly ring-width indices and the above stated periods of climate variables (Supplementary Table 4.1). All climate variables were detrended with a 15-year spline function in R (dplR packages, version 1.5.6) to avoid the inclusion of long-term trends in climate data.

To determine which climatic variables explain most short-term variation of the chronology, we performed a stepwise forward multiple regression analysis in SPSS (version 16) between tree-ring indices and the detrended climate variables. We tested the model for multi-collinearity in SPSS and analysed its strength using Akaike Information Criterion and Bayesian Information Criterion in R, using R Commander (Fox 2005). Model statistics and coefficients presented in Tables S2 and S3.

Supplementary Table 4.1. Overview of the monthly mean climatological data used in this study. Provided are the available years, origin of the data set and the distance to the study site. A linear regression analysis was performed to detect significant long-term trends in different climate variables over time.

Climate variable	**Available years**	**Origin of the data**	**Distance to Huai Kha Khaeng**	**Month or period with a significant linear trend in time (pearson's r; 1960 - recent available year)**
Precipitation	1911-2011	Climate Station Nakhon Sawan (N 15.80 E 100.20)	107 km	None
	1901-2009	CRU TS3.1 climate model (N 15.5-16.0 E 99.0-99.5)	0 km	None
Mean temperature	1949-2011	Climate Station Nakhon Sawan (N 15.80 E 100.20)	107 km	Oct (0.30), Oct-Dec (0.29)
	1901-2009	CRU TS3.1 climate model (N 15.5-16.0 E 99.0-99.5)	0 km	Jan (0.29), Oct (0.35), Oct-Dec (0.29)
Min temperature	1901-2009	CRU TS3.1 climate model (N 15.5-16.0 E 99.0-99.5)	0 km	Jan (0.28), Mar (0.34), Jan-Mar (0.38), dry season (0.31)
Max temperature	1901-2009	CRU TS3.1 climate model (N 15.5-16.0 E 99.0-99.5)	0 km	Sep (0.28), Oct (0.37)
Cloud cover	1901-2009	CRU TS3.1 climate model (N 15.5-16.0 E 99.0-99.5)	0 km	Mar (0.42), May (0.28), Jun (0.35), Jul (0.30), Jan-Mar (0.30), Apr-Jun (0.36)
Palmer drought severity index (PDSI)	1870-2005	UCAR Palmer Drought Severity Index (N 15.0-17.5 E 97.5-100.0)	0 km	Jan (-0.35), Feb (-0.34), Aug (-0.35), Sep (-0.34), Oct (-0.41), Nov (-0.34), Dec (-0.35), Jan-Mar (-0.32), Jul-Sep (-0.32), Oct-Dec (-0.37), rainy season (-0.34), dry season (-0.32), phenological year (-0.37)
ENSO: Niño 3.4 sea surface temperature anomalies	1882-2012	Global climate index	Global	None
Relative humidity	*1973-2003*	HadCRUH specific humidity model *(N 15.0-20.0 E 95.0-100.0)*	*0 km*	*1960 not available*
Solar irradiance	*1978-2012*	*Global climate index*	*Global*	*1960 not available*

Supplementary Table 4.2. Model summary for the climate-growth multiple regression.

Model	R	R Square	Adjusted R Square	Std. Error of the Estimate
[Cloud cover rainy season]	0.626	0.392	0.378	0.1549793
[Cloud cover rainy season] + [Temperature min October-November-December]	0.703	0.495	0.472	0.1428270
[Cloud cover rainy season] + [Temperature min October-November-December] + [Precipitation dry season]	0.740	0.548	0.516	0.1367273

Supplementary Table 4.3. Collinearity statistics multiple regression for climate-growth analysis.

Model	Unstandardised coefficients		Standardised Coefficients	t	Sig.	Collinearity statistics	
	B	Std. Error	Beta			Tolerance	VIF
[Constant]	-1.865	1.077	-1.731	0.091			
[Cloud cover rainy season]	4.868	0.889	0.580	5.477	0.000	0.938	1.066
[Temperature min October-November-December]	-2.111	0.643	-0.338	-3.283	0.002	0.993	1.007
[Precipitation dry season]	0.095	0.042	0.238	2.239	0.030	0.934	1.071

Appendix B – Growth series simulations

Tree-ring simulations were performed in Matlab v8.1 using a loop-structure in which every year 300 individuals were recruited over a period of 108 years (from 1901 to 2009). For each recruiting individual, growth in basal area was simulated and annually tracked until the tree died (random annual mortality chance of 1%). Each tree started with an initial basal area of <0.1 cm^2 (i.e. 1cm diameter) and a cambial age of 1 year. Modelled annual basal area growth was generated to mimic the growth of *Melia*. The model consisted of four main factors: (1) the ontogenetic curve, (2) climate-growth relations, (3) autocorrelation in growth and (4) a stochastic growth factor.

(1) The equation describing the ontogenetic curve was computed by fitting different non-linear functions (cf. Zeide 1993) to both the mean basal area increment and ring-width increment of *Melia* aligned to cambial age. We then choose the best model (highest R^2) to describe the ontogenetic trend of the modelled trees. The following Korf-model, fitted on mean basal area increment, showed the best-fit (R^2=0.93) and was therefore used:

Equation 1. $$BAIont_t = abct^{-c-1}e^{-bt^{-c}}$$

where *BAIont* is the basal area increment according to the ontogeny at annual interval t. Calibration parameter are presented by *a, b* and *c*.

(2) We used the same climate-growth relationships in the modelled trees as found for *Melia* in the multiple regression analysis from Appendix A. The following climate-growth model was used (R^2= 0.55; Equation 2):

Equation 2. $$BAIclim_t = a + b \cdot CC_{rs} + c \cdot TMi_{OND} + P_{dr}$$

where *BAIclim* is the growth determined by the cloud cover in the rainy season (CC_{rs}), mean minimum temperature in October to December (TMi_{OND}) and the precipitation in the dry season (P_{dr}). To simulate climatic variation in the model tree, we used detrended climatic data as input. Data were detrended to avoid any trends in the simulations other the imposed trends.

(3) Autocorrelation was included to simulate persistent differences between slow and fast growing individuals over time (e.g., Brienen *et al.* 2006). We included autocorrelation by adjusting annual growth for the mean growth in

previous years. Growth rates for each year were adjusted using the mean annual growth for the period *t* to *t* – n, in which *t* is the current year and n is the number of years used to cover autocorrelation (we used n = 15 years).

(4) Stochastic variation was included to mimic variation found in tree growth not caused by climate, autocorrelation or ontogenetic effects (i.e., caused by canopy dynamics, soil conditions, etc.). This factor was generated randomly, using a normal distribution.

Finally, variance in initial growth was increased to better mimic the variation in juvenile growth of *Melia*. For this purpose, a "pre-loop" was added, running before the creation of initial growth values, to assign variation in initial growth values to individual growth curves.

The stochastic factor sometimes created negative growth values for individual trees. In the case of negative growth, a tree was assigned a new, small positive growth value (normally distributed with $\mu = 0.25$, $\sigma = 1$) to allow for non-fatal slow growth. If the newly generated growth value was again negative, the simulation for that individual was terminated. The final ensemble of the model used a simple additive function for all factors.

Input parameters and weighing factors were iteratively calibrated to ensure that modelled growth showed mean basal area growth and standard deviations similar to *Melia*'s. After each simulation, we compared the distribution, means and standard deviations of growth rates between tree-ring simulations and the data for *Melia*. In the final model, mean growth rates and standard deviation showed similar patterns to *Melia*'s in both cambial age and calendar year arrangements. For instance, mean and standard deviation of the modelled trees till a cambial age of 45 years was almost equal to *Melia*'s ($\text{mean}_{\text{model}} = 59.7$; $\text{mean}_{\text{sample}} = 59.2$; $\text{STD}_{\text{model}} = 30.9$; $\text{STD}_{\text{sample}} = 34.1$).

Finally, different scenarios were simulated by introducing linear negative and positive trends to the base model (no trend). Trends were added by multiplying the model output by an annual direction coefficient of ±1.002 (i.e. a 2% growth increase/decrease per decade) and an annual coefficient of ±1.006 (i.e. a 6% growth increase/decrease). These growth changes are within range of changes found in tropical forests (Lewis *et al.* 2009). The Matlab code is available on request.

Appendix C: Accuracy and consistency of trend detection

The accuracy of a method represents how well the strength of the imposed trends is reflected in the detected trend (i.e., an imposed growth trend of 6% per decade translated to a detected trend of 6% per decade). We calculated the (relative) slope of the detected trends by the different GDMs and in Figure 4.5 assessed whether they coincided with the imposed trends. In Supplementary Table 4.5 we present the average of the slopes detected by each GDM in each growth trend scenario.

Supplementary Table 4.4: Average accuracy of the four growth-trend detection methods. Averages presented are average of all slopes detected for the ten repetitions of 100 random selections of 100 trees.

	Decrease 6%	Decrease 2%	No trend	Increase 2%	Increase 6%
CD	-0.8%	0.2%	0.3%	0.3%	0.3%
BAC	-9.2%	-2.2%	0.0%	1.6%	4.5%
RCS	-5.0%	-1.0%	0.0%	0.8%	2.0%
SCI	-11.2%	-3.5%	-1.3%	0.4%	2.8%

We assessed consistency in trend detection between the different GDMs on our modelled data as applied on *Melia*. For this purpose, we applied each GDM to a ‘fixed’ random selection of trees for all methods (i.e., the same selection of trees per GDM) in each growth-trend scenario. We compared whether trends were detected similarly on these corresponding random datasets and whether the slopes detected by the different GDMs were correlated. This correlation was calculated between the slopes detected for each method, with the slopes detected by RCS (used as the reference method).

On average, the slopes detected by BAC correlated well with the slopes detected by RCS (average $R^2 = 0.575$; Supplementary Table 4.6) whereas the slopes detected by SCI correlated (as expected) less strongly (average $R^2 = 0.244$). As CD detected nearly no trends, its slopes showed no correlation with the RCS’s (average $R^2 = 0.009$). For an overview of the correlations is provided in Figure S1 and a schematic overview of whether trends were detected by each method in the 100 random tree selections in figure S2.

Supplementary Table 4.5: Average consistency of the trend detection methods. Calculated as the R-squared between all slopes detected by the methods CD, BAC and SCI with the slopes detected by RCS. See also Figure S1 below.

	Decrease 6%	Decrease 2%	No trend	Increase 2%	Increase 6%	Average
CD	0.024	0.015	0.005	0.017	0.050	0.022
BAC	0.657	0.651	0.701	0.687	0.694	0.678
SCI	0.208	0.207	0.198	0.204	0.141	0.192

CD = conservative detrending; BAC = basal area correction; RCS = regional curve standardisation; SCI = size class isolation

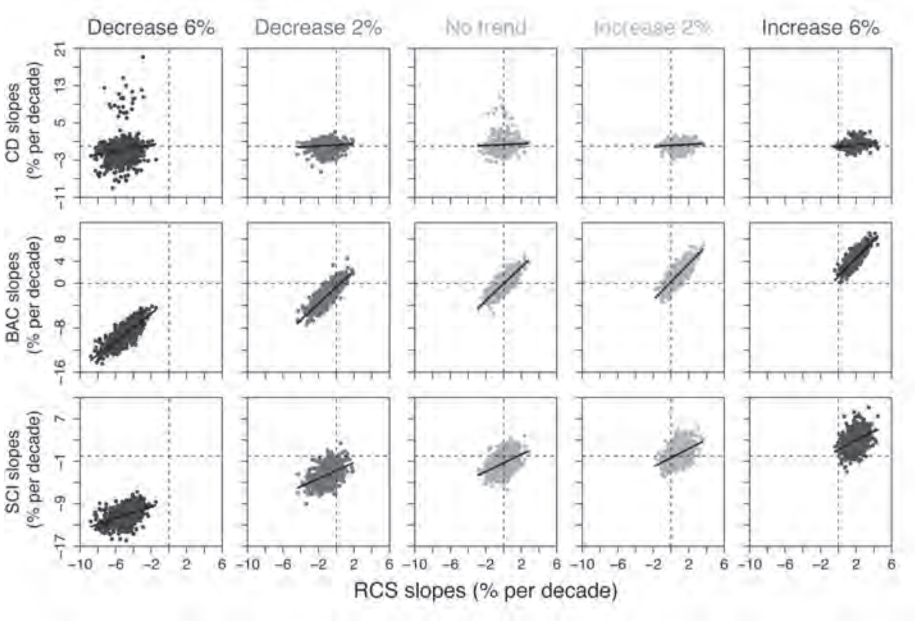

Figure S1: Slopes detected by CD, BAC and SCI against the slopes detected by RCS (as a reference) for each of the simulated growth-trend scenarios (6% and 2% growth decreases, no trend and 2% and 6% growth increases). Correlations between slopes are provided including R^2-values.

Appendix D – Literature review

Supplementary Table 4.6. Results of literature review on the use of GDMs. Provided are species name; research site; GDM used in study; detected long-term growth trend (growth rates increasing over time (+), decreasing growth rates (-), and no growth trend detected (0)); range in calendar year; tree ages covered by tree-ring series; and a brief explanation of the GDM from the methods section.

Species name[1]	Research site (Country, location)	GDM[2]	Long-term growth trend	Calendar year range	Age[3]	Authors	Explanation of methodology
Pinus sylvestris	Spain (Catalonia)	Basal Area Correction	+	1901 - 1997	96	Martínez-Vilalta *et al.* (2008)	Raw basal area data was compared to modeled Basal Area Increment (BAI) as a function of tree size and environmental variables (CO_2, temperature, precipitation, potential evapotranspiration) by means of mixed effects models.
*Cedrela odorata**	Bolivia (Los Indios/La Chonta/Purísima)	Size Class Isolation	+	1693 - 2003	310	Rozendaal *et al.* (2010)	We calculated the juvenile growth rate for each individual as the median basal area growth rate within a narrow range of diameters (i.e. diameter classes 0–1, 1–2, 2–3, 3–4, 4–6, 6–8, 8–10, 10–15, 15–20 and 20–30 cm) for all study species, except for the faster growing C. odorata and C. catenaeformis. For these species we used wider diameter classes at smaller sizes: 0–5 and 5–10 cm. By using different diameter classes for these species, we maintained a similar number of rings per diameter class for all species. The use of a median growth rate per diameter class allowed comparison of growth rates among trees at the same diameter, and thus at the same ontogenetic stage.
Cedrelinga catenaeformis			-	1860 - 2005	145		
*Clarisia racemosa**			+	1628 - 2005	377		
*Peltogyne heterophylla**			+	1773 - 2005	232		
*Pseudolmedia laevis**			+	1744 - 2005	261		
Picea abies	France (Alps)	Regional Curve Standardization	+	1750 - 1993	243	Rolland *et al.* (1998)	First, the average growth trend curve as a function of tree age was calculated for each species. This is done by averaging all measured ring-widths formed at the same cambial age for all different sites for a given species. These curves are then used for standardising the data, by dividing each measured ring-width at a given age of formation by the corresponding mean growth value at the same age. Second, the measured values are examined
Larix decidua			+	1750 - 1993	243		
Pinus cembra			+	1750 - 1993	243		
Pinus umcinata			+	1750 - 1993	243		

Supplementary Table 4.6. Continued

Species name[1]	Research site (Country, location)	GDM[2]	Long-term growth trend	Calendar year range	Age[3]	Authors	Explanation of methodology
Pinus cembra	Austria (Alps)	Size Class Isolation	+	1750 - 1989	239	Nicolussi *et al.* (1995)	In order to avoid any age dependent bias of ring width, we conducted our analysis only with discrete age phases of trees. In most cases we used the rings corresponding to an individual tree's age from 80 to 90 years. Since trees are "born" in different years, only those rings are utilized from each tree for any one decade in the calendar which falls in the 80 to 90 years age phase. This procedure requires the identification of the first growth ring, a rather demanding requirement, given the often asymmetric growth of trunks.
Quercus velutina	USA (Missouri)	Size Class Isolation	+	1850 - 2002	152	Voelker *et al.* (2006)	To more accurately align the pre-1850 *P. echinata* chronology along the cambial-age axis, we compared the last 10 cambial-age ring widths to similar cambial ages of the post-1850 chronology. Even when the pre-1850 cambialage chronology was aligned directly with the current cambial-age chronology, the ring widths for cambial ages 41–50 were visually and statistically indistinguishable.
Quercus coccinea			+	1850 - 2002	152		
Pinus echinata			+	1851 - 2002	151		
Populus tremuloides	USA (Wisconsin)	Regional Curve Standardization	+	1935 - 2003	68	Cole *et al.* (2010)	We modeled this response for each ramet (tree) in a nonlinear, mixed effects model, i.e. one that allows for factors to have both fixed effects (having the same magnitude for all individuals) as well as random effects, distributed as random variates among individuals. In this way, we accounted for the strong and highly nonlinear effect of age on growth, as well as variation arising from both genetic and environmental sources (e.g. soil type, slope, etc.). Thus, ring width is composed of an overall value common to all measurements, with an adjustment for each genet and for each ramet within that genet. This produced an age-specific growth curve. The model then analyzes how this age-specific growth would be affected by each of the other factors analyzed, alone and in combination.

*Annamocarya sinensis**	Vietnam (Cuc Phuong / Ba Vi / Bach Ma / Hang Kai – Pa Co)	Size Class Isolation	-	1898 - 2003	105	Zuidema *et al.* (2011)	To assess to the extent which growth differences among individuals persisted over time, we correlated the ranks of growth rates across diameter categories. For this purpose, we first calculated the average growth rate of 5-cm diameter categories for each individual (i.e., for 0-5, 5-10, 10-15 cm, etc.) to obtain a data set of average growth in 5-cm categories. Using this data set, we calculated the extent to which the ranks of individuals in terms of growth rates in a particular size category were correlated with those in the successive categories.
*Calocedrus ,macrolepus**			-	1950 - 2003	53		
*Dacrydium elatum**			-	1837 - 2003	166		
*Pinus kwangtungensis**			0	1811 - 2003	192		
Pinus sylvestris	France (Sainte-Baume)	Regional Curve Standardization	0	1900 - 2000	100	Vila *et al.* (2008)	Because growth trends also vary with tree age (i.e. increasing in the juvenile phase, stabilizing in the mature phase and decreasing in the senescent phase), data were also indexed to remove age effect by means of a Regional Curve Standardization. The Regional Curve (RC) was built for each species by ranking basal area series according to cambial age on trees from a wide ecological range and a wide range of tree age classes. These basal area series were averaged according to cambial age to build up the RC.
Pinus halepensis			+	1900 - 2000	100		
Picea abies	Switzerland (Rhone Valley, Jura), USA (Colorado Front Range), Cyprus (Troodos Mountain)	Conservative Detrending (S)	0	1921 - 1982	61*	Kienast & Luxmoore (1988)	Because the ring increment tends to decrease with increasing age, a potential growth increase is more likely underestimated by using a horizontal line. The growth trends of the raw chronologies were compared with those from the corresponding indexed series. To this end, the indexed chronologies were smoothed with a low-pass filtering technique, and increasing or decreasing growth trends were evaluated during the same time-periods using horizontal reference levels.
Picea pungens			0	1921 - 1982	61*		
Picea engelmanii			0	1921 - 1982	61*		
Pseudotsuga menziesii			+	1921 - 1982	61*		
Pinus sylvestris			0	1921 - 1982	61*		
Pinus brutia			0	1921 - 1982	61*		
Pinus nigra ssp. Pallasiana			+	1921 - 1982	61*		
Pinus ponderosa			0	1921 - 1982	61*		

Supplementary Table 4.6. Continued

Species name[1]	Research site (Country, location)	GDM[2]	Long-term growth trend	Calendar year range	Age[3]	Authors	Explanation of methodology
Pseudotsuga menziesii	Switzerland (Rhone Valley, Jura), USA (Colorado Front Range), Cyprus (Troodos Mountain)	Conservative Detrending (S)	+	1921 - 1982	61*	Kienast & Luxmoore (1988)	Because the ring increment tends to decrease with increasing age, a potential growth increase is more likely underestimated by using a horizontal line. The growth trends of the raw chronologies were compared with those from the corresponding indexed series. To this end, the indexed chronologies were smoothed with a low-pass filtering technique, and increasing or decreasing growth trends were evaluated during the same time-periods using horizontal reference levels.
Abies alba			0	1921 - 1982	61*		
Cedrus brevifolia			+	1921 - 1982	61*		
Pinus longaeva	USA (California)	Conservative Detrending (S)	+	1840 - 1970	130*	Lamarche *et al.* (1984)	Building a tree-ring chronology by using raw and standardization data and comparing different calendar year intervals.
Pinus aristata			+	1840 - 1970	130*		
Picea glauca	Northern-Hemisphere	Size Class Isolation	+	1760 - 1980	220	Briffa *et al.* (1998)	European tree-ring site collections were converted into basal area increment (BAI) values and stratified according to time and tree age. In other words, the mean BAI for particular tree genera in particular regions of Europe were calculated separately for pre-selected age bands of trees, and compared decade-by-decade from 1760 to 1980. This age stratification overcomes the age-related bias that confuses attempts to compare changing absolute growth rates where the data are made up of different aged trees through time.
Larix dahurica			+	1760 - 1980	220		

Quercus patraea	France (Loraine)	Regional Curve Standardization and Size Class Isolation	+	1838 - 1987	149	Becker et al. (1994)	Firstly, for a given cambial age class, the average radial growth was calculated for all those calendar years when at least 4 annual BAIs were available. It was then plotted vs calendar year. This was repeated for 10 cambial age classes from 10 (±2) to 100 (±2) years. Secondly, the effect of cambial age on BAI was taken into account using the following standardization method. The average BAI curve according to the cambial age (current age) was constructed for both species. As varying site conditions and varying calendar years of formation of the annual rings corresponded to every current year in the curve, the effects of the various environmental conditions tended to cancel each other out.
Quercus robur			+	1838 - 1987	149		
Picea glauca	Canada (Manitoba)	Conservative Detrending (C)	+	1900 - 1999	99	Wang et al. (2006)	Each ring-width series was conservatively detrended (i.e. negative exponential, linear regression, horizontal line). Mean, minimum and maximum monthly temperature and total monthly precipitation were use to construct a growth-climate model. The residual variation (i.e. actual indices minus estimated indices) was examined for any linear trends using simple linear regression.
Larix gmelinii	Russia (Siberia)	Conservative Detrending (C)	+	1580 - 1970	390	Jacoby et al. (2000)	Single detrending was done using curve fits of straight lines with horizontal or negative slopes or negative exponential curve fits. In less than 10% of the cases, a 200-yr spline was used.
Pinus palustris	USA (Georgia)	Regional Curve Standardization	+	1895 - 1987	92	West et al. (1993)	An exponential curve was fit on cambial age aligned tree-ring data, which represents a RCS. Additionally spearman correlation were performed between the chronology and climatic data (precipitation, temperature and PDSI) after which the residuals were analysed.
Juniperus occidentalis var. occidentalis	USA (Oregon)	Conservative Detrending (C)	+	1285 - 1998	713	Knapp et al. (2001)	All chronologies were produced using conservative standardisation techniques (i.e. negative exponential curve, linear regression of negative slope, or horizontal line) to preserve the variance attributable to such low-frequency processes as climate variability and CO_2 fertilization. Use of more flexible standardisation techniques (i.e. use of spline curves) would likely have removed many of the low-frequency CO_2 signals that were investigated in this study.

Supplementary Table 4.6. Continued

Species name[1]	Research site (Country, location)	GDM[2]	Long-term growth trend	Calendar year range	Age[3]	Authors	Explanation of methodology
Pinus balfouriana	USA (California)	Conservative Detrending (C)	o	1010 - 1986	976	Graumlich (1991)	Age-related trends in ring widths were removed by fitting negative exponential or horizontal growth curves to individual measurement series. A multiple regression analysis was performed in which the variables included summer temperature, previous-winter precipitation, and summer precipitation. The residuals were analyzed for trends.
Pinus contorta var. murrayana			o	1220 - 1986	766		
Juniperus occidentalis			o	1005 - 1981	976		
Abies religiosa	Mexico (from Pacific Ocean to Gulf of Mexico)	Basal Area Correction	-	1910 - 2010	100	Gómez-Guerrero et al. (2013)	The conversion of ring width into BAI is expressed here in annual time step resolution (1 year = 1 full ring, late and early wood), assuming that increment was uniform along each ring. This conversion is used to remove the ring width decline due to age effects. Additionally the trees where divided into time periods, namely; 1910-1950, 1950-1980 and 1980-2010.
Pinus hartwegii			-	1910 - 2010	100		
Picea glauca	USA (Alaska)	Conservative Detrending (C + S) and Regional Curve Standardization	+	1850 - 2002	152	Adreu-Hayles et al. (2011)	Individual tree-ring series were standardised using the program ARSTAN. Different detrending methods were applied: a spline function with a 50% frequency response of 140 yr (SP140); negative exponential or negative linear regression (NEXP); and regional curve standardization (RCS) after stabilizing the variance with a power transform (PT) technique. The signal free (SF) standardization method (Melvin and Briffa 2008) was also tested.
Araucaria angustifolia	Brazil (Rio Grande do Sul)	Basal Area Correction	o	1860 - 2005	145	Silva et al.(2009)	Ring width in mature trees declines with age, thus, if a declining growth trend is suspected, it may be impossible to investigate it on the basis of changes in ring width alone. The conversion of ring width into basal area increment (BAI) overcomes this problem. Here, the conversion of ring width into BAI is shown in 5-year pooled blocks, as the rings were pooled in sets of five adjacent rings before conversion in BAI.

