# LOOKING BACKWARDS:

## USING TREE RINGS TO EVALUATE LONG-TERM GROWTH PATTERNS OF BOLIVIAN FOREST TREES

**Danaë M.A. Rozendaal**

PROMAB Scientific Series 12

The Programa Manejo de Bosques de la Amazonía Boliviana (PROMAB) is a research, training and extension program advancing the sustainable exploitation and management of timber and non-timber forest resources in northern Bolivia. PROMAB is a joint effort of various Bolivian Institutes in Riberalta and Cobija, the Universidad Autónoma de Beni, Bolivia, the Universidad Autónoma de Pando, Bolivia, and Utrecht University and Tropenbos International in the Netherlands.

PROMAB, Casilla 107, Riberalta - Beni, Bolivia.
www.promab.org

**D.M.A. Rozendaal**
Looking backwards: using tree rings to evaluate long-term growth patterns of Bolivian forest trees
PROMAB Scientific Series 12
PROMAB, Riberalta, Bolivia
ISBN: 90-393-5268-7

**Keywords:** Bolivia, tree-ring analysis, long-term growth patterns, tropical forest, historical growth increase, forest dynamics, stem volume growth reconstruction, growth projections, timber yield

**Printed by:** GVO drukkers & vormgevers B.V. | Ponsen & Looijen, Ede
**Cover and layout:** Tonnie Jobse, www.jobse.nl
**Photos:** Adhemar Saucedo, Danaë Rozendaal

# Looking backwards: using tree rings to evaluate long-term growth patterns of Bolivian forest trees

# Terug in de tijd: de analyse van historische groeipatronen van Boliviaanse bomen met behulp van jaarringen

(met een samenvatting in het Nederlands)

# Retrocediendo en el tiempo: evaluación de patrones de crecimiento a largo plazo utilizando anillos de crecimiento de árboles en Bolivia

(con resumen ejecutivo en Español)

**Proefschrift**

ter verkrijging van de graad van doctor aan de Universiteit Utrecht
op gezag van de rector magnificus, prof.dr. J.C. Stoof,
ingevolge het besluit van het college voor promoties
in het openbaar te verdedigen op woensdag 3 februari 2010 des middags te 2.30 uur

door

**Danaë Mirthe Adriana Rozendaal**

geboren op 18 augustus 1981 te Amsterdam

**Promotor:** Prof.dr. M.J.A. Werger
**Co-promotor:** Dr. P.A. Zuidema

Financial support was obtained from the Netherlands Organisation for Scientific Research (NWO), WOTRO-grant W 01.53.2004.047.

*Voor mijn vader*

# Contents

**Chapter 1** General introduction 12

**Chapter 2** Tropical tree rings reveal preferential survival of fast-growing juveniles and increased juvenile growth rates over time 20
*with Roel J.W. Brienen, Claudia C. Soliz-Gamboa & Pieter A. Zuidema*
*New Phytologist*, doi: 10.1111/j.1469-8137.2009.03109.x

**Chapter 3** Assessing long-term changes in tropical forest dynamics: a first test using tree-ring analysis 36
*with Claudia C. Soliz-Gamboa & Pieter A. Zuidema*
*Submitted for publication*

**Chapter 4** Reconstructing stem volume growth of juvenile tropical forest trees: variability among individuals and trade-offs between stem diameter and height growth 50
*with Heinjo J. During, Daan Asscheman, Jeroen Wiegeraad & Pieter A. Zuidema*
*Submitted for publication*

**Chapter 5** Timber yield projections for tropical tree species: using plot data underestimates future yield if the large trees of today were the fast-growers of the past 66
*with Claudia C. Soliz-Gamboa & Pieter A. Zuidema*
*Submitted for publication*

**Chapter 6** Tropical dendroecology: a review and integrated summary 82

Resumen ejecutivo 96

Samenvatting 116

References 122

Dankwoord / Acknowledgements / Agradecimientos 140

Curriculum vitae 146

Publications 148

PROMAB publications 149

# CHAPTER 1

## General introduction

## Tree rings in the tropics

The existence of annual growth ring formation in the tropics has been denied for a long time (e.g. Lieberman *et al.*, 1985a). The absence of annual growth rings was thought to be a consequence of a lack of clear seasonality. However, already in 1927 the existence of annual growth rings in tropical trees has been described by Coster (1927; 1928). Annual ring formation in tropical forests occurs in areas where trees experience cambial dormancy in one period of the year due to unfavourable environmental conditions. Tree rings occur in seasonally dry forests, where one dry season per year induces cambial dormancy (e.g. Worbes, 1999). Also in floodplain forests and in mangroves seasonal flooding has been shown to result in annual ring formation (e.g. Schöngart *et al.*, 2002; Dezzeo *et al.*, 2003; Verheyden *et al.*, 2004). Seasonally dry forests and floodplain forests comprise a large area of the tropics. Thus, also in the tropics we may expect a large contribution of tree-ring analysis to the understanding of tree growth and ecology.

Tree rings of tropical tree species are often anatomically less distinct than in temperate areas, and are not always reliable. Climatic fluctuations within the seasons can cause formation of false rings (Priya & Bhat, 1998), wedging rings are common (Worbes, 2002) and also non-annual ring formation has been shown (Dünisch *et al.*, 2003; Wils *et al.*, 2009; Boninsegna *et al.*, 1989). Hence, the annual nature of the rings needs to be proved. This can be done through ring counts for trees of known age from plantations (e.g. Dünisch *et al.*, 2002), C14-bomb peak dating (e.g. Worbes & Junk, 1989; Fichtler *et al.*, 2003), by counting rings after cambial wounding (e.g. Nobuchi *et al.*, 1995; Lisi *et al.*, 2008) or through correlating growth with annual rainfall (e.g. Trouet *et al.*, 2006). Now, for an increasing number of species in many areas in the tropics annual rings have been shown (Baas & Vetter, 1989; Eckstein *et al.*, 1995; Worbes, 2002).

Recently, a start was made in exploring the potential of tree-ring analysis for answering ecological questions that require long-term growth data. The need for reliable data on ages and growth rates of tropical trees has been clearly expressed (Ashton, 1981; Bormann & Berlyn, 1981). First, tree-ring data were only used to study the relation between tree growth and climatic factors. Tree species have been found to show different responses to rainfall (e.g. Enquist & Leffler, 2001; Brienen & Zuidema, 2005) and El Niño-Southern Oscillation has been shown to influence tree growth (Schöngart *et al.*, 2004; Brienen *et al.*, 2009b). Second, the field of tropical dendroecology started to develop. Tree-ring analysis is a direct method to determine ages of tropical trees (Martínez-Ramos & Alvarez-Buylla, 1998; Worbes & Junk, 1999) and lifetime growth rates. Lifetime growth data were used to describe growth trajectories of trees to the canopy (Baker & Bunyavejchewin, 2006; Brienen & Zuidema, 2006a) and a combination with other age-estimation methods was applied to reconstruct the history and dynamics of a seasonal tropical forest in Thailand (Baker *et al.*, 2005). Recently, tree-ring analysis has also been applied to forest management studies (e.g. Brienen & Zuidema, 2006b; Schöngart, 2008). In this dissertation I apply tree-ring analysis for answering questions in tropical tree ecology that require long-term growth data.

### Pathways to the canopy

Tropical forests are highly diverse ecosystems in which many tree species with different life history strategies coexist. Light is often a limiting factor to tree growth in these forests, as only 1-2% of total light reaches the forest floor (Chazdon & Fetcher, 1984). The formation of canopy gaps through tree falls increases light availability temporarily and locally in the understorey, which leads to spatial and temporal variation in light conditions (Canham *et al.*, 1990). In addition, a vertical light gradient exists, as light availability increases with height in the forest. Tree species may partition the entire range of light environments and occupy different niches (Denslow, 1980; Poorter & Arets, 2003). Traditionally, species were classified either as pioneer, fast-growing species confined to gap environments, or as shade tolerant, slow-growing species which complete their lifecycle in the understorey (Whitmore, 1998). Turner (2001) proposed a broader classification scheme based on light requirements for regeneration and maximum adult height. In the category of canopy trees a division is often made into species that regenerate in the understorey and in gaps (cf. Poorter *et al.*, 2006). Thus, also among canopy species differences in shade tolerance can be found. These differences have been assessed through studying the relation between height and crown exposure from static data, as a proxy for a species-specific growth pattern towards the canopy (Poorter *et al.*, 2005; Sheil *et al.*, 2006).

For trees of canopy species it is of key importance to attain the canopy, to ensure light availability and the possibility to reproduce. So far, few studies described actual growth trajectories of tropical trees towards the canopy, as these long-term growth patterns cannot be derived from permanent sample plots. Permanent plots usually do not span more than ~30 years (cf. Clark, 2007), which is a short time period compared to a tree's lifespan. Thus, growth trajectories towards the canopy were studied based on growth projections from plot data (e.g. Clark & Clark, 1992; Clark & Clark, 2001). A more suitable approach is the reconstruction of historical growth patterns of individual trees through application of tree-ring analysis. In this way, prolonged periods of slow growth (suppressions) and prolonged periods of fast growth (releases) can be detected. The occurrence of suppressions and releases is generally thought to be caused by changes in light levels due to gap formation and closure (Nowacki & Abrams, 1997). Recently, also growth patterns of tropical trees towards the canopy have been reconstructed using tree ring analysis (Baker & Bunyavejchewin, 2006; Brienen & Zuidema, 2006a). Canopy tree species differed in growth patterns towards the canopy, which most likely is caused by differences in shade tolerance among species. Trees of most species required a gap at some stage to guarantee access to the canopy (Baker & Bunyavejchewin, 2006; Brienen & Zuidema, 2006a). The age at which trees of the same species attained the canopy varied strongly. Hence, growth rates differed largely among individual trees, probably due to large spatial and temporal variation in growth conditions (Brienen & Zuidema, 2006a).

Such large growth variation among trees has also been observed among juvenile trees in the forest (Clark & Clark, 1992), although the vast majority of juveniles is suppressed and exhibits low growth rates. A key question then is: which of these trees do attain the canopy?

Slow-growing juvenile trees have higher cumulative mortality risk (Terborgh *et al.*, 1997; Wyckoff & Clark, 2002), as they take longer to reach the canopy. This would mean that only fast-growing juveniles are expected to reach the canopy ('juvenile selection effect'). This hypothesis has been put forward frequently (e.g. Enright & Hartshorn, 1981; Swaine *et al.*, 1987), but has never been explicitly tested for tropical trees. Through comparing growth rates of juvenile trees at this moment in the forest with past growth rates of 'successful' canopy trees at the time they were juveniles, the existence of a juvenile selection effect can be evaluated. Landis and Peart (2005) found evidence for a juvenile selection effect in three temperate tree species by applying tree ring analysis. In this thesis I evaluate the existence of a juvenile selection effect for five tropical tree species using a similar approach (Chapter 2).

Most studies on tropical tree growth focused on growth in stem diameter, as it is more difficult to measure height growth accurately for larger trees. In studying temporal growth patterns in stem diameter, one assumes that growth in height shows similar patterns. The static, species-specific, relation between tree height and diameter was used to compare investment patterns in height and diameter growth among species (e.g. O'Brien *et al.*, 1995; Osunkoya *et al.*, 2007). So far, only one study evaluated long-term (16-y timespan) height growth for tropical trees to evaluate growth patterns to the canopy (Clark & Clark, 2001), although growth in height is of prime importance for attaining the canopy. In temperate forests, shifts in investment in height and diameter growth have been found (e.g. Zenner, 2008). Suppressed trees have been shown to grow relatively more in height than in diameter (Niklas, 1995; Naidu *et al.*, 1998) and the existence of a trade-off between diameter and height growth has been shown (Sumida *et al.*, 1997). Coomes and Grubb (1998) evaluated the relation between height and diameter growth for saplings of tropical tree species using short-term growth measurements. Large variation in the height/diameter-ratio was found, although this did not differ between saplings growing in gaps and in the understorey. The lack of differences has been attributed to ignoring the growth history of the saplings (Coomes & Grubb, 1998). Long-term height growth can also be reconstructed from tree rings, as only at the base of the tree all rings are present. Through counting rings in discs collected over the entire height of the tree, the time needed to grow through these height intervals can be determined (cf. Gutsell & Johnson, 2002). In Chapter 4 long-term diameter, height and stem volume growth are reconstructed for three tropical tree species.

## Tropical forests are changing

A growing amount of evidence from permanent sample plots suggests that tropical forests are changing. Over the last decades, aboveground biomass (Baker *et al.*, 2004), tree growth (Laurance *et al.*, 2004b; Phillips *et al.*, 2008) and stem turnover (Phillips & Gentry, 1994; Lewis *et al.*, 2004b; Phillips *et al.*, 2004) increased over the whole Amazon region. In addition, some changes in forest composition have been observed: a shift towards faster-growing species (Laurance *et al.*, 2004b) and increasing dominance of lianas (Phillips *et al.*, 2002). The cause of these changes is hotly debated (Chambers & Silver, 2004; Lewis *et al.*, 2004a; Wright, 2005; Lewis *et al.*, 2006). The increase in atmospheric $CO_2$ has been put forward as a likely cause of these changes (e.g. Lewis *et al.*, 2004a). Increased atmospheric $CO_2$ may stimulate growth, which results in an increase in stand-level basal area and recruitment. Similarly, tree density and stand-level mortality increase, which means an acceleration in tree turnover, thus in forest dynamics (Lewis *et al.*, 2004a; Phillips *et al.*, 2008). Nevertheless, others argue that due to the inclusion of plots in forests in different stages of recovery from disturbance, increases in biomass are resulting from differences in successional status among the forests evaluated (Feeley *et al.*, 2007a; Chave *et al.*, 2008; Fisher *et al.*, 2008; but see Gloor *et al.*, 2009). Similarly, the increase in growth has been questioned, as also decreasing growth rates have been found (Feeley *et al.*, 2007c).

It is important to unravel the causes of these changes, as tropical forests play a major role in the global carbon cycle (Malhi *et al.*, 2008), and increased forest dynamics may cause tropical forests to shift from carbon sink to carbon source (cf. Körner, 2004; Phillips *et al.*, 2009). The first issue to address is whether individual tropical trees respond to the increase in atmospheric $CO_2$. Artificial $CO_2$-enrichment has been shown to enhance growth of *in situ* tropical tree seedlings (Würth *et al.*, 1998). However, atmospheric $CO_2$ is steadily increasing since the Industrial Revolution, with a steep increase since 1950 (IPCC, 2007). It is not known whether tropical trees have responded to this gradual increase in $CO_2$, and whether a response would occur in trees of all sizes. To address this question long-term growth data of tropical trees are required. In a modelling study, Lloyd and Farquhar (2008) showed that a response to increased atmospheric $CO_2$ also can be expected for tropical trees, in particular when they are light-limited.

In temperate forests more research has been conducted on the response of trees to increased atmospheric $CO_2$. Tree-ring analysis has been applied, which allows the reconstruction of tree growth over the entire lifespan of a tree. Temperate trees indeed showed an increase in growth over the last 150 years (e.g. Rolland *et al.*, 1998; Voelker *et al.*, 2006). When correcting for tree age or comparing the response of small and large trees, the growth increase was found to be more pronounced for smaller trees (Voelker *et al.*, 2006; Wang *et al.*, 2006). Tree-ring analysis may also provide a means to analyze historical growth changes for tropical trees, as long-term growth can be reconstructed. In Chapter 2 I explore the long-term growth changes for five tropical tree species.

Apart from reconstructing long-term tropical tree growth, tree-ring analysis can also be applied in reconstructing historical forest dynamics (cf. Baker *et al.*, 2005). As an increase in tree turnover implies that tree fall, and thus gap formation, increased over time, it may be possible to observe these periods of growth release in tree-ring series of the remaining trees. If tree turnover increased over time, one would thus expect to find more releases recently than further back in time. This issue is assessed in Chapter 3.

### Sustainable logging?

To define criteria for sustainable logging schemes for tropical tree species, growth data are necessary. Nevertheless, growth data obtained from permanent sample plots may result in an underestimation of future timber yield. Most slow-growing trees are not expected to reach the canopy and survive to harvestable size (Landis & Peart, 2005), thus growth rates of faster-growing individuals are likely to give more reliable estimates (cf. Condit *et al.*, 1995a). Tree-ring data from trees of harvestable size have been used to evaluate timber yield recuperation after initial harvest (Brienen & Zuidema, 2006b; Brienen & Zuidema, 2007). The advantage of this approach is the inclusion of growth rates of trees that reached harvestable size, and the possibility to include temporal variation in growth rates in growth simulations. The inclusion of autocorrelated growth in growth simulations has been shown to give higher, and probably more realistic estimates of future timber yield (Miina, 1993; Brienen & Zuidema, 2006b; Brienen & Zuidema, 2007). Still, it is not known whether timber volume recuperation is underestimated when using growth data from permanent sample plots. This question is addressed in Chapter 5.

### This study

In this study I collected tree-ring data of extant trees over the entire size range for five tropical tree species (Table 1). These data were used to investigate long-term growth patterns of tropical trees. First, the existence of a juvenile selection effect was evaluated with its consequences for projections of future timber yield. Second, I assessed changes in growth and forest dynamics over time. Last, stem volume growth of juvenile trees of tree tropical tree species was reconstructed to study long-term investments in stem diameter and height growth.

### Specifically, the objectives of this thesis are:

- to determine whether only fast-growing juvenile trees attain the canopy.
- to evaluate whether juvenile growth rates have increased over time.
- to assess changes in the frequency of the occurrence of releases and strength of within-tree autocorrelation over time.
- to evaluate the relation between diameter, height and stem volume growth for juvenile tropical trees.
- to determine whether there is a trade-off between diameter and height growth.
- to analyze the consequence of the inclusion of fast-growing juveniles on timber volume recuperation at the second harvest.
- to quantify the percentage of the harvested timber volume at initial harvest that has recuperated at the time of second harvest.

### Study areas in Bolivia

In Bolivia, forests are situated along a rainfall-gradient: north of La Paz wet forests occur, then seasonally dry forests can be found towards the southeast of the country with a gradual change to dry shrublands (Killeen *et al.*, 1993). Fieldwork was conducted in three lowland moist forests in Bolivia. Two of these were situated in the Bolivian Amazon region in the department of Pando, Los Indios (10°26'S, 65°33'W) and Purísima (11°24'S, 68°43'W). The third study area was situated in the transitional region from the Bolivian Amazon to the dry Chiquitano forest in the department of Santa Cruz (La Chonta, 15°47'S, 62°55'W; cf. Fig. 1). Five canopy tree species were included, of which four are harvested for timber, and the fifth is a potential timber species (Table 1).

The Bolivian Amazon region consists of semi-evergreen moist forest. Annual precipitation is 1690 mm (Riberalta). The area experiences a dry season from May until September (<100 mm per month). Canopy height ranges between 25 and 35 m. Species richness is ~80 tree species ha$^{-1}$ (Poorter *et al.*, 2001).

La Chonta has an annual precipitation of 1580 mm with a dry season from May until September (<100 mm per month). During the dry season around 30% of the canopy trees drop their leaves (Peña-Claros *et al.*, 2008a). The forest has a canopy height of 27 m, stem density of 367 ha$^{-1}$ (of stems >10 cm dbh, diameter at breast height) and species richness of 59 tree species ha$^{-1}$. The most abundant species are *Pseudolmedia laevis*, *Ampelocera ruizii* and an *Ocotea* species (Peña-Claros *et al.*, 2008a).

**Table 1** List of the study species with their scientific and local names and the chapters in which they are included.

| **Species** | **Family** | **Local name** | **Chapter** | **Study site** | **Use** |
|---|---|---|---|---|---|
| *Cedrela odorata* L. | Meliaceae | cedro | 2 | Purísima | Timber |
| *Cedrelinga catenaeformis* (Ducke) Ducke | Fabaceae | mara macho | 2,4,5 | Los Indios | Timber |
| *Clarisia racemosa* Ruíz & Pavón | Moraceae | mururé | 2,3,4,5 | Los Indios | Timber |
| *Peltogyne* cf. *heterophylla* M.F. Silva | Fabaceae | morado | 2,3,4,5 | Los Indios | Timber |
| *Pseudolmedia laevis* (Ruíz & Pavón) J.F. Macbr. | Moraceae | ojoso colorado | 2 | La Chonta | Potential timber |

## Outline of this dissertation

Chapter 1 provides a general introduction to the conducted research.

Chapter 2 evaluates two hypotheses: (1) fast-growing juvenile trees have a higher chance to attain the canopy ('juvenile selection effect'), and (2) tree growth has increased over time ('historical growth increase').

Chapter 3 explores the potential of tree ring analysis in assessing changes in forest dynamics over time. Two methods are proposed: the frequency of occurrence of releases over time and autocorrelation in growth within individual trees.

Chapter 4 shows the potential of stem volume growth reconstruction in juvenile tropical trees. Variation in stem volume growth among trees and its persistence over time was evaluated. I evaluate whether there is a trade-off between the two components of volume growth: height growth and diameter growth.

Chapter 5 evaluates the influence of fast juvenile growth on future timber yield estimations. Projections of timber volume recuperation at second harvest were compared between two types of growth data: lifetime growth rates of trees of harvestable size and the last ten years of growth of extant trees over the whole size range of the species as a proxy for growth data from permanent sample plots.

Chapter 6 gives a review on tropical dendroecology with an integrated summary of the results presented in this dissertation.

### Programa de Manejo de Bosques de la Amazonía Boliviana (PROMAB)

This research was conducted within the framework of Asociación PROMAB in Riberalta, Bolivia, in cooperation with the Instituto Boliviano de Investigación Forestal (IBIF) in Santa Cruz, Bolivia. PROMAB is a research, education and extension program of various Bolivian Institutes in Riberalta and Cobija, Universidad Autónoma de Beni (Riberalta, Bolivia), Universidad Autónoma de Pando (Cobija, Bolivia), and Utrecht University and Tropenbos International in the Netherlands. The main activities of the program, which started in 1995, are ecological and socio-economic research, technical assistance, training of forest users (in particular farmers and rural communities), training of forestry students, and dissemination of information to forest users and governmental organizations. This dissertation is the 12th publication in the PROMAB Scientific Series. Earlier dissertations in this series dealt with the influences of light and water availability on seedling growth of rainforest tree species (Poorter 1998), the demography of tree species and exploitation of non-timber forest products (Zuidema 2000), mechanisms of secondary forest succession (Peña-Claros 2001), an economic analysis of the export of local forest products (Bojanic 2001), an exploration of the potentials of sustainable livelihoods for forest residents (Henkemans 2002), the role of seed trees and seedling regeneration for maintenance of commercial tree species (van Rheenen 2005), a study on growth patterns of commercial tree species using tree-ring analysis (Brienen 2005), and a study on the mechanisms of co-existence and replacement of tropical tree species at early stages of succession (Selaya 2007). Three other dissertations are forthcoming in this series. Claudia Soliz-Gamboa is studying gap dependence of three tropical tree species using tree-ring data. Mario Zenteno and Walter Cano study the contribution of forest management to the income of households and the consequences of community forest management on social relations within communities.

**Fig. 1** Map of Bolivia with the study sites indicated: La Chonta, Los Indios and Purísima.

# CHAPTER 2

## Tropical tree rings reveal preferential survival of fast-growing juveniles and increased juvenile growth rates over time

with Roel J.W. Brienen, Claudia C. Soliz-Gamboa & Pieter A. Zuidema

*New Phytologist*, doi: 10.1111/j.1469-8137.2009.03109.x

## SUMMARY

Long-term juvenile growth patterns of tropical trees were studied to test two hypotheses: (1) fast-growing juvenile trees have a higher chance to attain the canopy ('juvenile selection effect'), and (2) tree growth has increased over time ('historical growth increase').

Tree-ring analysis was applied to test these hypotheses for five tree species from three moist forest sites in Bolivia, using samples from 459 individuals. Basal area increment was calculated from ring widths, for trees <30 cm diameter.

For three out of five species, a juvenile selection effect was found in rings formed by small juveniles. Thus, extant adult trees in these species have had higher juvenile growth rates than extant juvenile trees. In contrast, rings formed by somewhat larger juveniles in four species showed the opposite pattern: a historical growth increase. For most size classes >10 cm diameter none of the patterns was found.

Fast juvenile growth may be essential for tropical trees to attain the forest canopy, especially for small juvenile trees in the dark forest understorey. The historical growth increase requires a cautious interpretation, but may be partially due to $CO_2$-fertilization.

**Key words:** tropical forest, long-term tree growth, historical growth increase, climate change, tree ring analysis, Bolivia

## INTRODUCTION

Most juvenile trees in the understorey of tropical forests are strongly light-limited, resulting in very low diameter growth rates (Chazdon & Fetcher, 1984; Clark & Clark, 1999). Slow-growing juveniles experience higher mortality rates (Wyckoff & Clark, 2002) and remain longer in the understorey where risk of damage by falling debris is high (Clark & Clark, 1991). They therefore may have a considerably lower chance to attain the canopy, compared to fast growers (Enright & Hartshorn, 1981; Swaine *et al.*, 1987; Baker, 2003). If fast growers preferentially reach the canopy, this implies that extant canopy trees would on average have grown faster as juveniles compared to extant juveniles (Fig. 1a). Or, when expressed against time, that juvenile growth rates realized in the distant past (i.e. in extant adults) would be higher than those attained in the recent past (i.e. in extant juveniles, Fig. 1b). In a temperate forest, Landis and Peart (2005) indeed found higher juvenile growth rates for extant canopy trees compared to extant juveniles using the same approach.

Another factor that may influence juvenile tree growth in tropical forests is climatic change (Clark, 2007; Lloyd & Farquhar, 2008; Malhi *et al.*, 2008). There is strong evidence that the growth rates of tropical forest trees have increased over the last few decades (Laurance *et al.*, 2004b; Phillips *et al.*, 2008), probably invoked by increased atmospheric $CO_2$ concentration (cf. Lloyd & Farquhar, 2008). Thus, for juvenile trees in tropical forests, one would expect that growth rates in the distant past (i.e. in extant canopy trees) are lower than those in the recent past (i.e. in extant juveniles), the 'historical growth increase' (Fig. 1c).

Clearly, the ‘juvenile selection effect’ and a ‘historical growth increase’ have opposing consequences for temporal patterns in juvenile growth (Fig. 1). It is unclear which of these factors has a stronger effect. This may depend on the size of juvenile trees under consideration. For instance, one could expect the juvenile selection effect to be stronger for juvenile trees in the forest understorey, as these typically experience higher mortality risk (e.g. Lieberman *et al.*, 1985b; Condit *et al.*, 1995b). On the other hand, a historical growth increase may also be stronger in smaller trees, as $CO_2$-fertilization is expected to have a stronger effect on light-limited trees (Lloyd & Farquhar, 2008). Artificial $CO_2$-enrichment indeed increased seedling growth in a forest in Panama (Würth *et al.*, 1998), although this was not compared to responses of larger individuals. It is therefore likely that both the juvenile selection effect and a historical growth increase influence growth patterns of juvenile trees, although their relative magnitude remains unclear.

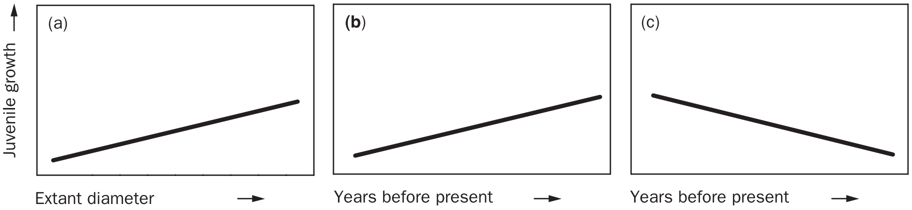


**Fig. 1** Graphical representation of the hypotheses. (a, b) ‘juvenile selection effect’ and (c) ‘historical growth increase’.

Here we present results of a tree-ring study on five tree species from the Bolivian Amazon in which we tested whether temporal patterns in juvenile growth rates are consistent with the juvenile selection effect and/or a historical growth increase in various diameter classes. Tree rings provide a very effective tool for doing so, as historical growth rates over the last centuries can be obtained, a period much longer than that for which plot data are available (Condit, 1995; Clark, 2007). Specifically, we tested the hypotheses, as depicted in Figure 1: (1) juvenile growth rates increase with extant tree size (‘juvenile selection effect’), and (2) juvenile growth rates increase over time (‘historical growth increase’). To our knowledge, this is the first study testing the juvenile selection hypothesis and evaluating centennial-scale growth changes for tropical forest trees.

## MATERIALS AND METHODS

### Study sites and species

Fieldwork was done in three lowland semi-deciduous moist forests in Bolivia: Los Indios, La Chonta and Purísima, which are 200-600 km apart. Los Indios (10°26’S, 65°33’W) and Purísima (11°24’S, 68°43’W) are situated in the department of Pando, La Chonta (15°47’S, 62°55’W) in the department of Santa Cruz. Mean annual precipitation is similar for Purísima and Los Indios, ~1700 mm $y^{-1}$, and somewhat lower for La Chonta, 1580 mm $y^{-1}$, which is located in the transitional region from moist to dry forest. All sites experience a dry season (<100 mm per month) from May until September.

Forests in the three locations have canopy heights of 25 to 35 m. Stem densities vary somewhat across sites: 367 ha$^{-1}$ (of stems >10 cm dbh, diameter at breast height) in La Chonta (Peña-Claros *et al.*, 2008a), 423 ha$^{-1}$ in Los Indios (Toledo *et al.*, 2008), and ca. 544 ha$^{-1}$ in northern Bolivia in forest similar to Purísima (R.J.W. Brienen, unpublished data).

Our study included five tree species (Supporting Information Table S1): *Cedrela odorata* (from Purísima), *Cedrelinga catenaeformis*, *Clarisia racemosa*, *Peltogyne* cf. *heterophylla* (all three from Los Indios) and *Pseudolmedia laevis* (from La Chonta). Species will be referred to by their generic name from now on. All species tolerate shade, but to a different extent (cf. Brienen & Zuidema, 2006a). *Cedrela* and *Cedrelinga* are light-demanding, while *Clarisia*, *Peltogyne* and *Pseudolmedia* are shade-tolerant species. The annual character of the juvenile and adult rings was proven with C14-bomb peak dating for *Cedrelinga*, *Clarisia* and *Peltogyne* (Soliz-Gamboa *et al.*, submitted), and using rainfall correlations for *Cedrela* (Brienen & Zuidema, 2005) and *Pseudolmedia* (see Supporting Information).

### Sample collection and ring width measurements

Selective logging had taken place during 2002 in Purísima, and during 2006 in both Los Indios and La Chonta. Fieldwork in Purísima and Los Indios was done just after selective logging, and for La Chonta just before. For each species, we randomly selected 60-69 trees of <50 cm dbh and 29-53 trees of >50 cm dbh (not possible for *Pseudolmedia*, due to small stature only three trees >50 cm dbh were included). We selected individuals of <50 cm dbh such that they were evenly distributed over diameter categories. In order to reduce spatial autocorrelation in growth rates, selected individuals needed to be at least 20 m apart. Damaged juveniles (<10 cm dbh) were not included. In *Cedrelinga* we checked for hollowness by pre-coring trees, and preferentially selected non-hollow trees to allow measurement of juvenile rings.

Discs or increment cores were obtained from the selected individuals. In the case of large trees (>50 cm dbh), we always collected discs from stumps of felled trees. For small trees, increment cores were obtained for *Cedrela* (2-3 per tree), and discs for all other species. Sampling height varied from 0.5-1.5 m in *Cedrela* and was kept constant within all other species, at either 0.5 or 1 m.

A digital picture of each disc was taken, to calculate fresh disc area using pixel-counting software (SigmaScan Pro 5.0). Discs were air-dried and sanded with progressively finer sandpaper until a grit of 1000. Rings were marked in three or four radii (one to three for *Cedrela*) – selected to correspond to total disc area – using a stereomicroscope (6.3-40x). Every tenth ring was connected over the whole disc to control for errors in ring identification. Ring widths were measured perpendicular to the ring boundaries using a LINTAB 5 (Rinntech) measurement device. For *Cedrelinga*, *Clarisia* and *Peltogyne* the last ring (2006, growth period 2006-2007) was left out for the trees <50 cm dbh, as this ring was formed after selective logging. For all species we succeeded in cross-dating part of the samples. Cross-dating proved difficult or impossible for the juvenile phase due to non-climatic influences on growth, such as suppressions and releases due to canopy dynamics (cf. (Brienen & Zuidema, 2006a). This means that juvenile growth may have been slightly overestimated due to missing rings for slow-growing trees. Missed rings may have lead to a slight underestimation of both the juvenile selection effect and the historical growth increase. Ring widths of all radii of the discs were averaged, corrected for desiccation and irregular growth using the mean radius of the fresh disc area. For the increment cores of *Cedrela*, average ring width was corrected with dbh of the tree. Ring width was then converted to basal area growth, as this provides a better proxy for biomass growth.

### Data analysis

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 class; 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 *Cedrela* and *Cedrelinga*. For these species we used wider diameter classes at smaller sizes: 0-5 and 5-10 cm. By applying 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 in the same ontogenetic stage. For each individual and each diameter class, we also calculated the mid-point of the ages of all rings, which we termed year before present (YBP). The calendar year for the 'present year' in the calculation of YBP was 2002 for *Cedrela* and 2006 for all other species.

We then related median growth rates (diameter and basal area) for a given diameter class to the extant diameter of all the trees using Pearson's correlation. For instance, for the diameter class of 0-1 cm, we correlated the median growth rates of all individuals with their current, extant size (as in Fig. 1a). A positive correlation between these variables indicates that juvenile growth rates of extant adults have been higher than those of extant juveniles, consistent with the 'juvenile selection effect'.

Similarly, we related median growth rates to the year before present (YBP) in order to find out whether growth rates of similarly-sized trees have changed over time. Relations between growth rate and YBP are expected to be comparable to those for growth rate and extant diameter, as age and size are not independent over the studied extant size range. Temporal autocorrelation in growth and persistent growth differences among trees may cause the relation of growth and extant dbh to deviate from that between growth and YBP, but the effect is probably small for juvenile growth (Brienen *et al.*, 2006). We checked whether correlations for diameter growth differed to those for basal area growth: this was not the case for 76 out of 80 correlations performed. All statistical analyses were conducted in SPSS 16.0 (SPSS Inc.).

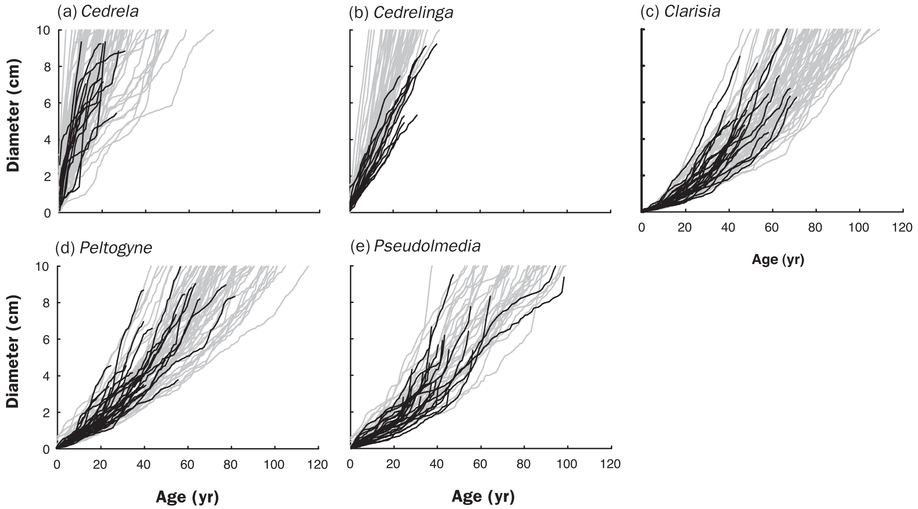


**Fig. 2** Growth trajectories until 10 cm diameter for five tropical tree species. Grey lines indicate trees >10 cm diameter at breast height (dbh), black lines indicate trees <10 cm dbh. Hollow trees were not included, as for those trees exact age could not be determined. (a) *Cedrela* (86 trees), (b) *Cedrelinga* (63 trees), (c) *Clarisia* (95 trees), (d) *Peltogyne* (85 trees), (e) *Pseudolmedia* (60 trees).

## RESULTS

### Ages and juvenile growth rates

Growth rates varied considerably across species, with *Cedrela* and *Cedrelinga* showing much faster juvenile growth than the other species (Fig. 2). On average, juveniles of *Cedrelinga* and *Cedrela* reached 10 cm diameter in 26 years and 24 years, respectively, a period more than three times shorter than that of the other species, which took 77-80 y (Fig. 2).

### Juvenile growth and extant diameter

In *Cedrela*, extant trees >10 cm dbh showed a much wider range in growth trajectories than trees <10 cm dbh (Fig. 2a). *Cedrelinga* juveniles of 1-10 cm dbh showed slower initial growth than extant trees >10 cm dbh of the same species (i.e. less steep growth trajectories, Fig. 2b). For *Clarisia*, *Peltogyne* and *Pseudolmedia* this pattern was less strong (Fig. 2c-e). In four out of five species we found significant correlations between juvenile growth and extant diameter (Figs 3,4,7). Positive as well as negative correlations were observed. For *Cedrelinga*, *Clarisia* and *Peltogyne*, positive correlations between juvenile growth and extant diameter were found mostly in the smallest diameter classes, whereas negative correlations were observed at larger sizes for *Clarisia* and *Pseudolmedia*. For all diameter classes >6 cm, we only found significant correlations for *Cedrelinga* in the diameter class from 5-10 cm and from 20-30 cm diameter (Fig. 7). For *Clarisia* and *Peltogyne* a positive correlation between growth and extant diameter was found from 0-1 cm diameter (Fig. 3c,d), showing that extant large trees had faster juvenile growth than extant juveniles. Similarly, juvenile growth was positively correlated with extant diameter in *Cedrelinga* juveniles (0-5 cm, 5-10 cm, 15-20 cm and 20-30 cm diameter, Figs 3b, 4b, 7b).

Negative correlations between juvenile growth and extant diameter were apparent in three of the five study species: in *Clarisia* (2-4 cm diameter), *Peltogyne* (1-2 cm diameter) and *Pseudolmedia* (2-6 cm diameter) juvenile growth rates decreased significantly with extant dbh (Figs 4c,e, 7). Thus, in those species extant juveniles grew faster than extant adult trees had done as a juvenile.

## Juvenile growth and time before present

As expected, the relations between juvenile growth rates and year before present (YBP, Figs 5,6) were similar to those for growth and extant diameter (Figs 3,4), although for the former we found slightly more significant correlations (Fig. 7). Positive correlations between juvenile growth and YBP were found for the growth of small juveniles of *Clarisia* and *Peltogyne* (0-1 cm dbh, Fig. 5c,d) and *Cedrelinga* (0-5 cm and 5-10 cm dbh, Fig. 5b). This is in accordance with the findings presented above that larger extant trees grew faster in their juvenile stage than extant juveniles in these diameter classes.

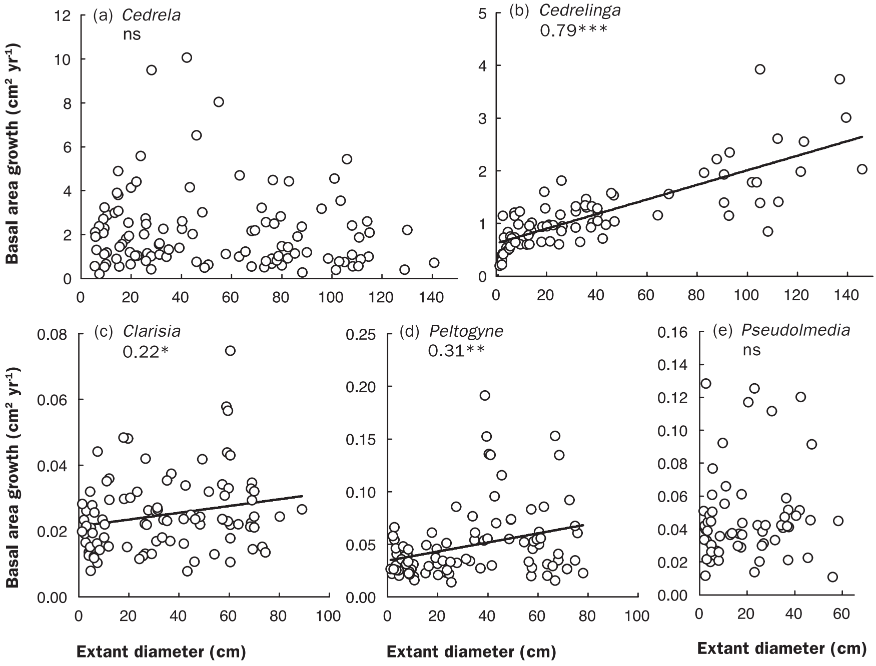


**Fig. 3** Relation between basal area growth in the 0-1 cm diameter class (0-5 cm for *Cedrela* and *Cedrelinga*) and extant diameter for five tropical tree species. Pearson's correlation coefficient is indicated. *= *P*<0.05, **=*P*<0.01, ***=*P*<0.001.

For juveniles of intermediate size, we found negative correlations between juvenile growth and YBP in four species (Fig. 7), suggesting increased juvenile growth rates over time. In *Cedrela* such correlations were found for juveniles of 10-15 cm diameter, for *Clarisia* from 2-4 cm diameter, for *Peltogyne* from 1-3 and 6-8 cm diameter and for *Pseudolmedia* in the diameter categories from 2-8 cm (Figs 5,6). Thus, except for one diameter class in *Cedrela*, no negative correlations between juvenile growth and YBP were observed for trees >8 cm diameter (Fig. 7).