Quercus rubra	Canada (Ontario)	Basal Area Correction	-	1901 - 2007	106*	Silva et al. (2010)	We determined ring width and annual BAI through standard dendrochronological methods. In mature trees, ring width declines with age; thus, declining growth may be impossible to detect based on changes in ring width alone. The conversion of ring width to BAI overcomes this problem. We used multiple regression models to identify significant correlations between BAI, WUE (water use efficiency), and climatic variables over the past century. Additionally a distinction was made between old and young trees.
Acer rubrum			-	1901 - 2007	106*		
Picea mariana			-	1901 - 2007	106*		
Pinus resinosa			-	1901 - 2007	106*		
*Chukrasia tabularis**	Thailand (Huai Kha Khaeng)	Basal Area Correction	-	1940 - 2006	66	Nock et al.(2011)	To distinguish between the effects of ontogeny and long-term environmental changes on stable isotopes ratios and tree growth, trees were selected nonrandomly so all size classes >10cm diameter at breast height (dbh) were represented (e.g. 20, 30, 40, 50, 450).
*Melia azedarach**			-	1970 - 2006	36		
*Toona ciliata**			-	1940 - 2006	66		
Fagus sylvatica	Spain (Montseny Mountains)	Basal Area Correction	-	1914 - 2003	89	Peñuelas et al. (2008)	Ring width in mature trees declines with age; thus, if a declining growth trend is suspected, it may be impossible to investigate it on the basis of changes in ring width alone. The conversion of radial increment (ring width) into BAI overcomes this problem.
Picea glauca	USA (Fairbanks Alaska)	No standardisation	-	1908 - 1996	88	Barber et al. (2000)	We did not transform ring widths into de-trended normalized ring-width index values for two reasons. First, we wanted to preserve the weighting effect of tree increments of different sizes because this reflects annual production more closely than normalized values, which remove this effect. Second, most white spruce of the age range in this study exhibit little age-related growth trend, and the removal of trend is user-specified and risks the loss of information on long-term climate variability that may actually influence tree growth.
Larix cajanderi	Russia (Yakutsk Siberia)	Conservative Detrending (S)	+	1588 - 2000	412	Kirdyanov et al. (2008)	The individual ring width series were standardised to remove non-climatic, tree-geometry and/or age-related trends A 300-year cubic smoothing spline with 50% frequency-response cutoff was fitted to the individual records and residuals calculated in ARSTAN. This standardised was used because it is reported to be one of the most appropriate detrending approaches for records of 300–500-year length.

Supplementary Table 4.6. Continued

Species name[1]	**Research site (Country, location)**	**GDM**[2]	**Long-term growth trend**	**Calendar year range**	**Age**[3]	**Authors**	**Explanation of methodology**
Pinus ponderosa	Germany (Bralitz)	Conservative Detrending (S + C)	+	1901 - 2001	100	Wagner et al. (2007)	A double detrending process (first: negative exponential curve, second: 67-year smoothing Spline with 50% cutoff) was applied to detrend tree-ring chronologies derived from 17 individuals for each species using the program ARSTAN. The two-sample Kolmogorov-Smirnov statistic was applied as a relative indicator of curve fit between two empirical data sets to test whether the tree-ring data and the discrimination differed significantly between the species. Additional the tree-ring width was recalculated into BAI.
Pinus sylvestris			+	1901 - 2001	100		
Pinus banksiana	Canada (Winnipeg Manitoba)	Conservative Detrending (S)	0	1912 - 1999	87	Girardin et al. (2008)	Tree-ring samples were treated using standard procedures. Measurement series were crossdated, detrended using a cubic smoothing spline giving a 50% frequency response of 60 years, and biological persistence (autocorrelation) was removed using autoregressive modelling. Additionally a modelling approach and an integration of the model outcomes and the empirical data was used.
Populus tremuloides			0	1912 - 1999	87		
Picea mariana			0	1912 - 1999	87		
Pinus ponderosa	USA (Oregon)	Conservative Detrending (C)	+	1493 - 1999	506	Soulé & Knapp (2006)	Because flexible standardisation techniques (e.g. spline curves) may remove low-frequency signals, we used conservative standardisation techniques such as negative exponential curve fitting or negative linear in the development of our chronologies.
Picea schrenkiana	China (Tianshan Mountains Tibet)	Conservative Detrending (C)	+	1851 - 2002	151	Su et al. (2007)	To focus on the common growth variations associated with climate, growth trends were removed from individual series using conservative detrending (negative exponential curves or straight lines).

Pinus halepensis	France (Provence)	Regional Curve Standardization	+	1894 - 1994	100	Rathgeber et al. (2000)	A standardisation was applied to reduce the age effect within the chronologies. A regional age-related growth trend was calculated for the four climatic variables using a polynomial adjustment for density variables and an exponential growth function for ring width variables.
Fagus sylvatica	Italy (Apennine Mountains)	Conservative Detrending (S) and Basal Area Correction	-	1655 - 2002	347	Piovesan et al. (2008)	Two methods for tree-ring series were used. First the Past annual BAI was estimated by subtracting twice the annual ring width (wt) from the annual outside bark. A raw BAI chronology was built for each site as the average by year of individual-tree BAI series. Additionally a prewhitened (i.e. without time-series autocorrelation) BAI chronologies were produced by using a 50-year cubic smoothing spline on the series at calendar year.
Abies cephalonica	Greece (Cephalonia)	Conservative Detrending (C)	+	1840 - 2005	165	Koutavas (2008)	Standardised TRW indices for each tree were calculated as I = R/G, where I is the value of the index, R the measured ring width, and G the modelled ring width based on the best-fit exponential growth trend.
Pinus contorta	USA, (Mammoth Mountain California)	Conservative Detrending (C)	-	1815 - 1995	180	Biondi & Fessenden (1999)	We computed the Mammoth Mountain tree-ring chronology in order to minimize individual variability in ring-width series, as follows: I=+i(w/y)it; with I t, chronology value at year t; w, crossdated ringbwidth; y, modified negative exponential or straight line with slope ≤0; +i, biweight robust mean of the i values, i = 1, . . . , nt; and nt, number of measured specimens that include year t.
Abies pinsapo	Iberian Peninsula (Spain and Portugal)	Basal Area Correction	-	1946 - 2005	59	Linares et al. (2009)	The trend of decreasing ring width with increasing tree size was removed by converting radial increment into BAI.

Supplementary Table 4.6. Continued

Species name[1]	Research site (Country, location)	GDM[2]	Long-term growth trend	Calendar year range	Age[3]	Authors	Explanation of methodology
Pinus longaeva	USA (Sheep Mountain California)	No standardisation	+	-2650-2006	4656	Salzer et al. (2009)	In all cases, we chose not to standardise to tree-ring indices to avoid any potential data-transformation biases that might be introduced by standardisation. The absence of standardization does not affect our ability to interpret tree-growth anomalies in terms of climate over these time scales, because the vast majority of our hundreds of samples are old rings that are not from the juvenile period of the trees' lives. There is little, if any, age-related change in ring width in such old rings.
Abies cephalonica	Greece (Ainos Mountain)	Conservative Detrending (C)	+	1820 - 2007	187	Koutavas (2013)	Most samples exhibit declining ring width with age typical of open canopy forests with limited competition and can be modeled well with negative exponential or linear growth curves. In several samples (18 of 31 radii, 13 of 23 trees), the declining trend with age is interrupted by growth reversals (increases) in the late 20th–early 21st centuries. In the remaining samples, such reversals cannot be discerned with certainty because of pronounced negative biological/geometric growth trends. The standardisation approach was designed to preserve low frequency variations while removing age and geometry-related trends.
Fagus sylvatica	Spain (Montseny Mountains)	Basal Area Correction	-	1960 - 2003	43	Jump et al. (2006)	To examine the mean growth trend of the dominant and codominant canopy trees for each site, BAI for each year was averaged over all individuals at each site. BAI series for dominant and codominant trees in mature stands typically show a period of early growth suppression (suppression phase) before a rapid increase in annual basal area growth (release phase). BAI may continue to increase in mature healthy mature trees.
Picea glauca	Alaska and Canada (Arrigetch Peaks, Brooks Range,Franklin Mountains, Northwest Territories, Churchill and Manitoba)	Conservative Detrending (C)	+	1585 - 1990	405	D'Arrigo & Jacoby (1993)	Only very conservative (negative exponential, straightline, or regression)curve fits were included in the standardisation process in order to ensure that the low-frequency trends of interest to this study were retained.

Pinus cembra	Romania (Calimani Mountains)	Regional Curve Standardization	+	1163 - 2005	842	Popa & Kern (2009)	The growth series were standardised to eliminate the non-climatic trends and to maximize the climatic information from the individual series. To preserve the low frequency variation in the tree-ring chronology the regional curve standardization (RCS) method was applied.
Pinus cembra	Italy (Piedmont)	Basal Area Correction	+	1453 - 1994	541	Motta & Paola (2001)	In order to give a better estimate of net productivity of a tree, the simple tree-ring widths were converted into basal area increments (BAI). This ought to eliminate the effect of reduction in ring widths due to the diameter increase of tree (and therefore a question of geometry) without eliminating the patterns of increase or decrease in ring width due to other causes.
Larix decidua			+	1426 - 1997	571		
Pinus sibirica	Mongolia (Tarvagatay Mountains)	Conservative Detrending (C)	+	1550 - 1994	444	Jacoby et al. (1996)	Cores were dated by means of basic dendrochronological techniques and were standardised with only conservative negative-exponential or straight-line fits.
Larix sibirica			+	1550 - 1994	444		
Picea rubens	USA (Virginia and North Carolina)	Conservative Detrending (C)	0	1860 - 1988	128*	Goelz et al. (1999)	We chose to concentrate on cross-sectional area increment, as radial increment is known to decline with age, thus obscuring whether the decrease is due to ontogeny or some extrinsic factor. We used Hoerl's special functions to describe the trend of growth.
Abies Fraseri			0	1945 - 1988	43*		
Quercus robur	Romania (Vlăsia Plain region)	Size Class Isolation	-	1809 - 2009	200	Neagu 2010	Data on annual ring width were processed for each individual year, and stratified in four major age classes, i.e., between 1 and 50 years, 51 to 100 years, 101 to 150 years, and between 151 and 200 years. Confidence intervals were determined and analysed for the significance (p=1%) of differences between the means. Direct comparison of mean increment of trees belonging to different generations has the advantage of not requiring standardisation to eliminate the influence of age from treering series and mathematical modelling, and may be considered an indicator of site productivity variation over time.

Supplementary Table 4.6. Continued

Species name[1]	Research site (Country, location)	GDM[2]	Long-term growth trend	Calendar year range	Age[3]	Authors	Explanation of methodology
Pinus sylvestris	Russia (along border with Norway and Finland)	Size Class Isolation	+	1660 - 1992	332	Alekseev & Soroka (2002)	Data for 3 523 tree-rings were place in the 0–20 year age class, 2 920 tree-rings in the 21–40 year age class, 2 052 tree-rings in the 41–60 year age class, 1 664 tree-rings in the 61–80 year age class, 1 373 tree-rings in the 81–100 year age class and 5 422 tree-rings in the older than 101 year age class. In order to reveal growth trends in our time series data, we needed to remove the influence of age bias. For this purpose a method of forest growth reconstruction was used that randomizes the growth process by splitting tree-ring time series into single rings with subsequent regrouping. Each ring width is assigned a tree age and a calendar year.
Fagus sylvatica	France (north-eastern France)	Regional Curve Standardization	-	1900 - 1990	90	Bontemps & Esper (2011)	The basic principle of standardisation techniques is to remove agerelated signals in growth series to obtain a bias-free chronology. Standardisation is achieved by dividing the size of each available ring by the value expected from its cambial age in a reference curve.
Austrocedrus chilensis	Southern Hemisphere (South America)	Conservative Detrending (C)	-	1559 - 1999	440	Villalba et al. (2012)	To conserve the low-frequency signal in the tree-ring records, conservative methods of standardisation were selected, fitting negative exponential or linear curves with zero or negative slope to each individual series, or by smoothing each series with a robust median filter.
Araucria araucana	Southern Hemisphere (South America)		-	1559 - 1999	440		
Nathofagus betuloides	Southern Hemisphere (South America)		-	1559 - 1999	440		
Lagarostrobos franklinii	Southern Hemisphere (Tasmania)		+	1559 - 1999	440		

Phyllocladus aspleniifolius	Southern Hemisphere (Tasmania)	Conservative Detrending (C)	+	1559 - 1999	440	Villalba et al. (2012)	To conserve the low-frequency signal in the tree-ring records, conservative methods of standardisation were selected, fitting negative exponential or linear curves with zero or negative slope to each individual series, or by smoothing each series with a robust median filter.
Halocarpus biformis	Southern Hemisphere (New Zealand)		+	1559 - 1999	440		
Larix sibirica Ledebour	Mongolia (Khentey Mountains)	Regional Curve Standardization	-	1800 - 2006	206	Dulamsuren et al. (2010)	Long-term (low-frequency) climate trends can be identified by removing the annual variation of climate from the tree-ring series and conserving the age-related trend. If the annual increment is not related to the calendar year, but to tree age, a mean age-related growth curve [regional growth curve (RGC)] can be established for a given site, largely independently of the annual variation of climate.
Pinus halepensis ssp. Brutia	Greece (Samos Island)	Size Class Isolation	-	1951-2000	49	Sarris et al. (2007)	Because tree rings get narrower as trees get older it is a common practice to 'detrend' chronologies of tree rings. However, if the age trend coincides with an environmental trend, age detrending also removes the environmental signal of interest (age-climate confounding). Therefore, we did not detrend our data, but compare tree-ring width for similar life (age) stages only. We first compare radial growth rates for similarly young life stages over the ca. 100-year observation period. In a second approach, we compared decadal mean tree-ring width, of each individual tree, for equal cambial growth periods (classes) of 20–29, 30–39 and 40–49 years. Decadal means for each of these periods were used to test effects of precipitation on growth.

[1] Tropical species indicated with *

[2] Two types of Conservative Detrending indicated: detrending by mathematical curve fitting (C) and detrending with flexible splines (S)

[3] For studies not indicating exact ages or calendar year ranges, values were estimated and are indicated with *

Appendix E – Additional analysis for BAC

The C-method standardization is an adaptation of BAC that further 'detrends' the growth rates expressed in basal area. This method assumes that the age-trend in growth is mostly caused by the distribution of a fairly constant basal area increment over an expanding surface. Thus, the C-method standardizes growth by calculating the ratio of tree growth (ring-width) divided by the expected width for a tree-size. The expected width is calculated from the expected basal-area growth (which is assumed to be constant) for that size. We performed the C-method standardization in R, following Biondi and Qeadan (2008) using the *cms* function in the dplR package (Bunn *et al.* 2008).

The method detected either no-trends or negative growth trends in all simulations. However, C-method did never detect growth increases, even for the simulations with the highest imposed positive growth trends (Supplementary Table 4.7 and Figure S3). This detection of only negative trends may be induced because of the assumption that ring widths show very rapid decreases in the early years of a tree. However, for most (simulated) curves, this reduction is much weaker than assumed/expected by the C-curves (Figure S4). Especially for the juvenile years in large/old trees, the fit of the C-curves is weak and initial growth rates are overestimated (Figure S4). These overestimations in the juvenile years of large trees probably resulted in lower residuals in the recent past than further back in time, thus inducing negative trends to be detected. This weak fit of the curves by the C-method was also noted by Biondi and Qeadan (2008). We believe that these negative trends are induced by the fact that we also include young/small trees in the analysis. The (expected basal area) curves fitted by the C-method do not correctly account for the age trend in young/small trees – overestimating actual growth in the more resent past – resulting in lower residuals for young trees (and thus relatively more "low residuals" in the recent past than further back in time).

Supplementary Table 4.7. Results for the C-method standardization for the five growth-trend simulations (no trend; 2% and 6% imposed growth increases; and 2% and 6% decreases). Provided are sensitivity (percentage of correctly detected imposed growth trend), reliability (100% minus the amount of erroneously detected growth trends) and the average detected trends per decade (i.e., average of slopes detected by linear models fitted on 100 simulations per imposed trend).

	Decrease 6%	Decrease 6%	No trend	Increase 6%	Increase 6%
Sensitivity	100%	100%	0%	0%	0%
Reliability	100%	100%	0%	1%	13%
Trend (per decade)	-13.0%	-7.4%	-6.0%	-4.5%	-2.8%

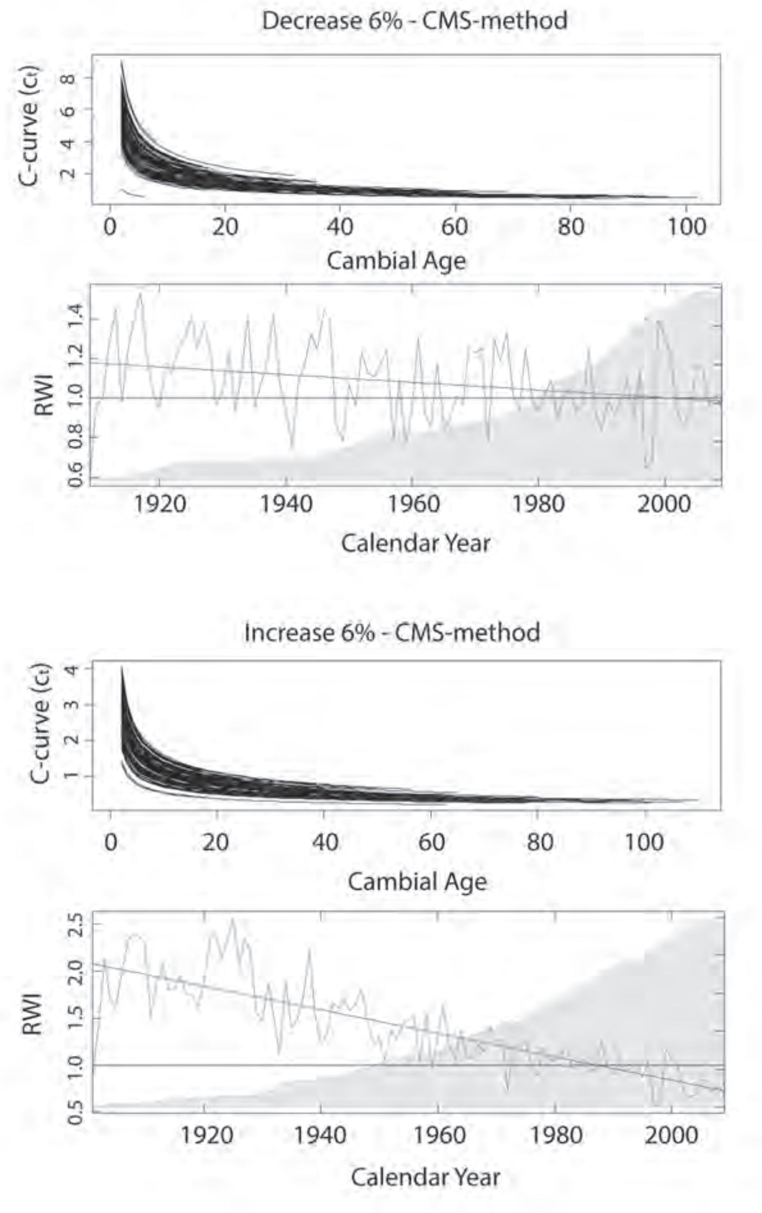

Figure S2: C-curves (cf. Biondi & Qeadan, 2008) fitted through random subsets of 100 simulated growth series and the resulting chronologies for two different growth-trend scenarios: growth increases and decreases of 6%. Both chronologies show negative trends over time.

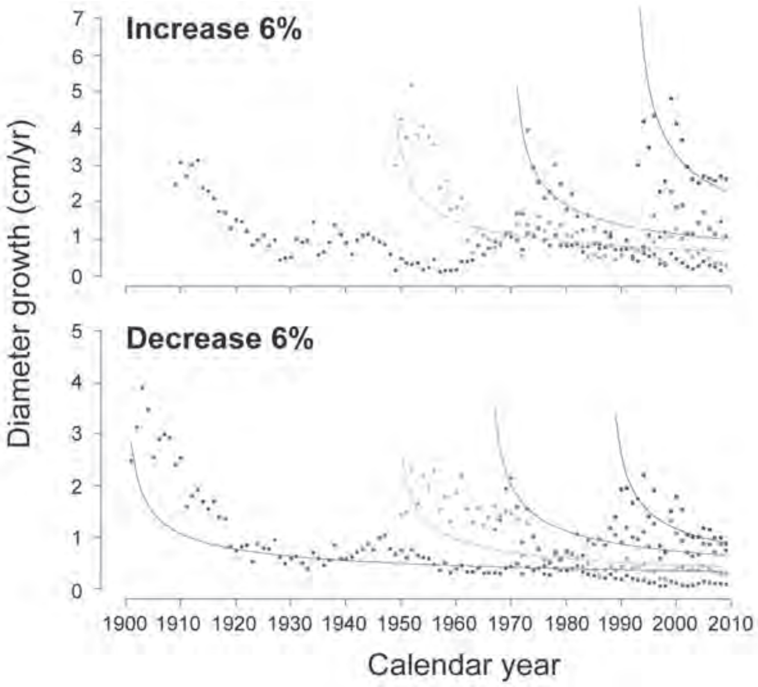

Figure S3: Examples of the fitted C-curves (cf. Biondi & Qeadan, 2008) through four simulated growth series with differing ages, for two different growth-trend scenarios: growth increases and decreases of 6%. Both chronologies show negative trends over time.

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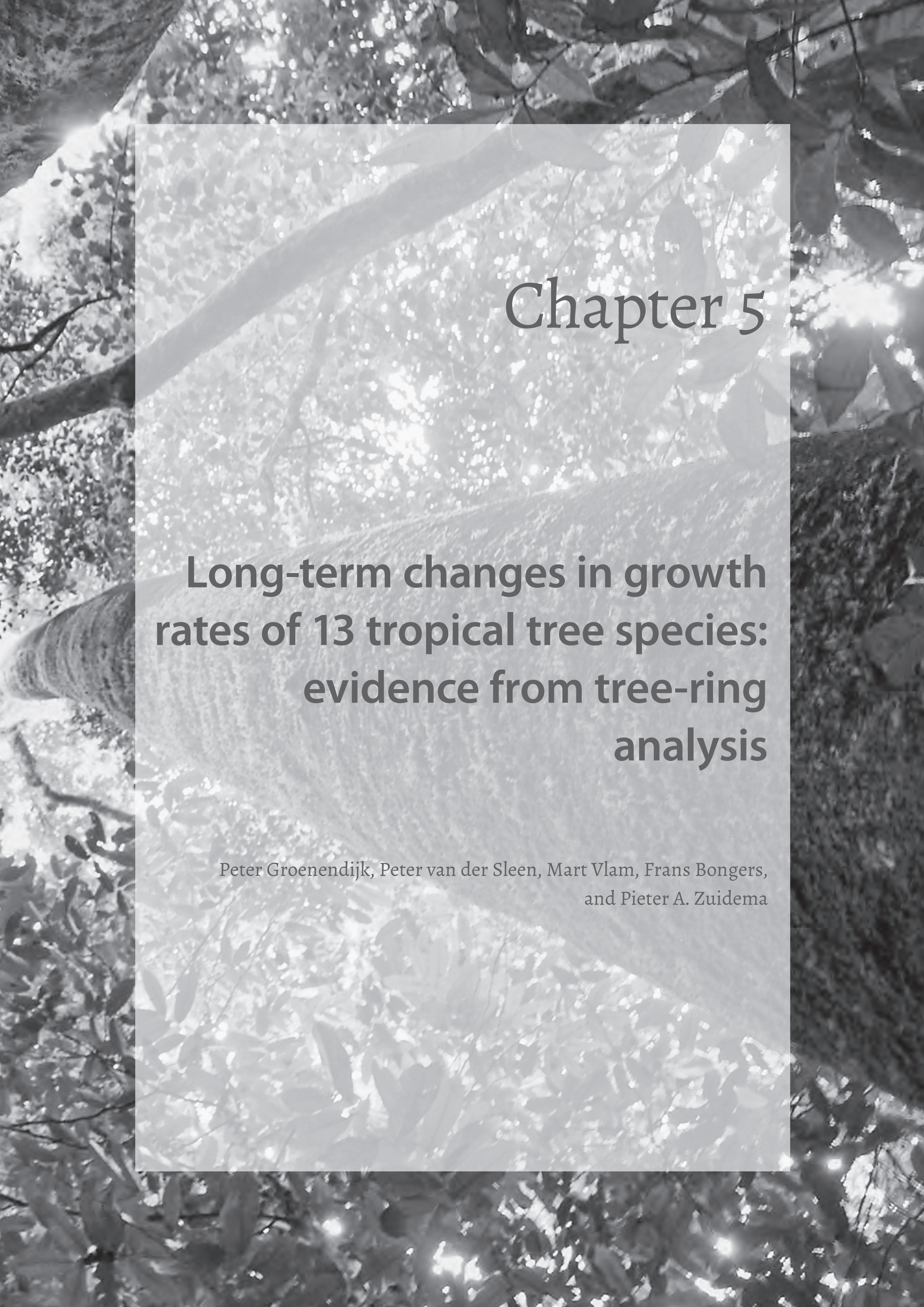

Chapter 5

Long-term changes in growth rates of 13 tropical tree species: evidence from tree-ring analysis

Peter Groenendijk, Peter van der Sleen, Mart Vlam, Frans Bongers,
and Pieter A. Zuidema

Abstract

The important role of tropical forests in the global carbon cycle makes it imperative to assess changes in their carbon dynamics when accurately projecting future climate change. Forest monitoring studies conducted over the past decades have found contrasting evidence for both increasing and decreasing growth rates of tropical forest. These changes are often ascribed to anthropogenic climatic changes and suggest that tropical forests acted either as carbon sinks or sources in the recent past. The limited length of these studies, however, restrains analyses to decadal scales and it is still unclear whether growth changes occurred over longer time scales. Furthermore, these studies often focussed on plot-level changes and rarely on the level of species. These community-wide dynamics are the aggregate result of species-specific responses to changes in climatic conditions or disturbances, but virtually nothing is known about species-level responses so far. Here we analyse species-specific growth changes on a centennial scale, using growth data obtained from tree-ring analysis for 13 tree species (~1300 trees), from three sites distributed across the tropics. We used an established and a new growth trend detection method and explicitly assessed the influence of biases on the detection of trends. In addition, we assessed whether aggregated trends were present within and across the study sites. We found evidence for decreasing growth rates over time for 10 species, whereas increases were noted for two species and one showed no trend. Additionally, we found evidence for weak aggregated growth decreases in the species from Thailand and when analysing all sites simultaneously. These growth reductions suggest worsening growth conditions in tropical forests, possibly due to temperature increases. However, other causes cannot be excluded, such as recovery from large-scale disturbances or changing forest dynamics. Our findings contrast the growth patterns that would be expected if increased CO_2 would stimulate tree growth. This suggests that the commonly assumed growth increases of tropical forests may be incorrect, which could lead to erroneous predictions of carbon dynamics in tropical forest under climate change.