## DISCUSSION

### Juvenile selection effect

Many researchers hypothesized that fast-growing juvenile trees in tropical forests have a higher chance to reach the canopy, the 'juvenile selection effect' (e.g. Enright & Hartshorn, 1981; Swaine *et al.*, 1987; Baker, 2003; Terborgh *et al.*, 1997; Brienen & Zuidema, 2006a). To our knowledge, our study is the first to actually test this hypothesis for tropical tree species through a direct comparison between current and historical juvenile growth rates. For three out of five study species we found that extant canopy trees have had faster growth as

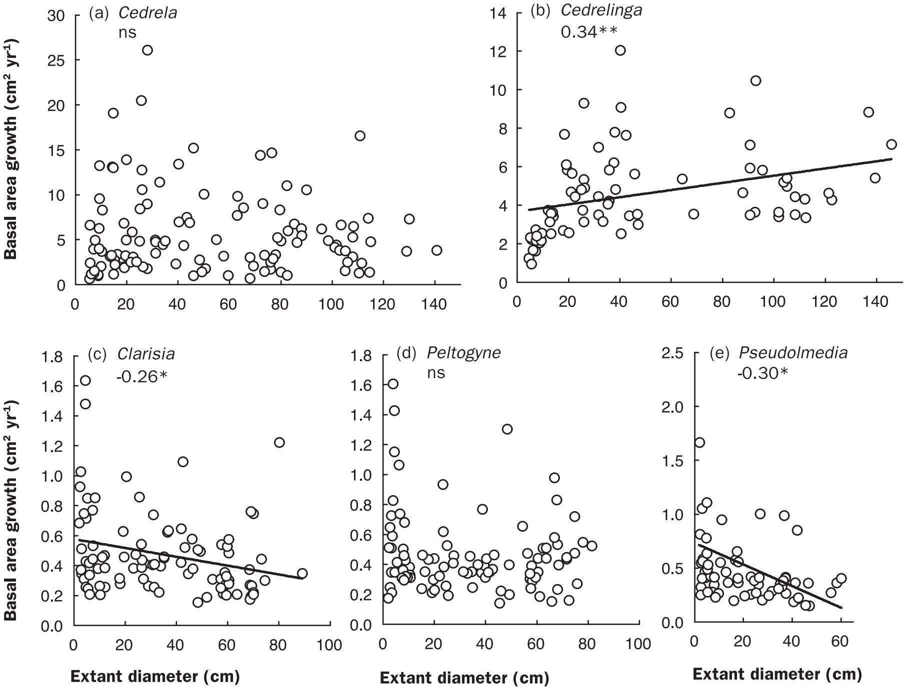


**Fig. 4** Relation between basal area growth in the 2-3 cm diameter class (5-10 cm for *Cedrela* and *Cedrelinga*) and extant diameter for five tropical tree species. Pearson's correlation coefficient is indicated. *= $P<0.05$, **=$P<0.01$, ***=$P<0.001$.

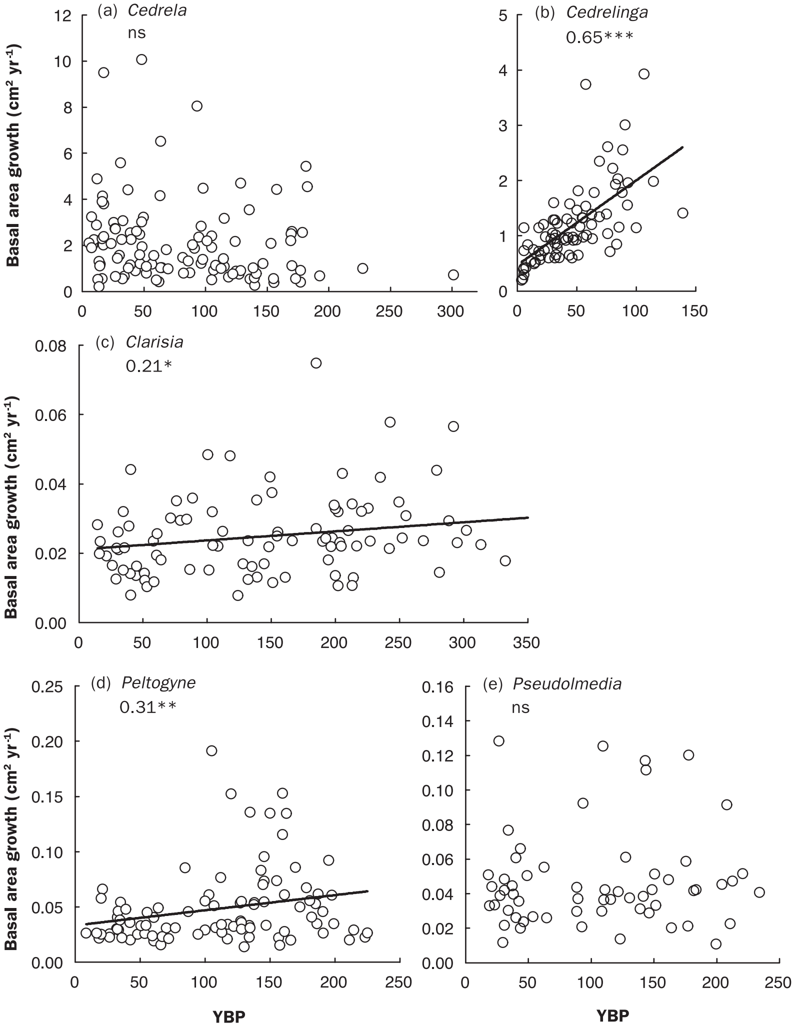


**Fig. 5** Relation between basal area growth in the 0-1 cm diameter class (0-5 cm for *Cedrela* and *Cedrelinga*) and year before present (YBP; year before 2006, year before 2002 for *Cedrela*) for five tropical tree species. YBP is the median value per tree. Pearson's correlation coefficient is given. *= $P$<0.05, **=$P$<0.01, ***=$P$<0.001.

small juveniles compared to extant juveniles, consistent with this juvenile selection effect. Our results suggest that fast growth until reaching 1 cm diameter (until 30 cm in *Cedrelinga*) increases the chance to attain the canopy. These findings are in accordance with those of Landis and Peart (2005), who showed higher juvenile growth in extant adult trees compared to extant juveniles in three temperate forest species until 5 cm diameter.

Our results likely underestimate the strength of the juvenile selection effect, as all trees included in our sample had already survived until 1 cm diameter. Therefore, the effects of slow growth on survival until 1 cm diameter were not taken into account here. As slow growth

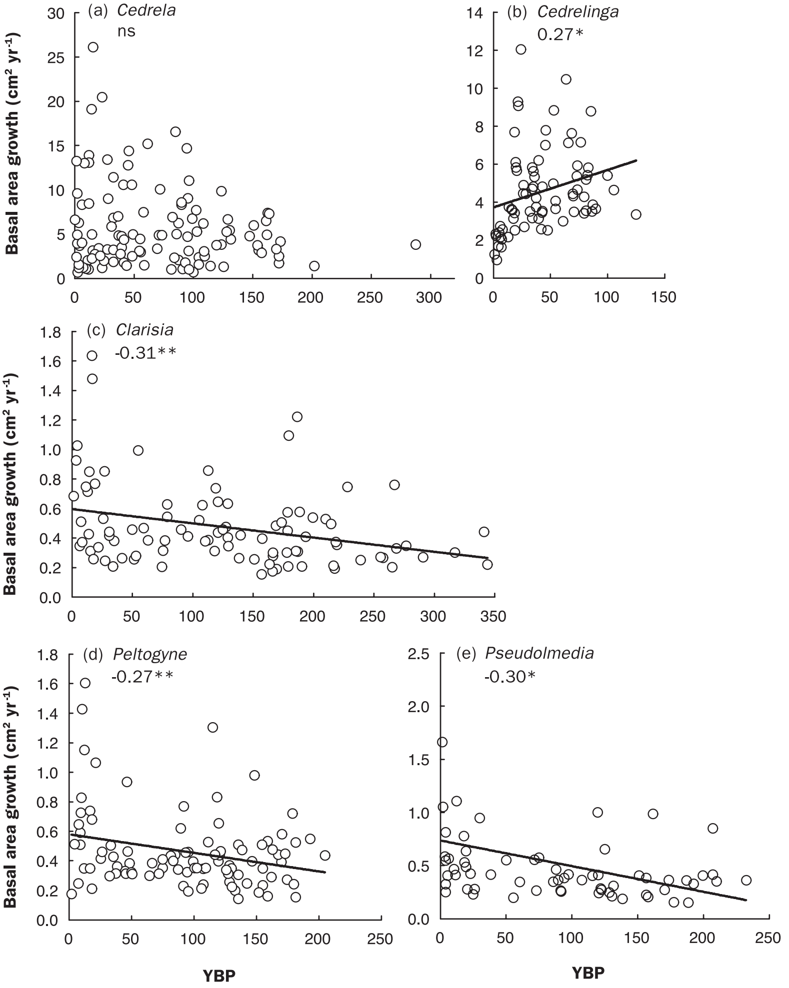


**Fig. 6** Relation between basal area growth in the 2-3 cm diameter class (5-10 cm for *Cedrela* and *Cedrelinga*) and year before present (YBP; year before 2006, year before 2002 for *Cedrela*) for five tropical tree species. YBP is the median value per tree. Pearson's correlation coefficient is given. *= $P<0.05$, **=$P<0.01$, ***=$P<0.001$.

leads to low survival (Terborgh *et al.*, 1997; Wyckoff & Clark, 2002), the consequences of slow growth in the 0-1 cm diameter class are likely larger than we quantified here. On the other hand, finding a juvenile selection effect in trees that have already survived until 1 cm diameter indicates that fast growth until that size has implications for survival until larger diameters. Such enhanced survival of initially fast-growing saplings may be the result of continued favourable growing conditions or a larger leaf area and larger carbohydrate reserves that these individuals had developed early in life (cf. Landis & Peart, 2005).

Most likely, the juvenile selection effect is driven by differences in light availability among trees, but we cannot exclude other factors which may have caused a growth decline over time. Nevertheless, in case of a climate-related growth decline, we would expect a growth decrease for all species over more diameter classes. It is possible that successful trees have established in high light conditions. This agrees with results of Brienen and Zuidema (2006a), who found fast early growth for *Amburana cearensis*. Similarly, Baker and Bunyavejchewin (2006) found that almost 40% of the canopy individuals of the shade-tolerant *Neolitsea obtusifolia* had recruited in gaps, while this was even >90% for the shade-intolerant species *Melia azederach*. Thus, juvenile trees that establish in a canopy gap may have a larger chance to attain the canopy.

The preferential survival of fast-growing juveniles to large size implies that fast growers have a higher chance to reach reproductive size. Thus, fast-growing juvenile trees likely have

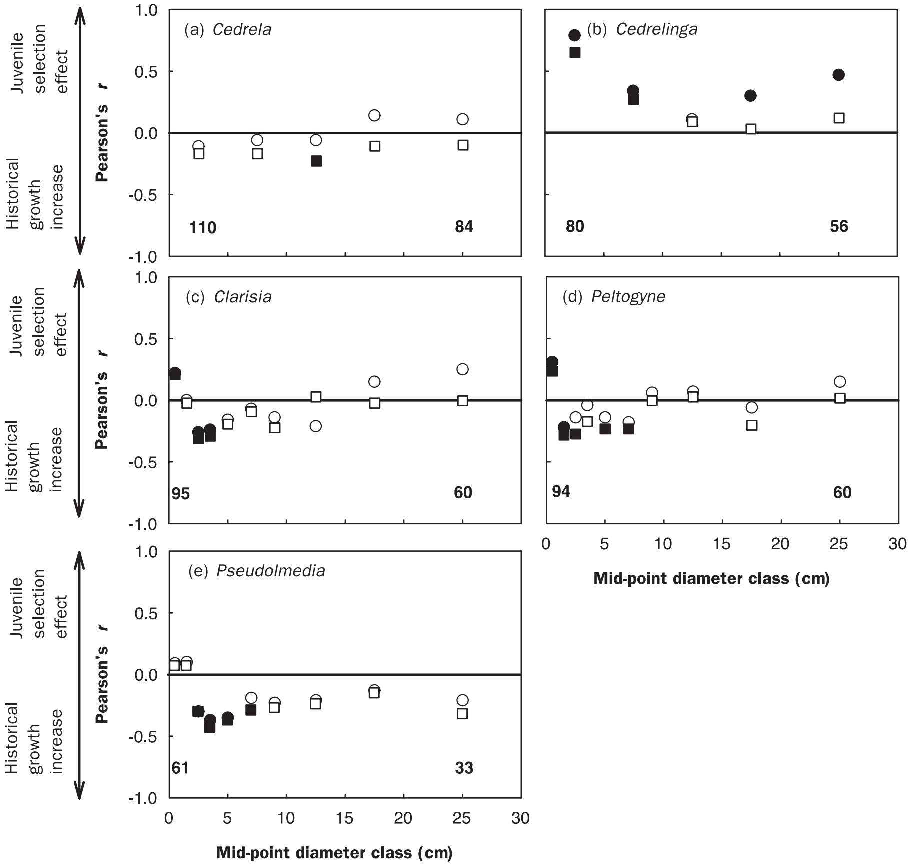


**Fig. 7** Pearson's correlation coefficients between basal area growth, extant diameter at breast height (dbh, circles) and year before present (YBP, squares) in diameter classes until 30 cm. Non-significant correlations are indicated with open symbols, filled symbols are used for significant correlations ($P$<0.05). YBP is expressed as number of years before present (median for all rings considered per diameter class; years before 2006, years before 2002 in *Cedrela*). A positive correlation indicates a juvenile selection effect, whereas a negative correlation indicates a historical growth increase. The minimum and maximum sample sizes are indicated in the lower part of the graphs.

a large contribution to population growth and fitness (Zuidema *et al.*, 2009). That means that selection pressure would act to increase the ability for fast growth in juvenile trees. On the other hand, the majority of saplings in the understorey of tropical rainforest are growing in the shade (Chazdon & Fetcher, 1984; Clark & Clark, 1999) and trajectories to the canopy can be long (Brienen & Zuidema, 2006a; Clark & Clark, 2001), putting strong selection pressure on traits that increase survival in shade. Thus, one would expect the juvenile selection effect to be absent or smaller in shade-tolerant species compared to light-demanding species. Landis and Peart (2005) found evidence for juvenile selection also in shade-tolerant species, but less strong compared to the shade-intolerant species. We found that the juvenile selection effect is weaker in two of the three shade-tolerant species, compared to *Cedrelinga*, a light-demanding species (Brienen & Zuidema, 2006a). Also the effect in the two shade-tolerant species is restricted to much younger life stages (i.e. until 1 cm diameter) compared to *Cedrelinga*, which needs high light conditions up to a diameter of 30 cm. These differences probably indicate differences in shade tolerance among species. However, we did not find a juvenile selection effect in the light-demanding species *Cedrela*. This is at odds with findings of Terborgh *et al.* (1997), which showed that slow-growing *Cedrela* juveniles had lower survival chances. This may partly be due to not having included trees from 1-5 cm dbh for this species, or to lower consistence of height at which samples were taken.

Our results have implications for modelling tropical tree growth. In presence of a juvenile selection effect, the average growth rate of extant juveniles is unlikely to be the correct measure to use in growth models or projections (e.g. Lieberman & Lieberman, 1985). Some researchers have already recognized this problem, and apply only above-average growth rates in tree growth projections (e.g. Condit *et al.*, 1995a; Terborgh *et al.*, 1997; Laurance *et al.*, 2004a) or include the link between growth and light conditions (Metcalf *et al.*, 2009). Although our sample of tree species is limited, our findings suggest that using above-average growth rates is generally recommended. The degree to which growth rates need to be adjusted depends on the shade tolerance of the species. Baker (2003) found that for shade-tolerant species mean growth rates may give relative accurate estimations of tree ages, whereas the use of mean growth rates for shade-intolerant species will strongly underestimate long-term growth rates and hence overestimate tree ages. To accurately predict long-term growth rates and model growth dynamics, species-specific data on the relation between growth and mortality are needed (e.g. SORTIE, Kobe *et al.*, 1995; Pacala *et al.*, 1996). As a short-cut to such modelling techniques, a comparison of (long-term) tree-ring data and increment data of extant trees may give valuable insights into the degree to which adjustments of growth rates are needed for different species.

### Increasing juvenile growth rates over time?

Juvenile growth rates increased over time in four out of five species in certain size classes (Fig. 7). In temperate forests, similar increases in growth over time have been found (Rolland *et al.*, 1998; Soulé & Knapp, 2006; Voelker *et al.*, 2006; Wang *et al.*, 2006; Johnson & Abrams, 2009; but see Landis & Peart, 2005). A cautious interpretation of our results and those of others is required, as sampling biases may result in spurious correlations between growth and time. Imagine that individual trees differ in long-term growth rates, such that slow-growing trees remain slow-growers, and fast-growers keep growing fast (Brienen *et al.*, 2006). Combined with some degree of size-dependence in the mortality probability at larger diameters, this will lead to a shorter lifespan of persistently fast-growers compared to slow-growers (i.e. subgroups with different mortality in the population; cf. Sheil & May, 1996). In temperate forests, slow-growing trees had indeed a longer lifespan than fast-growing trees of the same species (Black *et al.*, 2008; Bigler & Veblen, 2009). Thus, when sampling a population of large trees at a specific moment in time, the subpopulation of trees recruited in the distant past contains a smaller proportion of fast-growing trees than the subpopulation of trees recruited in the more recent past. This may lead to an apparent increase in growth rates in the recent past, even when growth rates did not increase (sampling bias I). A second sampling bias may occur when trees are sampled from some size threshold onwards. Then, slow-growing trees will not have reached this threshold at the moment of sampling, which could mean that more recently the sample may be biased towards fast-growing individuals (sampling bias II). Sampling bias I, II, or their combination may yield spurious positive correlations between growth and time.

Sampling bias I may have affected our results, although we do not have evidence for size-dependent mortality in the study species. There may have been some impact of sampling bias II too, as we sampled relatively many large trees. The sampling threshold in our study was 1 cm dbh (for *Cedrela* 5 cm dbh), which is rather low. Still, we did not sample in proportion to the population structure, thus trees in larger size classes have been overrepresented in our sample. If we assume that equal proportions of slow- and fast-growers establish at every time step, fast-growers reach larger size classes at a younger age than slow-growers. Even when evaluating growth at small tree sizes, we might include relatively more fast-growers than slow-growers and have a bias towards fast, recent growth.

We judge that our findings of historical growth increases are likely not the result of the above-mentioned sampling biases, although we cannot rule out that there has been some impact. If such sampling biases would have occurred, this should have led to historical growth increases also for the larger diameter categories, but these were not found. It is clear that the sampling biases described may importantly affect historical growth patterns. A full understanding of their magnitude requires a combination of empirical and modelling studies.

There are various explanations for the observed historical growth increase. Long-term changes in precipitation could have affected tree growth, but this is not likely as precipitation did not increase over the last decades in our study region (Malhi & Wright, 2004). Another explanation is the occurrence of recent large-scale disturbances leading to increased growth over recent time periods. We did not find strong, synchronous increases in growth rates that would indicate large-scale disturbances, nor do we have indications that such disturbances have taken place in our study areas over the last two centuries. A final – and often proposed – cause of historical increase in juvenile growth is the rise in atmospheric $CO_2$. The observed historical growth increase may be consistent with growth stimulation by elevated atmospheric $CO_2$. Remarkably, the historical growth increase in our study was confined to very small trees. This agrees with the stronger growth increase for young trees found in temperate forests (Voelker *et al.*, 2006; Wang *et al.*, 2006), although in those studies only non-light-limited trees were included. We found hardly any indication of an historical growth increase for larger trees. Only for *Cedrela* increasing growth rates over time were found for trees from 10-15 cm diameter, and for none of the species we observed a growth increase over time in larger size classes (Fig. 7).

### Concluding remarks

The juvenile selection effect and the historical growth increase likely interact. This could be the reason for not finding evidence for any of the two effects in certain diameter classes and species, as they cancel out. Thus, not finding a historical growth increase could be due to a strong juvenile selection effect. Similarly, this interaction may cause an underestimation of the historical growth increase in certain diameter classes.

The strength of the two effects likely varies among species. The juvenile selection effect is likely to be strongest in shade-intolerant species, while a historical growth increase may be stronger in shade-tolerant species. These species-specific patterns may have contributed to the switch from a juvenile selection of small (0-1 cm diameter) trees to a historical growth increase in slightly larger trees that we observed in two shade-tolerant species. We do not know whether a historical growth increase is associated with shade-tolerant species (cf. Kerstiens, 2001) or whether it is just harder to detect in shade-intolerant species that show strong selection of fast-growing juveniles.

Given the importance of changes in tropical forest biomass for atmospheric $CO_2$ concentrations (Malhi *et al.*, 2008), there is a clear need to understand the drivers of long-term growth patterns of tropical trees. Our study shows that tree-ring analysis is a promising tool to evaluate temporal changes in growth of tropical forest trees, at decadal to centennial scales. When combined with measurements on stable isotopes (e.g. McCarroll & Loader, 2004; Hietz *et al.*, 2005) or analysis of recruitment patterns (e.g. Baker *et al.*, 2005), tree-ring analysis may help unravelling causes of such temporal growth changes.

## ACKNOWLEDGEMENTS

We are grateful to Mart Vlam for help with the ring measurements. We thank Nazareno Martínez, Miguel Cuadiay, Adhemar Saucedo, Don Eugenio Mercado, Jeroen Wiegeraad, Edwin Rodríguez, Jan Rodenburg, Adhemar Cassanova Arias, and many others for help with fieldwork. We are grateful to staff and personnel of PROMAB-UAB, IBIF and to the Universidad Autónoma Gabriel Rene Moreno for logistic support. Logging companies 'La Chonta Woods' and 'Maderera Boliviana Etienne S.A.' are acknowledged for permission to work in their concessions and for logistic support. Niels Anten, Heinjo During, Marinus Werger and three anonymous reviewers provided constructive comments on earlier versions of the manuscript. DMAR was supported by grant W 01.53.2004.047 from the Netherlands Foundation for the Advancement of Tropical Research (WOTRO).

## SUPPORTING INFORMATION

**Table S1** Characteristics of the study species and sample size. Growth potential is indicated as the 99th-percentile of all observed diameter growth rates per species.

| **Species** | **Family** | **Shade tolerance** | **Deciduousness** | **Growth potential** (cm yr$^{-1}$) | **Study site** | **Sampling** area (ha) | **Sample size** 1-50 cm dbh | **Sample size** >50 cm dbh |
|---|---|---|---|---|---|---|---|---|
| *Cedrela odorata* L. | Meliaceae | Light-demanding | Deciduous | 2.25 | Purísima | 850 | 61 | 53 |
| *Cedrelinga catenaeformis* (Ducke) Ducke | Fabaceae | Light-demanding | Brevi-deciduous | 2.92 | Los Indios | 2500 | 60 | 29 |
| *Clarisia racemosa* Ruíz & Pavón | Moraceae | Shade-tolerant | Evergreen | 0.95 | Los Indios | 400 | 65 | 30 |
| *Peltogyne* cf. *heterophylla* M.F. Silva | Fabaceae | Shade-tolerant | Brevi-deciduous | 1.4 | Los Indios | 170 | 69 | 29 |
| *Pseudolmedia laevis* (Ruíz & Pavón) J.F. Macbr. | Moraceae | Shade-tolerant | Evergreen | 0.95 | La Chonta | 50 | 60 | 3 |

### NOTE S1 ANNUAL CHARACTER OF JUVENILE AND ADULT RINGS OF *PSEUDOLMEDIA LAEVIS*

#### Relation between growth and rainfall

For *Pseudolmedia* a chronology from 1985-2005 was constructed using a total of 92 ring-width series from 32 trees (13 juvenile trees of 1-10 cm diameter at breast height (dbh) and 19 trees >10 cm dbh) with an interseries correlation of 0.49. The age-trend was removed from the ring-width series with negative exponential or linear detrending. The chronology was constructed from the residuals using the program ARSTAN. Rainfall-data (1994-2005) were from the sawmill in the concession 'La Chonta', at a distance of about 30 km from the research area (M. Peña-Claros, unpublished data).

The ring width index showed a strong, positive correlation with annual precipitation calculated from September until August the subsequent year, which corresponds to the annual growth of the tree (Fig. S1; Pearson's $r$=0.66, $P$=0.02). This result strongly indicates that juvenile, as well as, adult rings of *Pseudolmedia* are formed annually.

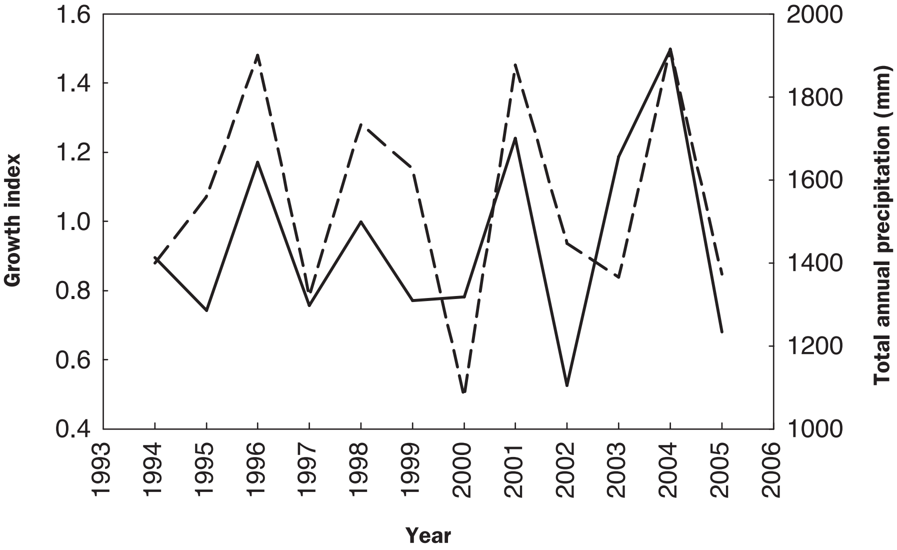


**Fig. S1** Chronology (1994-2005) of *Pseudolmedia laevis* (straight line) and annual precipitation from the sawmill in La Chonta (dashed line).

# CHAPTER 3

## Assessing long-term changes in tropical forest dynamics: a first test using tree-ring analysis

with Claudia C. Soliz-Gamboa & Pieter A. Zuidema

## SUMMARY

There is growing evidence that tree turnover in tropical forests has increased over the last decades. This change is generally attributed to climatic change but may also be the result of a response to disturbance. The evaluation of patterns and causes of changes in tree turnover requires data over much longer periods than currently available from forest dynamics plots. Here, we propose two methods to detect evidence for long-term changes in tree turnover from tree-ring data. We then apply these to two Bolivian non-pioneer species, evaluating temporal changes in growth patterns over 200-300 y. First, we checked for synchronization of growth releases in time, to identify possible large-scale disturbances. Second, we related the frequency of growth releases to time with the aim to determine whether the frequency of releases has increased over time. Finally, we calculated the degree of temporal autocorrelation, a measure that is indicative for the temporal changes in growth rates due to canopy dynamics. We checked whether the degree of autocorrelation has changed over time. As the occurrence of releases and the strength of autocorrelation may be partly caused by the ontogenetic increase in growth, we analyzed release frequency and degree of autocorrelation based on the residuals from a relation between tree size and diameter growth.

Overall, we did not detect changes in autocorrelation or release frequency over the last 200-300 years in both species. The exception to this general pattern was the first size category (a 20-y period starting at 0 cm diameter), in which we did find an increase in release frequency over time. This relation is probably the result of the structure of our dataset or of a remaining ontogenetic effect due to fast growth of some individuals.

In all, we found no evidence for a long-term change in tree turnover in the study area over the last two to three centuries. We discuss the suitability of the proposed methods in reconstructing long-term changes in tree turnover.

**Key words:** Forest dynamics, growth release, autocorrelated growth, ontogeny, tree turnover, tropical trees, Bolivia

## INTRODUCTION

There is a growing amount of evidence that tropical forests are changing. Growth rates of individual trees increased over the last decades in permanent sample plots (Laurance *et al.*, 2004b; Phillips *et al.*, 2008), as did aboveground biomass (Baker *et al.*, 2004), and tree turnover (Phillips & Gentry, 1994; Lewis *et al.*, 2004b; Phillips *et al.*, 2004; Laurance *et al.*, 2009). These changes have been attributed to climate change, in particular to the increase in atmospheric $CO_2$ (Lewis *et al.*, 2004a). Elevated levels of $CO_2$ may have increased rates of photosynthesis and as a result stimulated tree growth. At stand level, such changes may have increased rates of growth, recruitment and mortality, resulting in a higher stem density and increased aboveground biomass (Lewis *et al.*, 2004a; Phillips *et al.*, 2008). An alternative explanation for the observed change in tropical forest biomass is the occurrence of historical (large-scale) disturbances (Chave *et al.*, 2008). If forests are recovering from such disturbances, an increase in biomass over time is observed.

Although the evidence for increased biomass and tree turnover in tropical forests is now quite strong, the causes of these increases are widely and intensively debated (e.g. Wright, 2005; Lewis *et al.*, 2004a; Lewis *et al.*, 2006). Methodological problems have been proposed as causes, including sampling biases related to the size, amount and location of the permanent sample plots, which may have led to observing increases in biomass (Feeley *et al.*, 2007a; Chave *et al.*, 2008; Fisher *et al.*, 2008). Similarly, the varying intervals between re-measurements of the plots have been suggested to result in an increase in tree turnover (Sheil, 1995b). To account for the latter bias, corrections have been applied (cf. Lewis *et al.*, 2004b; Lewis *et al.*, 2004c; Phillips *et al.*, 2004). No evidence was found for a sampling bias due to intrinsic temporal patterns of forest biomass growth and decline (Gloor *et al.*, 2009).

So far, temporal patterns in forest dynamics have been evaluated over relatively short time periods, spanning just the last few decades (e.g. Phillips *et al.*, 2004). Atmospheric $CO_2$, however, has increased over the last 150 years (IPCC, 2007). Also, any recovery from past disturbances is a long-term process that would take many decades. Thus, to study these effects, long-term data are required. One option to obtain such data is the application of tree-ring analysis. Tree-ring analysis has been successfully used to show that diameter growth of four Bolivian tree species has gradually increased over the last centuries (Chapter 2). In order to detect changes in tree turnover, it is necessary to analyze the temporal variation in tree-ring width instead of the average or median values. An increase in tree turnover over time implies an increase in the frequency of canopy gap formation. The formation of canopy gaps back in time can be reconstructed using tree-ring analysis, as growth rates of the remaining trees temporarily increase when a gap is formed. These growth releases can be found in tree-ring data as periods of a sudden increase in growth, which is sustained over time (Nowacki & Abrams, 1997). Thus, an increase in the frequency of occurrence of releases over time may indicate an increase in tree turnover. Tree-ring analysis has been widely applied to reconstruct the disturbance history of temperate forests (e.g. Runkle, 1982; Lorimer & Frelich, 1989; Lusk & Smith, 1998) and recently also in the tropics for a seasonally dry forest in Thailand (Baker *et al.*, 2005).

Another way of evaluating whether tree growth patterns have changed over time considers the temporal patterns in growth autocorrelation. Tree growth tends to be autocorrelated in time (e.g. Kohyama & Hara, 1989; Kammesheidt *et al.*, 2003; Grogan & Landis, in press), i.e. the growth of a tree in one year is correlated with that in the subsequent year. Such growth autocorrelation of individual trees – ‘within-tree autocorrelation’ – has been found to be strong for a number of tropical tree species (Brienen *et al.*, 2006). Within-tree autocorrelation has been suggested to increase, when a tree switches more often between periods of slow and fast growth (Brienen *et al.*, 2006). As the occurrence of periods of suppression and release in growth are associated with gap dynamics, we expect within-tree autocorrelation to increase with increasing tree turnover.

In this study we evaluate the suitability of these two methods – detection of releases and analysis of autocorrelation – to assess evidence for long-term changes in tropical forest dynamics. The following research questions were addressed: (1) Has the frequency of occurrence of releases changed over time? and (2) Has the strength of within-tree autocorrelation increased over time?

We applied these methods to two Bolivian non-pioneer tree species using long-term growth data from tree-ring measurements. Trees over the entire diameter range of the species were sampled to evaluate changes in within-tree autocorrelation and frequency of growth releases over the last 2-3 centuries.

## MATERIALS AND METHODS

### Study area and species

Fieldwork was conducted in a semi-deciduous moist forest area, 'Los Indios' (10°26'S, 65°33'W), in the department of Pando, Bolivia. Mean annual precipitation is 1660 mm (Riberalta), with a dry season (<100 mm per month) from May until September. The forest has an average canopy height of 33 m and stem density of 423 stems ha$^{-1}$ (of stems >10 cm diameter at breast height (dbh; Toledo *et al.*, 2008). Fieldwork was conducted in 2006 and 2007, just after selective logging (2-3 trees ha$^{-1}$) had taken place. Before that, the forest was not harvested, and no evidence for large-scale historical disturbances exists. Two shade-tolerant canopy tree species were included: *Clarisia racemosa* and *Peltogyne* cf. *heterophylla*, which will be further referred to by their generic name only. Both species form annual rings in both the juvenile and the adult stage (Soliz-Gamboa *et al.*, submitted). Fieldwork for *Clarisia* was done in an area of ~400 ha and for *Peltogyne* in an area of ~170 ha. Research areas for the two species did not overlap.

### Sample collection and ring width measurements

We randomly selected 57 and 62 trees of <50 cm dbh and 30 and 29 trees of >50 cm dbh for *Clarisia* and *Peltogyne*, respectively (cf. Chapter 2). We selected individuals of <50 cm dbh such that they were evenly distributed over diameter categories. In order to reduce spatial autocorrelation in growth rates, selected individuals needed to be at least 20 m apart. Damaged juveniles (<10 cm dbh) were not included.

Discs were obtained from the selected individuals at 0.5 m height for *Clarisia* and at 1 m height for *Peltogyne*. In the case of trees >50 cm dbh, we always collected discs from stumps of logged trees. A digital picture of each disc was taken, to calculate fresh disc area using pixel-counting software (SigmaScan Pro 5.0). Discs were air-dried and sanded with progressively finer sandpaper until a grit of 1000. Rings were marked in three or four radii – selected to correspond to total disc area – using a stereomicroscope (6.3-40x). Every tenth ring was connected over the whole disc to control for errors in ring identification. Ring widths were measured perpendicular to the ring boundaries using a LINTAB 5 (Rinntech) measurement device. The last formed ring (2006, growth period 2006-2007) was left out for the trees >50 cm dbh, as this ring was formed after selective logging. Ring widths of all radii of the discs

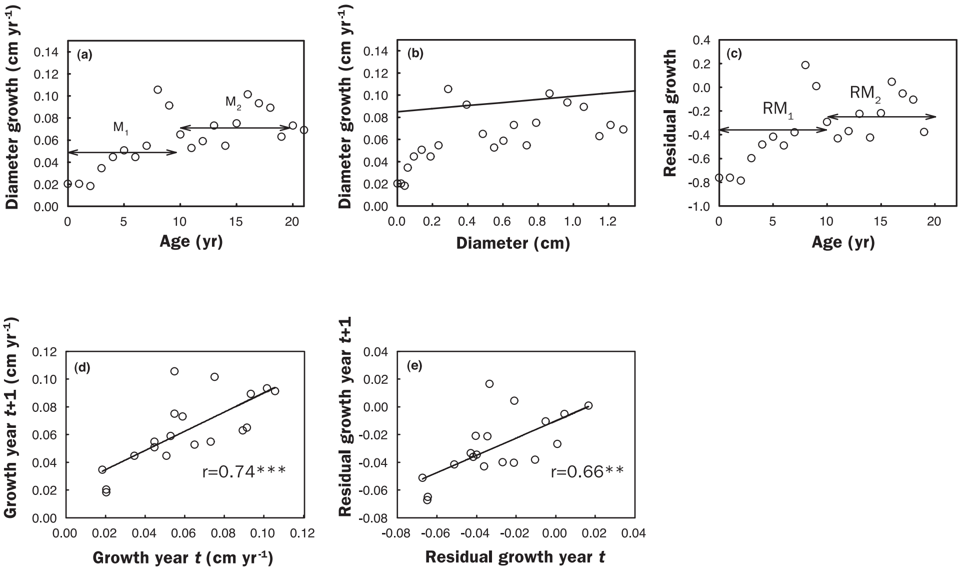


**Fig. 1** Example of growth patterns of a *Clarisia* tree. (a) Diameter growth over the first 20 years (initial diameter is 0 cm) of the lifespan of an individual tree. Moving averages $M_1$ and $M_2$ are indicated. (b) Relation between size and diameter growth. The line represents the average relation between size-and growth rate for *Clarisia*. (c) Residuals from the average relation between tree size and growth rate in proportion to the average relation between tree size and growth rate. Moving averages are indicated. (d) Within-tree autocorrelation for the initial diameter of 0 cm. (e) Autocorrelation in the residuals for the initial diameter of 0 cm.

were averaged, corrected for desiccation and irregular growth using the mean radius of the fresh disc area.

### Calculating and analyzing growth releases

Relative changes in diameter growth were calculated. A moving average of ten years was applied to remove long-term age-effects and short-term climatic fluctuations. Percent growth change was calculated following the approach of Nowacki and Abrams (1997):

$$\%GC_i = [(M_2 - M_1) / M_1] \times 100$$

where %GCi = percentage growth change between the preceding and subsequent 10-year means of year *i*, $M_1$ = mean diameter growth over the preceding ten years (including year *i*), and $M_2$ = mean diameter growth over the subsequent ten years. A period with %GC >50%, which lasted for at least ten years was regarded as a release. Nevertheless, growth rates increase with tree size (e.g. Clark & Clark, 1999). If this ontogenetic increase in growth is strong, in spite of the application of a moving average, it may result in a high %GC and even lead to the detection of a release (cf. Fig. 1a). To correct for this size-related effect, we determined residual growth: the residuals of a species-specific linear regression between average size (for trees up to 20 cm diameter) and growth (Fig. 1b). These residuals were used to calculate growth changes, corrected for the ontogenetic increase in growth. We expressed the residuals in proportion to the average relation between size and growth. Then, we calculated a measure similar to the percentage change of growth residuals (residual growth change; $\%RGC_i$; cf. Fig. 1c):

$$\%RGC_i = (MR_2 - MR_1) \times 100$$

where $\%RGC_i$ = percentage change in growth residuals between the preceding and subsequent 10-year averages, $MR_1$ = mean residual diameter growth over the preceding ten years (including year *i*), and $MR_2$ = mean residual diameter growth over the subsequent ten years. A period with %RGC>50%, which lasted for at least ten years was regarded as a release. Note that here growth of each year is standardized for the relation between average size and growth rate. The difference between $MR_1$ and $MR_2$ is not expressed in proportion to $MR_1$, but in proportion to the average relation between size and growth rate. We chose to use this approach, instead of the boundary-line method for detecting releases (Black & Abrams, 2003), as that method does not fully correct for tree size and requires a large amount of points to establish the boundary line (Black *et al.*, 2009).

First, we evaluated whether there was evidence for the occurrence of a large-scale disturbance in the study area (cf. Baker *et al.*, 2005). To do so, the dataset was divided into 25y-periods, among which the percentage of trees with a release starting in each time period was compared. Second, the occurrence of releases in growth was related to time. To allow comparison of the occurrence of releases and strength of autocorrelation among trees at the same diameter, and thus in the same ontogenetic stage, we expressed all variables for a timespan of 20 years starting at different tree diameters (i.e. initial diameter; 0, 2.5, 5, 10, 15 and 20 cm) per individual tree. Presence or absence of a release was scored for the same 20 years. For each individual and each initial diameter, we also calculated the midpoint of the ages of those 20 years, which we termed year before present (YBP; the time axis, cf. Chapter 2). The calendar year for the ‘present year’ in the calculation of YBP was 2006, the year of data collection. A logistic regression was performed to relate the presence or absence of a release to YBP for each initial diameter.

### Calculating within-tree autocorrelation

Within-tree autocorrelation was calculated as the correlation of growth of an individual tree in a certain year *t* with its growth in the subsequent year *t*+1 using Pearson’s correlation. We expressed autocorrelation in time periods of 20 years starting at the same initial diameters as for the frequency of releases. In this way, the comparison of the strength of autocorrelation among trees was facilitated. Additionally, we calculated strength of autocorrelation corrected for tree size. A fast-growing individual tree passes in 20 years through a larger diameter range than a slow-growing tree, which could mean that in those 20 years a fast-growing tree has a larger ontogenetic increase in growth rate, and thus, stronger within-tree autocorrelation. Autocorrelation was calculated from the residuals of a linear regression between size and average growth rates up to 20 cm diameter. Then, strength of autocorrelation was related to YBP using a mixed modelling approach, as data points were not independent due to the inclusion of multiple values per tree (one value per initial diameter). Initial diameter was included as a factor, and YBP as a covariate. To analyze the influence of ontogeny, we also included the mean diameter growth rate over the same 20y-period as a covariate. This approach was applied for within-tree autocorrelation and the autocorrelation in the residuals. All statistical analyses were performed using SPSS 16.0 (SPSS Inc.).