5.1 Introduction

Tropical forests form an important element of the global carbon cycle. While covering only 7% of the Earth's terrestrial surface, they are responsible for one third of the terrestrial net primary production and store approximately 40% of all carbon in terrestrial vegetation (Houghton, 2005). Due to their high storage and processing of carbon, changes in net uptake or loss of carbon has large implications for the global carbon cycle (Pan *et al.*, 2011). Shifts in climate, in atmospheric CO_2 levels or in nutrient depositions, may influence growth and mortality rates of trees and alter the dynamics of tropical forests (Lewis *et al.*, 2009a; Alvarez-Clare *et al.*, 2013). For instance, decreases in growth rates have been interpreted to reflect the limiting effect of increased temperature on growth (Feeley *et al.*, 2007), while growth increases interpreted to reflect the stimulating effect of increasing CO_2 concentrations (e.g., Phillips *et al.*, 2008; Lewis *et al.*, 2009a).

Monitoring studies of permanent sample plots (PSP) have provided valuable insights in the growth and dynamics of tropical forests. Evidence on the climate sensitivity of forest growth in these plots (Clark *et al.*, 2010) has been used to explain changes in growth rates, dynamics and biomass accumulation (e.g., Phillips *et al.*, 2008; Murphy *et al.*, 2013). Yet, community-level responses consist of the aggregate reaction of different species – with different life strategies – which will react differently to changing conditions. It is therefore essential to understand these species-level responses when assessing changes in tropical forests. However, the high biodiversity of tropical forests – combined with the usually small size of plots – has restricted analyses of changes to the community (Phillips *et al.*, 2008; Lewis *et al.*, 2009b) or genus level (Laurance *et al.*, 2004b). Studies on the responses of individual species are sparse in the tropics, with only one PSP study analysing growth changes at species level (Feeley *et al.*, 2007). This study reported decreasing growth rates for most species studied, suggesting a reduction in the potential of forests to sequester carbon from the atmosphere (Feeley *et al.*, 2007).

Climatic changes are often suggested as the drivers of detected changes in tropical forest (Feeley *et al.*, 2007; Lewis *et al.*, 2009a). However, the same changes could also appear when forests recover from (large-scale) disturbances (Muller-Landau, 2009; Chambers *et al.*, 2013). Although PSP studies have provided valuable insights on changes in tropical forests, these studies are limited by their relative short duration compared to the time-span of the changes they want to assess: climatic changes or recovery from disturbances take place at the scale of multiple decades up to centuries. To improve the understanding of tropical forests' responses to climate change, there is a need for long-term approaches analysing growth changes. These long-term approaches are needed, as growth trends detected in plot studies may simply reflect decadal fluctuations in climatic factors (e.g., temperature; Feeley *et al.*, 2007) or be a result of the relatively small size of most plots (Chambers *et al.*, 2013).

Tree-ring analysis offers the opportunity to extend insights on growth changes of individual tree species to the scale of multiple decades to centuries. In temperate regions, tree-ring analysis has widely been used to assess effects of climate on tree growth and to analyse historical growth changes (e.g., Esper *et al.*, 2012; Villalba *et al.*, 2012). In the tropics, tree-ring analysis has only recently been applied to analyse changes in growth (Rozendaal *et al.*, 2010a; Nock *et al.*, 2011). Tree-ring analysis usually provides growth data that goes back to the establishment of trees and allows for the analysis of growth changes at species level. It thus has a great potential to assess historical growth changes and to improve the understanding of how tropical forests react to climate change (Bowman *et al.*, 2013; Zuidema *et al.*, 2013).

Here, we use tree-ring analysis to assess long-term growth changes in tropical forests. We sampled 1262 trees of 13 species from three tropical forests sites across the tropics: in Bolivia, Cameroon and Thailand. We addressed the following questions: (i) are growth rates changing over time for our study species?; (ii) is the detection of growth changes affected by sampling biases?; and (iii) do species from the same site an across sites show similar growth changes?

Growth data for the 13 species were obtained from tree-ring analysis and growth trends were analysed for the last ~150 years on the level of species, site and for all sites combined. In the analysis of trends, we explicitly evaluated possible effects of biases inherent to working with tree-ring data (Brienen *et al.*, 2012a; Nehrbass-Ahles *et al.*, 2014). Trend detection may be affected by the choice of method to disentangle inherent age/size trends present in tree growth from long-term trends (CHAPTER 4). Therefore, we combine an established and a new trend-detection method to ensure trend detection is robust. Additionally, we explicitly test for the presence of two important biases in our data – the 'juvenile selection' bias (cf. Rozendaal *et al.*, 2010a) and the 'pre-death slow growth' bias (cf. Brienen *et al.*, 2012a) – to evaluate whether and how strongly these biases may have affected our results.

5.2 Material and Methods

Study areas and sample collection.

We sampled trees from undisturbed tropical forests located in the three continents: South America (in Bolivia), Africa (in Cameroon) and Southeast Asia (in Thailand). In Bolivia, trees were collected in the 'La Chonta' logging concession, situated at 15.84° S, 62.85° W, ca. 300 km northeast of Santa Cruz de la Sierra. The vegetation at La Chonta consists of semi-deciduous moist forest, on the transition between dry-forest (Chiquitano) and moist Amazonian forests (Peña-Claros *et al.*, 2008). Precipitation in the region is unimodal, with an annual average of 1580 mm and a four month dry season (with <100 mm rainfall) from May to September. In Cameroon, samples were collected inside the Forest Management Unit 11.001 of the logging company Transformation REEF Cameroon (TRC, 2008). The area is situated at 5.23° N, 9.10° E, adjacent to the Korup National park in the Southwest region. Vegetation consists of semi-deciduous lowland rainforest of the Guineo-Congolian type (Kenfack *et al.*, 2006). Precipitation is also unimodal, with average annual precipitation around 4100mm (Nchanji & Plumptre, 2003) and a three-month dry season from December to February. In Thailand, the study site was situated in the Huai Kha Khaeng Wildlife Sanctuary (HKK), situated at 15.60° N 99.20° E, around 250 km northwest of Bangkok. The vegetation in HKK consists of semi-deciduous moist forest (Bunyavejchewin *et al.*, 2009). Precipitation is unimodal, with an annual average of 1473 mm and a 4-6 months dry season from November to April.

At each study site, we sampled trees of four to five species (Figure 5.1 and Table 5.1), selected based on the possession of clear annual growth rings and on their local abundance (i.e., relatively common species). Trees were sampled using a stratified random approach inside large (144-297 ha) areas of undisturbed forest, i.e., where no previous logging activities had taken place and not showing sign of major anthropogenic disturbances. We worked in undisturbed forests to avoid any effects of disturbances on the detection of trends. At each large study area, we created a virtual grid of several 300 × 300 m cells and at random coordinates inside each cell, we installed circular plots of ca. 1 ha (radius of ~56m) that were located using a GPS device (Garmin GPSmap 60CSx). Inside these plots, all trees >5 cm diameter at breast height (dbh, at 130 cm height) of our target species were sampled. We installed 16-25 plots per study area, distributed across the entire area, to ensure sample sizes of around 100 trees per species (Table 5.1). We also collected samples outside the circular plots for some of the species, to include some large (and presumably old) trees or to ensure sample sizes were reached. For two species in Cameroon – *Daniellia ogea* and *Terminalia ivorensis* – we also sampled trees outside the large study area to increase sample sizes.

In Bolivia and Cameroon, samples were collected inside logging concessions, allowing for the collection of stem discs for ~30% of the sampled trees. The remaining samples in Bolivia and Cameroon and all samples from Thailand were collected using 5 mm diameter increment borers of different lengths (Suunto, Finland and Haglöf, Sweden) in three to four directions per tree. All samples were taken at 1 m height or above buttresses or anomalies when present.

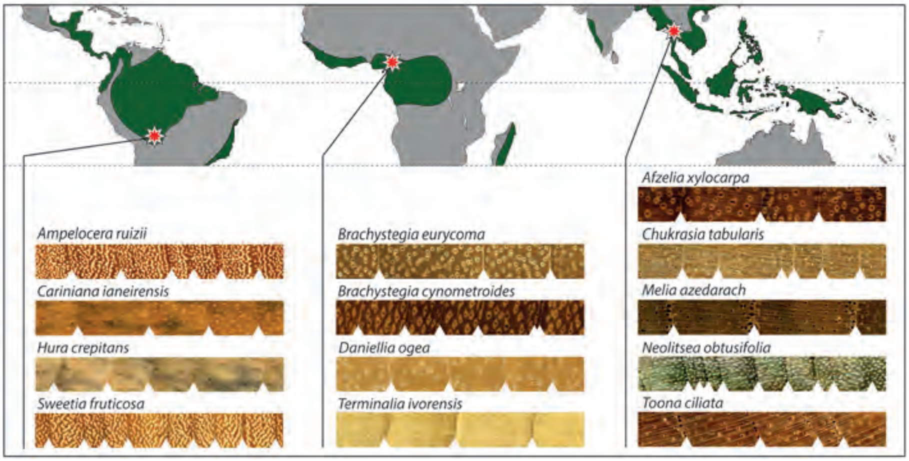

Figure 5.1. Location of study areas and ring structures for the species studied. Wood samples were collected in wet tropical forests (precipitation >1500 mm yr^{-1}) in three locations (red stars): in Bolivia at the La Chonta forest concession; in Cameroon in the TRC 11.001 logging concession, adjacent to Korup National park; and in Thailand in the Huai Kha Khaeng Wildlife Sanctuary. Growth-ring boundaries in the wood are indicated with white triangles.

Ring measurements

Prior to measurements, samples were air dried and either cut or polished to increase ring-boundary visibility. Ring-widths were measured using a LINTAB 6 measuring table and TSAPWin software (Rinntech, Germany) or using high-resolution scans (1600-2400 dpi) and the WinDendro software (Regent

Instruments, Canada). Ring widths were measured in three to four different directions for each tree following standard dendrochronological approaches (for more details see Groenendijk *et al.*, 2014; Vlam *et al.*, 2014b). Finally, tree-ring width measurements were converted to cross-sectional area growth (basal area increment, BAI) as BAI better represents a tree's biomass growth.

The annual nature of ring formation has been previously demonstrated for the Bolivian species by Lopez *et al.* (2012). For the Cameroonian species, annuality of ring formation for *T. ivorensis* was established by Détienne *et al.* (1998). For the remaining three species, annual ring formation was assessed through radio-carbon dating (Groenendijk *et al.*, 2014). Two of the species – *B. eurycoma* and *D. ogea* – showed high-quality dating, while the third – *B. cynometroides* – showed some discrepancies in dating that lead to tree-age underestimations of about 10%. For the species from Thailand the annual character of ring formation was proven by Baker *et al.* (2005). Furthermore, for the samples used here, Vlam *et al.* (2014b) was able to confirm annuality by building chronologies and analysing climate-growth relations (Table 5.1).

We checked the quality and dating of the tree-ring measurements by crossdating the measured ring series. Crossdating is standard practice in tree-ring analysis and consists of matching the patterns of variation in ring-widths between different series: within trees (i.e. among different radii) and among trees (i.e., among individuals). Crossdating measurements within a tree ensures the same (amount of) rings are measured between the different radii of an individual and helps in identifying wedging rings (rings that merge on certain parts of the circumference of the tree) and 'false' ring structures (intra-annual growth variations). For nearly all 1262 measured trees, internal crossdating proved successful, i.e., variation in ring-width for the different radii within a tree matched well, both visually and statistically.

Crossdating among individuals proved more challenging and we were only able to build crossdating for four Thai species (Vlam *et al.*, 2014b) but not for the Bolivian and Cameroonian species (Groenendijk *et al.*, 2014). We acknowledge that without chronologies, we lack proof that dating of all rings was absolute. However, the design of this study aimed at detecting growth changes and not at establishing chronologies. Although unavoidable, we assume that possible shifts in calendar year values due to dating errors do not strongly affect growth-trend detection, nor induce the detection of erroneous trends. Thus, we believe that the quality of our measurements is still high enough to address our (ecological) research questions, as lacking chronologies does not imply that dating accuracy is low (cf. Fichtler *et al.*, 2003; Groenendijk *et al.*, 2014).

Table 5.1. Characteristics of the 13 species studied. Included are family, shade-tolerance guild (ST = shade-tolerant; PST = partial shade-tolerant; LLP = long-lived pioneer, definitions cf. Poorter *et al.* (2006); and leaf phenology (E, evergreen; D = deciduous; BD = brevi-deciduous).

County	Species	Family	Guild[1]	# trees	Leaf phenology[2]	Annual rings
Bolivia	*Ampelocera ruizii*	Ulmaceae	ST	91	E	Lopez *et al.* (2012)
	Cariniana ianeirensis	Lecythidaceae	PST	102	D	Lopez *et al.* (2012)
	Hura crepitans	Euphorbiaceae	PST	95	D	Lopez *et al.* (2012)
	Sweetia fruticosa	Fabaceae	LLP	105	BD	Brienen and Zuidema (2003)
Cameroon	*Brachystegia cynometroides*	Fabaceae	PST	122	BD	Groenendijk *et al.* (2014)
	Brachystegia eurycoma	Fabaceae	PST	124	BD	Groenendijk *et al.* (2014)
	Daniellia ogea	Fabaceae	LLP	104	BD	Groenendijk *et al.* (2014)
	Terminalia ivorensis	Combretaceae	LLP	62	D	Détienne *et al.* (1998)
Thailand	*Afzelia xylocarpa*	Fabaceae	LLP	100	D	Vlam *et al.* (2014b)
	Chukrasia tabularis	Meliaceae	PST	104	BD	Vlam *et al.* (2014b)
	Melia azedarach	Meliaceae	LLP	89	D	Vlam *et al.* (2014b)
	Neolitsea obtusifolia	Lauraceae	ST	104	E	Vlam *et al.* (2014b)
	Toona ciliata	Meliaceae	LLP	61	D	Vlam *et al.* (2014b)

[1] Ecological Guilds: Bolivia (Peña-Claros *et al.*, 2008), Cameroon (Hawthorne, 1995), Thailand (Baker *et al.*, 2005); definitions cf. Poorter *et al.* (2006)

[2] Phenology: Bolivia (Mostacedo *et al.*, 2003), Cameroon (Hawthorne, 1995; Lemmens *et al.*, 2012), Thailand (Williams *et al.*, 2008)

[3] Ring boundary definition cf. Worbes (1995)

Ontogenetic vs. long-term trends in growth

To detect long-term growth changes from tree rings requires disentangling age/size dependent trends in growth from long-term growth changes. Several methods have been developed for this purpose. However, the detection power and reliability of these methods vary (CHAPTER 4) and method choice affects the trend detection. Here we applied the well-established regional curve standardisation (RCS) together with the less common size class isolation (SCI) method. The RCS was shown to have a high detection power and to be reliable when detecting long-term growth trends (CHAPTER 4), whereas the SCI is a more conservative (i.e., less sensitive) when detecting trends, but analyses trends more directly, using raw growth rates. These methods complement each other and combining them provides the most robust results when assessing growth changes (CHAPTER 4).

In the RCS, an average ontogenetic growth trend for a species (the 'regional curve', dashed line under 'Age/size correction'; Figure 5.2) is calculated and individual tree-ring series are divided by this average curve (Briffa *et al.*, 1992; Esper *et al.*, 2003)1992; Esper et al., 2003. The regional curve is usually calculated by aligning ring-widths of all individuals to cambial age (i.e., age from the pith) and calculating the average expected growth for each age. For shade-tolerant species or for species showing periods of growth suppression (e.g., slow growth due to overshadowing) size rather than age is often a better indicator for an individual's ontogenetic stage (King *et al.*, 2005; Nock *et al.*, 2011). Therefore we calculated the regional curve using small diameter classes instead of age (the 'regional size curve'; cf. Bontemps & Esper, 2011). We used diameter classes of 0.5 cm and calculated average growth rates of all individuals in each class (>10 individuals per class). We then fitted four different non-linear functions to these average growth rates per size class: Chapman-Richards, Hossfeld, Korf, and Weibull (cf. Zeide, 1993). The function that best described the size - BAI relationship for each species (i.e., with the highest R^2) was chosen to represent the regional curve. We then calculated residual growth rates by dividing each growth-year by the expected growth for its size (as calculated from the regional curve). Finally, to ensure residuals were calculated for the same diameter classes as used for the regional curve, we averaged (annual) residual growth rates for each 0.5 cm diameter class.

In the Size Class Isolation, growth rates are compared inside the same size classes for extant small (and thus young) and extant large (thus old) trees (cf. Landis & Peart, 2005; Rozendaal *et al.*, 2010a), i.e., growth rates of small trees are compared with those of large trees when they were small (Figure 5.2 and CHAPTER 4). The SCI assumes that the size dependent growth-trend does not affect the detection of long-term growth trends if analysed within fixed size classes. We computed the SCI using 4-cm diameter classes and calculated growth rates as an average BAI of five rings: the year at which a tree reaches the diameter class (e.g., 4, 8, 12 cm; Figure 5.2) and the two rings prior and after that year. Trends in the SCI are calculated over raw growth data (in BAI) making this method independent of decisions made during curve fitting procedures. However, due to its lower sample sizes (the unit of measurement are individual trees) the power to detect trends using the SCI is lower than the RCS' (CHAPTER 4). For the sake of simplicity, in the main text we will focus mostly on the RCS, providing more extensive results for SCI in the Supplementary materials.

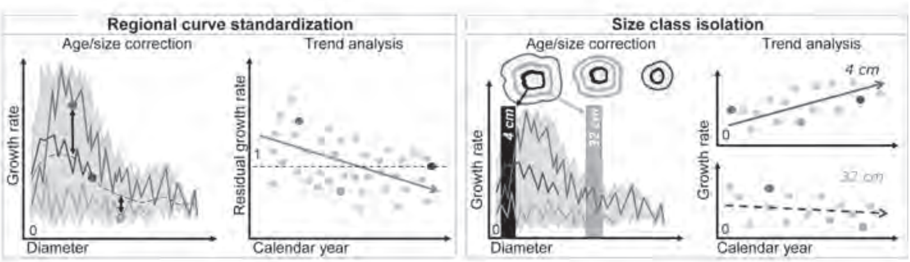

Figure 5.2. Schematic overview of the application of the regional curve standardisation (RCS) and size class isolation (SCI) to disentangle age/size from long-term trends in tree growth. Left panels indicate how the age/size trend (i.e., the ontogenetic signal) is disentangled from long-term growth changes: for the RCS, by dividing individual growth curves by the average age/size trend (dashed line); for SCI, by analysing trends within size-classes (e.g., in class 4cm, black bar). The second column illustrates how trends are computed: on residual growth rates for the RCS and on raw rates for the SCI. See Methods section for more detailed explanation of the methods.

Analysis of species-level growth trends

We tested for long-term growth trends for each species using the RCS and the SCI. In the RCS trends were analysed by computing Pearson's correlation coefficients (significance level $p < 0.05$) between the residual growth data and calendar year ('Trend analysis'; Figure 5.2). In the SCI, for each species trends were analysed for all size classes simultaneously using mixed-effect models, including 'calendar year' as fixed factor and 'size class' as random factor. For all analyses, we used the natural logarithm of the (raw) growth data to normalize the data and stabilize variation. We tested the mixed-effect models with random intercept and with random intercept and slope, and tested whether calendar year had a significant effect on the model. For each test, the most parsimonious model was chosen, i.e., the model yielding the lowest Aikaike's Information Criteria (AIC), and we computed estimated p-values.

Assessing biases in trend detection

When analysing growth trends, it is imperative to account for several biases (Brienen *et al.*, 2012a; Nehrbass-Ahles *et al.*, 2014; CHAPTER 4). Two biases may have affected our results: the 'juvenile selection' bias (Rozendaal *et al.*, 2010a), and the 'pre-death slow growth' bias (Brienen *et al.*, 2012a). Therefore we explicitly evaluate whether these biases were present in our data.

The 'juvenile selection' bias may lead to the detection of growth decreases over time, or mask growth increases. This bias occurs if slow-growing juvenile trees have a lower chance to reach maturity than fast growers. This lower survival implies that the large canopy trees of today were relatively fast growing in the past. Evidence for this bias has been found for temperate (Landis & Peart, 2005) and tropical species (Rozendaal *et al.*, 2010a). We evaluated whether the juvenile selection bias affected our results by analysing if slow growing juvenile trees (<20 cm dbh) in the distant past were selectively 'removed' from our dataset. For this purpose, we performed the equivalent of a quantile regression on the 25% slowest and fastest growing juvenile trees. The lower quantile represents the slowest growers of a population and a negative trend in this quantile may indicate that these individuals have selectively been removed from the population further back in time (grey area, Figure 5.3). Such a negative trend may also be induced by worsening growth condition in time, e.g., as induced by increases in temperature. However, such worsening growth conditions would also lead to changes in the growth potential of a species, thus on the quantile with the fastest growers. By simultaneously analysing trends in both the slowest and fastest growers, it is possible to assess the juvenile selection bias and disentangle it from changing growth conditions. In the case of the juvenile selection bias, the two quantiles will show a differential direction of trends, with the slowest growers showing a negative growth trend while the fastest growers may show either no or a positive trend (Figure 5.3). Additionally, in the case of a strong external driver forcing growth changes, we expect to find congruent growth trends in both quantiles: worsening growth conditions in time would lead to negative trends (Figure 5.3), whereas improving growth conditions to growth increases (Figure 5.3).

In short, the slowest growers in a population (i.e., the lower quantile) can be used to assess the presence of a juvenile selection bias, while the fastest growers provide information on changing growth conditions over time. We performed the quantile regressions on the RCS data only, as it provides a higher detection power than the SCI after splitting up the data (i.e. larger sample sizes). For each decade, we selected the 25% fastest and 25% slowest growing individuals (in residual growth rates) and analysed the trends over the quantile growth data (log transformed) using Pearson's correlations.

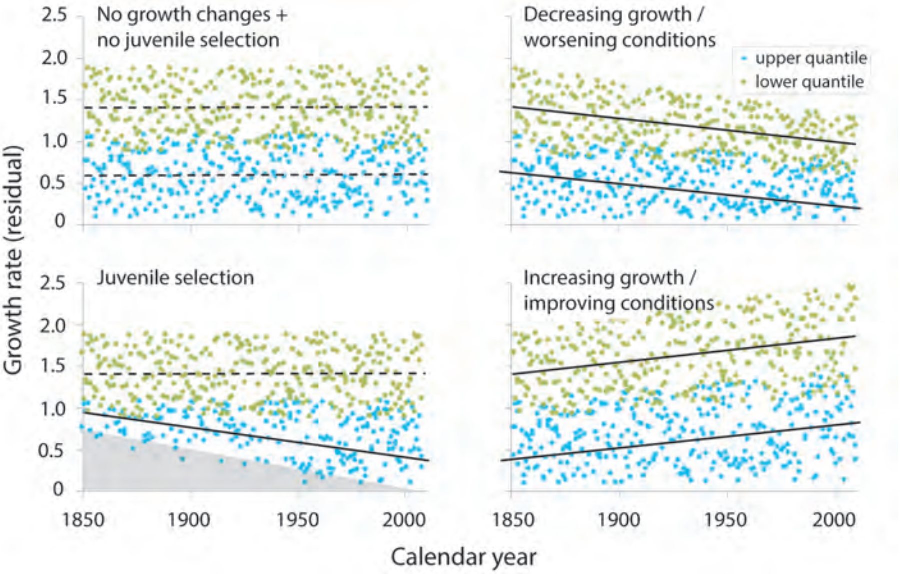

Figure 5.3: Schematic overview of the approach to detect the juvenile selection bias using quantile regressions. Juvenile selection occurs if fast-growing juvenile trees have a higher chance to reach maturity than slow growers. Simultaneous analyses of trends in the slowest and fastest quantiles of juvenile growth allows assessing the juvenile selection and disentangling it from changing growth conditions. In the case of juvenile selection, the two quantiles will show a differential direction of trends, with the fastest growers (green dots) showing either no or a positive trend in growth, while slowest growers (blue dots) will show a negative growth trend (as slow growers are selectively removed from the data further back in time; grey area). In the case of strong external drivers forcing growth changes (right panels), the quantiles will show congruent growth trends. Solid black lines indicate significant trends and dashed lines non-significant. Quantiles were calculated as the 25% fastest and slowest growers per decades.