## RESULTS

### Size-dependent growth rates, growth releases and autocorrelation

Growth rates strongly increased with tree size for both species (Fig. 2). In *Clarisia*, average growth rate at 0 cm diameter, 0.04 cm yr$^{-1}$, showed a ninefold increase to 0.36 cm yr$^{-1}$ at 20 cm diameter. For *Peltogyne*, this initial increase was also strong, eightfold, from 0.06 cm yr$^{-1}$ at 0 cm diameter to 0.48 cm yr$^{-1}$ at 20 cm diameter. This increase is probably due to larger leaf area available for assimilation and to some extent an increase in light with increasing tree height.

The occurrence of releases showed a strong pattern with tree size and differed between species (Fig. 3a). *Clarisia* showed more releases at the initial diameters of 0, 2.5 and 5 cm. A lower percentage of trees experienced a release at larger diameters. For *Peltogyne* the opposite pattern was found as releases mostly occurred at the initial diameters of 10 and 15 cm (Fig. 3a). *Clarisia* showed strong within-tree autocorrelation in the 20y-period starting at 0 cm diameter; autocorrelation was lower for the larger initial diameters (Fig. 3c). For *Peltogyne*, autocorrelation was low in the time period starting at 2.5 cm diameter. Hence, for this species autocorrelation does not seem to increase or decrease with increasing tree size. The strong autocorrelation at small size for *Clarisia* may be a consequence of the relatively

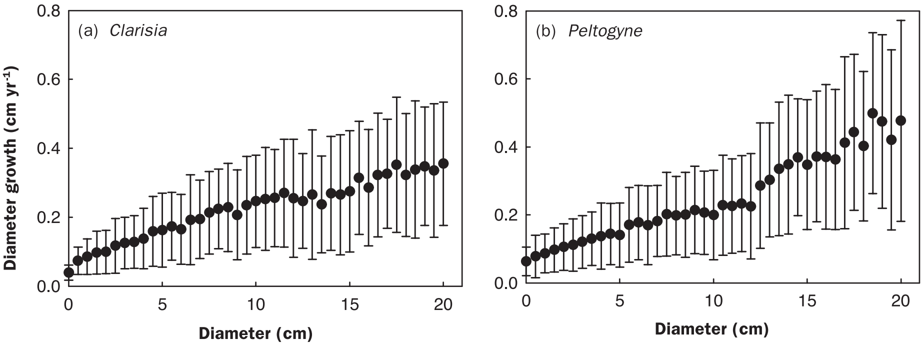


**Fig. 2** Average relation between tree diameter and diameter growth for two tropical tree species. Error bars are standard deviations.

steep increase in growth from 0 cm to 2.5 cm diameter compared to the increase at larger diameters (cf. Fig. 2). In contrast, *Peltogyne* showed a less steep increase until ~12.5 cm diameter, but a steeper increase from 12.5 cm onwards (Fig. 2b).

### Assessing changes in release frequency over time

To evaluate the degree of synchronization in time in the occurrence of releases, we compared the occurrence of releases in 25-year periods. In general, there was no clear pattern in the occurrence of releases for both species, but the percentage of trees with a release varied somewhat over the past 200-300 y (Fig. 4). As *Clarisia* reaches a higher age than *Peltogyne*, there were >10 trees present in the sample from 1700 onwards, while for *Peltogyne* this was from 1825 onwards. We found releases in all time intervals for both species and did not detect a clear clustering of releases at any moment in time in the past centuries (Fig. 4). To determine whether recently the occurrence of releases increased over time, we related the presence or absence of a release to year before present (YBP) with a logistic regression for each initial diameter. At most initial diameters we did not find a relation between the occurrence of releases and YBP (Fig. 5). For both species, we found a significant increase in

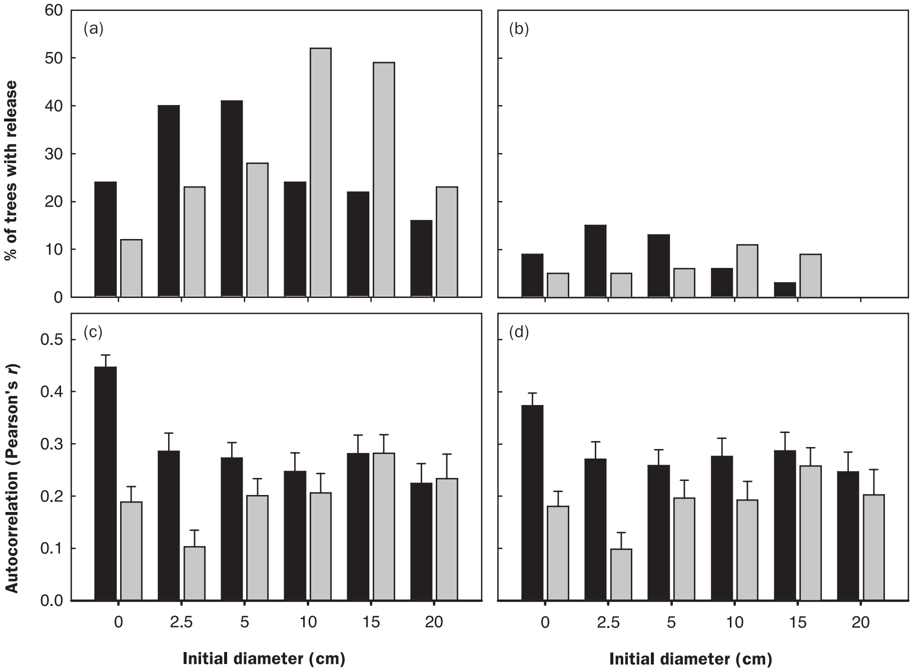


**Fig. 3** Average within-tree autocorrelation with standard error and percentage of trees with a release in a 20-year time period starting at different initial diameters. Black bars indicate values for *Clarisia*, grey bars represent values for *Peltogyne*. (a) Percentage of trees with a release. (b) Percentage of trees with a release after correction for the relation between size and growth rate. (c) Within-tree autocorrelation. (d) Within-tree autocorrelation in residuals from a regression between tree size and growth rate.

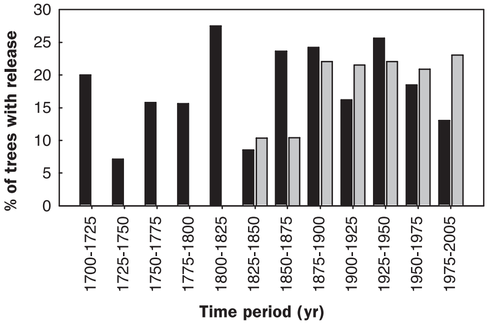


**Fig. 4** Percentage of trees with a release in 25-year time periods for *Clarisia* (black bars) and *Peltogyne* (grey bars). Percentages were only indicated for time periods with at least ten trees present.

releases over time in the 20y-interval at an initial diameter of 0 cm and for *Peltogyne* also at 2.5 cm diameter (Fig. 5). This may be partially due to the structure of the dataset, as sample sizes are largest at small tree size. At those sizes, both juvenile growth rates of large trees and growth rates of extant juvenile trees are included. Additionally, the range in YBP is largest at small tree sizes, as growth rates of the oldest and youngest trees are included.

When evaluating the occurrence of releases corrected for growth releases caused by the ontogenetic pattern in growth, much less releases were detected for both species (Fig. 3b). However, at an initial diameter of 0 cm an increase in the occurrence of releases over time was still observed for *Clarisia*, as well as for *Peltogyne*. Nevertheless, the number of trees with a release was very low, eight for *Clarisia* and only five for *Peltogyne* (cf. Fig. 3b).

**Table 1** Results of a mixed model analysis to determine the effects of start diameter (tree size) on autocorrelation and on autocorrelation in the residuals from the relation between tree size and growth in a 20-year period. Year before present (YBP; year before 2006) and average diameter growth for the same 20 years were included as covariates. Bold values indicate significant effects at $P<0.05$.

| | *Clarisia* | | | | *Peltogyne* | | | |
|---|---|---|---|---|---|---|---|---|
| | Autocorrelation | | Residuals | | Autocorrelation | | Residuals | |
| | *F* | *P* | *F* | *P* | *F* | *P* | *F* | *P* |
| Initial diameter | 0.507 | 0.771 | 0.881 | 0.494 | **2.430** | **0.035** | **3.064** | **0.010** |
| YBP | **4.032** | **0.045** | 2.855 | 0.092 | 0.006 | 0.941 | 0.018 | 0.894 |
| DGR | 0.000 | 0.985 | 0.118 | 0.732 | **12.622** | **0.000** | **8.696** | **0.003** |
| Initial diameter x YBP | 0.369 | 0.870 | 0.409 | 0.842 | 1.049 | 0.388 | 0.886 | 0.491 |
| Initial diameter x DGR | 1.733 | 0.126 | 1.840 | 0.104 | **3.494** | **0.004** | **3.801** | **0.002** |
| YBP x DGR | **3.885** | **0.049** | 2.714 | 0.100 | 0.369 | 0.544 | 0.136 | 0.713 |

## Changes in autocorrelation over time

Temporal patterns in the strength of autocorrelation were evaluated using a mixed modelling approach. For *Clarisia* a significant negative relation between within-tree autocorrelation and YBP was observed, which indicates an increase in within-tree autocorrelation over time (Table 1; Fig. 6). In *Peltogyne* we found no relation between within-tree autocorrelation and YBP (Table 1; Fig. 6). Within-tree autocorrelation did not vary with tree size in *Clarisia*, where-

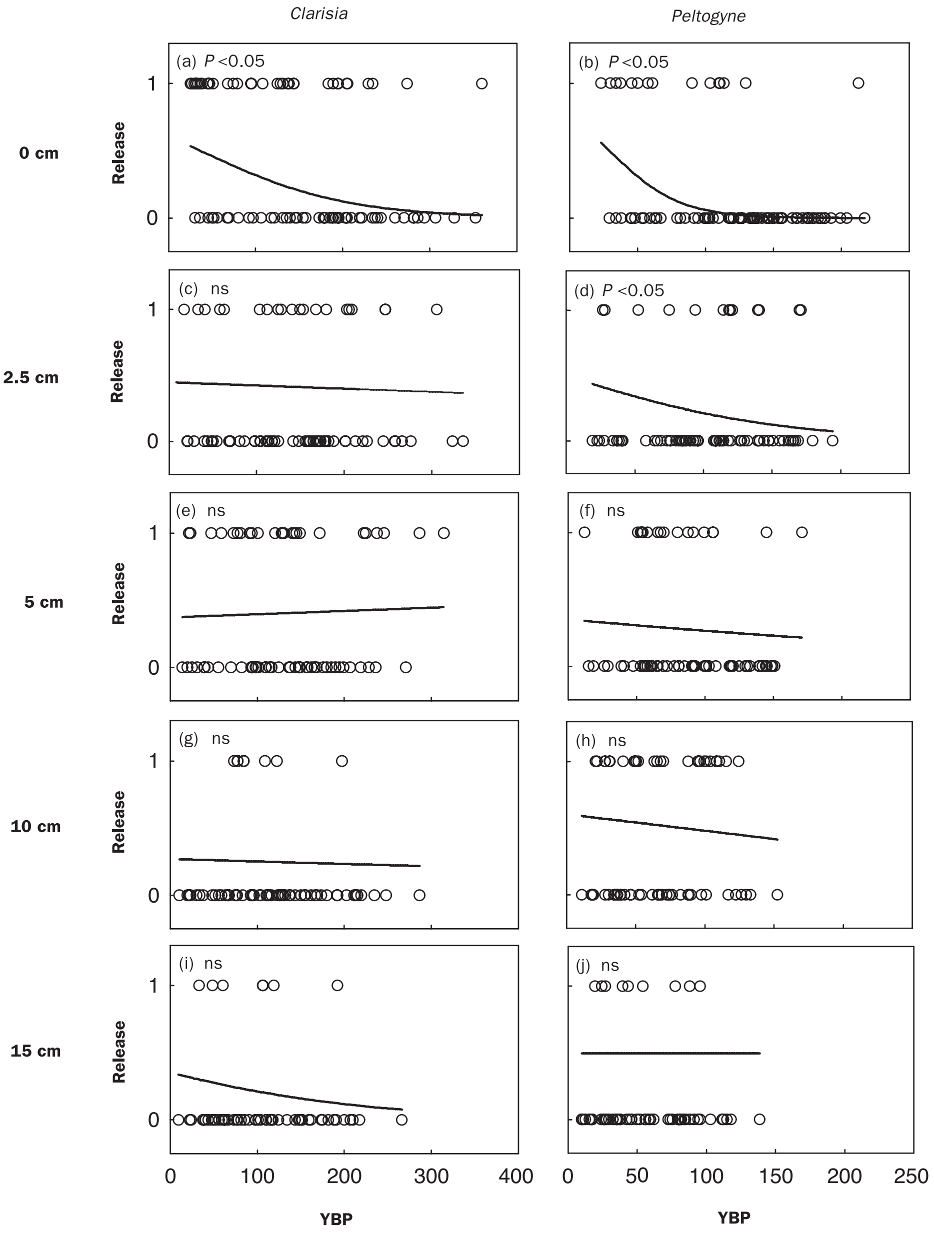


**Fig. 5** The occurrence of releases (based on ring widths, not on residual growth) related to the number of years before present (YBP; year before 2006) for two tropical tree species at different tree sizes.

as for *Peltogyne* within-tree autocorrelation differed among initial diameters and increased with average diameter growth rate (Table 1).

When correcting for the relation between tree size and growth rate, autocorrelation was somewhat lower in *Clarisia* at an initial diameter of 0 cm (Fig. 3b). When using autocorrelation in growth residuals, no significant effect of YBP was found for any of the species (Table 1). For *Peltogyne* a positive relation between average growth rate and within-tree autocorrelation was still found, even when using residual growth (Table 1). Similarly, there was still an effect of initial diameter on within-tree autocorrelation for *Peltogyne*.

## DISCUSSION

### Ontogeny and the occurrence of releases and strength of within-tree autocorrelation

Tree growth is known to increase with tree size (e.g. Clark & Clark, 1999). With increasing tree size, trees have larger leaf area available for assimilation. Additionally, growth rates are known to increase with increasing tree height (Claveau *et al.*, 2002), probably as a consequence of the increase in light availability with increasing tree height (cf. Sterck *et al.*, 2001). An ontogenetic growth increase may lead to the detection of a release. If the ontogenetic increase is strong, the difference between the moving average of the preceding 10 years may differ strongly from that of the subsequent ten years and result as such in a large growth change. This may be the case for *Clarisia* in particular, as in this species the initial increase in growth with tree size is relatively steep (cf. Fig. 2). Similarly, the larger number of releases for *Peltogyne* at the initial diameters of 10 and 15 cm may be the consequence of the steeper ontogenetic increase in growth at those tree sizes. The detection of a much lower number of releases after correcting for size-related growth confirms this idea.

An ontogenetic growth increase may cause strong autocorrelated growth. Brienen *et al.* (2006) attributed the stronger autocorrelation for trees <10 cm dbh to the frequent alternation of suppressions and releases at that tree size. However, they also show that the use of residual growth results in lower within-tree autocorrelation, although the decrease differed among species (Brienen *et al.*, 2006). Our results show that accounting for the relation between size and growth did not result in a large reduction in within-tree autocorrelation. After correcting for the average relation between size and growth, autocorrelation still increased with growth rate in *Peltogyne* (Table 1). This may be due to the fact that we calculated residuals based on an average relation between size and growth rate, rather than the observed relation for individual trees. Thus, differences among fast- and slow-growing trees at the same tree size were still present in the dataset of residuals and may be largely responsible for the strong autocorrelation that we observed.

### Evidence for changing forest dynamics over time?

Two methods were proposed to assess changes in forest dynamics over time using tree-ring analysis: the occurrence of releases and the strength of within-tree autocorrelation. In addi-

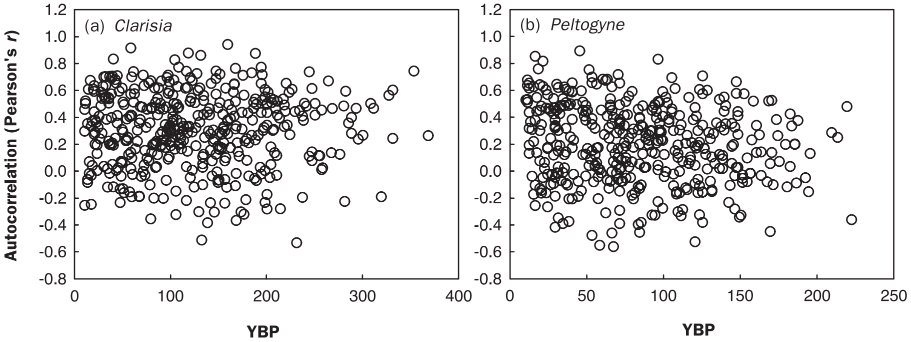


**Fig. 6** Relation between within-tree autocorrelation for a 20-year timespan and average year before present (YBP; year before 2006). Values for all tree sizes are shown, based on ring widths instead of residual growth.

tion to that, we evaluated synchrony in the occurrence of releases over time to identify possible large disturbances. Although some variation in the occurrence of releases over time was observed, evidence for a large-scale disturbance was not found. At small tree diameters, we observed an increase in the frequency of releases over time in both species and an increase in within-tree autocorrelation over time for *Clarisia*. These patterns were likely caused by an ontogenetic increase in growth. When accounting for an ontogenetic increase in growth, neither temporal changes in within-tree autocorrelation, nor reliable temporal changes in the occurrence of releases were found. At an initial diameter of 0 cm, still a temporal change in the occurrence of release was found for both species, but only very few trees showed a release (cf. Fig. 3b). Thus, we did not find evidence for a change in forest dynamics over time in the study area.

## Future directions

The application of tree-ring analysis may be a promising tool in evaluating temporal patterns in tropical forest dynamics, but causes of growth releases and within-tree autocorrelation should be unravelled further to develop more suitable methods to detect light-related growth changes. It may be more appropriate to define criteria to detect releases specifically for tree species and forest types (cf. Rubino & McCarthy, 2004). Baker and Bunyavejchewin (2006), for instance, defined releases based on threshold values in observed light levels and also in temperate forests releases have been defined in a similar way (e.g. Lorimer *et al.*, 1988). Another way of defining releases is a direct comparison of growth before and after canopy gap formation for the same tree, which has been done for temperate tree species in silvicultural studies about thinning treatments (cf. Bebber *et al.*, 2004; Bevilacqua *et al.*, 2005), but not for tropical trees. Using these approaches, there is larger chance to detect growth releases which are indeed triggered by improved light conditions.

It should be taken into account that we worked on a rather coarse spatial scale as we included, on average, less than one tree per 2 ha (*Peltogyne*) or per 4 ha (*Clarisia*). To capture all variation in canopy dynamics and to be able to define forest turnover (e.g. Hartshorn,

1978) or that proportion of the forest canopy that is annually opened through gap formation (e.g. van der Meer & Bongers, 1996), gap dynamics should also be evaluated on smaller spatial scales. A possible sampling design may be the inclusion of various clusters of trees, with the clusters distributed over a larger area. In this way changes at different spatial scales can be detected (cf. Baker *et al.*, 2005). Additionally, our sample size was small. To determine changes in forest structure in a single area a sample of at least 1000 trees has been suggested to be sufficient (cf. Hall *et al.*, 1998; Clark, 2007). For our approach probably fewer trees would suffice, as only trees that survived, or that did not experience a gap event, were included. Nevertheless, a larger sample size than presented here is probably required.

To obtain full insight in temporal patterns in forest dynamics, the complete disturbance history of the forest needs to be reconstructed. This entails inclusion of all trees of the dominant (canopy) tree species in a certain area to allow reconstruction of time of establishment, synchronization of the occurrence of releases in time and the spatial scale of disturbances. In temperate forests, this approach is commonly applied (e.g. Lusk & Smith, 1998; Rentch *et al.*, 2003). For tropical forests, however, this approach may be somewhat far-fetched as these forests are more diverse and usually not all species form (reliable) annual growth rings (Baker *et al.*, 2005; but see Worbes *et al.*, 2003). Still, such an approach can be applied for the species that do form reliable annual rings. When adjusting the techniques for the detection of releases and improving the sampling strategy, the reconstruction of release frequencies over long time periods will help understanding long-term patterns of tropical forest dynamics.

## ACKNOWLEDGEMENTS

We are grateful to Mart Vlam for help with the ring measurements. We thank Nazareno Martínez, Miguel Cuadiay, Adhemar Saucedo, Jeroen Wiegeraad, Edwin Rodríguez, and many others for help with fieldwork. We are grateful to staff and personnel of PROMAB-UAB for logistic support. Logging company 'Maderera Boliviana Etienne S.A.' is acknowledged for permission to work in their concession and for logistic support. We thank Heinjo During for discussions on the data analysis and for providing constructive comments on an earlier version of the manuscript. DMAR was supported by grant W 01.53.2004.047 from the Netherlands Foundation for the Advancement of Tropical Research (WOTRO).

# CHAPTER 4

## Reconstructing stem volume growth of juvenile tropical forest trees: variability among individuals and trade-offs between stem diameter and height growth

with Heinjo J. During, Daan Asscheman, Jeroen Wiegeraad & Pieter A. Zuidema

## SUMMARY

Understanding how tropical trees attain the forest canopy requires availability of long-term growth data. Ideally, such growth data are directly related to biomass growth. Growth rates in stem volume may be appropriate, as it is closer related to biomass growth than diameter or height growth. So far, long-term stem volume growth patterns have not been reconstructed for tropical trees.

In this study we reconstruct long-term stem volume growth of individual juvenile trees belonging to three tropical tree species. We evaluate growth variation among trees within a species and its persistence over time and we detect whether there is a trade-off between the two components of volume growth: height growth and diameter growth.

Tree-ring analysis was applied using stem discs collected along the entire height of a tree. This approach allowed the reconstruction of lifetime diameter, height and stem volume growth for 21-27 juveniles per species. Relations between stem volume growth, diameter growth and height growth were evaluated in tree height classes.

Growth in stem volume, height and diameter varied strongly among individuals of the same height, probably as a consequence of differences in growth conditions among trees. Among-tree differences in volume growth persisted over height classes, while this was less so for diameter growth and height growth. Hence, shifts in investment in height and diameter growth occurred over time, whereas stem volume growth remained the same.

No correlations between diameter growth and height growth were found in any of the height classes. We found negative correlations between stem volume growth and height growth, for small trees of all species. Thus, trees that grew fast in stem volume invested relatively less in height growth compared to slow-growing trees. Even though height growth and diameter growth are unrelated, these results may be consistent with a trade-off between diameter and height growth.

Our results show that fast juvenile growth is associated with low height growth, suggesting that trees in favourable (light) conditions invest relatively more in stability and crown development than in height growth.

**Key words:** Bolivia, juvenile trees, long-term growth patterns, trade-off, tree rings, tropical forest, volume growth reconstruction

## INTRODUCTION

Growth of juvenile trees in tropical forest shows strong variation over time and among individuals (Clark & Clark, 1992). Rates of diameter growth may vary by more than an order of magnitude among equally-sized trees of the same species (Clark & Clark, 1999), and also show strong fluctuations over time within trees (Baker & Bunyavejchewin, 2006; Brienen & Zuidema, 2006a). Similar strong variation is observed in height growth (Clark & Clark, 2001). This variation is generally thought to be caused by spatio-temporal variation in the availability of light and water (Clark & Clark, 1992; Baker *et al.*, 2003), differences across individuals in architecture (King *et al.*, 1997; Sterck *et al.*, 2003), as well as herbivory and damage (Clark & Clark, 1991). Analyzing this growth variation improves our understanding of factors determining successful growth to the canopy. As this may take many decades, reconstruction of long-term growth rates is required. Recently, several studies have used tree-ring data to analyze long-term diameter growth rates for tropical trees (e.g. Worbes, 1999; Fichtler *et al.*, 2003; Brienen & Zuidema, 2006a). Although such studies do provide valuable insights into long-term growth rates, diameter growth cannot always be interpreted as a proxy for biomass growth, as there are likely trade-offs between diameter and height growth (Sumida *et al.*, 1997). Instead, a more suitable proxy for biomass growth can be obtained by reconstructing stem volume growth. Historical rates of volume growth can be quantified from tree-ring analysis at various heights along a tree's stem (cf. Sumida *et al.*, 1997).

Stem volume growth depends on growth in stem diameter and growth in height. Thus, variation between individuals in volume growth is explained by differences in these two rates. Height and diameter growth are thought to play different roles in tree functioning. Height growth is a means to escape shade in the forest understorey, but it comes at a cost of increased risk of buckling or breakage. Diameter growth reduces these mechanical stresses (King, 1986). Investments in height growth and in diameter growth occur in response to different environmental cues and the existence of a trade-off relation between height growth and diameter growth has been suggested (Larson, 1963). Height growth increases under low light availability and low red/far red ratios (Smith, 1982; Schmitt & Wulff, 1993), whereas mechanical stress results in higher investment in diameter growth (Jaffe & Forbes, 1993). Complex responses of investments in height and diameter growth have been observed in response to changes in environmental conditions for various tree species in temperate forests (Bevilacqua *et al.*, 2005; Collet & Chenost, 2006; Zenner, 2008). For tropical trees, much less is known about relative investment in height and diameter growth (cf. Coomes & Grubb, 1998).

Stem volume growth is closely related to biomass growth. Thus, differences in volume growth among individuals may indicate variation in growing conditions. When sustained over

**Table 1** Characteristics of the study species and sample size

| **Species** | **Family** | **Shade tolerance** | **Deciduousness** | **Growth strategy** | **Adult growth potential** (cm yr$^{-1}$) | **Wood specific gravity** (g cm$^{-3}$)* | **Sample size** 1-15 cm dbh |
|---|---|---|---|---|---|---|---|
| *Cedrelinga catenaeformis* (Ducke) Ducke | Fabaceae | Light-demanding | Brevi-deciduous | Height-growth type | 2.92 | 0.48 | 24 |
| *Clarisia racemosa* Ruíz & Pavón | Moraceae | Shade tolerant | Evergreen | Lateral-growth type | 0.95 | 0.57 | 27 |
| *Peltogyne* cf. *heterophylla* M.F. Silva | Fabaceae | Shade tolerant | Brevi-deciduous | Lateral-growth type | 1.4 | ~0.7-0.8 | 21 |

* from Chave *et al.* 2006

time, this variation in growing conditions may lead to persistent differences in volume growth over time. Thus, fast-growing individuals may maintain high volume growth over time, while slow-growers remain slow-growers. Such persistent variation has been observed for diameter growth rates (Brienen *et al.*, 2006), but has not been investigated for volume growth. As stem volume growth is closer related to biomass growth, it may be a better measure to evaluate temporal persistence in growth differences among trees.

Here, we reconstruct volume growth of juveniles of three Bolivian non-pioneer tree species. We use these lifetime data to answer the following questions: (1) To what extent does stem volume growth vary among individual trees?; (2) Can variation in volume growth be explained by height growth, diameter growth or both?; (3) Do differences in volume growth among juvenile trees persist over time?; and (4) Is there a trade-off between diameter and height growth?

We apply tree-ring analysis to reconstruct growth in diameter, height and stem volume over the entire lifetime of juvenile trees. Height growth was reconstructed through ring counts at different heights in the tree (cf. Gutsell & Johnson, 2002): differences in ring counts taken at different heights represent the time spent to grow from the lower to the upper height. This approach allows studying the investment patterns in height and diameter growth of individual trees over long timespans.

## MATERIALS AND METHODS

### Study area and species

Fieldwork was conducted in a semi-deciduous moist forest area, 'Los Indios' (10°26'S, 65°33'W), in the department of Pando, Bolivia. Mean annual precipitation is 1660 mm (Riberalta), with a dry season (<100 mm per month) from May until September. The forest has an average canopy height of 33 m and stem density of 423 stems ha$^{-1}$ (of stems >10 cm diameter at breast height (dbh; Toledo *et al.* 2008).

Three canopy tree species were included: *Cedrelinga catenaeformis*, *Clarisia racemosa* and *Peltogyne* cf. *heterophylla* (Table 1). Species will be referred to by their generic name only. All species tolerate shade, but to a different extent. *Cedrelinga* is relatively light-demanding, whereas *Clarisia* and *Peltogyne* are more shade-tolerant (cf. Brienen & Zuidema, 2006a). The light-demanding species *Cedrelinga* with large, compound leaves can be considered a species of the 'height-growth' type, whereas *Clarisia* and *Peltogyne* tend to the 'lateral-growth' type based on their morphology (cf. Kohyama & Hotta, 1990). Height-growth species predominantly invest in height growth by avoiding investment in branching and crown development, particularly in gap conditions. Lateral-growth species, in general, invest more in stem diameter and branching (Coomes & Grubb, 1998; Takahashi *et al.*, 2001; but see Aiba & Nakashizuka, 2007). Species differ in wood density (cf. Chave *et al.*, 2006), for *Peltogyne* dry mass costs to realize a unit of growth are higher than for *Clarisia* and *Cedrelinga* (Table 1). All species form annual rings in both the juvenile and the adult stage (Soliz-Gamboa *et al.*, submitted).

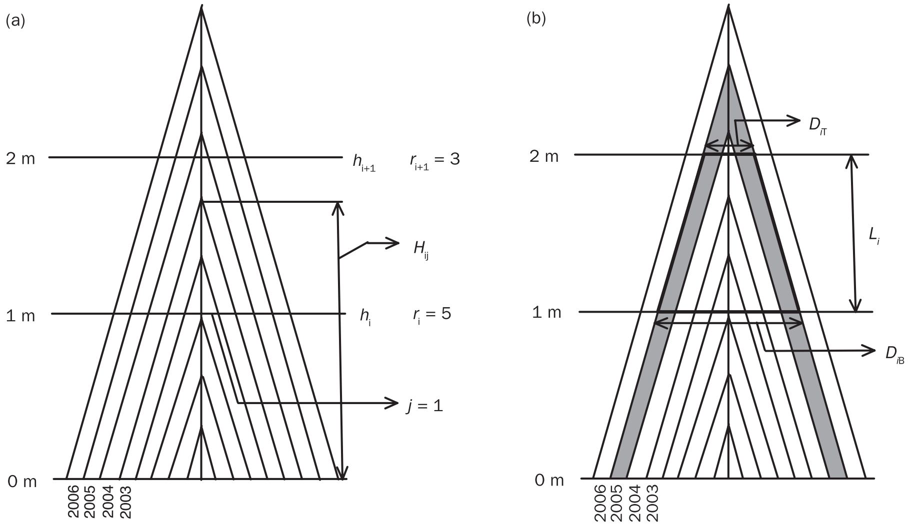


**Fig. 1** Schematic representation of the reconstruction of height growth and volume growth using tree-ring counts on discs collected along the entire stem of the tree. (a) Height growth reconstruction. $h_i$ is the height of the tree at the *i*th disc, $r_i$ is the number of rings at the *i*th disc, *j* is the number of the ring and $H_{ij}$ is the estimated total tree height for a certain year. (b) Volume growth reconstruction using the volume of the frustrum of a cone. $D_{iT}$ is the diameter of the top, $D_{iB}$ is the radius of the base and $L_i$ is the height. Volume growth of the year 2005 is indicated in grey.

## Sample collection and ring measurements

Fieldwork was conducted in 2007, after the area had been selectively logged in 2006 (2-3 trees were felled per ha). For each species, we randomly selected 21-27 trees from 1-15 cm dbh (Table 1). In order to reduce spatial autocorrelation in growth rates, we selected individuals that were located at least 20 m apart. Trees with signs of damage to the stem or crown were not included in the sample.

Discs were collected at different heights along the stem of selected trees. The lowest disc was collected at the stem base (0 m), and the subsequent discs were taken at 1 m intervals along the entire height of the tree. We measured fresh disc area for all collected discs, using calliper measurements in two directions for small discs and digital pictures for large discs. Discs were air-dried and sanded with progressively finer sandpaper until a grit of 1000. Rings were marked in three radii using a stereomicroscope (6.3-40x). Every tenth ring was connected among the three radii, over the whole disc, to control for errors in ring identification. Ring widths were measured perpendicular to the ring boundaries using a LINTAB 5 (Rinntech, Heidelberg, Germany) measurement device.

Ring widths of all radii were averaged and corrected for desiccation and irregular growth using the fresh-disc radius. The last formed ring (2006, growth period 2006-2007) was not included in our analyses, as it was formed after selective logging took place. Diameter growth was reconstructed based on the ring widths at a height of 1 m, except for diameter growth of the years corresponding to the height growth in the height class from 0-1 m. In this height class diameter growth was expressed based on ring widths in the disc collected at 0 m height, as the inner rings were not present in the disc collected at 1 m height.

### Calculation of annual height and volume growth

Height growth was reconstructed using the ring counts of discs collected at 1 m intervals over the entire height of the tree (Fig. 1a). Annual height growth was estimated using Carmean's method (Carmean, 1972), which assumes that height growth is constant within a stem segment between two consecutive collected discs and that, on average, a disc is collected at the middle of the height growth of a year. Estimated tree height $H_{ij}$ at a certain tree age was calculated as (Dyer & Bailey, 1987; Fig. 1a):

$$H_{ij} = h_i + (h_{i+1} - h_i) / [2(r_i - r_{i+1})] + (j - 1)(h_{i+1} - h_i) / (r_i - r_{i+1}) \qquad \text{(eqn.1)}$$

In which $h_i$ = height in the stem at which the ith disc was collected, $r_i$ = number of rings at the ith disc and $j$ = ring number, counted from the innermost ring in a disc. Carmean's method has been found to give an accurate estimation of annual height growth (Dyer & Bailey, 1987). In case of an equal number of rings in two consecutive discs, i.e. height growth >1 m $yr^{-1}$, we used longer segments for the reconstruction of annual height growth until a difference in ring number between two discs was obtained.

Volume growth was reconstructed for every year. Total annual volume growth, corresponding to the volume of one ring, was calculated as the sum of volumes of that ring in all height segments of 1 m length of a tree (cf. Fig. 1b). The volume of a ring in a 1 m segment was calculated as the difference in volume of the frustrum of a cone including the ring and without the ring (cf. Fig. 1b). To calculate the volume of the frustrum of a cone its height is needed and the radii of the top and the base. Hence, to calculate the total volume $V$ of a tree in a certain year the following formula was used (Nilsson & Albrektson, 1993; cf. Fig. 1b):

$$V = \pi/12 \sum_{i=1}^{n} L_i(D_{iT}^2 + D_{iB}^2 + D_{iT} * D_{iB}) \qquad \text{(eqn. 2)}$$

where $i$ is the number of the stem segment between two consecutive discs, $n$ is the number of stem segments, $L_i$ is the length of stem section $i$, $D_{iT}$ is the diameter at the top of the stem section $i$ and $D_{iB}$ is the diameter at the base of stem section $i$. To obtain the volume of a ring, i.e. annual stem volume growth of that year, the total tree volume of the preceding year was subtracted from the total of the year evaluated.

### Data analysis

To enable comparison of trees at the same height, we divided the dataset into tree height classes. Height classes coincided with the 1m segments used for height growth reconstruction over the entire height of the tree: 0-1 m height, 1-2 m, 2-3 m, 3-4 m, etc. For each individual, we calculated diameter growth, height growth and volume growth as an average per

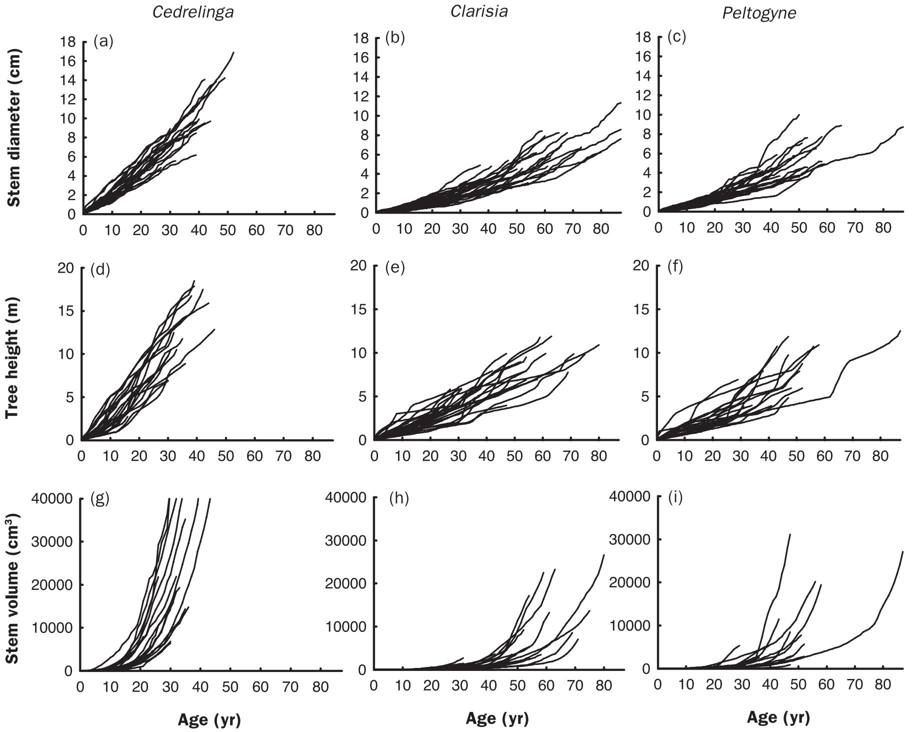


**Fig. 2** Growth patterns of individual juvenile trees of *Cedrelinga*, *Clarisia* and *Peltogyne*. (a-c) Diameter-age trajectories; (d-f) Height-age trajectories; (g-i) Volume-age trajectories.

height class. Growth rates of trees that grew >1 m per year in a certain height class were included in the lower height class.

Spearman's rank correlations were calculated to relate volume growth to height growth and diameter growth per height class. As few larger trees (>10 m height) were included in the study, correlations were only performed in height classes which included growth rates of at least ten trees. To evaluate persistent differences in volume, height and diameter growth rates among trees over time, average growth rates were related among height classes with Spearman's rank correlation. Spearman's rank correlation was performed using SPSS 16.0 (SPSS Inc.).

## RESULTS

### Growth patterns in height, diameter and stem volume

Diameter growth showed large variation among and within species (Fig. 2a-c). The fast-growing *Cedrelinga* attained a stem diameter of 3 cm in 15 years on average, while *Clarisia* and *Peltogyne* took on average 43 and 34 years, respectively, to reach the same diameter

(Fig. 2a-c). For all species, large variation in diameter growth rates was observed. The time needed to grow until 3 cm diameter varied from 9-20 years in *Cedrelinga*, from 26-55 years in *Clarisia* and from 17-49 years in *Peltogyne* (Fig. 2a-c).

Height growth also varied widely, both among and within species. *Cedrelinga* attained a tree height of 3 m in 12 years on average, while *Clarisia* and *Peltogyne* needed on average 25 and 27 years, respectively, to attain the same height (Fig. 2d-f). Within species, the time needed to reach 3 m height varied two- to fivefold among individuals. For *Cedrelinga* time needed to reach 3 m height varied from 6-19 years among individual trees, for *Clarisia* from 8-39 years and for *Peltogyne* from 13-43 years, respectively (Fig. 2d-f). As a consequence, trees of a species differed up to fifteenfold in the time to grow from one height class to the next (Fig. 3). In *Clarisia*, for example, in the height class from 1-2 m, average height growth ranged from 0.04-0.6 m $yr^{-1}$.

Similar within-species variation was observed for stem volume growth, when comparing trees in the same height class (Fig. 3). For example, in *Cedrelinga* average stem volume growth varied from 1 $cm^3$ $yr^{-1}$ for the slowest-growing tree up to 30 $cm^3$ $yr^{-1}$ for the fastest grower in the height class from 0-1 m. Growth in stem volume showed a strong increase with age, and with tree height in all species (Fig. 2d-f; cf. Fig. 3).

Within species, the relation between tree height and diameter differed among individual trees (Fig. 4). For example, at a height of 3 m the observed diameters ranged from 1.4-4.9 cm in *Cedrelinga*, 0.6-2.4 cm in *Clarisia* and from 0.4-3.1 cm in *Peltogyne*. Within individual trees, the relation between tree height and diameter did not follow a straight line (Fig. 4). Probably, small fluctuations in the height/diameter-ratio occurred over the lifespan of a tree. Overall, the three species showed a similar relation between tree height and diameter (Fig. 4), which suggests that there was no difference in stem slenderness among the three species.

### Relation between investment in height growth and volume growth

We investigated whether trees that differed in their volume growth in a certain height class, also showed different investment in height growth. We expected that trees with fast growth in stem volume would also exhibit a high rate of height growth. In contrast with our expectation, most relations between height growth and volume growth were non-significant or negative (Table 2, Fig. 3). For instance, in the first height class (0-1 m) a negative correlation between height growth and volume growth was found for all species (Fig. 3). For *Clarisia* and *Peltogyne*, height growth and volume growth were also negatively correlated in the height class from 1-2 m (Fig. 3). This means that fast growers in terms of stem volume realized relatively low growth in height, while those growing more slowly in volume invested relatively more in height growth.