The 'pre-death slow growth' bias (cf. Brienen *et al.*, 2012a) may lead to the detection of growth decreases over time or may mask positive trends. This bias arises if growth reductions occur in the years preceding tree death (Wyckoff & Clark, 2002; Chao *et al.*, 2008). In this case, the most recent years in the tree-ring data will include growth data from individuals that are dying (but still alive) and that show reduced growth rates. In temperate forests, growth reductions prior to death were found between 6 up to more than 12 years prior to a tree's death (Wyckoff & Clark, 2002). In the tropics however, it is unclear how long these growth reductions persist, as existing analyses do not cover more than 10 years (e.g., Chao *et al.*, 2008; Rüger *et al.*, 2011; van den Berg *et al.*, 2012). We expect this to play a role on only the last 15-20 years of growth. Therefore, to evaluate the effect of the pre-death slow growth bias, we re-analysed trends after excluding the last 15 years of growth. If negative trends detected in all data disappear or become positive after the removal of the last 15 years, this indicates that the pre-death slow growth bias may have influenced trend detection.

Growth trends within and across sites

If growth changes are driven by a common external factor, we expect that all species of a site – or across sites – will show trends in the same direction. We used linear mixed-effect models to analyse aggregated trends in growth for all species from a site. In these models, we included 'calendar year' as fixed factor and 'species' as random factor. For the analysis of aggregated trends for all sites, we combined all data and analysed trends on a similar way as for the site-level analysis, but nested all random factors further inside site. The natural logarithm of residual or raw growth data was used, to normalize data and stabilize variation. All linear mixed-effect models were tested with random intercept only, and with random intercept and slope, and the most parsimonious model was chosen, i.e., the model yielding the lowest Aikaike's Information Criteria (AIC). All analyses were performed in R (version 3.0.2; R Core Team 2013), using the package NLME (Pinheiro *et al.*, 2009).

5.3 Results

Species specific trends

We assessed long-term growth changes in tropical forests at three levels: at species level, site level and for all sites combined. In the species-level analysis using RCS, 12 of the 13 species showed significant changes in (log transformed) growth rates over time and one species (*Afzelia xylocarpa*) showed no changes (Figure 5.4). Two of these 12 species showed significant growth increases, whereas for 10 species growth rates decreased over time.

For the Bolivian species we found growth decreases for three species (*A. ruizii*, *C. ianeirensis*, and *S. fruticosa*) and an increase for one (*H. crepitans*; Figure 5.4). The Cameroonian species showed similar trends: growth decreases in three species (*B. eurycoma, B. cynometroides* and *T. ivorensis*) and a growth increases for one (*D. ogea*; Table 5.2). For the Thai species, growth decreases were found for four species (*C. tabularis, M. azedarach, N. obtusifolia,* and *T. ciliata*) and no growth change for one (*A. xylocarpa*). In Supplementary materials Supplementary figure 5.1 we show a similar analysis, but with trends computed on the raw residuals (i.e., not transformed) using non-parametric tests (Spearman's rho).

Detected trends using RCS ranged from significant to highly significant (*p*-values from ~0.02 to < 0.001, Table 5.2) and the period over which trends were assessed depended on the longevity of the species analysed and ranged from ~70 years (for e.g., *M. azedarach* and *A. ruizii*) up to ~250 years (e.g., for *D. ogea*, Table 5.2).

For the species level analysis with SCI, we applied a linear mixed-effect model for each species with 'calendar year' as fixed and 'diameter category' as a random factor. SCI showed similar trends as the RCS, but with a lower detection power: trends detected for 8 instead of 10 species. Only for one species – *A. ruizii* in Bolivia – did the detected trends not coincide: a growth decrease was found using RCS and an increase using SCI (Supplementary table 5.1).

Analysis of biases

We assessed whether the juvenile selection bias affected the detection of trends by analysing trends on the slowest and fastest growth quantiles for juvenile trees (dbh <20 cm). For most species, trends in the quantiles were similar to the trends found when analysing all growth data (Figure 5.5, Supplementary table 5.1), indicating the juvenile selection bias does not affect the trends detected. The only species that showed a possible effect of the juvenile selection bias was the Thai species *A. xylocarpa*. For this species, the lower quantile showed a negative trend, whereas trends were not significant in the upper quantile and in all data (Supplementary table 5.2). This negative trend may indicate that slow growing individuals were selectively removed from the dataset further back in time. Additionally, for three species presenting growth reductions in the analysis of all data – *C. ianeirensis, T. ivorensis* and *T. ciliata* – trends were not significant anymore in the quantile analysis (Figure 5.5).

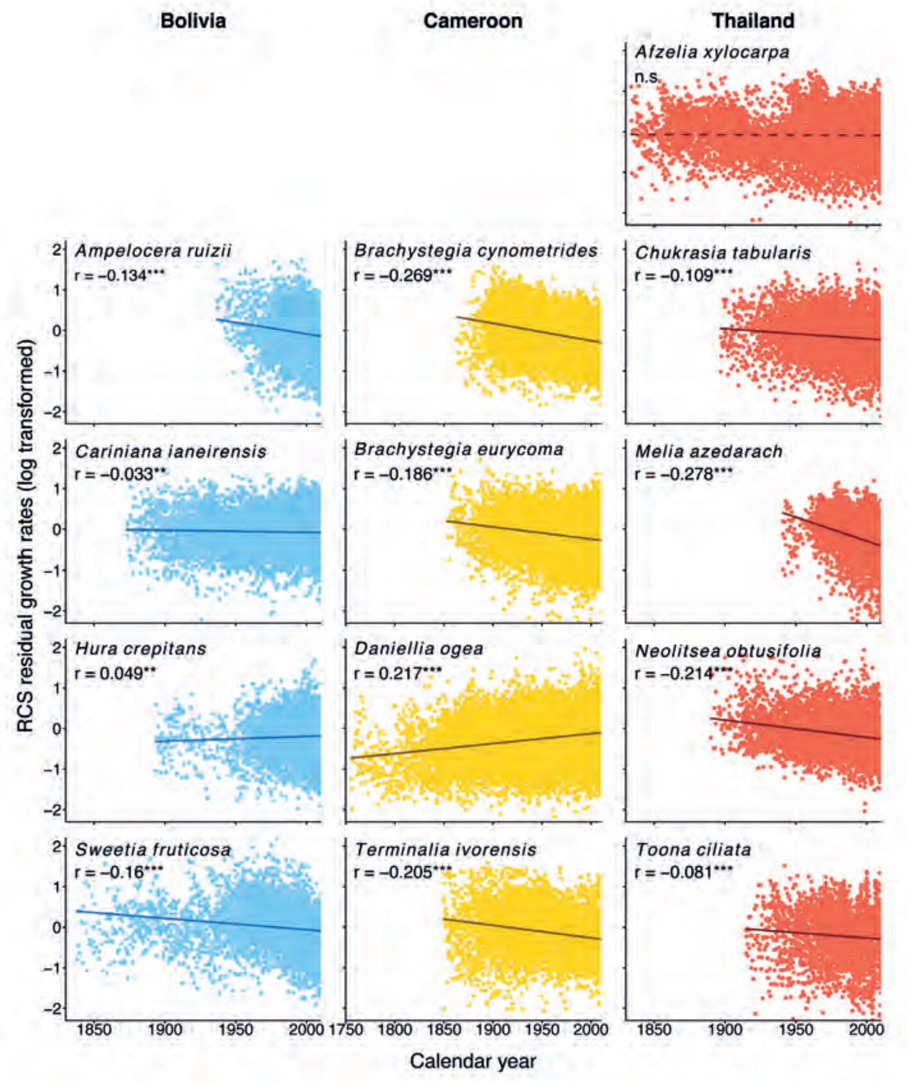

Figure 5.4. Long-term trends in in growth for 13 species from three tropical sites, using the regional curve standardisation. Trends computed with Pearson's correlations between (log transformed) standardised growth rates and against calendar year. Note the varying x-axis. Solid lines indicate significant trends in the quantiles, dashed lines non-significant trends.

Table 5.2. Long-term trends in residual growth rates for the 13 tree species. Residual growth calculated using the regional curve standardisation (RCS) method. Significant trends marked in bold (red = growth decreases, green = growth increases) and sample size (n) and period of analysis are also provided.

Study site	Species	Pearson's r year[1]	Sample size	Period of analysis
Bolivia	*Ampelocera ruizii*	**-0.134*****	2304	1937-2010
	Cariniana ianeirensis	**-0.033***	5202	1874-2010
	Hura crepitans	**0.049***	2725	1894-2010
	Sweetia fruticosa	**-0.160*****	3463	1838-2010
Cameroon	*Brachystegia cynometroides*	**-0.269*****	8814	1864-2010
	Brachystegia eurycoma	**-0.186*****	7761	1854-2010
	Daniellia ogea	**0.216*****	9693	1756-2010
	Terminalia ivorensis	**-0.205*****	5601	1850-2010
Thailand	*Afzelia xylocarpa*	-0.010	6427	1834-2010
	Chukrasia tabularis	**-0.109*****	4416	1897-2010
	Melia azedarach	**-0.278*****	2619	1941-2010
	Neolitsea obtusifolia	**-0.214*****	3989	1890-2010
	Toona ciliata	**-0.081*****	2415	1915-2010

[1] RCS analysis: trends computed with Pearson's correlations of (log transformed) standardised growth rates against calendar year

Significance trends indicated as: * $p < 0.05$; ** $p < 0.01$; and *** $p < 0.001$)

To assess whether the 'pre-death slow growth' bias has influenced the species-level results, we re-analysed all growth trends after removing the last 15 years of growth (i.e., on years prior to 1985). Removing these growth years hardly affected the detected trends for most species (Supplementary figure 5.2, Supplementary table 5.3). However, for two species trends disappeared, i.e., changed from significantly positive (in *H. crepitans*) or significantly negative (in *T. ciliata*) to non-significant, while for another two species – *S. fruticosa* and *M. azedarach* – trends changed from positive to negative (Supplementary figure 5.2, Supplementary table 5.3).

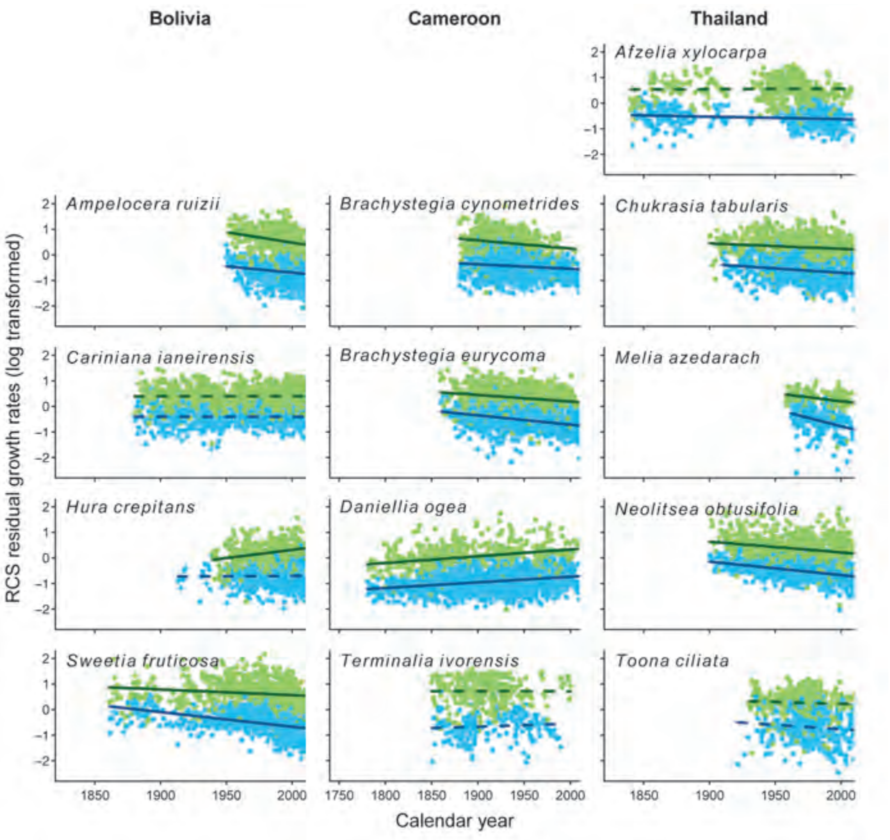

Figure 5.5. Quantile regression of growth trends for 13 tropical tree species from three tropical sites. Trends computed on the 25% fastest (green dots) and 25% slowest growers (blue dots) to assess the effect of juvenile selection bias (see Figure 5.3) using with Pearson's correlations between growth rates and calendar year. Solid lines indicate significant trends in the quantiles, dashed lines non-significant trends.

Aggregated growth trends per site

To identify whether aggregated growth trend were present per site, we analysed trends for all species in each site simultaneously. In Bolivia, species-level increases and decreases in growth were both detected. However, when simultaneously analysing trends for all species, using both the RCS as the SCI, we found no evidence for aggregated changes in growth rates for all species in the Bolivian site (i.e., no significant 'calendar year' effect in the linear mixed-effect model). Results for Cameroon were similar to the Bolivian results: although trends were present at species level, no aggregated growth changes were detected among the species using the both detection methods. For Thailand, in four of the five species we detected growth decreases. When analysing for aggregated trends for all Thai the mixed-effect models using RCS data showed a weak growth decrease over time (year effect = -0.0041, $p = 0.033$, n= 19860; Table 5.3). Although significant ($p < 0.05$), the model that included the year effect only differed slightly from the no-trend model in Akaike's information criterion (ΔAIC = 1.83) and this difference is thus inconclusive (cf. Burnham *et al.*, 2011; Murtaugh, 2014). The mixed-effect models using SCI did not detect significant trends when analysing all species of the Thai site simultaneously (Supplementary table 5.2).

Growth trends across sites

To assess whether a common factor (e.g., increasing temperatures, or CO_2-fertilisation) is driving growth changes over all three research sites, we analysed growth changes for all species from all sites simultaneously. Using the linear mixed-effect model for all sites, we found a weak reduction in growth over time (year effect = -0.0027, $p = 0.005$, DF= 65415; Table 5.3).

In short, both growth increases and decreases were present at the species-level, but on site level, consistent growth changes were only found for the Thai study site. Additionally, we found evidence for a congruent growth decrease across all species and sites. Again, the model including the year effect differed slightly from the no-trend model (ΔAIC = 2.80), indicating again that the detected trend was weak (cf. Burnham *et al.*, 2011; Murtaugh, 2014). The mixed-effect models using SCI analyse aggregated trends for all sites did not detect significant trends (Supplementary table 5.2).

Table 5.3: Linear mixed-effect model results for trend analyses per site and for all sites combined. Trends in growth were analysed on residual growth rates (from the regional curve standardisation) using mixed-effect models, with 'calendar year' as fixed factor (Effect year). In the analysis per site, 'species' were included as random effects. For the analysis for all sites, random effects were 'species' nested in 'country'. Growth data were log transformed to normalize data and stabilize variation. Also provided: degrees of freedom (DF), ΔAIC, and period of analysis. Two-tailed significance indicated with: * $p < 0.05$; ** $p < 0.01$.

Study site	Intercept	Effect year (± std error)	DF	ΔAIC effect year[1]	Period of analysis
Bolivia	-0.033	-0.0018 ± 0.0014	13689	0.24	1838-2010
Cameroon	-0.144	-0.0019 ± 0.0015	31864	0.20	1756-2010
Thailand	-0.051	-0.0041 ± 0.0019*	19860	1.83	1834-2010
All sites	-0.073	-0.0027 ± 0.0010**	65415	2.80	1756-2010

ΔAIC: differences in Akaike's information criterion between models with and without a year effect (cf. Burnham *et al.*, 2011; Murtaugh, 2014)

5.4 Discussion

This is one of the first studies to assess species-specific long-term growth changes in tropical forest trees. We assessed these changes using tree-ring data from three sites across the tropics. Of the 13 species analysed, 10 showed growth decreases over time, two showed growth increases and for one species no growth changes were detected. When analysing trends on site-level, an aggregated negative trend was found in the for the trees from Thailand. Finally, we found indications of an aggregated growth decrease when analysing trends in all species across the three sites.

Species specific trends

For the majority of the tree species analysed here (12 out of 13), growth rates have changed in the past two centuries and, in 10 cases, growth has declined over time (Figure 5.4). The growth reductions found for many species may indicate worsening growth conditions in time. Similar growth reductions have also been found in other studies, though for much shorter periods of time (Feeley *et al.*, 2007), or analysed using smaller sample sizes (Nock *et al.*, 2011). In both studies, these growth decreases have been linked to increasing temperatures, which for tropical species may already be reaching limiting values, especially during the hottest periods of the day (Doughty & Goulden, 2008).

That growth conditions may be worsening is supported by the quantile regressions (Figure 5.5) and by the fact that several species in Thailand and Cameroon show weak regeneration in the last 20-80 years (Vlam, 2014). Weak or failing regeneration is common in tropical forests (e.g., Poorter *et al.*, 1996; Newbery *et al.*, 2013; Vlam, 2014) and may indeed reflect changing climatic conditions (Vlam *et al.*, 2014a). However, it may also be caused by changes in (anthropogenic) disturbance (Muller-Landau, 2009), be part of the life-history strategy of a species (Newbery *et al.*, 2013) or be caused by the lack of large-scale disturbances (Baker *et al.*, 2005). A lack of regeneration, or regeneration in pulses, has large consequences for the detection of trends. Age clustering may affect the detection of (growth) trends in studies based on tree-ring data as well as in studies based on permanent sample plots (Muller-Landau, 2009). In tree-ring data, such age clustering may cause apparent growth decreases (conditions in the past better than conditions now), whereas in plot studies, age clustering may induce apparent increases in biomass (while growth rates may decrease).

If regeneration only occurs under large-scale disturbance, which are rare, trends in growth may be apparent that are induced by the recovery of forests from this disturbance (Fisher *et al.*, 2008; Chambers *et al.*, 2013). Disentangling trends caused by changing regeneration conditions from long-term trends induced by climatic changes (e.g., in temperature of CO_2 concentrations) is very challenging, for both tree-ring and PSP based studies.

Robustness of growth trends results

Detecting trends in forest tree growth is challenging, irrespective of working with growth data obtained from PSPs or from tree-ring measurements (Bowman *et al.*, 2013) and several biases may erroneously induce trends. In PSP studies, these biases may be induced if plots have not been installed at random locations (Phillips *et al.*, 2004) or by the relatively small size of plots (Chambers *et al.*, 2013). For tree-ring studies, biases may be induced by sampling design (Nehrbass-Ahles *et al.*, 2014), due to the nature of growth data (Brienen *et al.*, 2012a; Bowman *et al.*, 2013), or by the choice of trend detection method (CHAPTER 4). As we sampled trees randomly in space and following their size distribution in the forest, biases caused by sampling design probably did not affect our results. Next, we will discuss the two biases that may have influenced the detection of trends.

To assess for the presence of the 'pre-death slow growth' bias, we tested whether the removal of the last 15 years of growth caused a change in the detected trend. For only two species – *M. azedarach* and *Sweetia fruticosa* – did this removal result in a change in trend consistent with this bias: trends changed from negative to positive (Supplementary figure 5.2). This bias may thus have induced the negative trends detected for these species. However, the sample size for *M. azedarach* reduced considerably after removing the last 15 years of growth data (from 2619 to 942, Table 5.2 + Supplementary table 5.1), due to the species' short lifespan (maximum ~60 years). Whether this inversion in the trend for *M. azedarach* was caused by the pre-death slow growth bias or due to the exclusion of a large part of the 'population' is difficult to ascertain. Individuals of *Sweetia fruticosa* may indeed be showing a growth trend due to the 'pre-death slow growth' bias. Sampling dead trees could be used to ascertaining whether this bias takes place. However, this is difficult in the tropics, due to high decomposition rates.

The 'juvenile selection bias' may lead to the detection of growth decreases over time or to the masking of growth increases. We expect this bias to be present mostly for light-demanding tree species (e.g., the long-lived pioneers *M. azedarach* and *Terminalia ivorensis*) as young individuals of these species require high light conditions and fast growth to reach maturity. Although several of the species analysed here are light demanding species (Table 5.1), only for one species – *Afzelia xylocarpa* – evidence was found that slow growers in the distant past were 'removed' from the dataset, i.e., the lower quantile showed a growth reduction (Figure 5.5). This species shows a spatial and temporal pattern in regeneration (Vlam *et al.*, 2014a), which may hamper assessing the effect of the juvenile selection bias on the trends. For most species growth trends in the quantiles were similar to the trends detected in all data, reinforcing the suggestion that these trends were caused by changing growth conditions and not by the juvenile selection bias.

Aggregated trends per site

In the analysis of consistency in trends per site, only for the Thailand sites did we find evidence that growth changes have occurred consistently among different species. In Thailand, the aggregated negative trend suggest worsening growth conditions for all species. Such growth reductions were also found in a large-scale (50 ha) monitoring plot adjacent to our study site (Dong *et al.*, 2012) and also using tree-ring analysis for three of the species also studied here: *Chukrasia tabularis, M. azedarach* and *Toona ciliata* (Nock *et al.*, 2011), though for much smaller sample sizes (from 14-36 trees). Paradoxically, Nock *et al.* (2011) found growth reductions together with increases in intrinsic water-use efficiencies, suggesting that growth decreased while the photosynthetic capacity of trees increased over time. Unravelling the causes for these growth changes and assessing whether growth conditions have indeed changed is challenging. Growth of most Thai species analysed here is positively related to precipitation amount and negatively to temperature (Vlam *et al.*, 2014b). Rising temperatures and respiration costs, and more frequent El Niño events may have induced these growth declines (Nock *et al.*, 2011). The hump-shaped age distributions found for many of the Thai species (Vlam, 2014) supports the suggestion of worsening conditions in the more recent past. Additionally, we believe that the recovery from (large-scale) disturbances may also be driving the growth reduction detected for the Thai site (Baker *et al.*, 2005), perhaps in combination with the climatic changes mentioned above.

The lack in consistent growth changes in Bolivia and Cameroon suggest that growth is not driven by a single factor in these sites. The Bolivian site is the second dryest forests in this study and temperature increases noted for the area (Seiler *et al.*, 2013) could explain decreases in growth found on species-level (Seiler *et al.*, 2013). However, the Bolivian species showed no regeneration problems (Vlam, 2014), suggesting unaltered conditions – at least for regeneration – in the recent past. On the other hand, forest fires have disturbed parts of the forest in the last two decades (Blate, 2005; Lopez *et al.*, 2012) and may thus have enhanced the regeneration of light-demanding species.

Several species in Cameroon showed growth reductions and no regeneration in the recent past (Vlam, 2014), suggesting changing conditions in the area. Increases in temperature have been noted (for the past ~50 years) in the study area, while precipitation did not change (Molua & Lambi, 2006). However, no aggregated trends were noted for the Cameroonian site, suggesting not external factor changed growth for all species. A reduction in human-induced disturbances (Pourtier, 1989; Oslisly *et al.*, 2013) may in part explain the worsening conditions (i.e., by closing of the canopy, while defaunation due to the bush meat hunting (Abernethy *et al.*, 2013)2013 could explain the lacking regeneration in Cameroon. Lacking regeneration does not necessarily mean a growth reduction as *Daniellia ogea* showed a growth increase (Figure 5.4) while lacking regeneration (Vlam, 2014).

Trends across sites

We found evidence for a growth reduction across all study sites. Although not conclusive (ΔAIC = 2.8, Table 5.3; cf. Burnham *et al.*, 2011), these results suggest tropical forests tree growth has reduced in the past ~150 years. These results contrast strongly with the growth increases expected under a strong CO_2-fertilization effect (Lloyd & Farquhar, 2008), and with several studies that found decadal-scale increases in forest biomass (Phillips *et al.*, 2008; Lewis *et al.*, 2009b) and in growth rates (Laurance *et al.*, 2004b). Surprisingly, growth did not increase in spite of increases in intrinsic water-use efficiency over time being found in trees of 12 of our study species (Nock *et al.*, 2011; van der Sleen, 2014). Tropical forest growth is sensitive to temperature (Clark *et al.*, 2010) and the increasing temperatures may have induced the growth decreases (Feeley *et al.*, 2007; Nock *et al.*, 2011). The effects of rising CO_2 concentrations and rising temperatures on growth could cancel each other out. Also, tree growth might not be carbon limited in tropical forests, with other nutrients limiting growth (e.g., phosphorus Lloyd *et al.*, 2001). Additionally, the suggested gains in photosynthesis due to the higher CO_2 levels may not be invested in stem growth, as diameter growth is low on the carbon allocation hierarchy (Sala *et al.*, 2012; Richardson *et al.*, 2013).

Implications and outlook

Tropical forests are as complex as the combination of all species and their interactions. Understanding how growth changes occur on the species level thus forms the basis to understand whether site or forest changes are taking place. We found species-level growth changes for most of the species analysed, but that these changes were not necessarily reflected in the aggregated trends for the sites. That these results may vary illustrates the importance of assessing trends on both the level of species and sites.

Our results showed decreasing growth rates for most of the species analysed. However, when analysed for all species together trends were less pronounced, with only weak (non-conclusive) aggregated trends being detected. Still, these results contrast strongly with the increases in growth of tropical forest trees found in several studies (Laurance *et al.*, 2004b; Lewis *et al.*, 2009a) and expected under CO_2-fertilization (Lloyd & Farquhar, 2008). If growth of tropical forest trees is indeed decreasing – or at least not changing – this will have large consequences for the projections of the carbon dynamics of tropical forests under increasing ambient CO_2 (Huntingford *et al.*, 2013). Currently, models used to predict vegetation development under changing climate – dynamic global vegetation models – assume a CO_2-fertilization on the growth of tropical forests (Sitch *et al.*, 2008; Huntingford *et al.*, 2013), with tropical forests predicted to act as a carbon sink in the coming century. This widespread assumption of CO_2-fertilisation is controversial (Körner, 2009) and may not be valid for the species studied here (van der Sleen, 2014). Our results support the assumption that elevated ambient CO_2 does not directly lead to higher tree growth. Furthermore, changing growth rates may lead to shifts in competition between species, which may lead to and may species shifts and dominance of more drought adapted species (e.g., if temperatures increase; Feeley *et al.*, 2011). These shifts may be already happening in tropical forests (Laurance *et al.*, 2004b) as suggested by the lacking regeneration for many our study species (Vlam, 2014).

Detecting whether changes have or are taking place in tropical forest growth is challenging (Bowman *et al.*, 2013), and every method used to assess these changes – tree-ring analysis, monitoring plots, etc. – has limitations and biases

(Phillips *et al.*, 2004; Brienen *et al.*, 2012a; Chambers *et al.*, 2013). Understanding the drivers of these changes is possibly even more challenging – and arguably even more important – than only detecting them. We argue that to know whether and why tropical forests are changing requires an integrative approach, combining long-term growth data (from tree-rings) with field measurements from monitoring plots; e.g. (Lewis *et al.*, 2009b), carbon flux estimates (e.g., Saleska *et al.*, 2003), and large-scale experimental studies (e.g., Nepstad *et al.*, 2007; Tollefson, 2013). Monitoring plots provide the most complete data on the dynamics and changes in tropical forests as it includes growth, mortality and regeneration rates, and allows to assess changes in species composition (Laurance *et al.*, 2004b). Carbon flux measurements provide large-scale estimates of the carbon dynamics and net primary productivity of forests (e.g., Saleska *et al.*, 2003; Gatti *et al.*, 2014). Large-scale experimental approaches allow to directly quantify the effects of (predicted) climatic changes on plant processes and growth (e.g., Nepstad *et al.*, 2007), and the foreseen CO_2-enrichment experiment in the Amazon (Tollefson, 2013) will fulfil an important knowledge gap on topical forest responses to higher CO_2 concentrations. Tree-ring analysis can provide a long-term perspective to extrapolate results from short-term measurements and experiments to the scale of centuries. Such integrative approaches have been applied in temperate forests (Girardin *et al.*, 2008; Babst *et al.*, 2014b; Belmecheri *et al.*, 2014), but are still lacking in the tropics. More tree-ring studies are needed in the tropics and many species throughout the tropics produce annual rings (Zuidema *et al.*, 2012). Tree-ring analysis provides the species-specific and long-term growth data necessary to assess changes in tree-growth on relevant time-scales. A standardized sampling protocol, analogous to the existing protocols for sampling plots (e.g. RAINFOR, AfriTRON, CTFS), would greatly increase the potential of using tree rings to detect and compare growth changes in forests trees worldwide. In the tropics, further studies should focus on widespread or dominant species (e.g., 'hyperdominant' species;Ter Steege *et al.*, 2013), of which many produce rings and that can be sampled in large number over large areas. Additionally, the analysis of stable-isotopes in the tree-rings provides additional information on both environmental (Fichtler *et al.*, 2010; Brienen *et al.*, 2012b), and physiological processes (Nock *et al.*, 2011; van der Sleen, 2014) that drive tree growth. Integrated with other methods and combined with the analysis of stable isotopes, well-designed tree-ring sampling can provide the (missing and) important long-term contextual information that is needed to understand growth changes.

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Supplementary materials

Appendix A - Results SCI analysis

Supplementary table 5.1: Species-level analysis of long-term trends for the 13 tree species using the regional curve standardisation (RCS) and size class isolation (SCI) methods. Trends indicated as the year effect of analysis (red = growth decreases, green = growth increases) and significant trends marked in bold. Also indicated: sample size (n), and period of analysis.

Study site	Species	RCS year effect[1]	Sample size	Period of analysis	SCI year effect[2]	Sample size	Period of analysis
Bolivia	*Ampelocera ruizii*	**-0.134*****	2304	1937-2010	**0.015*****	341	1945-2009
	Cariniana ianeirensis	**-0.033***	5202	1874-2010	0.001	833	1876-2009
	Hura crepitans	**0.049***	2725	1894-2010	**0.002****	635	1856-2009
	Sweetia fruticosa	**-0.160*****	3463	1838-2010	-0.001	448	1802-2010
Cameroon	*Brachystegia cynometroides*	**-0.269*****	8814	1864-2010	**-0.008*****	1367	1870-2010
	Brachystegia eurycoma	**-0.186*****	7761	1854-2010	**-0.001***	1551	1857-2010
	Daniellia ogea	**0.216*****	9693	1756-2010	**0.001*****	1585	1749-2010
	Terminalia ivorensis	**-0.205*****	5601	1850-2010	**-0.003****	1392	1838-2010
Thailand	*Afzelia xylocarpa*	-0.010	6427	1834-2010	0.000	1218	1826-2010
	Chukrasia tabularis	**-0.109*****	4416	1897-2010	-0.001	702	1835-2010
	Melia azedarach	**-0.278*****	2619	1941-2010	**-0.007*****	855	1894-2010
	Neolitsea obtusifolia	**-0.214*****	3989	1890-2010	**-0.002***	515	1906-2010
	Toona ciliata	**-0.081*****	2415	1915-2010	-0.001	533	1864-2010

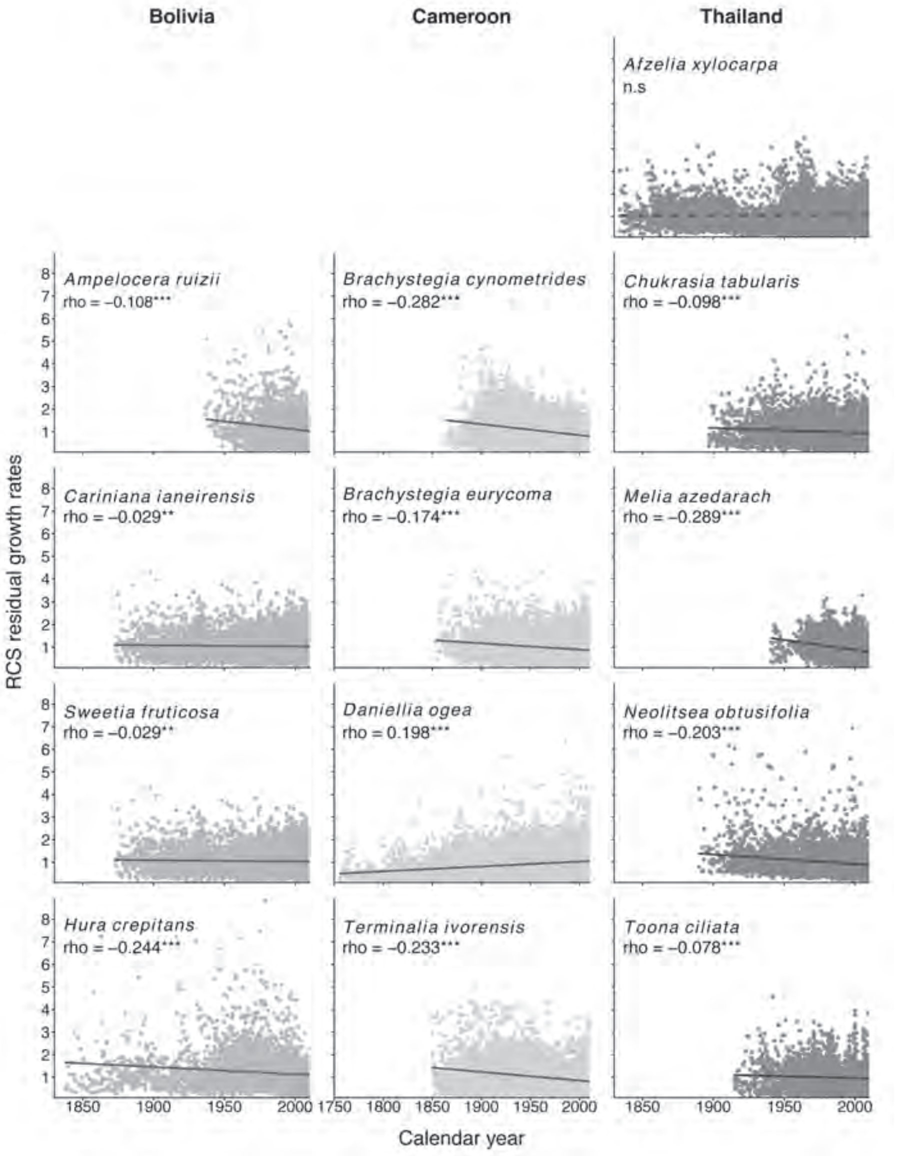
[1] RCS analysis: trends computed with Pearson's correlations of (log transformed) standardised growth rates against calendar year

[2] SCI analysis: trends assessed with linear mixed-effect models on (log transformed) basal area increment, with 'calendar year' as fixed factor and 'size class' as random factor.

Significance trends indicated as: * $p < 0.05$; ** $p < 0.01$; and *** $p < 0.001$)

Supplementary table 5.2: Linear mixed-effect model results for the regional curve standardisation (RCS) and the size-class isolation (SCI) methods. We analysed temporal trends in growth using 'calendar year' as fixed factor (Effect year). In the analysis per site, 'species' were included as random effects in the RCS and 'diameter category' nested in 'species' for the SCI. For the analysis for all sites, these random factors were further nested in 'site'. For the RCS, input data were the log transformed residual growth rates and for the SCI log transformed basal area increment. Two-tailed significance indicated with * = $p < 0.05$.

Detection method	Study site	Intercept	Effect year	Sample size	Period of analysis
RCS	Bolivia	-0.0326	-0.0018	13694	1838-2010
	Cameroon	-0.1444	-0.0019	31869	1756-2010
	Thailand	-0.0513	-0.0041*	19866	1834-2010
	All sites	-0.0743	-0.0027**	65429	1756-2010
SCI	Bolivia	3.1328	0.0037	2257	1802-2010
	Cameroon	3.9786	-0.0027	5895	1749-2010
	Thailand	3.1136	-0.0020	3823	1826-2010
	All sites	3.5853	-0.0008	11975	1749-2010



Supplementary figure 5.1. Long-term trends in in growth for 13 species from three tropical sites, using the raw residuals from the regional curve standardisation. Trends computed with Spearman's rank correlation between (log transformed) standardised growth rates against calendar year. Solid lines indicate significant trends in the quantiles, dashed lines non-significant trends. Note the varying x-axis.

Appendix B – Assessing the presence of biases

Juvenile selection bias

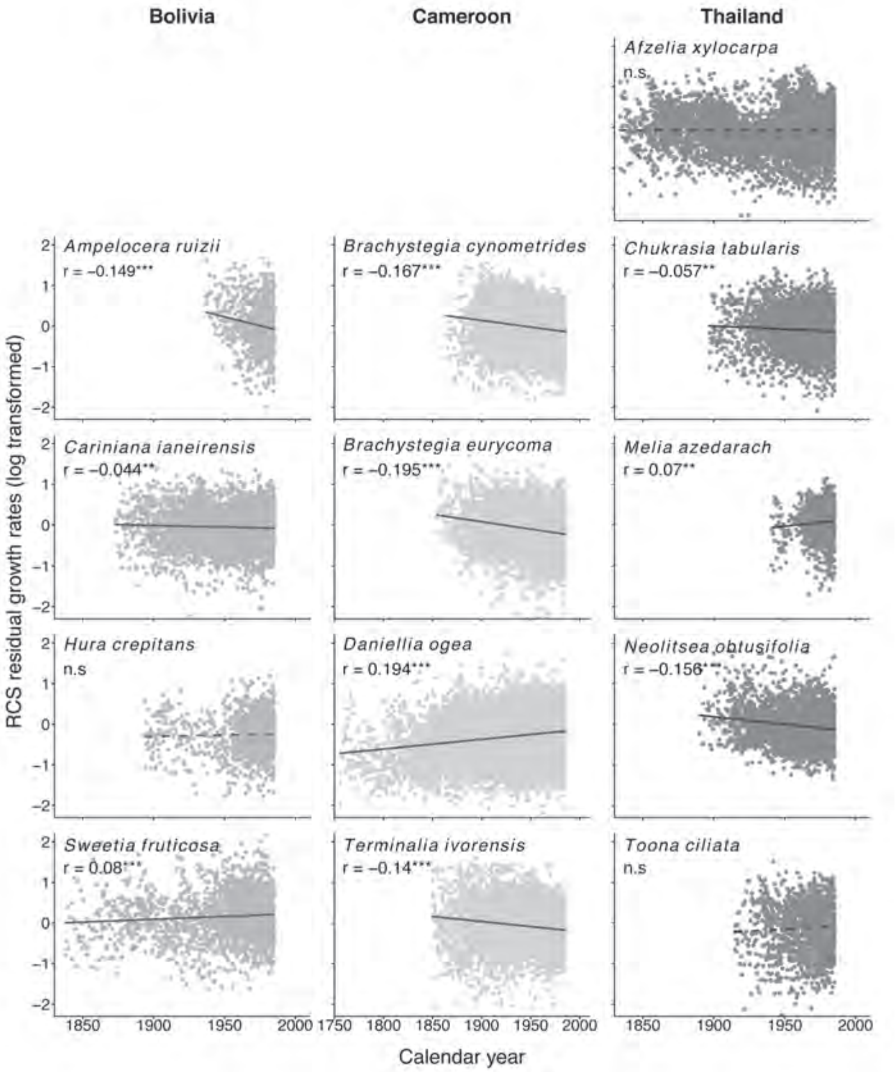
Supplementary table 5.3: Analysis of long-term trends in growth on the upper and lower quantiles for 13 tropical tree species. Trends calculated with Pearson's r and significance indicated with * $p < 0.05$; ** $p < 0.01$; and *** $p < 0.001$.

Study site	Species	Guild	All data	Lower quantile	Upper quantile
Bolivia	*Ampelocera ruizii*	ST	$\mathbf{-0.134}^{***}$	$\mathbf{-0.151}^{***}$	$\mathbf{-0.246}^{***}$
	Cariniana ianeirensis	PST	$\mathbf{-0.033}^{*}$	-0.003	0.009
	Hura crepitans	PST	$\mathbf{0.049}^{*}$	0.010	$\mathbf{0.231}^{***}$
	Sweetia fruticosa	LLP	$\mathbf{-0.160}^{***}$	$\mathbf{-0.430}^{***}$	$\mathbf{-0.152}^{***}$
Cameroon	*Brachystegia cynometroides*	PST	$\mathbf{-0.269}^{***}$	$\mathbf{-0.126}^{***}$	$\mathbf{-0.171}^{***}$
	Brachystegia eurycoma	PST	$\mathbf{-0.186}^{***}$	$\mathbf{-0.339}^{***}$	$\mathbf{-0.185}^{***}$
	Daniellia ogea	LLP	$\mathbf{0.216}^{***}$	$\mathbf{0.283}^{***}$	$\mathbf{0.291}^{***}$
	Terminalia ivorensis	LLP	$\mathbf{-0.205}^{***}$	0.084	-0.003
Thailand	*Afzelia xylocarpa*	LLP	n.s.	$\mathbf{-0.148}^{**}$	0.015
	Chukrasia tabularis	PST	$\mathbf{-0.109}^{***}$	$\mathbf{-0.200}^{***}$	$\mathbf{-0.111}^{**}$
	Melia azedarach	LLP	$\mathbf{-0.278}^{***}$	$\mathbf{-0.356}^{***}$	$\mathbf{-0.255}^{**}$
	Neolitsea obtusifolia	ST	$\mathbf{-0.214}^{***}$	$\mathbf{-0.399}^{***}$	$\mathbf{-0.202}^{***}$
	Toona ciliata	LLP	$\mathbf{-0.081}^{***}$	-0.103	-0.049

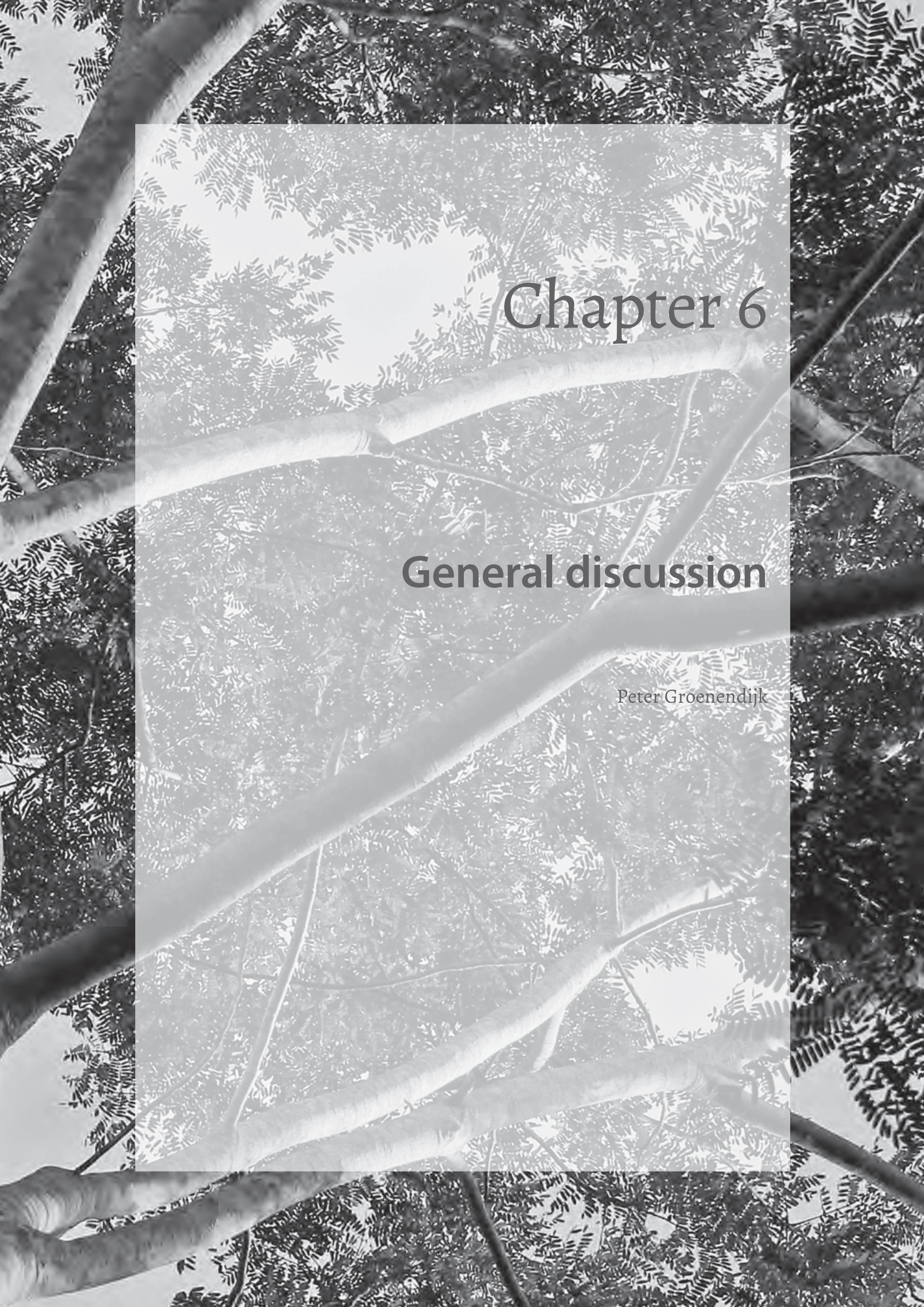
Pre-death slow growth bias

Supplementary table 5.4: Test for 'pre-death slow growth' bias: linear mixed-effect model results for analysis of trends per site and for all sites combined. We removed the last 15 years of growth (years after 1985) and re-analysed long-term trends in growth in residual growth rates. We used the same mixed-effect models, with 'calendar year' as fixed factor (Effect year), including in the analysis per site, 'species' as random effects; and for the analysis for all sites, 'species' was further nested in 'site'. Growth data were log transformed to normalize data and stabilize variation. Two-tailed significance indicated with: * $p < 0.05$; ** $p < 0.01$.

		Intercept	St error Intercept	p-value	Year effect	St error Year	p-value	DF
Bolivia	Intercept	0.022087	0.117501	0.8509	-0.001623	0.002167	0.4539	7258
Cameroon	Intercept	-0.106406	0.056784	0.0610	-0.001746	0.001402	0.2131	24598
Thailand	Intercept	-0.067501	0.032346	0.0369	-0.000049	0.001316	0.9701	12245
All	Intercept	-0.051774	0.039397	0.1888	-0.001060	0.000806	0.1886	44103



Supplementary figure 5.2. Long-term trends in in growth for 13 species from three tropical sites after removal of the last 15 years of growth data to assess the 'pre-death slow growth' bias (cf. Brienen *et al.*, 2012a). Trends computed on residual growth rate from the regional curve standardisation with Pearson's correlations between (log transformed) growth rates and calendar year. Solid lines indicate significant trends in the quantiles, dashed lines non-significant trends. Note the varying x-axis.



Chapter 6

General discussion

Peter Groenendijk

Tropical forests harbour an incredible diversity, are a key element of the global carbon cycle (Bonan, 2008) and provide many goods and services (e.g., fruits, timber and non-timber forest products). Due to the high storage and processing of carbon by tropical forests, changes in forest cover and in the net uptake or loss of carbon by forests have large implications for the global carbon cycle (Pan *et al.*, 2011). Tropical forests are under increasing pressure and undergoing rapid changes due to deforestation, conversion to other land uses and logging. Additionally, there is evidence that intact tropical forests are undergoing changes due to the effects of climate change. Most notably, there is evidence for increases in biomass of intact tropical forests (Lewis *et al.*, 2009a), suggesting that intact tropical forests have acted as carbon sinks over the past decades. As monitoring plots usually cover only a few decades, it is still unclear if these changes are driven by long-term alterations in the forest or by short-term climatic fluctuations (e.g., Feeley *et al.*, 2011). Assessing whether changes have occurred over centennial scales is thus crucial to understanding whether and how tropical forests are reacting to climatic changes.

In this thesis we used tree-ring analysis to assess long-term changes in growth of tropical forests (over the last ~150 years). Additionally, we applied growth data derived from tree rings to evaluate the sustainability of forest management practices in Cameroon. In CHAPTER 2 of this dissertation, we assessed the potential for using tree-rings in wet tropical forests in Central Africa and evaluated the presence and annual formation of ring boundaries in the wood of commercially exploited tree species. In CHAPTER 3, we used the growth rates obtained from tree rings to assess future timber productivity for four Cameroonian timber species. For this purpose we simulated their logging yields (i.e., volume of timber logged) in the next logging cycle and compared these yields to the volume cut at the first cycle (i.e., can yields be sustained over time). In CHAPTER 4 we used measured tree-ring data and simulated growth trajectories to evaluate how different detrending methods affect the detection of long-term trends in growth data from tree-rings. In CHAPTER 5 we analysed centennial-scale changes in growth rates of 13 tropical tree species collected in three sites throughout the tropics.

In this chapter the main findings of this dissertation and discuss their consequences. Finally, we provide an overview of the main methods used to detect changes in tropical forests and provide recommendations on how to integrate them.

6.1 Potential of tree-ring analysis is the tropics

For more than a century it has been known that tropical tree species may form annual growth rings (Brandis, 1898; Coster, 1927; Worbes, 2002). However, for long the formation of annual rings in tropical rainforests trees has been denied (Swaine, 1994; Chambers *et al.*, 1998; Kurokawa *et al.*, 2003). Researcher often believed that rainforests lack seasonality and therefore, that growth in these ecosystems is continuous throughout the year (i.e., no period of cambial dormancy). The passing of the Intertropical Convergence Zone, however, induces seasonality throughout tropical regions (Waliser & Somerville, 1994) and most tropical forests are considered to be seasonal (Underwood *et al.*, 2014). This seasonality influences tree growth and even in wet evergreen tropical rainforests growth of trees is driven by climate (Clark *et al.*, 2010). In the 'dry' season cambial activity stops (Moya & Tomazelo-Filho, 2009) and some tree species form annual growth rings (Fichtler *et al.*, 2003; CHAPTER 2). Furthermore, the strength of the seasonality also varies, ranging from regions with strongly seasonal climates and well demarcated dry seasons to regions with (nearly) ever-wet climate. This variation in seasonality raises the questions whether tree rings are formed across all tropical climatic zones, and what proportion of tropical tree species form annual ring boundaries.

The last two decades have seen an increase in tree-ring analyses in the tropics (Worbes, 2002, and references therein) and in its application for forest ecology (Worbes *et al.*, 2003) and forest management (Brienen & Zuidema, 2006a; De Ridder *et al.*, 2013b). In CHAPTER 2 of this dissertation, we further explored the potential to use tree rings in tropical rainforests. We evaluated whether growth rings are formed annually in the wood of tree species growing under very high levels of precipitation (>4000 mm) and in conditions considered improper for ring formation (Swaine, 1994; Whitmore, 1998). For this purpose, we assessed whether ring structures are formed in the wood of the 22 tree species, which were selected as they were commercially exploited in the region. We showed that ring structures are formed in the wood of more than half of them (in 14 species), with variation in ring clarity between species. On four species, out of a subset of five evaluated, we proved the annual character of ring formation using radiocarbon bomb-peak dating.