At larger tree heights, the negative correlation between height growth and volume growth disappeared, and only in two height classes in *Cedrelinga*, and one height class in *Peltogyne*, a positive correlation was observed (Table 2). Hence, a tree that grew relatively fast in height, did not grow necessarily fast in stem volume, too. This scarcity of significant correlations is

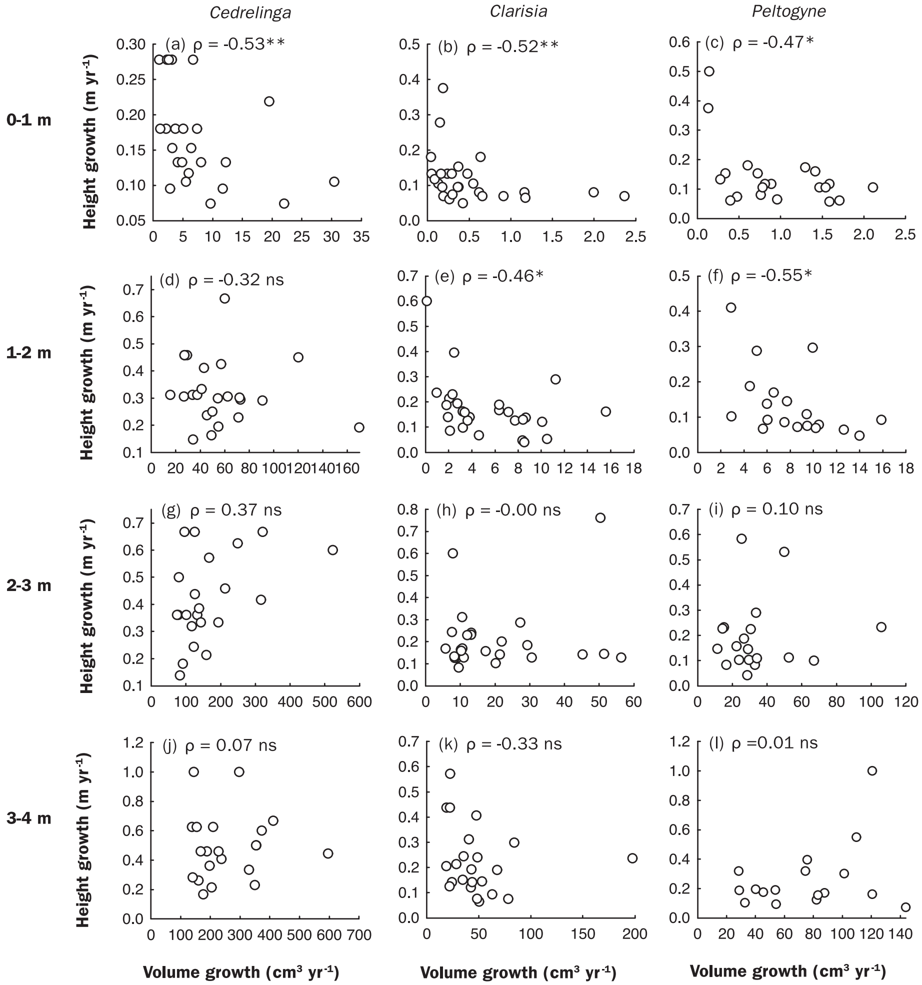


**Fig. 3** Relation between volume growth and height growth of juvenile trees of *Cedrelinga*, *Clarisia* and *Peltogyne*. Average volume growth and height growth were calculated per tree, per height class. Spearman's rank correlation coefficients (ρ) and significance levels are indicated (*= $P<0.05$, **=$P<0.01$, ***=$P<0.001$). (a-c) Height class 0-1 m; (d-f) height class 1-2 m; (g-i) height class 2-3 m; (j-l) height class 3-4 m.

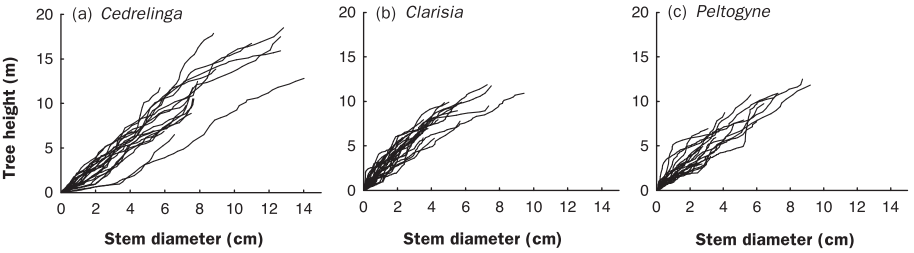


**Fig. 4** Height-diameter relationships over time for individual juvenile trees of three Bolivian tree species. (a) *Cedrelinga*; (b) *Clarisia*; (c) *Peltogyne*.

obviously also related to the limited number of trees included in the study, in particular in the larger height classes.

We expected a positive relation between diameter growth and volume growth, as the relation between diameter growth and volume growth is quadratic. Moreover, diameter growth is added each year along the entire stem of the tree, while height growth only contributes to stem volume growth in the slender top of the tree. Indeed, diameter growth showed a significant, positive relation with volume growth in all species in all height classes (Table 2).

### Persistent volume growth differences among trees

The large differences in volume growth among individuals (Fig. 3) tended to persist over time (Table 3). For example, in *Cedrelinga* trees that had fast volume growth in the height class of 0-1 m were still the fast-growing trees in the height class from 4-5 m. In *Clarisia* and *Peltogyne*, volume growth differences in the height class from 0-1 m lasted over less height classes, until the height class from 1-2 m and from 2-3 m, respectively (Table 3). Most likely, this is a consequence of the long passage time of *Clarisia* and *Peltogyne* through these height classes, compared to *Cedrelinga*. Also in height classes at larger tree heights, among-tree differences in volume growth were persistent over time. For all species, among-tree differences in volume growth rate persisted at least in the next height class (Table 3).

For diameter and height growth not many significant correlations in growth rates over height classes were found (Table 3). Only in *Cedrelinga*, among-tree differences in height growth rates in the height class from 0-1 m persisted in the height class from 1-2 m. Thus, in general among-tree differences in diameter and height growth were not strongly persistent over time in contrast to the results for stem volume growth.

**Table 2** Correlations between growth in stem volume, height and diameter for three Bolivian tree species. Spearman's rank correlations are given per height class. Significant correlations are given in bold (*= $P<0.05$, **=$P<0.01$, ***=$P<0.001$). - indicates that the correlation was not evaluated due to a sample size <10. V = stem volume growth, H = height growth, D = diameter growth.

| Height class | *Cedrelinga* | | | | *Clarisia* | | | | *Peltogyne* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | H - V | D - V | D - H | | H - V | D - V | D - H | | H - V | D - V | D - H | |
| | ρ | ρ | ρ | n | ρ | ρ | ρ | n | ρ | ρ | ρ | n |
| 0-1 m | **-0.53**** | **0.72**** | -0.20 | 24 | **-0.52*** | **0.59**** | 0.02 | 27 | **-0.47*** | 0.43 | 0.28 | 21 |
| 1-2 m | -0.32 | **0.46*** | -0.05 | 24 | **-0.46*** | **0.60**** | -0.21 | 27 | **-0.55*** | **0.64**** | 0.02 | 19 |
| 2-3 m | 0.37 | **0.60**** | **0.50*** | 22 | -0.00 | **0.65**** | 0.31 | 26 | 0.10 | **0.47*** | 0.03 | 19 |
| 3-4 m | 0.07 | 0.35 | 0.27 | 21 | -0.33 | **0.51*** | 0.11 | 23 | 0.01 | 0.36 | 0.25 | 17 |
| 4-5 m | -0.07 | 0.45 | 0.00 | 18 | -0.06 | **0.60**** | 0.22 | 21 | **0.78**** | **0.94**** | **0.66*** | 12 |
| 5-6 m | 0.17 | **0.79**** | 0.04 | 18 | 0.18 | **0.82**** | **0.46*** | 20 | 0.37 | **0.85**** | 0.25 | 13 |
| 6-7 m | **0.64**** | **0.63**** | 0.42 | 18 | 0.24 | **0.89**** | 0.40 | 15 | - | - | - | - |
| 7-8 m | **0.54*** | 0.50 | 0.04 | 14 | 0.54 | **0.83**** | **0.59*** | 12 | - | - | - | - |
| 8-9 m | 0.47 | **0.98**** | 0.46 | 13 | - | - | - | - | - | - | - | - |
| 9-10 m | -0.21 | 0.46 | -0.16 | 13 | - | - | - | - | - | - | - | - |

**Table 3** Spearman's rank correlation coefficients for growth rates in diameter, height and volume between tree height classes for three Bolivian tree species. Significant correlations are given in bold (*= *P*<0.05, **=*P*<0.01, ***=*P*<0.001).

| | | Height class | 1-2 m | 2-3 m | 3-4 m | 4-5 m | 5-6 m |
|---|---|---|---|---|---|---|---|
| *Cedrelinga* | Diameter growth | 0-1 m | -0.04 | 0.40 | 0.36 | 0.26 | 0.11 |
| | Height growth | 0-1 m | **0.60**** | 0.26 | -0.01 | 0.16 | -0.34 |
| | Volume growth | 0-1 m | **0.68**** | **0.57**** | **0.45*** | **0.47*** | 0.26 |
| | Diameter growth | 1-2 m | - | 0.24 | 0.26 | 0.00 | **0.66**** |
| | Height growth | 1-2 m | - | 0.07 | -0.11 | 0.24 | **-0.50*** |
| | Volume growth | 1-2 m | - | **0.78**** | **0.72**** | **0.49*** | **0.58*** |
| | Diameter growth | 2-3 m | - | - | 0.29 | -0.07 | 0.09 |
| | Height growth | 2-3 m | - | - | 0.38 | 0.00 | -0.30 |
| | Volume growth | 2-3 m | - | - | **0.62**** | **0.55*** | **0.75**** |
| | Diameter growth | 3-4 m | - | - | - | 0.12 | 0.16 |
| | Height growth | 3-4 m | - | - | - | 0.37 | -0.17 |
| | Volume growth | 3-4 m | - | - | - | **0.54*** | 0.39 |
| *Clarisia* | Diameter growth | 0-1 m | 0.27 | 0.06 | -0.23 | -0.37 | -0.40 |
| | Height growth | 0-1 m | 0.28 | 0.10 | 0.15 | 0.06 | -0.34 |
| | Volume growth | 0-1 m | **0.54**** | 0.34 | 0.32 | 0.08 | 0.26 |
| | Diameter growth | 1-2 m | - | 0.25 | 0.04 | 0.19 | -0.17 |
| | Height growth | 1-2 m | - | -0.14 | -0.17 | 0.18 | 0.09 |
| | Volume growth | 1-2 m | - | **0.78**** | 0.37 | 0.07 | 0.23 |
| | Diameter growth | 2-3 m | - | - | 0.15 | 0.24 | -0.25 |
| | Height growth | 2-3 m | - | - | 0.04 | 0.13 | -0.21 |
| | Volume growth | 2-3 m | - | - | 0.16 | 0.02 | 0.08 |
| | Diameter growth | 3-4 m | - | - | - | **0.79**** | 0.29 |
| | Height growth | 3-4 m | - | - | - | 0.04 | -0.25 |
| | Volume growth | 3-4 m | - | - | - | **0.80**** | **0.69**** |
| *Peltogyne* | Diameter growth | 0-1 m | 0.21 | 0.09 | -0.42 | 0.22 | -0.02 |
| | Height growth | 0-1 m | 0.03 | 0.18 | -0.33 | -0.26 | -0.04 |
| | Volume growth | 0-1 m | **0.55*** | **0.69**** | 0.39 | 0.13 | 0.53 |
| | Diameter growth | 1-2 m | - | 0.42 | -0.20 | -0.41 | **0.71*** |
| | Height growth | 1-2 m | - | -0.15 | -0.07 | **-0.77**** | -0.29 |
| | Volume growth | 1-2 m | - | **0.59*** | **0.79**** | 0.56 | 0.60 |
| | Diameter growth | 2-3 m | - | - | -0.21 | 0.35 | 0.32 |
| | Height growth | 2-3 m | - | - | 0.14 | -0.01 | -0.20 |
| | Volume growth | 2-3 m | - | - | **0.65**** | 0.39 | **0.60*** |
| | Diameter growth | 3-4 m | - | - | - | 0.37 | 0.33 |
| | Height growth | 3-4 m | - | - | - | 0.30 | -0.08 |
| | Volume growth | 3-4 m | - | - | - | **0.81**** | **0.58*** |

## DISCUSSION

### Growth patterns in stem volume, diameter and height of tropical trees

We observed large variation in stem volume, diameter and height growth among trees in the same height class. Such variation is most likely caused by differences in light conditions among trees, as juvenile tree growth is strongly related to light availability (e.g. Clark & Clark, 1992; King, 1994; Pacala *et al.*, 1994). Large intraspecific variation in diameter growth in tropical trees has been documented for many species (e.g. Lieberman *et al.*, 1985a; Swaine *et al.*, 1987; Clark & Clark, 1992; Korning & Balslev, 1994). Large variation in height growth was also observed in a study on annual height growth of juvenile trees over a 16-year time span in Costa Rica, although in that study the variation in height growth rates is not explicitly shown (Clark & Clark, 2001). Our study is the first to document such strong growth variation at the scale of two to seven decades.

Differences in volume growth among trees were persistent over time (Table 3). Thus, a slow-growing tree probably continues to do so in the next height class, and fast-growing trees remain fast-growing over time. These results suggest that differences among trees in growth conditions remain the same over long periods of time. Probably, differences in light conditions among small trees persist over time in tropical forest, as canopy closure after gap formation may take around 15 years (van der Meer & Bongers, 1996). As a consequence, fast-growing individuals need less time to reach the canopy, have a larger chance to reproduce and may therefore be more important for population growth (cf. Zuidema *et al.*, 2009).

Among-tree differences in diameter and height growth were less persistent over time than differences in stem volume growth (Table 3). This may indicate that relative investment in height and diameter growth changed over time, while among-tree differences in volume growth remained the same. Brienen *et al.* (2006) found strong among-tree autocorrelation in diameter growth with a 1-year time lag, but in our study variation in diameter growth may be not persistent over time due to the longer time lags evaluated (i.e. the passage time of a tree through a height class). A reason for not finding strong persistence over time in among-tree differences in height growth may be the confounding effect of height loss due to damage (cf. Clark & Clark, 2001). Arets (2005) excluded negative height growth rates from analysis and found strong autocorrelation in height growth between two measurement intervals for saplings of groups of species from tropical forest in Guyana. We avoided including damaged trees, but it is likely that small setbacks in height have occurred during the lifetime of our sampled trees, as height loss due to damage is common in juvenile trees (Clark & Clark, 1991; Paciorek *et al.*, 2000).

### A trade-off between early height and stem diameter growth?

We did not find an indication for a trade-off between diameter and height growth when directly correlating these two variables (Table 2). A reason for not finding negative (or positive) relations may be the large variation in growth among individual trees within a height class.

Van Noordwijk and de Jong (1986) argued that if the total amount of resources which can be invested in two life history traits varies strongly among individuals, positive instead of the expected negative correlations may be observed. Thus, if among-tree differences in volume growth are large, negative correlations between height growth and diameter growth may disappear or change into a positive correlation between height and diameter growth (cf. van Noordwijk & de Jong, 1986). For this reason, we chose to evaluate the relation between volume growth and height growth, rather than relating diameter growth and height growth directly. Volume growth is a proxy for the total (biomass) growth of a tree, and of this total amount of wood volume, part is allocated to height growth and part to diameter growth (cf. Sumida *et al.*, 1997).

Our results show that small trees are able to change relative investment in stem volume and height growth. Trees of <2 m height which grew fast in stem volume, invested less in height growth. This supports the idea that in low light conditions – that is, in case of strong competition for light – relatively more resources are allocated to height growth compared to a high-light situation (Weiner & Thomas, 1992; Niklas, 1995; Naidu *et al.*, 1998; Poorter & Werger, 1999). At larger tree heights, however, no negative correlations between stem volume growth and height growth were observed (Table 2). This may be due to the different scaling between diameter growth and height growth with increasing tree height. To maintain a similar mechanical stability with increasing tree height a larger investment in diameter growth is needed per unit height growth. Additionally, light conditions will be more heterogeneous among small trees. Therefore, differences in light conditions will be large among small trees, and relative investment in height growth is likely to vary strongly among individuals. Large trees, to the contrary, most likely experience more homogeneous light conditions closer to the canopy. Additionally, as a consequence of their larger crown size, they may sample a larger range of environmental conditions leading to smaller differences in growth conditions among trees. For this reason, the difference in relative investment in height and diameter growth among large trees may be less than for small trees.

The observed negative relation between early stem volume and height growth may be consistent with a trade-off between diameter and height growth. A trade-off between height and diameter growth implies that a tree can invest relatively more assimilates in height growth, with an increased mechanical risk, or invest more in diameter growth to increase its safety factor. Nevertheless, by preferentially increasing its diameter growth, a tree does not increase light capture, as would be the benefit of a higher investment in tree height. Indications for such a trade-off have been found in temperate forest in *Quercus glauca* (Sumida *et al.*, 1997). In contrast to our results, investment in diameter growth, associated with increased foliage growth, was higher than investment in height growth under suppressed conditions (Sumida *et al.*, 1997). Juvenile trees of *Acer saccharum* showed a different pattern (Bonser & Aarssen, 1994). Investment in lateral growth, defined as the degree of branching, was higher at high light availability, whereas at low light availability investment in height growth increased (Bonser & Aarssen, 1994). These results are comparable to our results, although we do not have information on historical crown shape and size. Ideally, data on crown growth should be included to improve understanding on total aboveground investment patterns.

Tree species may display different growth strategies under similar variations in growth conditions. Nevertheless, all three study species showed a negative relation between early height and stem volume growth, despite the differences in growth strategy among the species (cf. Table 1). These results contrast those found for temperate forest trees. For instance, Hara *et al.* (1991) showed that suppressed saplings of the height-growth species *Betula ermanii* grow relatively more in height while suppressed saplings of the lateral-growth species *Abies veitchii* and *A. mariesii* grow relatively more in diameter.

## RECONSTRUCTING VOLUME GROWTH OF TROPICAL TREES

As far as we know, this is the first study to reconstruct volume growth over the lifespan of juvenile tropical trees. Studies on relative investments in height and diameter growth so far have predominantly used static data (e.g. O'Brien *et al.*, 1995; Sterck & Bongers, 1998; Osunkoya *et al.*, 2007). For instance, such species-specific allometric relations have been used to estimate biomass growth of tropical trees (e.g. Chave *et al.*, 2005). An important shortcoming of this approach is that relative investment in height and diameter growth is assumed not to vary. This assumption often does not hold, as the actual diameter/height-ratio of a stem is the result of the accumulation of height and diameter growth over time (cf. Bongers & Sterck, 1998; Henry & Aarssen, 1999). The actual height/diameter-ratio of the stem is indeed known to vary among individuals of the same height within a species (Coomes & Grubb, 1998; Kooyman & Westoby, 2009). Thus, relative investment in stem diameter and height growth can only be understood through the quantification of these processes over time.

Is it necessary to reconstruct volume growth, or do diameter growth rates yield the same insights? It clearly is more labour intensive to reconstruct stem volume growth, as ring widths in discs collected over the whole height of the tree need to be measured. At first sight, diameter growth rates may appear to be a good estimator for stem volume growth as volume and diameter growth rates are strongly correlated in most height classes. However, when evaluating temporal persistence in growth rate variation among trees, growth in stem volume and stem diameter showed remarkably different results. Hence, diameter growth is not a good proxy for biomass growth and should be interpreted cautiously. A second advantage of using volume growth is the inclusion of differences in diameter growth along the tree stem, as the width of a ring varies with height (Bouriaud *et al.*, 2005; Ikonen *et al.*, 2006). In all, the reconstruction of stem volumes represents an additional tool to obtain insight in factors governing the long-term growth of juvenile trees.

## ACKNOWLEDGEMENTS

We are grateful to Claudia Soliz-Gamboa for help with fieldwork and discussion on the methodology. We thank Nazareno Martínez, Miguel Cuadiay, Adhemar Saucedo and many others for help with fieldwork. We are grateful to staff and personnel of PROMAB-UAB for logistic support. Logging company 'Maderera Boliviana Etienne S.A.' is acknowledged for permission to work in their concession and for logistic support. We thank Feike Schieving for discussion on volume growth calculations. Marinus Werger provided constructive comments on earlier versions of the manuscript. DMAR was supported by grant W 01.53.2004.047 from the Netherlands Foundation for the Advancement of Tropical Research (WOTRO).