That ring structures are formed under high levels of rainfall, as is the case in our site in Cameroon, is remarkable. Water is probably not a strong limiting factor for growth in these forests, and trees thus do not have to avoid drought by shedding leaves and entering a period of cambial dormancy (Borchert, 1999). In spite of the high levels of rainfall, many of the species studied in CHAPTER 2 do shed their leaves and, together with the formation of ring structures in the wood, this suggests that these species show periods of cambial dormancy. For several species, individual trees growing near or on the banks of permanent rivers were observed to also shed their leaves. These trees probably do not experience a drought signal at all, suggesting that the deciduous character of these species – and therefore their ring formation – is genetically determined. Leaf-shedding might thus simply be genetically built in, perhaps as a remnant adaptation to drier conditions in the past (Maley & Brenac, 1998), or as a physiological necessity for trees to renew their photosynthetic apparatus (Wright & van Schaik, 1994).

The observed proportion of species forming tree-ring structures in this thesis, 64%, is higher than proportions observed in other studies in dryer regions. Across ecosystems in Brazil ring structures were found in 48% of the species (Alves & Angyalossy-Alfonso, 2000), in dryer forests in Mexico for ~ 40% of species (Roig *et al.*, 2005; Brienen *et al.*, 2009), and in the Amazon region between 25% and 50% (Roig, 2000; Worbes, 2002). This higher proportion seems contradictory to the expectation that tree-ring formation is inhibited by the lack of a strong environmental signal at the study site in Cameroon. One of the reasons for this higher proportion is that finding ring structures does not entail that these structures are formed annually. Studies merely assessing the presence of ring-structures (e.g., this study; and Alves & Angyalossy-Alfonso, 2000) may thus report higher proportions than studies that really prove annual ring formation. Often, annual formation is only assessed for a subset of species and, if proven, 'extrapolated' to the remaining species (e.g., Worbes *et al.*, 2003; Brienen *et al.*, 2009). Additionally, it is important to note that the species analysed in CHAPTER 2 were all commercially exploited species. This set of species thus formed a non-random selection of the community with certain (wood) characteristics that make them attractive as a source of timber, e.g., ease of working, resistant to rotting, large and straight boles. This subset of wood and tree characteristics may reflect certain physiological traits (Westoby & Wright, 2006; Chave *et al.*, 2009) that may also influence ring formation. Whether the proportion of species forming ring structures would be similar when performing a randomised or a complete screening of the species in the forest – thus also including shade-tolerant and small stature tree species – is hard to tell. Yet, we believe that this proportion will be lower if including all species and that growth rings will be more difficult to discern (due to slow growth of trees in the shade). Notwithstanding, shade-tolerant species may still form rings and high-quality annual rings have been found in several understory tree species (Couralet *et al.*, 2010), albeit under much drier conditions (rainfall of ~1200 mm yr^{-1}). All things considered, care should thus be taken when extrapolating this higher than expected proportion of species forming rings to the community level. Clearly, structured screenings of all species in a forest are needed to improve the estimations of the proportion of ring-forming species. Nonetheless, that a significant proportion of species forms growth rings under the wet conditions in this study, suggests that the potential of using tree-rings is more or less similar throughout the tropics, at least for forest regions showing some sort of seasonality (Worbes, 1989; Alves & Angyalossy-Alfonso, 2000). Ultimately, we estimate that tree rings can be used to measure growth and ages for around a quarter to a third of the tree species growing in tropical forests with some kind of seasonality.

When considering only species that present high-quality annual rings, i.e., that allow for the construction of chronologies to ensure exact dating, the proportion of species is lower than those mentioned above, e.g., for only ~10% of the species in drier African forests (Tarhule & Hughes, 2002). Although only possible for a restricted number of species, the chronologies built for these species can be used as a proxy to reconstruct climate. Such climate reconstructions are very relevant and extremely important in the tropics, because of the doubtful quality (Aguilar *et al.*, 2005) and usual short timespans covered by meteorological data in tropical countries (Clark, 2007). Tree-ring research on species with such high-quality rings should thus be stimulated, especially for species with large geographical distributions, such as *Cedrela odorata* (in Central and South America), *Toona cilliata* (in tropical Asia and tropical Australia) and *Entandrophragma spp.* (in West and Central Africa). At the same time, care needs to be taken not to blindly focus on the handful of high-potential species at the expense of analysis on other species that also form rings. For these other species, tree-ring analysis can still be used and provides high value data on long-term (lifetime) growth rates of trees. These growth data, although having a lower precision (e.g., for *B. cynometroides*; CHAPTER 2), are still very useful to answer ecological questions (such as in CHAPTERs 5) and to aid sustainable management of tropical forests (e.g., in CHAPTER 3).

For the remaining species that do not produce visible rings, or no ring structures at all, several techniques exist to aid ring identification or to measure annual (growth) signals in the wood. X-ray densitometry can be used to help recognizing tree-ring boundaries (Worbes, 1995). High resolution measurements of isotope concentrations (e.g., ^{13}C and ^{18}O) also shows great potential to provide growth data and ages for ringless species (Poussart *et al.*, 2004; Loader *et al.*, 2007; Pons & Helle, 2011). However, these isotope measurements require specialist knowledge and infrastructure, need be corroborated with radiocarbon dating and are very labour intensive, thus limiting their widespread application (van der Sleen, 2014). Finally, the analysis of trace elements in the wood (e.g., calcium) by synchrotron X-ray microanalysis may also reveal annual or seasonal signals in the wood (Poussait *et al.*, 2006). Synchrotron analysis is non-destructive and relatively fast, thus allowing for a widespread application that can aid in ring-boundary recognition (Poussait *et al.*, 2006). However, the underlying (ecological) drivers of trace elements in wood are still poorly understood and it is imperative to understand these drivers prior to interpreting synchrotron results.

Increasing (tree-ring) research efforts in the tropics would be especially relevant for African tropical forests. These forests form the second largest tropical forest tract worldwide, have a strong impact on the carbon cycle (Cao *et al.*, 2001; Williams *et al.*, 2007) and strongly influence local and global climate (Washington *et al.*, 2013). Despite their importance, African forests are the least studied of the world's tropical forests (Malhi *et al.*, 2013) and most ring studies have focussed on the drier extents of these forests (Trouet *et al.*, 2001; Tarhule & Hughes, 2002; Therrell *et al.*, 2007). Tree-ring analysis can provide vitally important data to understand the growth and (carbon) dynamics of African forests (Worbes *et al.*, 2003; CHAPTER 5) and can also be used to extend climatic records further back in time (Schöngart *et al.*, 2006). Very old trees of species with high-quality rings can still be found in tropical African forests, e.g. *Entandrophragma cylindricum* >500 years old (Détienne *et al.*, 1998). Growth variation in such old trees can be used as a proxy to reconstruct climate far beyond any instrumental record (Nzogang, 2009; van der Sleen, 2014) and these 'low hanging fruits' (in tree-ring analysis terms) should receive more research attention As logging continues and pristine forests become more scarce, such vital records of growth and climate are being lost. It is thus pertinent to further explore the full dendrochronological potential of these species. Additionally, these ring-forming species are among the commercially most important species in Africa (CHAPTER 2) and tree-ring analysis can be used to obtain growth data in a relatively fast way. In this way tree rings can fill the knowledge gap on growth rates needed to evaluate the sustainability of forest management practices (De Ridder *et al.*, 2013b; CHAPTER 3).

6.2 A recipe for finding ring-producing tropical tree species?

Future tree-ring studies would be greatly facilitated if there would be a 'recipe' for finding (high-quality) growth rings in tropical tree species. The presence of growth rings is probably driven by genetic, environmental and physiological factors. The formation of anatomical structures demarcating annual growth may be genetically built in (Alves & Angyalossy-Alfonso, 2000; Eilmann *et al.*, 2014), and some (sub)families show species with high quality rings in all tropical regions, e.g., Meliaceae and Ceasalpinoideae (Dünisch *et al.*, 2003; Schöngart *et al.*, 2006; Vlam *et al.*, 2014b; CHAPTER 2). However, these families also contain species that do not form rings (Détienne *et al.*, 1998; CHAPTER 2), or species that only form rings in the dryer parts of their geographical distribution (Tarhule & Hughes, 2002). Working with species from these families may thus already raise the odds of finding high-quality tree rings. However, these chances may be higher if working in sites with strong seasonality in climate (Alves & Angyalossy-Alfonso, 2000) or with trees growing under more limiting conditions (e.g., at extremes of their distribution ranges, or on well-drained slopes). For species that form tree-rings in wet tropical conditions and that have large geographical distributions (e.g., *Terminalia ivorensis*, *Entandrophragma utile*), we expect that rings will be easier to distinguish under drier, more seasonal climates (Moya & Tomazelo-Filho, 2009; De Ridder *et al.*, 2013a).

A physiological factor that influences the formation of growth ring boundaries is the shedding of leaves. Species that shed their leaves enter a period of cambial dormancy and are therefore most prone to produce annual growth rings (Worbes, 1989; Tarhule & Hughes, 2002). The chance of finding annual growth rings thus increases when working with deciduous tree species. However, tree-ring analysis is also possible for tropical species that are evergreen (Couralet *et al.*, 2010), semi- deciduous (only partially shedding leaves, e.g., *Daniellia ogea*; CHAPTER 2), or brevi-deciduous (leafless for a brief period of time; e.g., *Bracystegia spp*). For these species, however, ring formation should be analysed with care as cambial dormancy may not occur over the entire circumference of the stem or not be annually returning (but note that *D. ogea* showed nice rings while being semi-deciduous, CHAPTER 2).

A clear recipe for finding growth rings in tropical tree species is thus not evident. However, choosing deciduous species from families or genera that show ring-forming species increases the chance of finding rings. Databases that contain descriptions of ring boundaries (e.g., Insidewood; Richter & Dallwitz, 2000) are helpful to finding suitable species. However, ring descriptions in these databases are often either erroneous or ambiguous (see Fact sheets, CHAPTER 2), and should thus be seen as indicatory. Also, tropical tree-ring analysis can be difficult due to the lack of clear ring boundaries in certain species or on certain portions of the stem, e.g., the inner or outer most rings. Additionally, rings may be locally absent in certain parts of the tree's circumference (i.e., wedging rings) and false structures can be present in the wood that resemble ring boundaries (e.g., intra-annual growth variations). These problems are not limited to, but seem to be ubiquitous for tropical species (Worbes, 2002; Rozendaal & Zuidema, 2010). Thus, a simple recipe to finding ring-producing species does not exist. This lacking recipe combined with the difficulties of working with tropical tree rings, implies close scrutiny is needed when assessing ring formation in tropical tree species.

6.3 Ages of tropical trees and prospects for sustainable timber exploitation

Large and old trees play a very important role in the carbon balance of tropical forests. These trees are key drivers of carbon retention and its variation in tropical forests (Saatchi *et al.*, 2011; Slik *et al.*, 2013). In addition, biomass growth in large trees may continuously increase over their entire lifespan (Stephenson *et al.*, 2014). Knowledge on the age of tropical trees is thus important to understand the dynamics and accumulation rates of carbon in tropical forests and to model their carbon retention potential (Galbraith *et al.*, 2013). Tree-ring analysis provides accurate age estimates of trees, which can be used to better understand carbon dynamics and can be used to validate age estimates from permanent plot studies (Martínez-Ramos & Alvarez-Buylla, 1998). Such age estimates, using indirect projections, have ranged from 22 (Martínez-Ramos & Alvarez-Buylla, 1998) to over 1000 years (Condit *et al.*, 1995; Laurance *et al.*, 2004a). On the other hand, ages derived directly from tree rings provided more conservative estimates: maximum ages of ~ 500 year (Détienne *et al.*, 1998; Fichtler *et al.*, 2003; Brienen & Zuidema, 2006a). Tree ages found in this study ranged from ~22 years (*T. ivorensis* of ~80 cm dbh) to a maximum of nearly 300 years (*D. ogea* and *E. utile*), thus suggesting that tree ages in wet tropical forests in Africa are in range, or slightly lower, than those from other tropical (Détienne *et al.*, 1998; Brienen & Zuidema, 2006a; Vlam *et al.*, 2014b), and temperate regions (Loehle, 1988). These results also reaffirm that the high age estimates for tropical trees found in some studies – up to 2000 years (Chambers *et al.*, 1998) – are either highly overestimated or belonging to very exceptional individuals or species.

Tree ages can also be used for forest management purposes, for instance to evaluate and improve (the sustainability of) logging operations. The potential to use tree-rings for this purpose is high for many important commercial species in South-America and Africa (Détienne *et al.*, 1998; Schöngart *et al.*, 2006; CHAPTER 2). This potential is however, lower in Asia, where the most important family of commercial species – the Dipterocarpaceae – generally lack visually detectable rings (Poussart *et al.*, 2004; Baker *et al.*, 2005; Ohashi *et al.*, 2009).

Assessing the sustainability of forest exploitations is complex and depends first on defining sustainability and requires clarity about what is to be sustained (Putz *et al.*, 2012). Different elements of sustainability have been suggested and assessed: maintenance of forest cover, the retention of biodiversity or of carbon stocks, or achieving sustained logged volumes over subsequent logging cycles. Obviously, financial sustainability often precedes these elements. Also, several techniques exist to measure and evaluate each of these elements. All these dimensions imply that evaluating sustainability is complex and no consensus exists yet on the best definition of sustainability.

In CHAPTER 3 of this thesis, we integrated growth data from tree-rings with logging inventory data to forecast whether timber yields can be sustained in the next harvest round for four timber species in Cameroon. Yields at the next harvest, simulated using the standard 30-year logging cycle and under the maximum logging intensity, were predicted to reduce strongly for all species: between 23.9% and 36.0%. Additionally, these simulations also showed that volume ingrowth from trees that were below MCD in the first harvest accounted for only ~10% of the total yield in the next harvest (CHAPTER 3). Doubling the logging cycle length resulted in higher yields and commercial ingrowth, but did not result in yields being sustained (remained under 48% for all species). Using species specific field-based logging intensities lead to remarkable increases in yields: between 52-73% for the less valuable timber species. For the species with the highest commercial value, *E. utile*, field-based logging intensities were similar to the maximum allowed and thus using them did not result in yield increases.

These low yields clearly suggest that volumes exploited at the first logging round will not be sustained in the following cycle, even for a fast growing species such as *T. ivorensis*. Declining yields are in line with other studies summarized in Putz *et al.* (2012), and are considered almost inevitable, as the remaining trees cannot grow back the volume accumulated over many years within current (or reasonable) logging cycle lengths. This amount of accumulated volume over the years is also called the 'primary forests premium' (cf. Keller *et al.*, 2007). For the species studied here, trees often grew more than 50 years between reaching the MCD and being logged (e.g., up to 180 years for *E. utile*, CHAPTER 3), suggesting a large primary forest premium for these species, and consequently, supporting the suggestion that yields will be lower in the next logging cycle.

Most simulations of future logging yields are limited to one or two logging cycles, as accurate data on tree regeneration, mortality and growth after logging are scarce. Many of the exploited species occur at low densities (<1 adult tree per ha) and show little regeneration (Schulze, 2008). Ultimately, the sustainability of logging will depend on the successful regeneration of these rare species and measures such as enrichment planting or tending of natural regeneration may be needed to guarantee future timber stocks (Schwartz *et al.*, 2013). Additionally, other silvicultural measures may be taken to enhance the growth of future crop trees, such as liberating them from lianas (Peña-Claros *et al.*, 2008) and thinning of the forest after logging (Gourlet-Fleury *et al.*, 2013). However, depending on their intensities, these silvicultural measures may be expensive (Mostacedo & Fredericksen, 1999) and long-term monitoring is required to evaluate their effectiveness and economic viability (Peña-Claros *et al.*, 2008; Gourlet-Fleury *et al.*, 2013). Ideally, such evaluations should also include the demographic consequences of logging (Verwer *et al.*, 2008; Free *et al.*, 2014; Grogan *et al.*, 2014), using population models that incorporate the effects of logging on the regeneration, mortality and growth rates of a tree species. One of the possible approaches to do so is to use integral projection models (cf.

Zuidema *et al.*, 2010) to combine the long-term growth data from tree-rings with results from monitoring of these silvicultural measures (Verwer *et al.*, 2008). These models accurately incorporate the variation in vital rates (e.g., growth, reproduction, survivor) with a species and can be used to accurately predict future population growth. For a large number of tropical timber species tree-ring data are already available that can be used in such simulations (see Table 6.1 for a non-exhaustive list).

Although species-specific yield declines may be inevitable, care is needed avoid forest use becomes financially unsustainable. Forests with reduced financial value due to forest-level overexploitation of timber resources run a higher chance to be converted to other non-forest land uses. Ideally, measures should be taken to ensure logging occurs more sustainably. Increasing logging cycle lengths or minimum cutting diameters (MCD), or decreasing logging intensities, are some of these measures. Increasing logging cycle lengths, however, requires long-term commitment and investments from logging companies. These commitments are hampered by the unstable politico-economical environments in many tropical countries. Thus, increasing the MCD or reducing logging intensities remain as more viable options. That actual intensities in the field for three of the species are lower than the maximum allowed, and projected yield higher, is hopeful. The lower field-based intensities imply that the primary forest premium is 'spread' over subsequent logging cycles, increasing the long-term financial viability of timber exploitation. Timber exploitation throughout the tropics usually focusses on only a handful of these high-value species (Holmes *et al.*, 2002; Ruiz-Pérez *et al.*, 2005), and we expect that for most of them logging intensities are consistently high. Increasing MCD is then crucial to not overexploit these species. Additionally, shifting exploitation focus to 'lesser known timber species' is fundamental to maintain forest-level timber yields (Putz *et al.*, 2012). Any measures to stimulate the use of alternative species are highly encouraged (e.g., ITTO, 1990), and these shifts in exploitation should ideally already be implemented in current harvest.

Table 6.1: List of commercial tree species from moist and wet tropical forests for which growth rates have been measured from tree-rings (>25 individuals measured). These growth data can be used with demographic models to increase the accuracy of timber yield simulations and to assess the consequences of logging on tree populations.

Species name	Family	Country	# trees	Reference
Amburana cearensis	Fabaceae	Bolivia	36	Brienen and Zuidema (2006a)
Cedrela odorata	Meliaceae	Bolivia	60	Brienen and Zuidema (2006a)
Cedrelinga catenaeformis	Fabaceae	Bolivia	33	Brienen and Zuidema (2006a)
Terminalia superba	Combretaceae	Democratic Republic Congo	60	De Ridder *et al.* (2013b)
Terminalia superba	Combretaceae	Ivory Coast	29	De Ridder *et al.* (2013b)
Aucumea klaineana	Burseraceae	Gabon	83	Détienne *et al.* (1998)
Entandrophragma cylindricum	Meliaceae	Central African Republic	104	Détienne *et al.* (1998)
Entandrophragma utile	Meliaceae	Central African Republic	59	Détienne *et al.* (1998)
Triplochiton scleroxylon	Malvaceae	Central African Republic	101	Détienne *et al.* (1998)
Cedrela odorata	Meliaceae	Brazil	64	Dünisch *et al.* (2003)
Swietenia macrophylla	Meliaceae	Brazil	47	Dünisch *et al.* (2003)
Tabebuia barbata	Bignoniaceae	Brazil	40	Da Fonseca Júnior *et al.* (2009)
Vatairea guianensis	Fabaceae	Brazil	40	Da Fonseca Júnior *et al.* (2009)
Microberlinia bisulcata	Fabaceae	Cameroon	46	Newbery *et al.* (2013)
Entandrophragma candollei	Meliaceae	Cameroon	41	Nzogang (2009)
Entandrophragma cylindricum	Meliaceae	Cameroon	75	Nzogang (2009)
Entandrophragma utile	Meliaceae	Cameroon	25	Nzogang (2009)
Erytrophleum ivorense	Fabaceae	Cameroon	52	Nzogang (2009)
Milicia excelsa	Moraceae	Cameroon	34	Nzogang (2009)
Cedrelinga catenaeformis	Fabaceae	Bolivia	29	Rozendaal *et al.* (2010b)
Clarisia racemosa	Moraceae	Bolivia	35	Rozendaal *et al.* (2010b)
Peltogyne cf. heterophylla	Fabaceae	Bolivia	29	Rozendaal *et al.* (2010b)

Table 6.1: Continued

Species name	Family	Country	# trees	Reference
Piranhea trifoliata	Euphorbiaceae	Brazil	28	Rozendaal *et al.* (2010b)
Anogeissus leiocarpus	Combretaceae	Benin & Ivory Coast	60	Schöngart *et al.* (2006)
Daniellia oliveri	Fabaceae	Benin & Ivory Coast	45	Schöngart *et al.* (2006)
Diospyros abyssinica	Ebenaceae	Benin & Ivory Coast	25	Schöngart *et al.* (2006)
Pterocarpus erinaceus	Fabaceae	Benin & Ivory Coast	25	Schöngart *et al.* (2006)
Ilex inundata	Aquifoliaceae	Brazil	47	Schöngart (2008)
Luehea cymulosa	Malvaceae	Brazil	34	Schöngart (2008)
Piranhea trifoliata	Euphorbiaceae	Brazil	74	Schöngart (2008)
Garcinia brasiliensis	Clusiaceae	Brazil	80	da Silva Marinho *et al.* (2013)
Hevea spruceana	Euphorbiaceae	Brazil	25	da Silva Marinho *et al.* (2013)
Schizolobium amazonicum	Fabaceae	Bolivia	100	van der Sleen, *unpublished*

The measures mentioned above may however, lead to a dilemma. Lowering timber exploitation at the first harvest may lead to sustained yields in the future, but will also diminish current financial gains from the forest, possibly making logging economically unfeasible. On the other hand, high yields now may lead to economically unfeasible logging in the near future, thus only postponing de devaluation of forests' value. If exploiting the forest is economically unattractive, the risk of conversion to non-forest land uses increases (e.g., to palm-oil plantation; Oakland Institute, 2012). Avoiding such conversion, and thus maintaining forest cover, is one of the highest priorities to conserve tropical forests in the future (Edwards *et al.*, 2011).

Clearly, a simple solution for this dilemma is not at hand. The proposed measures will lead to lower timber production or may reduce revenue for the logging companies (e.g., through increased exploitation costs, or lower timber prices of alternative species). Ensuring financial viability of logging in the future may require additional compensatory measures to exacerbate the lower revenues of applying such measures. Although prices of certified timber (i.e., from well-managed forests) are usually higher than of conventional timber, they have until now remained too low to induce significant shifts in forest management practices (Meijaard *et al.*, 2005). Prices of timber may inevitably increase in the near future, as tropical timber production is expected to decline in the near future (Shearman *et al.*, 2012), which may possibly increase the financial viability of logging. However, to further stimulate sustainable timber production, measures such as payment for ecosystem services of tropical forests may also be required. Logged forests still retain large stocks of carbon (Gourlet-Fleury *et al.*, 2013; Sist *et al.*, 2014), and carbon recovery can be relatively fast, especially if exploitation follows reduced impact logging protocols (RIL; West *et al.*, 2014). The retention and fast recovery of carbon stocks from logged forests imply that carbon-offset schemes (e.g., REDD+) can be applied to compensate logging companies for wood volumes not extracted (Loarie *et al.*, 2009).

6.5 Detecting growth changes in the tropics, what can tree rings tell us?

Most carbon in forests worldwide is stored in the form of wood and tree-rings register the variation in wood growth over time. Wood increment represents the final balance of photosynthate production in the leaves and its allocation of carbon to diameter growth. Photosynthates generated in the leaves are controlled by the availability of light, water, CO_2 and nutrients, whereas the allocation of photosynthates to wood is related to plant strategies (Kuptz *et al.*, 2011), and to water, nutrients and carbon availability (Trouet *et al.*, 2012; Chen *et al.*, 2013). Several lines of evidence show that wood growth has the lowest priority in carbon allocation of trees (Sala *et al.*, 2012; Richardson *et al.*, 2013), in particular during periods of (environmental) stress, when carbon allocation is prioritized to reserves, i.e., non-structural carbon (Smith & Stitt, 2007), possibly as a strategy to increase survival chances (O'Brien *et al.*, 2014). Wood having the lowest carbon-allocation priority implies that wood increment (i.e., diameter growth) shows strong annual variation between favourable and adverse growing conditions(Rocha, 2013). The width of tree rings thus registers environmental signals, making ring-width a good proxy for climatic variations, and this has led to the wide application of tree-ring studies in climate reconstructions (e.g., Esper *et al.*, 2002; Schöngart *et al.*, 2006).

Ring width is also a good proxy for the carbon sequestration of trees (Bouriaud *et al.*, 2005). Due to the long-term coverage of growth variability, tree-ring analysis can thus also be used to assess long-term changes in tree (biomass) growth, that can be related to the reaction of (tropical) forests to climatic changes. Despite the potential for long-term analyses of growth change, tree rings have only rarely been applied for this purpose in the tropics (Rozendaal *et al.*, 2010b; Nock *et al.*, 2011). In CHAPTER 5 of this thesis, we assessed these long-term growth change using tree-rings measured across three tropical locations. Detecting these long-term trends using tree-rings is, however, not straightforward and has restrictions that need to be accounted for. Next, we discuss several of these restrictions and possible adaptations in sampling and analysis that we believe will help to overcome them.

The first restriction emerges from classical sampling strategies and analyses methods in dendrochronology. Classical dendrochronological studies (in temperate regions) usually focus on long-term climate reconstructions and therefore concentrate sampling on the largest and oldest trees in a community and preferably those growing under extremely limiting conditions (e.g., on mountain slopes). Then, of these very old samples, only those that show a common growth signal (i.e., that crossdate well to one another) are chosen for further analysis. Trends in growth are then computed on these subsets of well-crossdating old trees, using methods that are arbitrarily chosen, based either on the method yielding the 'best results' (e.g., highest inter-series correlations; Holmes, 1983) or based on *a priori* assumptions (e.g., Silva *et al.*, 2009). This workflow results in long data series that are very valuable for climatic reconstructions. These studies usually cover long timespans (up to several centuries; Esper *et al.*, 2002)2002 and many are based on large amount of measured trees, distributed over large areas. These climatic reconstructions are therefore robust and these climatic reconstructions are pivotal to understand growth variations in the last millennia. However, the focus on only large old trees combined with the different steps of 'subsetting' data, makes these analysis flawed when detecting long-term growth trends. This workflow causes biases to arise especially for the more recent periods of analysis. These more recent periods are important if assessing climate change effects on tree growth, and it is therefore important to account for these limitations and adapt sampling and analysis protocols.

To use tree-rings in assessing the carbon dynamics of the world's forests, several changes in methods are required: sampling trees in more 'normal' forests (i.e., with less extreme climates) and following the natural size-distribution of a species (cf. Nehrbass-Ahles *et al.*, 2014), including non-crossdatable samples in the analysis of trends, and applying several growth-trend detection methods simultaneously (CHAPTER 4). Shifting to normal forests will allow to infer conclusions on long-term growth changes over large areas, while still allowing for climate reconstructions spanning more than a century (Schöngart *et al.*, 2006), to several centuries (Dunwiddie & LaMarche, 1980). More emphasis is also needed on tropical tree-ring analysis, for instance by focussing on species that are known to form annual rings (Zuidema *et al.*, 2012) or on widespread and abundant species (i.e., "hyperdominant" species; Ter Steege *et al.*, 2013). By sampling trees in size classes following their natural distribution in the field, the effect of several (sampling) biases can be avoided or at least reduced (Brienen *et al.*, 2012a; Nehrbass-Ahles *et al.*, 2014). Standardising sampling designs would also allow the comparison of growth changes between different species and sites, both within and across forest biomes (e.g., CHAPTER 5). Samples that cannot be crossdated may yield lower quality growth data, as wedging and missing rings cannot be detected with certainty and dating of all rings in these samples is thus not absolute. Therefore, these samples cannot be used for climatic reconstructions. Notwithstanding, these samples represent ecologically relevant individuals – those that show different or limited growth conditions – and including these samples is therefore essential when assessing growth changes over time. Finally, we showed that the choice of trend-detection method influences the detection of trends (CHAPTER 4). Each of the methods assessed has specific limitations that need to be accounted for when analysing trends in growth (Table 4.2) and all depend of arbitrary decisions at some point in the analysis. However, we also show that methods are often consistent in detecting trends and we recommend combining methods for a robust analysis.

6.6 Integrating approaches to assess tropical forest changes

Tree-ring analysis in the tropics is still in in its early stages and only recently more attention has been given to issues that may arise from sampling design (Nehrbass-Ahles *et al.*, 2014), biases related to the nature of tree-ring data (Brienen *et al.*, 2012a) and from the choice of trend-detection methods (CHAPTER 4). Working with tree-rings in the tropics has its limitations, some of which apply specifically to working in the tropics (e.g., only a subset of species forms rings), whereas others apply to tree-ring analysis in general (e.g., methodological limitations). Yet, in spite of the limitations, well-designed tree-ring studies open a window to the past and provide long-term, species-specific information on growth changes in tropical forests. Such long-term, species-specific information is urgently needed if we wish to understand how tropical forests are reacting to climatic changes. Finally, there are several methods to detect (growth) changes in tropical forests (see Textbox 6.1), but none provide a panacea for resolving the discussion whether tropical forests are changing: all methods fill knowledge gaps while also having limitations. Combining different methods may allow for a cross-validation of results and tree-ring analysis can be used to place results in a long-term perspective. There are several possibilities of combining the strengths of tree-ring analysis with other existing methods, we will discuss four of them.

An essential first step, is to better understand the cycles of cambial activity and wood growth (and anatomy) in tropical species. Studying intra-annual changes in wood formation can for instance be done by taking periodic wood samples using micro-cores (cf. Die *et al.*, 2012; Pumijumnong & Buajan, 2012). These cycles form the basis to understand tree growth – and thus the basis for tree-ring analysis – and are directly related to cycles of biomass increment in forests. Thus, understanding the drivers of wood growth is key to better understand the dynamics of biomass growth and storage in tropical forests. Cycles of cambial activity and the drivers for its onset and variation need to be studied in relation to fluctuations in local environmental conditions, e.g., precipitation (Die *et al.*, 2012) and in tree phenology, e.g., leaf flushing (Wagner *et al.*, 2013). Phenology can be measured locally, by periodical registration of leaf characteristics, or can be measured remotely, by relating it to remotely sensed phenological indices, e.g., NDVI (Pennec *et al.*, 2011). Furthermore, cambial activity variation should also be coupled to measurements of carbon fluxes (Rocha *et al.*, 2006; Babst *et al.*, 2014b) (Belmecheri *et al.*, 2014). For instance using Eddy-covariance towers, see Textbox 6.1). Coupling cambial activity, tree phenology and large scale analyses of carbon fluxes can be used to better understand how carbon sequestration is related to cycles of wood formation and its onset. Carbon sequestration of tropical forests may vary strongly from year to year (Gatti *et al.*, 2014) and tree-ring chronologies may be used as proxy to reconstruct (variation in) carbon sequestration over time. Additionally, a better understanding of the relationship between tree growth and carbon sequestration helps interpreting and extrapolating findings on long-term changes in tree growth (CHAPTER 5).

Second, tree-ring analysis can be used to put growth changes detected in monitoring plots into a long-term context. Tree-ring analysis can provide valuable insights on the climate sensitivity of tree growth (Brienen & Zuidema, 2006a; Vlam *et al.*, 2014b) that can be used to explain growth changes found in plots. Also, tree ages derived from rings can be used to assess whether large-scale disturbances have taken place in an area (Baker *et al.*, 2005; Vlam, 2014). Such large scale disturbances may have occurred long before plots were installed and, leaving an imprint on the dynamics of plots that may affect growth trends detected in plot data (Wright, 2005) and from rings (Vlam, 2014). Identifying such disturbances is thus important when interpreting detected changes. Indications for such past disturbances can be derived from tree ages and its temporal and spatial aggregation (Vlam, 2014), and when performed in or near monitoring plots, can help identifying whether disturbance drives growth changes found in plots. Data from monitoring plots can also be used to help interpret results from rings, for instance, mortality and regeneration data from plots can be used to assess the underlying mechanisms of several biases that may affect the detection of growth trends (e.g., "juvenile selection" bias, CHAPTER 5).

Third, tree-ring analysis can be integrated to *in situ* experimental approaches (e.g., rainfall exclusions, heating, CO_2 fertilisation; Table 6.2), to provide a long-term baseline to which the effects of such experiments can be tested. With this baseline, changes in growth rates of trees as a consequence of the experimental treatment can be tested using rings. Likewise, the analysis of isotopes in the wood can be used to assess the physiological consequences of such experiments. For instance, analysis of ^{13}C isotopes in rings can be used to analyse changes in the intrinsic water use efficiency (iWUE) of trees (Nock *et al.*, 2011; van der Sleen, 2014) that are expected to occur in the drier experimental conditions (Nepstad *et al.*, 2007) or under the addition of CO_2 to the atmosphere (Tollefson, 2013).

Finally, results from these different methods (i.e., tree-rings, plots, remote sensing, etc.) need to be combined with modelling approaches to better simulate climate change effects on tree growth. Growth data from tree-rings, combined with the results from experimental approaches and plot data, can be used to parameterize individual based models (Sterck & Schieving, 2011; Fyllas *et al.*, 2014) to simulate the (combined) effect of changes in precipitation, CO_2 concentrations, temperature, and nutrients on the growth and survival of trees. Such integrative approaches can also be used to assess large-scale responses of tropical forests to climatic changes e.g., using Dynamic Global Vegetation Models (DGVMs; Sitch *et al.*, 2008). For such large-scale approaches, the long-term and species-specific growth data from tree rings may be very valuable, especially if combined with information on physiological changes that is stored in the wood (e.g., iWUE; Nock *et al.*, 2011; van der Sleen, 2014). At the moment, most DGVMs predict increases in the biomass of tropical forests as a consequence of CO_2 fertilization (Sitch *et al.*, 2008; Huntingford *et al.*, 2013), thus suggesting that tropical forests will act as carbon sinks in the coming century, therefore mitigating climate change.

Detecting whether changes have or are taking place in tropical forest growth is challenging (Bowman *et al.*, 2013), and every method used to assess these changes – tree-ring analysis, monitoring plots, etc. – has limitations and biases (Phillips *et al.*, 2004; Brienen *et al.*, 2012a; Chambers *et al.*, 2013). Understanding the drivers of these changes is possibly even more challenging – and arguably even more important – than only detecting them. We argue that only by integrating approaches will it be possible to assess the causes of recent changes in tropical forest growth and dynamics. Integrative approaches are being applied in temperate forests (Girardin *et al.*, 2008; Babst *et al.*, 2014b; Belmecheri *et al.*, 2014), but are still lacking in the tropics. Ultimately, tree-ring analysis can be used in these integrative approaches to place results from short-term measurements and experiments into a long-term perspective.

Text box 6.1 – Methods to measure and monitor tropical forests

Tropical forests store and process large quantities of carbon (Bonan, 2008). Measuring this carbon pool and assessing the divers of its dynamics is important to understand the role tropical forests play in the earth's carbon cycle and to assess whether and how tropical forests will react to predicted climate changes in the future. The importance of understanding these dynamics has led to the development and application of several methods to monitor and detect changes in tropical forests. In this textbox we briefly introduce each method and its main products, and discuss some of their variations. Figure 6.1 provides a schematic overview of the methods and Table 6.2 an overview of their primary use, strengths and limitations.

1. Carbon flux measurements

The absorption and emission of carbon by tropical forests, and how it varies over time, can be estimated by measuring the fluxes of carbon dioxide (CO_2) and other gasses in the atmosphere above these forests. Common methods of measuring CO_2 fluxes are Eddy-covariance towers (Saleska *et al.*, 2003), airborne CO_2 measurements (Gatti *et al.*, 2014), and more recently satellite based estimates of atmospheric CO_2 concentrations (Basu *et al.*, 2013). The Eddy covariance method measures vertical transport of CO_2 in the atmosphere above the forest canopy. Fluxes are computed from three-dimensional measurements of air transport (using ultrasound anemometers) combined with high-frequency sampling (5 to 10 s^{-1}) of fluctuations in carbon dioxide concentrations. By accumulating these measurements, the general fluxes of carbon dioxide of the forest (absorption and release) can be computed (usually done per 30 minute intervals). Airborne measurements use small aircraft to take air sample profiles from just above the forest canopy (~300m high) up to the mid troposphere, at ~9 km (Stephens *et al.*, 2007). The concentrations of CO_2 and other gases, such as carbon monoxide, are then analysed in these air samples. Samples are taken on a monthly basis (Gatti *et al.*, 2014), and when performed over different areas, such airborne measurements allow assessing carbon fluxes at regional (ca. 10^5–10^6 km^2) to global scales (Stephens *et al.*, 2007). Since 2009, a Japanese satellite (GOSAT) tracks total column atmospheric CO_2 concentrations worldwide. These space-based measurements can also be used to estimate CO_2 fluxes (Basu *et al.*, 2013), have a large spatial coverage and provide information not available from the sparse surface network, albeit with a lower accuracy (Buchwitz *et al.*, 2007).

2. Remote sensing

Remotely sensed measurements (i.e., from satellite instruments or from airplanes) can be used to analyse vegetation cover and its changes, to assess the productivity of tropical forests and to estimate forest cover biomass. Optical satellite observations have been used to determine the area of land covered by tropical forests (Mayaux *et al.*, 2013) and to detect forest disturbances (Espírito-Santo *et al.*, 2014)2014 and land-cover change (Hansen *et al.*, 2013). By measuring changes in certain spectral ranges (e.g., NDVI uses 'greeness' of images), satellite images can be used to estimate photosynthetic activity of the vegetation and to assess seasonal and interannual cycles of forest productivity (Brando *et al.*, 2010). Using lasers to scan the earth surface, satellite lidar (laser imaging, detection and ranging) has been used to measure canopy heights and forest structure to estimate tropical forest above ground biomass globally (Drake *et al.*, 2002; Saatchi *et al.*, 2011). Such lidar measurements can also be performed using small airplanes or from the ground. Airborne lidar provides similar measurements as satellite lidar, but measures smaller areas with much higher resolution (Asner *et al.*, 2012). Ground-based lidar have only more recently been used and provide measurements of the structure of forests from the ground (Calders *et al.*, 2014), allowing to build two- and three-dimensional models of the structure of the forest. Remotely sensed data allow for estimating productivity and biomass of tropical forests over large areas, but need to be calibrated with field data to be scaled up (Mascaro *et al.*, 2011) and are prone to several artefacts in measurements (Morton *et al.*, 2014).

3. Experimental approaches

Experiments allow to directly measure the effects of (expected) climatic changes on plant processes and growth. Experimental studies on the level of leaves (Slot *et al.*, 2014)2014 and seedlings (Way & Oren, 2010) are relatively common and have provided a good understanding of plant physiological responses (e.g., photosynthetic rates, respiration) to changing environmental conditions, such as drought and increasing CO_2 concentrations (Huang *et al.*, 2007). On the other hand, manipulative experiments on the tree or community level – crucial to upscale leaf-level responses and to understand forest-level changes – are rare (Zuidema *et al.*, 2013). Examples of such large-scale approaches in on tropical forest include experiments on: the effect of fire (Brando *et al.*, 2014), drought (Nepstad *et al.*, 2007; da Costa *et al.*, 2014) and nutrient addition (Alvarez-Clare *et al.*, 2013). Maintaining these experiments over several years to decades is crucial to understand possible adaptations to and the long-term effects of different changing conditions on (the growth of) plants. Integrating different effects will be even more interesting, as these integrative effects on ecosystem level are unknown or have only poorly been studied (Zuidema *et al.*, 2013). Experiments for assessing the effects of CO_2-addition in humid tropical forests are on the way (Tollefson, 2013) and will fulfil an important knowledge gap on topical forest responses to higher CO_2 concentrations.

4. Forest monitoring plots

Monitoring plots are fixed forest areas in which diameter growth, mortality and regeneration of all trees (above a diameter threshold) are monitored periodically, usually every one to five years. In the tropics, these plots are usually ~1 hectare in size, but studies with larger plots also exist (e.g., CTFS; Gourlet-Fleury *et al.*, 2013). In many countries monitoring plots were initially installed to measure forests for timber exploitation or to measure biodiversity but are now also increasingly used to assess forest biomass stocks and growth. Most measurements in these plots usually cover a few years (Lewis *et al.*, 2009b) to a couple of decades (Gourlet-Fleury *et al.*, 2013). Plot data provide a complete assessment of changes in forests as they include growth, mortality and regeneration of trees, but also register forest dynamics, such as disturbances or shifts in species composition. Monitoring plots have been crucial for reporting changes in tropical forest biomass, growth and dynamics (Phillips *et al.*, 2002; Lewis *et al.*, 2009a). However, due to their relatively low measurement resolution, plot studies have so far contributed little to identify the causes of the observed (biomass) changes, but see Clark and Clark (2011). More recently, different plots have been united in large networks (e.g., AfriTron, CTFS) to assess changes in biomass over large areas of forests and over longer periods of time (Phillips *et al.*, 2008; Lewis *et al.*, 2009b).

5. Tree-ring analysis

Tree-ring analysis is increasingly being used in tropical forests to measure the growth and ages of tropical trees (Worbes, 2002; Rozendaal & Zuidema, 2010). Tree-ring data can be used for climate reconstructions (Schöngart *et al.*, 2006), forest ecology (Worbes *et al.*, 2003) and management (Schöngart, 2008). Tree-rings are formed (annually) by a subset of tropical tree species (~25 - 40% of species form rings) and the annuality of ring formation needs to be ascertained, especially when working with new species. Measuring tree-rings requires specialized knowledge on wood anatomy, to identify the anatomical structures that demarcate ring boundaries. Although restricted to the subset of species forming rings and requiring specialized knowledge, tree-ring analysis is the only method that provides century-long growth data that cover relevant timespans when assessing the effects of recent climatic changes on tropical trees (i.e., the last ~150 years, since the industrial revolution). Tree-rings have been used to analyse growth changes in tropical tree species (Rozendaal *et al.*, 2010a; Nock *et al.*, 2011). Additionally, stable isotopes in the wood of trees, can be used as archives of physiological (Nock *et al.*, 2011) and environmental signals (Brienen *et al.*, 2012b). Isotope measurements can be used to provide a contextual information for the growth changes detected from tree rings on the same trees (Nock *et al.*, 2011; van der Sleen, 2014).

Text box 6.1 – Continued

6. Modelling approaches

Modelling approaches can be used to integrate results from forest monitoring, experiments, and tree-rings to predict tree and forest responses to climatic changes over different temporal and spatial scales. Different models exist that simulate growth and development on individual- or species level (Sterck *et al.*, 2006), that model the growth and development of populations (Uriarte *et al.*, 2012) or of entire ecosystems (Sitch *et al.*, 2008). Individual level simulations can be used to understand the carbon allocation in trees (Sterck & Schieving, 2011), to assess forest productivity and its climatic drivers (Fyllas *et al.*, 2014) and to predict how trees react to integrated effects of climatic changes on plant growth (van Loon *et al.*, 2014). Population level models can be used to assess the demographic consequences of expected climatic changes, such as population growth, changes in recruitment rates and expected tree lifespans. At ecosystem level, models can integrate species traits with predicted climatic changes, to assess large-scale responses of tropical forests to climate change (Huntingford *et al.*, 2013; Fyllas *et al.*, 2014).

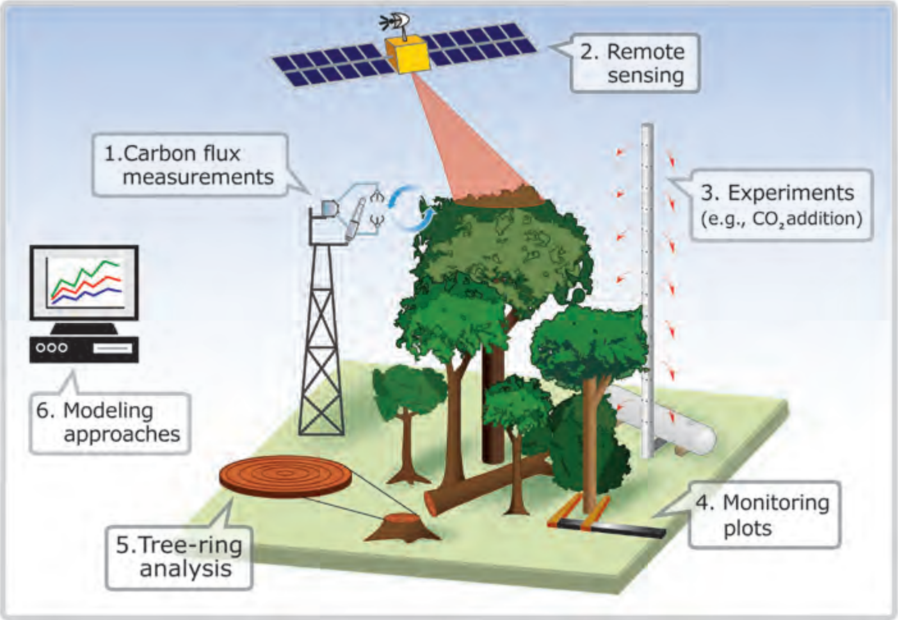


Figure 6.1. Schematic overview of the most important methods used for measuring and monitoring tropical forest biomass: 1. Carbon Flux Measurements; 2. Remote sensing techniques; 3. Experimental approaches; 4. Forest Monitoring plots; 5. Tree-ring analysis and; 6. Modelling approaches. See Textbox 6.1 for further explanation of the models and Table 6.2 for an overview of their strengths and limitations.

6.7 Changing tropical forest growth rates and biomass

One of the key results in this thesis are the growth reductions found for most of the species analysed in CHAPTER 5. These long-term growth reductions may have important demographic consequences for these species, potentially leading to shifts in the species composition of tropical forests. These shifts may be already happening in tropical forests (Laurance *et al.*, 2004b) and the lacking regeneration observed for many of the species studied here (Vlam, 2014) also points in this direction. Growth reductions indicate worsening growth conditions, possibly reflecting the negative effect of temperature increases on tree growth. However, other causes for these reductions cannot be excluded, such as recovery from large-scale disturbances or (anthropogenic) changes in forest dynamics.

No strong growth changes were found when analysing aggregated trends on site level and across sites: aggregated growth reductions were detected for the Thai site and across sites but these reductions were weak (i.e., non-conclusive). These findings do, however, contrast growth increase expected to occur if tree growth is stimulated by increased ambient CO_2. This discrepancy is on the one hand rather surprising, considering that there are strong indications that increased ambient CO_2 has led to higher intrinsic water-use efficiency in tropical trees (Nock *et al.*, 2011; Peñuelas *et al.*, 2011; van der Sleen, 2014). On the other hand, in spite of the increased iWUE, no concurrent increases in tree growth were observed in those studies. Additionally, free Air CO_2 Enrichment (FACE) experiments under field conditions have shown that elevated CO_2 initially stimulates growth, but that plants acclimate and growth increases are not sustained (Norby, 2011). Furthermore, the additional photosynthetates produced due to higher ambient CO_2 may not be invested in wood production, but rather on non-structural carbon, reproduction or in growth of other plant parts (Sala *et al.*, 2012; AbdElgawad *et al.*, 2014). Finally, accelerated growth may also be inhibited by the negative effect of increased temperature on growth (Feeley *et al.*, 2011) or may be limited by nutrient availability, e.g. nitrogen of phosphorus (Alvarez-Clare *et al.*, 2013). Taken together, these results suggest that a long-term CO_2-fertilization of the diameter growth of tropical trees is absent. If growth of tropical forest trees is indeed decreasing – or at least not changing – this implies that DGVM projections of the carbon dynamics of tropical forests overestimate the carbon sink potential of these ecosystems (Sitch *et al.*, 2008; Huntingford *et al.*, 2013).

Table 6.2 The most important methods used for measuring and monitoring tropical forest biomass and how it is affected by climate change. Adapted from Babst *et al.* (2014a). Provided are the method's main characteristics; timespan covered by measurements (and their temporal resolution); principal products delivered by each method; and their strengths and limitations. Numbers correspond to those in Textbox 6.1 and Figure 6.1.

#	Data source	Temporal covered (resolution)	Principal products	Primary use	Advantages	Limitations
1	Carbon flux measurements (airborne; Eddy-covariance towers)	Several years (half-hourly)	Large scale net carbon balance + derivatives (e.g., primary productivity; TER)	Terrestrial carbon dynamics	High temporal resolution; integral carbon budgets; large areas; network measurements (e.g., FLUXNET)	Requires highly specialized infra-structure and training; Short-term records; gaps in data (e.g., in bad weather; at night)
2	Remote sensing (satellite imagery; terrestrial or airborne LiDAR)	Point measurements; Years to decades (bi-weekly to monthly)	Vegetation cover and indices (e.g., NDVI); Estimates above ground biomass; Three dimensional forest structure (terrestrial LiDAR)	Quantify land-use changes; photosynthesis strength and cycles; stand structure and biomass	Covers large areas; multispectral information; accurate 3D estimates biomass forest (LiDAR)	Satellite images requires daytime and cloudless conditions; indirect estimates (needs corroboration with field measurements); cost-; labour- and data intensive
3	Experiments: e.g., artificial drought; CO_2 addition (FACE)	Several years (hourly to yearly)	Reaction plants to changing conditions (CO_2; drought); changes in physiology; growth rates; phenology	Direct understanding effects environmental changes on plants	Effect changes can be measured directly ; both individual and stand level reactions (e.g, on growth) can be measured	Expensive and labour intensive, limiting size and replication of experiments
4	Forest monitoring plots	Years to decades (annual to five-year)	Diameter growth; height growth; mortality and regeneration rates; stand dynamics	Forest management; growth and biomass monitoring; biodiversity measures	Ease and low costs of application; present in most countries; large networks measurements (e.g., AfriTRON, CTFS)	Most plots short term (<30 yrs); relatively small (usually 1 ha); needs periodic measurements; old plots installed with different purposes leading to biases

5	Tree rings	Decades to centuries (annual)	Diameter growth; wood anatomical features; stable isotopes ratios ($\delta^{13}C$; $\delta^{18}O$; $\delta^{2}H$; $\delta^{15}N$)	Climate reconstructions; ecology; physiology; management	Long-term data; life history of trees with annual resolution; species specific; records environmental conditions	Limited to species with rings; requires specialized training; several biases; limited to growth data (no direct regeneration and mortality data)
6	Modelling approaches	Variable from days to centuries (daily to yearly)	Individual tree growth models; carbon cycle dynamics (GDVMs); climate change (e.g., IPCC 2013); NPP	Understand and predict climate change and responses of tree / vegetation to it.	Use to generalize measurements and understand theories and processes; flexible input and temporal scales	Limited to quality input data (e.g., plant functional types, climate sensitivity); different models give divergent output (use average models?)

Abbreviations: NDVI normalised difference vegetation index; LIDAR light detection and ranging; GPP gross primary production; NPP net primary production; DGVM dynamic global vegetation modelling; IPCC Intergovernmental Panel on Climate Change; TER terrestrial ecosystem respiration; FACE Free-air concentration enrichment.

Example references: 1. Drake *et al.* (2002), Calders *et al.* (2014); 2. Gatti *et al.* (2014), Vourlitis *et al.* (2011); 3. Phillips *et al.* (1998), Lewis *et al.* (2009b); 4. Nepstad *et al.* (2007), Brando *et al.* (2014), Tollefson (2013); 5. Nock *et al.* (2011), Rozendaal *et al.* (2010a); 6. Sitch *et al.* (2008), Sterck and Schieving (2011)

6.8 Outlook

In this thesis we showed that tree-ring analysis is possible for several tree species growing in a Central African wet tropical forest. The potential to use tree-ring analysis to acquire lifetime growth data of trees seems to be considerable throughout the tropics. These lifetime growth data were then used to show that exploited volumes of timber for four tree species in Cameroon may not be sustained in the following cutting cycle. Such calculations can be used as a basis to implement more sustainable forest management practices in tropical forests. Finally, we show that the growth rates for several species is declining in tropical forests but that aggregated across sites no strong growth trends are present.

If one message becomes clear from this thesis it is that long-term data are crucial to enhance the management of tropical forests and to understand long-term changes happening in these forests. Tropical forests are highly complex ecosystems as they harbour a large amount of interacting tree species. Analysing species-level changes in growth, survival and regeneration of trees thus forms the basis to assess and interpret community-level changes. Such species-level analysis are however rare. To our knowledge, only one study using forest monitoring data has assessed these trends (Feeley *et al.*, 2011). Tree-rings allow conducting species-specific and long-term assessments of growth changes. Now that tropical tree-ring studies are becoming more common and many tropical species are found to produce annual rings (Zuidema *et al.*, 2012), it is high time that more analyses of long-term growth trends are conducted and published (Rozendaal *et al.*, 2010a; Nock *et al.*, 2011).

One of the most important finding of this thesis is that many tropical species show long-term growth decreases. That species-level growth trends were not reflected in the aggregated trends for all sites illustrates the importance of assessing trends on both the level of species and sites. Several studies have found long-term increases in intrinsic water-use efficiency of tropical trees, as a response to the increasing CO_2 concentrations in the atmosphere. These increases should lead to an increase in photosynthesis (or a decrease in transpiration) that could thus lead to growth increases in tropical trees. That increases in water-use efficiency were not reflected in growth increases is surprising and suggest that growth is limited by other factors than carbon availability. Additionally, these results suggest that the commonly assumed growth increases of tropical forests may be incorrect, which could lead to erroneous predictions carbon dynamics of tropical forest under climate change. There is a strong need to integrate research approaches if we wish to assess the evidence for climate change effects on tropical forests. A possible integrative approach is combining monitoring plot and remotely sensed data with the long-term growth data from tree rings. Such integrative approaches may be the best way forward to relate recent findings of changes in forest growth and biomass to changes over the past centuries.

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Summary

Tropical forests cover only 7% of the earth's land surface, but harbour almost half of the world's biodiversity. These forests also provide many ecosystem services, such as the storage of carbon and the regulation of local and regional climate, and many goods such as timber and fruits. Furthermore, tropical forests contribute disproportionately to the global carbon cycle, storing an estimated 25% of the carbon stocks on land and accounting for a third of the terrestrial net primary productivity. Therefore, changes in forest cover or in the net uptake or loss of carbon by forests directly influences the global carbon cycle. Tropical forests are under increasing anthropogenic pressure and are undergoing rapid changes due to deforestation, conversion to other land uses and logging. Additionally, there is evidence that pristine and intact tropical forests are undergoing changes due to the effects of climate change. Concerted increases in biomass and tree growth have been found in studies monitoring intact tropical forests, suggesting that they acted as considerable carbon sinks over the past decades. On the other hand, decreasing or fluctuating forest growth and biomass have also been noted. These different changes have been attributed to different climatic drivers: growth increases have been suggested to arise from growth stimulation by increasing atmospheric CO_2 concentrations, while growth decreases have been interpreted to reflect the limiting effects of increased temperature on growth. As monitoring plots usually cover only a few decades, it is still unclear whether these changes are pervasive or whether they simply reflect the effect of short-term climatic fluctuations on tree growth. Assessing whether changes have occurred over centennial scales is thus crucial to understanding whether and how tropical forests are reacting to climatic changes.

In this thesis we apply tree-ring analysis on a pantropical study to assess long-term changes in growth of tropical forest trees. Tree-ring analysis was used to measure long-term growth rates of ~1350 trees of different species coming from three sites across the tropics. Trends in growth over the last two centuries were then analysed using an established an a new trend-detection method. Additionally, we applied the long-term growth data from rings to improve the evaluation of forest management practices in Cameroon. All samples were collected and measured within the TROFOCLIM project led by Pieter Zuidema.

The project also includes two other PhD theses and sample collection was divided among the three PhD projects and the three sites: in Bolivia (samples collected by Peter van der Sleen), Cameroon (by me) and in Thailand (by Mart Vlam).
The main objectives of this thesis were: (1) to assess the potential for using tree-rings in a wet tropical forest in Central Africa; (2) to project timber yields in the next logging round for four Cameroonian tree species; (3) to evaluate the sensitivity and accuracy of four commonly used methods to detect long-term trends in tree-ring data; and (4) to detect whether growth rates of tropical forest trees have changed over the past ~150 years.

In Chapter 2 of this dissertation, we evaluated whether growth rings are formed annually in the wood of tree species growing under very high levels of precipitation (>4000 mm) in an African tropical forest. For this purpose, we assessed whether ring structures are formed in the wood of the 22 commercially exploited tree species and found that ring structures are indeed formed by more than half of these species (in 14 species), though with varying ring clarity. On four species we proved the annual character of ring formation using radiocarbon bomb-peak dating. That rings are formed under such high levels of precipitation is surprising, as these conditions are considered improper to induce ring formation. These results suggest that the potential of tree-rings analysis is more or less similar across the tropics. Based on our results and that of other studies, we estimate that tree rings can be used to measure tree growth and ages for around a quarter to a third of tropical tree species.

Worldwide, over 400 million hectares of tropical forests are set aside for timber production. Attaining sustainable use of these forests is very important, in the light of the important role of tropical forests in retaining biodiversity and storing carbon. Ensuring that timber species are not overexploited is key to ensure that forest use is sustainable and entails finding a balance between economic gains and the (ecological) sustainability of logging operations. In Chapter 3, we integrated growth data from tree-rings with logging inventory data to forecast whether timber yields can be sustained in the next harvest round for four timber species in Cameroon. Under current logging practices, future logging yields were predicted to reduce moderately to strongly for all species. These yield reductions are worrisome for forest conservation, as loss of economic value may lead to conversion of forests to other land uses. We recommend that such calculations are needed for more species and argue that these simulations should include the effects of logging and eventual silvicultural measures on the growth and survival of trees.

Lifetime tree growth data – as acquired by tree-ring analysis – contains long-term trends in growth that reflect the ontogenetic development of an individual or species, i.e., these data contains an age/size signal in growth. In Chapter 4 we evaluate the sensitivity, accuracy and reliability to detect long-term trends in growth of four methods that are commonly used to disentangle these age/size trends from long-term growth trends. We applied these growth-trend detection methods to measured growth data from tree rings and to simulated growth trajectories on which increasing an decreasing trends were imposed. The results revealed that the choice of method influences results of growth-trend studies. We recommend applying two methods simultaneously when analysing long-term trends – the Regional Curve Standardization and Size Class Isolation – as these methods are complementary and showed the highest reliability to detecting long-term growth changes.

In Chapter 5, we analysed long-term growth trends in tropical forest trees using a pantropical approach applying the two recommended growth-trend detection methods. We showed that growth rates for most of the 13 tropical tree species, from the three sites across the tropics, decreased over the last centuries. These species-level changes may have important demographic consequences and may eventually lead to shifts in the species composition of tropical forests. We found no strong growth changes when analysing trends aggregated per site or across sites: only weak growth reductions were detected for the Thai site and across sites. These findings contrast growth increases that would be expected if tree growth is stimulated by increased ambient CO_2. These growth reductions suggest worsening growth conditions for several tropical tree species, and could result from the negative effect of temperature increases on tree growth, or reflect the effect of large-scale disturbances on these forests.

If one image becomes clear from this thesis it is that long-term data are crucial to enhance the management of tropical forests and to quantify changes happening in these forests. Tree-ring analysis provides this long-term perspective for tree growth and is thus a great tool to evaluate changes in the growth of trees, including for tropical species. One of the most important finding of this thesis is that many tropical species show long-term decreases in growth. These results suggest that the commonly assumed growth increases tropical forests, based on measurements over the last couple of decades, may be incorrect. This discrepancy in results could have strong consequences, among others leading to erroneous predictions of the carbon dynamics of tropical forests under future climate change. Combining monitoring plot data (to analyse short-term changes in growth and species composition) with remotely sensed data (to accurately determine forest land cover) and with the long-term growth data from tree rings is probably the best way forward to relate recent findings of short-term changes in tree growth and forest biomass to changes over the past centuries. Such integrative approaches are needed to better quantify and understand the effects of climate change on tropical forests.

Samenvatting

Tropische bossen bedekken slechts 7% van het landoppervlak op aarde maar herbergen bijna de helft van de biodiversiteit. Ook verzorgen tropische bossen ecosysteemdiensten zoals het opslaan van koolstof en regelen van lokale klimaatcondities, en leveren ze verschillende goederen zoals hout en vruchten. Daarnaast dragen ze onevenredig veel bij aan de wereldwijde koolstofcyclus. Zo bevatten tropische bossen naar schatting 25% van de koolstofvoorraden op het land en zijn ze verantwoordelijk voor één derde van totale netto primaire productiviteit. Veranderingen in het bosareaal of in de netto opname of verlies van koolstof door bossen heeft daarom directe invloed op de wereldwijde koolstofcyclus, met mogelijke gevolgen voor klimaatsverandering.

Tropische bossen ondervinden steeds meer druk door menselijk handelen, onder meer door ontbossing en houtkap. Daarnaast zijn er aanwijzingen dat ongerepte en intacte tropische bossen veranderingen ondergaan als gevolg van klimaatverandering. In studies waarin bospercelen periodiek worden gemeten, zijn de groei van bomen en de totale boombiomassa per oppervlakte eenheid toegenomen gedurende de laatste decennia. Dit wijst erop dat tropische bossen grote hoeveelheden koolstof hebben opgeslagen in de afgelopen periode. Andere studies hebben tegenstrijdige resultaten opgeleverd: een verlaging of fluctuatie van boomgroei of biomassa in de loop van de tijd. Deze veranderingen in tropische bossen worden toegeschreven aan verschillende klimatologische factoren: de toename in groei en biomassa worden toegeschreven aan de verhoging van de atmosferische CO_2-concentraties, terwijl groeivertraging gerelateerd wordt aan de negatieve effecten van hogere temperatuur op boomgroei. Echter, omdat studies met bospercelen slechts een paar decennia overbruggen is het nog onduidelijk of deze veranderingen het gevolg zijn van een geleidelijke verhoging van temperatuur of CO_2-concentraties of een weerspiegeling van de effecten van andere factoren die op korte termijn boomgroei beïnvloeden, zoals fluctuaties in klimaat. Om te begrijpen of en hoe tropische bossen reageren op klimaatverandering is het dus cruciaal om veranderingen in de dynamiek van die bossen te bestuderen op lange termijn, dat wil zeggen gedurende enkele eeuwen.

In dit proefschrift gebruiken we jaarringanalyse om veranderingen in de groei van tropisch bomen te reconstrueren gedurende de afgelopen 150 tot 250 jaar.

Hiervoor maten we de jaarringen van 1350 bomen van verschillende soorten, afkomstig uit drie locaties in de tropen. Groeiveranderingen werden vervolgens geanalyseerd met behulp van zowel een bestaande als ook een nieuwe methode om veranderingen te detecteren. Daarnaast gebruiken we de groeigegevens van tropische bomen om de duurzaamheid van bosbeheer in Kameroen te bepalen. Alle monsters zijn verzameld en gemeten binnen het TROFOCLIM project onder leiding van Pieter Zuidema. Het project omvat ook twee andere proefschriften en het bemonsteren van bomen werd verdeeld over de drie promotieprojecten en de drie locaties: in Bolivia (monsters verzameld door Peter van der Sleen), in Kameroen (door mij) en in Thailand (door Mart Vlam).

De doelstellingen van dit proefschrift waren: (1) het evalueren van het potentieel voor het gebruik van jaarringmetingen in een nat tropisch bos in Centraal-Afrika; (2) het bepalen van toekomstige houtopbrengsten voor vier Kameroenese boomsoorten; (3) het evalueren van vier methodes die gebruikt worden om geleidelijke groeiveranderingen te detecteren in jaarringdata; en (4) het bepalen of de groei van tropische bomen is veranderd in de afgelopen ~ 150-250 jaar.

In hoofdstuk 2 van dit proefschrift hebben we onderzocht of er in het hout van boomsoorten in een zeer nat Afrikaans tropisch bos jaarringen worden gevormd. We deden onderzoek aan 22 boomsoorten die worden gekapt voor hardhout. Ringstructuren worden gevormd door meer dan de helft van deze soorten, maar de kwaliteit van de ringen varieerde aanzienlijk. Voor vier soorten hebben we het jaarlijkse karakter van de ringformatie bewezen met behulp van de datering van radioactief koolstof, met de zogeheten 'bombpeak dating'. Dat jaarringen worden gevormd in bomen die in zeer natte bossen groeien is verrassend en deze resultaten suggereren dat er veel potentie is voor jaarringonderzoek, in zowel redelijk droge als zeer natte tropische bossen. Op basis van onze resultaten en die van andere studies, schatten we in dat jaarringanalyse mogelijk is voor één vierde tot één derde van alle tropische boomsoorten.

Wereldwijd wordt meer dan 400 miljoen hectare tropisch bos gebruikt voor houtproductie. Het duurzaam beheren van deze bossen is zeer belangrijk, onder andere vanwege hun bijdrage aan het behoud van biodiversiteit en de opslag van koolstof. Eén aspect van duurzaam bosbeheer is het voorkomen van overexploitatie van de commerciële houtsoorten. Daarvoor is het nodig om een evenwicht te vinden tussen economische winst op korte termijn en de ecologische duurzaamheid van houtkap op de lange termijn. In hoofdstuk 3 hebben we gegevens over boomgroei die we verkregen op basis van jaarringmetingen gecombineerd met gegevens van bosinventarisaties om de hoeveelheid hout te bepalen die tijdens de komende oogst kan worden gerealiseerd. Onze berekeningen laten zien dat bij ongewijzigde praktijk van houtkap, die toekomstige hoeveelheid hout sterk zal verminderen voor de vier onderzochte soorten. Deze resultaten zijn zorgwekkend aangezien het verlies van economische waarde van het bos kan leiden tot de conversie van bos naar meer lucratief landgebruik. We bevelen aan dat vergelijkbare modellen voor houtopbrengst worden opgesteld voor alle commerciële houtsoorten in Kameroen.

In hoofdstuk 4 evalueren we de gevoeligheid, nauwkeurigheid en betrouwbaarheid van vier methoden die veelvoudig worden gebruikt om veranderingen in boomgroei te achterhalen op basis van jaarringmetingen. Om geleidelijke veranderingen in boomgroei te detecteren is het noodzakelijk om rekening te houden met groeiveranderingen die plaatsvinden gedurende de levensontwikkeling van een individu, de zogeheten ontogenetische groeitrend. Er bestaan verschillende methodes die dit trachten te doen. Deze methodes verschillen in aanpak en aannames, maar de gevolgen van methodekeuze op de gedetecteerde groeiveranderingen is nog niet eerder getest. In dit hoofdstuk hebben we de effecten van die methodes getest: we hebben vier veelgebruikte methodes toegepast op zowel de gemeten groei van een boomsoort uit Thailand als ook op gemodelleerde groei waarbij we groeivertragingen of –versnellingen hadden gesimuleerd. Uit de resultaten bleek dat de keuze van de methode in belangrijke mate de resultaten beïnvloedt. Twee methoden komen als beste uit de test: de ‘Regional Curve Standardisation’ en de ‘Size Class Isolation‘. Omdat deze methoden complementair zijn en de hoogste betrouwbaarheid gaven raden we aan om ze in het vervolg altijd toe te passen.

In hoofdstuk 5 hebben we veranderingen in boomgroei over de afgelopen 150 jaar geëvalueerd. We deden dat voor 13 tropische boomsoorten, op drie locaties (Bolivia, Kameroen en Thailand). Voor de meeste van de onderzochte soorten vonden we dat groeisnelheden afgenomen zijn in de afgelopen eeuw. Deze veranderingen op soortniveau kunnen belangrijke demografische gevolgen hebben voor deze soorten en kunnen uiteindelijk leiden tot verschuivingen in de soortensamenstelling in de onderzochte bossen. Echter, we vonden geen sterke groeiveranderingen als we alle soorten per locatie gezamenlijk analyseerden: alleen zwak significante groei afnames zijn gedetecteerd. Deze bevindingen contrasteren echter met de groeiversnelling die zou worden verwacht als boomgroei in belangrijke mate wordt gestimuleerd door de verhoogde atmosferische CO_2 concentraties. De gevonden groeivertragingen suggereren juist verslechterende groeiomstandigheden voor enkele tropische boomsoorten. Deze vertragingen zijn mogelijk het gevolg van het negatieve effect van temperatuurstijgingen op boomgroei of van het herstel van deze bossen na grootschalige verstoringen.

Als één beeld duidelijk wordt uit dit proefschrift, is het dat gegevens over de groei van bomen over lange periodes cruciaal zijn om het beheer van tropische bossen te verbeteren en om de veranderingen die in deze bossen plaatsvinden te kwantificeren. Jaarringanalyse levert dit langetermijnperspectief voor boomgroei en is een geweldig hulpmiddel om boomgroei veranderingen te evalueren, en is ook toe te passen in de tropen. Een van de belangrijkste bevindingen van dit proefschrift is dat de groeisnelheid van veel tropische boomsoorten over de lange termijn afneemt. Deze resultaten zijn verrassend en suggereren dat boomgroei beperkt wordt door andere factoren dan koolstofbeschikbaarheid. Bovendien suggereren onze resultaten dat de algemeen aangenomen groeitoename in tropische bossen, die gebaseerd zijn op groeimetingen over slechts de laatste decennia, wel eens onjuist zou kunnen zijn. Dit kan grote gevolgen hebben en kan onder meer leiden tot foutieve voorspellingen van de koolstofdynamiek van deze bossen onder klimaatverandering. Het combineren van bosinventarisatiestudies (voor korte termijn groeiveranderingen en veranderingen in de soortensamenstelling), satelliet waarnemingen (‘remote sensing’, voor nauwkeurige bepalingen van bosareaal) en de lange termijn groeigegevens uit jaarringanalyse is waarschijnlijk de beste manier om de recente bevindingen van veranderingen in de groeisnelheid van bomen en in bosbiomassa te relateren aan veranderingen gedurende de afgelopen eeuwen. Dergelijke integratieve benaderingen zijn essentieel om de effecten van klimaatverandering op tropische bossen beter te kwantificeren en te begrijpen.

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Doing a PhD is like a walk through a tropical forest: it is one of the most amazing and inspiring sights to behold, but it can sometimes be a rather hot and sweaty place, nearly impenetrable and encroached by spiny lianas. There are several people I would like to thank that have contributed to make this 'walk' both possible and pleasant.

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During the entire PhD track, one has to cut (or to bore) through several logs! Not an easy task when considering giant hard-wooded rainforest trees. One of the best parts of the PhD was doing this together with some very dedicated people. I had the pleasure to share fieldwork and ring measurements with several MSc students: William '*cause it looks Gangsta*' Mbia, Wouter Berendsen, Fintan '*Khalleeb*' Kelly, Guyso Singha, Evelien '*Dame de fer*' Louwers, Thomas '*the Coach*' Voswinkel, Richard '*riz chaud*' Peters, and Katrui Veldhuijzen. We shared good times in the forest and bad times too (you know, when all corers break, the car gets stuck, the rain is raining...) and you were all exceptional companions. Thanks for the great help! We are together!

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Written somewhere 10.972 m above Greenland,
13 December 2014

Short Biography

Peter Groenendijk was born on January 4th 1984 in Casa Branca, Brazil. He attended primary education at Colégio Objetivo in Casa Branca and finished his high school at the SG Marianum in Groenlo, the Netherlands. He studied Biology (BSc) at Utrecht University between 2003 and 2006. After his bachelor he travelled to Brazil for a year, of which he spent six months volunteering at a research project in the Brazilian state of Acre. In this project he interviewed inhabitants of the extractivism reserve Chico Mendes on the use and value of forest products (inside the PhD project of Amy Duchelle, University of Florida).

In 2008 he started his master in Plant Ecology at Utrecht University and for he did his first research internship at the Centro de Investigaciones en Ecosistemas (CIEco) in México. During his internship he was introduced to tree-ring analysis (under the supervision of Dr. Roel Brienen) and assessed the climate-growth relationships for a dry-forest tree species (*Cedrela salvadorensis*). For his second research internship, Peter travelled to Ethiopia where he worked on the dynamics of exploited and unexploited frankincense tree populations (*Boswellia papyrifera*). He completed is master in 2010 and immediately started his PhD research project aimed at better understanding the long-term effects of global change on tropical tree growth. This PhD, together with two other projects, was embedded in the TROFOCLIM project of Pieter Zuidema.

List of publications

- **Groenendijk, P.**, Eshete A., Sterck, F.J., Zuidema, P.A., Bongers, F. 2012. Limitations to sustainable frankincense production: blocked regeneration, high adult mortality and declining populations. Journal of Applied Ecology 49 (1), 164-173

- Zuidema, P.A., Baker, P.J., **Groenendijk, P.**, Schippers, P., Sleen, P. van der, Vlam, M. & Sterck, F.J. 2013. Tropical forests and global change: filling knowledge gaps. Trends in Plant Science 18, 1360-1385.

- **Groenendijk, P.**, Sass-Klaassen, U., Bongers, F., Zuidema, P.A. 2014. Potential of tree-ring analysis in a wet tropical forest: A case study on 22 commercial tree species in Central Africa. Forest Ecology and Management 323, 65-68.

- Peters, R.L., **Groenendijk, P.**, Vlam, M., Zuidema, P.A. 2014. Detecting long-term growth trends using tree rings: A critical evaluation of methods. Global Change Biology (*published online;* DOI: 10.1111/gcb.12826)

- Sleen, P. van der , **Groenendijk, P.**, Vlam, M., Anten, N.P.R., Boom, A., Bongers, F., Pons T.L., Terburg, G., Zuidema, P.A. 2015. No growth stimulation of tropical trees by 150 years of CO_2 fertilization but water-use efficiency increased, Nature Geoscience 8, 24-28.

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PhD Education Certificate

PE&RC Training and Education Statement

With the training and education activities listed below the PhD candidate has complied with the requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

Review of literature (4.5 ECTS)

- Long-term growth changes in tropical forest trees

Writing of project proposal (4.5 ECTS)

- Detecting long-term growth changes in tropical forest trees, a pantropical approach using tree rings

Post-graduate courses (3.3 ECTS)

- Introduction to R for statistical analysis; PE&RC (2010)
- Bayesian statistics; PE&RC (2010)
- Training in dendrochronological sampling techniques + Field visit CTFS Huai Kha Khaeng site and Thammasat University in Thailand; TROFOCLIM project (2011)
- Survival Analysis; PE&RC (2015)

Laboratory training and working visits (1.5 ECTS)

- Field visit 'La Chonta' forest and Instituto Boliviano de Investigación Forestal; Bolivia (2012)

Invited review of (unpublished) journal manuscript (2 ECTS)

- Oikos: Population dynamics tropical palm (2011)
- Book chapter: Liana anatomy (2012)
- Forest Ecology and Management: Use of tree rings for forest management (2013)
- Forests: Disturbance history of tropical forests (2014)

Competence strengthening / skills courses (2.9 ECTS)

- Reviewing a Scientific Paper; WGS (2012)
- Voice Matters - Voice and Presentation Skills Training; WGS (2013)
- Techniques for Writing and Presenting Scientific Papers; WGS (2013)
- Career assessment; WGS (2014)
- The Choice: Personal leadership and directing own performance; ESG (2014)

PE&RC Annual meetings, seminars and the PE&RC weekend (3 ECTS)

- PE&RC Weekend first year (2010)
- PE&RC Day (2010-2012)
- PE&RC Weekend last year (2013)

Discussion groups / local seminars / other scientific meetings (6.6 ECTS)

- FEM journal club (2011-2014)
- PE&RC Discussion Group Ecological Theory and Application (2010-2013)
- Symposium tropical ecology, University of Amsterdam; oral presentation (2011)
- Local seminars on tropical ecology, tree-rings, etc. (2012-2013)

International symposia, workshops and conferences (9 ECTS)

- ATBC meeting; poster presentation; Bonito, Brasil (2012)
- ATBC meeting; oral presentation; San José, Costa Rica (2013)
- TRACE meeting; oral presentation; Aviemore, Scotland (2014)
- AGU Fall meeting; oral presentation; San Francisco, USA (2014)

Lecturing / supervision of practicals / tutorials (1.2 ECTS)

- Tropical Ecology; Utrecht University (2010)
- Invited speaker course 'Biobois'; Laboratory for Wood Biology and Xylarium; Tervuren, Belgium (2013)
- Forest Resources (2013, 2014)

Supervision of MSc students

- William Mbia: Climate change effects on growth tropical tree species (2011)
- Guy Singha: Growth patterns and timber yield projections in Cameroon (2011)
- Fintan Kelly: Assessing climate-growth relationships and juvenile selection effect (2011)
- Wouter Berendse: Timber yield projections for *B. cynometroides* in Cameroon (2011)
- Evelien Louwers: Reconstruction disturbance history using *T. ivorensis* (2012)
- Thomas Voswinkel: Growth trajectories to the canopy (2012)
- Katrui Veldhuijzen: Traits to predict biomass growth in tropical trees (2013)

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