# CHAPTER 5

## Timber yield projections for tropical tree species: using plot data underestimates future yield if the large trees of today were the fast-growers of the past

with Claudia C. Soliz-Gamboa and Pieter A. Zuidema

## SUMMARY

Most growth and yield models for tropical tree species use diameter growth data obtained from permanent sample plots. A potential disadvantage of this data source is that such permanent sample plots include slow-growing, suppressed juvenile trees of which only a small fraction will attain harvestable size. If the faster-growing juvenile individuals are more likely to reach harvestable size, the average growth rate of extant juvenile trees will be lower than the historical, juvenile growth rate of trees of harvestable size. Thus, if juvenile growth rates are obtained from permanent sample plots, yield simulations may underestimate future timber yield. To determine the magnitude of this effect we contrasted growth of trees to harvestable size based on growth projections between two types of growth data: long-term tree-ring data from harvestable trees ('lifetime growth data') and the last ten years of growth of extant trees over the entire size range ('plot-type growth data'). The latter data type is a proxy for growth data from permanent sample plots. Second, we evaluated which percentage of the timber volume harvested at the initial harvest is available at second harvest using lifetime growth data. We obtained tree-ring data from 89-98 individuals of three Bolivian timber species, over their entire size range. Based on these data tree growth simulations were performed for two scenarios: a second harvest in 20, and in 40 years. A realistic degree of growth autocorrelation was incorporated in the growth projections, for both the lifetime and the plot-type growth data.

Observed ages at the minimum cutting diameter in tree-ring data of harvestable trees were high: average ages varied from 63 years to 179 years among species. Commercial ingrowth was 23-46% larger when using lifetime growth data than for plot-type growth data for two of the three species. Thus, the faster juvenile growth of trees that reach harvestable size indeed resulted in higher projections of timber yield.

In spite of the positive effect of higher juvenile growth on projected timber yield, our simulations showed that the recuperation of timber volume was low. Only 20-33% of the timber volume harvested at first harvest could be obtained at second harvest after 20 years. For a second harvest after 40 years this was 26-46%.

Based on our results we recommend the use of above-average growth rates in timber yield projections that apply permanent plot data. To determine what percentage of faster-growers should be used in such simulations, it is important that similar analyses are conducted for more species. In spite of the use of more realistic growth data, our simulations predicted low timber yields at second harvest, even when applying a cutting cycle of 40 years. To sustain timber yields at future harvests, long cutting cycles should probably be combined with silvicultural treatments.

**Key words:** tree rings, growth projections, timber yield, tropical forest, permanent sample plots, Bolivia

## INTRODUCTION

Sustainable selective logging may be a means to protect tropical forest areas from deforestation as this increases the economic value of these forests (Keller *et al.*, 2007; Zarin *et al.*, 2007). However, the potential of forest management to safeguard tropical forests is strongly debated (e.g. Rice *et al.*, 1997; Fredericksen *et al.*, 2003; Pearce *et al.*, 2003; Zarin *et al.*, 2007). It is therefore of key importance to obtain high-quality estimates of timber recovery after selective logging. Many timber yield studies have shown that current regulations and practices of selective logging do not sustain timber production in tropical forests (e.g. Dauber *et al.*, 2005; Sist & Ferreira, 2007; Schulze *et al.*, 2008b). Most of the calculations of future timber yields apply tree growth rates obtained from repeated diameter measurements in permanent sample plots (e.g. Clark & Clark, 1999; Finegan *et al.*, 1999). In combination with data on mortality, recruitment and size structure of the population, such data are then used to construct growth models to project future timber yield for individual tree species (e.g. Gourlet-Fleury *et al.*, 2005; Picard *et al.*, 2008), or species groups (e.g. Kammesheidt *et al.*, 2001; Sist *et al.*, 2003; Arets, 2005; van Gardingen *et al.*, 2006).

An important limitation of the use of growth data from permanent sample plots is that many of the slow-growing, suppressed juvenile trees are not expected to reach harvestable size (Wyckoff & Clark, 2002). Such preferential survival of fast-growing juveniles – the 'juvenile selection effect' - was first found in temperate forest trees (Landis & Peart, 2005). Recently, the juvenile selection effect was also detected in tropical forests (Chapter 2). The juvenile selection effect implies that, those individuals that have reached the canopy and harvestable size most likely have been fast growers as juveniles. In other words, many of the slow-growing trees will not make it to harvestable size. Thus, the average diameter growth rate of extant juvenile trees is lower than the historical growth rates of harvestable trees. This implies that if one uses diameter growth rates from extant juvenile trees in permanent sample plots to project tree growth and timber yields, this likely underestimates juvenile growth (cf. Sheil, 1995a). Although some researchers have anticipated to this effect by using above-average growth rates to estimate ages and future timber yield of tropical tree species (Condit *et al.*, 1995a; Laurance *et al.*, 2004a), most growth and yield models still apply average growth rates of extant trees.

Recently, tree-ring data have been used to obtain growth rates for timber volume calculations and evaluate the sustainability of logging regimes (Brienen & Zuidema, 2006b; Schöngart *et al.*, 2007; Schöngart, 2008). If ring data in such studies are obtained from large trees, they probably reflect the 'typical' growth rates of individuals that reach harvestable size. Therefore, growth rates obtained from tree-ring measurements of harvestable trees are likely to be most accurate for application in timber yield projections (Brienen & Zuidema, 2006b). Moreover, a second advantage of using tree-ring data is the possibility to include observed temporal growth variation in growth projections, which leads to more accurate and higher estimates of future timber yield (Brienen & Zuidema, 2006b; Brienen & Zuidema, 2007).

So far, a test of differences in timber yield projections based on tree rings and plot data is missing. It is therefore unknown whether and to what extent timber volume recuperation after logging is underestimated if one uses permanent plot data. In this study we provide a direct comparison between projected timber yield based on lifetime diameter growth rates of harvestable trees ('lifetime growth data') and recent growth rates of extant trees of all sizes ('plot-type growth data'). We use tree-ring analysis to obtain both types of data: for the life-time growth data we are using the full growth history of harvestable trees, while for the plot-type growth data we use the last 10 years of data for extant trees of various sizes. The latter type of data is therefore analogous to that obtained from permanent sample plots. The following research questions were addressed: (1) Is the predicted recuperation rate of timber volume influenced by the type of data used? and (2) What percentage of the timber volume harvested at first harvest is available in the second harvest after one cutting cycle? We obtained tree-ring data from three Bolivian timber species, and performed tree growth simulations based on current national logging legislation under a cutting cycle of 20 and 40 years.

## MATERIALS AND METHODS

### Study area and species

Fieldwork was conducted in a semi-deciduous moist forest area, the forest concession 'Los Indios' (10°26'S, 65°33'W) from the logging company 'Maderera Boliviana Etienne S.A.' (MABET), in the department of Pando, Bolivia. Mean annual precipitation is 1660 mm (Riberalta), with a dry season (<100 mm per month) from May until September. The forest has an average canopy height of 33 m and stem density of 423 stems ha$^{-1}$ (trees >10 cm diameter at breast height (dbh; Toledo *et al.*, 2008). Three canopy tree species were included in the study: *Cedrelinga catenaeformis*, *Clarisia racemosa* and *Peltogyne* cf. *heterophylla* (Table 1). Species will be referred to by their generic name hereafter. All species tolerate shade, but to a different degree. *Cedrelinga* is relatively light-demanding, whereas *Clarisia* and *Peltogyne* are more shade-tolerant (cf. Brienen & Zuidema, 2006a). All species form annual rings in both the juvenile and the adult stage (Soliz-Gamboa *et al.*, submitted). The minimum cutting diameter (MCD) varies among the three species: for *Cedrelinga* the MCD is 60 cm, for *Clarisia* 45 cm and for *Peltogyne* 50 cm.

### Sample collection and ring width measurements

Fieldwork was conducted in 2006 and 2007, just after selective logging (2-3 trees ha$^{-1}$) had taken place. For each species, we randomly selected 60-69 trees of <50 cm dbh and 29-30 trees of >50 cm dbh (Chapter 2). We selected individuals of <50 cm dbh such that they were evenly distributed over diameter categories. To reduce spatial autocorrelation in growth rates, we only included individuals that were >20 m apart. Individuals of <10 cm dbh that showed damage were not selected. In *Cedrelinga* we checked for hollowness by pre-coring trees, and preferentially selected non-hollow trees to allow measurement of juvenile rings.

Discs were obtained from the selected individuals at either 0.5 m height (*Clarisia*) or 1 m height (*Cedrelinga* and *Peltogyne*). In the case of trees >MCD, we always collected discs

**Table 1**. Overview of timber yield recuperation at second harvest in various Neotropical forests. MCD=Minimum Cutting Diameter

| Study | Species | Location | Type of growth data | Growth rates | MCD | Length of cutting cycle | Volume recuperation (%) |
|---|---|---|---|---|---|---|---|
| Brienen and Zuidema 2006 | *Amburana cearensis* | Bolivian Amazon | Tree-ring data | Lifetime growth rates | 50 cm | 20 years | 18% |
| Brienen and Zuidema 2006 | *Cedrela odorata* | Bolivian Amazon | Tree-ring data | Lifetime growth rates | 60 cm | 20 years | 24% |
| Brienen and Zuidema 2006 | *Cedrelinga catenaeformis* | Bolivian Amazon | Tree-ring data | Lifetime growth rates | 50 cm | 20 years | 22% |
| Brienen and Zuidema 2006 | *Peltogyne* cf. *heterophylla* | Bolivian Amazon | Tree-ring data | Lifetime growth rates | 50 cm | 20 years | 61% |
| Condit *et al.* 1995 | *Calophyllum longifolium* | Central Panama | Plot data | Above-average growth | 60 cm | 30 years | 21% |
| Condit *et al.* 1995 | *Hura crepitans* | Central Panama | Plot data | Above-average growth | 60 cm | 30 years | 5% |
| Condit *et al.* 1995 | *Platymiscium pinnatum* | Central Panama | Plot data | Above-average growth | 60 cm | 30 years | 14% |
| Condit *et al.* 1995 | *Prioria copaifera* | Central Panama | Plot data | Above-average growth | 60 cm | 30 years | 20% |
| Condit *et al.* 1995 | *Tabebuia guayacan* | Central Panama | Plot data | Above-average growth | 60 cm | 30 years | 14% |
| Condit *et al.* 1995 | *Tabebuia rosea* | Central Panama | Plot data | Above-average growth | 60 cm | 30 years | 11% |
| Dauber *et al.* 2005 | All commercial species | Bolivian Amazon | Plot data | Optimum growing conditions | 50 cm | 25 years | 22% |
| Gourlet-Fleury *et al.* 2005* | *Dicorynia guianensis* | French Guiana | Plot data | | 60 cm | 42 years | Max. 60% |
| Grogan *et al.* 2008 | *Swietenia macrophylla* | Brazilian Amazon | Inventory data | | 60 cm | 30 years | 23.1-46.5% |
| Schulze *et al.* 2008b | 5 commercial species** | Brazilian Amazon | Inventory data | Post-logging growth rates | 50 cm | 30 years | 40-50% |
| Schulze *et al.* 2008a | *Tabebuia impetiginosa* | Eastern Brazilian Amazon | Inventory data | Post-logging growth rates | 50 cm | 30 years | 12.9-14.3% |
| Schulze *et al.* 2008a | *Tabebuia serratifolia* | Eastern Brazilian Amazon | Inventory data | Post-logging growth rates | 50 cm | 30 years | 16.5-26.2% |
| Sist and Ferreira 2007 | All commercial species | Eastern Brazilian Amazon | Plot data | Optimistic scenario | 55 cm | 30 years | 50% |
| Valle *et al.* 2007 | All commercial species | Eastern Brazilian Amazon | Plot data | | 50 cm | 30 years | 83% |

* Initial stand conditions were stabilized at year 1999+450, using the model SELVA

** *Astronium lecointei*, *Cordia goeldiana*, *Hymenaea courbaril*, *Parkia pendula* and *Tabebuia serratifolia* from stumps of logged trees. A digital picture of each disc was taken, to calculate fresh disc area using pixel-counting software (SigmaScan Pro 5.0). Discs were air-dried and sanded with progressively finer sandpaper until a grit of 1000. Rings were marked in three or four radii – selected to correspond to total disc area – using a stereomicroscope (6.3-40x). Every tenth ring was connected over the whole disc to control for errors in ring identification. Ring widths were measured perpendicular to the ring boundaries using a LINTAB 5 (Rinntech) measurement device. The last formed ring (2006, growth period 2006-2007) was left out for the trees <MCD, as this ring was formed after selective logging. Ring widths of all radii of the discs were averaged, corrected for desiccation and irregular growth using the mean radius of the fresh disc area. In case of trees >MCD with missing rings in the centre, we used the mean

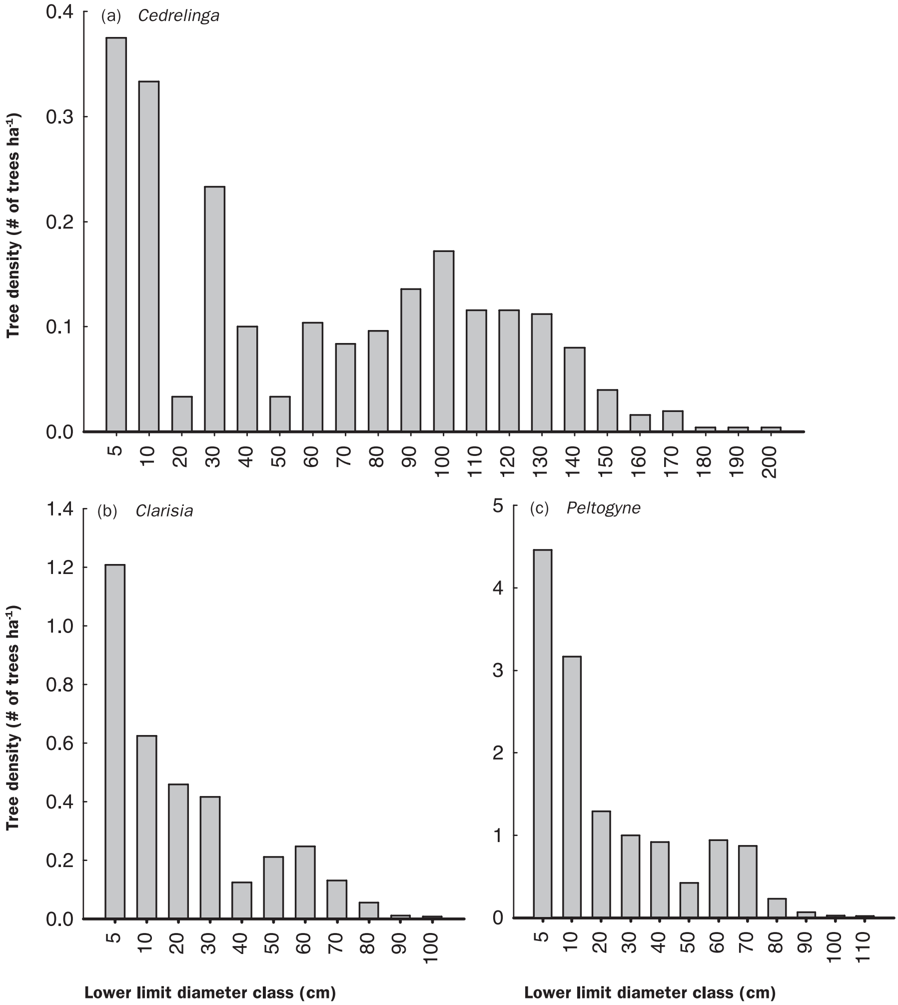


**Fig. 1** Tree density in diameter classes from 5 cm onwards for three Bolivian tree species.

age-diameter relation for non-hollow trees >MCD to reconstruct the age-diameter trajectory. In that way we could determine for all trees the age at which they attained the MCD. In growth simulations only the measured ring widths were included.

### Construction of growth curves

We used bootstrap simulations to obtain a large number of growth trajectories from tree-ring measurements, following the approach of Brienen *et al.* (2006). For the simulations of 'lifetime growth data' we used tree-ring data from the full set of historical ring width measurements. For the simulations of 'plot-type growth data' growth data of just the last ten years of ring width were used to perform simulations.

In these simulations, autocorrelation was incorporated as such that the link between growth in the previous and current growth interval was maintained by randomly choosing the current growth rates from trees with previous growth in the same 'growth rate class'. The incorporation of growth variation within and among individual trees in growth simulations leads to more reliable, and higher, estimates of timber volume recuperation in the second cutting cycle (Miina, 1993; Brienen & Zuidema, 2006b; Brienen & Zuidema, 2007).

To determine the appropriate level of growth autocorrelation to be applied in the simulations, we first performed several trial simulations. Brienen *et al.* (2006) found that using cumulative growth over a 5-year time interval as input in the simulations yielded a better match of the observed and simulated age distribution of large trees than using growth rates with a 1-year time interval. We determined which time interval would yield most reliable simulation output for our study species. A set of 1000 trees per species was simulated with variation similar to that observed in the growth trajectories reconstructed from tree-ring measurements of harvestable trees (lifetime growth data; Brienen *et al.*, 2006). We evaluated the 95%-confidence interval of simulated ages at the MCD when using (cumulative) growth rates over 1, 2, 3, 4 and 5 year, and then selected the time interval for expressing autocorrelation that resulted in the best fit with the observed ages at the MCD of harvestable trees. We assumed that the selected time interval for incorporating autocorrelated growth in the simulations for lifetime growth data would also be appropriate for plot-type growth data.

Then, using the selected time interval, we simulated 1000 trees based on the lifetime growth data and again 1000 individuals using the plot-type growth data. All growth simulations were executed in Matlab 5.3 (The Mathworks Inc.).

### Calculation of timber volumes and commercial ingrowth

The Forestry Law in Bolivia prescribes a minimum cutting cycle of 20 years and allows cutting 80% of the trees >MCD at each harvest. The 20% remaining trees need to be retained in the forest as seed trees (van Rheenen, 2005).

To project timber yield at second harvest the observed population density of the species was used as initial condition. Densities of trees in size classes >MCD were obtained from the logging company 'MABET'. We used data from 250 ha from the same area as the trees used for tree-ring analysis. For tree densities in size classes <MCD, population structures were constructed from counts of trees >5 cm dbh in 24 transects of 10 m x 1 km. As stem density for *Cedrelinga* in these transects was low, we added information on abundance of trees >10 cm dbh from six permanent sample 1 ha-plots in Los Indios (Instituto Boliviano de Investigación Forestal, unpublished data).

Species-specific relations between dbh and commercial height were established to calculate stem volume. Commercial height, i.e. height until the first branch, was measured for all trees in the 24 transects with a measurement pole for small trees and a clinometer for large trees. Additionally, commercial height was measured for the trees which were used for tree-ring analysis after they had been cut. Stem volume ($V$) was calculated as:

$$V = h(0.5\text{dbh}/100)^2\ \pi\ 0.65 \qquad (1)$$

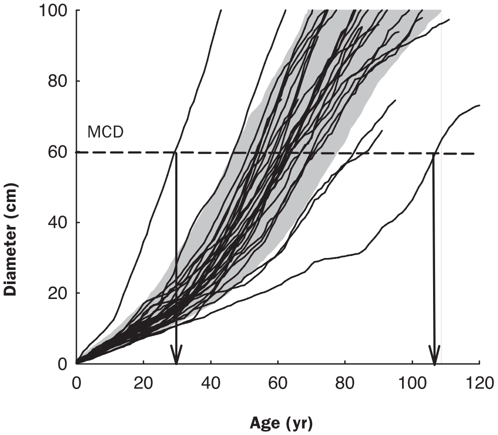
where $h$ is commercial height (in m), [(0.5dbh/100)2π] represents basal area ($m^2$) and 0.65 is the form factor which is applied in Bolivia to correct for stem taper (Dauber, 2003; Brienen & Zuidema, 2006b).

We compared the ‘commercial ingrowth’ – the growth of trees below the MCD into harvestable size classes – for both datatypes: lifetime growth data and plot-type growth data. To this end, we applied the prospective approach of Brienen and Zuidema (2006b; see below). Commercial ingrowth was calculated for two logging scenarios that differed in the timing of the second harvest: either 20 years or 40 years after initial logging. First, a list of 1000 trees of a randomly chosen size within each diameter class was established. We applied 5-cm wide diameter categories for 5-10 cm dbh and 10-cm wide categories for larger sizes, up to the MCD (40-45 cm diameter for *Clarisia*). For each of these simulated trees we determined whether it would attain harvestable size at second harvest by (1) randomly assigning one of the 1000 simulated growth trajectories to the tree and (2) determining its tree size at second harvest, after 20 or 40 years. For all trees that made it to the MCD within the 20-y or 40-y simulation period, we applied a mortality rate of 2% (the commonly observed mortality rate in the region (Poorter *et al.*, 2001), and in tropical forests elsewhere (e.g. Lieberman *et al.*, 1985b; Condit *et al.*, 1995b)). The percentage of trees that attained the MCD at the second harvest was multiplied with $(0.98)^{20}$ for the 20y-scenario and with $(0.98)^{40}$ for the 40y-scenario, to obtain the fraction of trees that survived. Finally, the percentage of the 1000 trees that survived and attained the MCD per diameter class <MCD was multiplied with the observed tree density per hectare and average stem volume at second harvest for each diameter class. In this way commercial ingrowth was obtained for each diameter category, in $m^3\ ha^{-1}$.

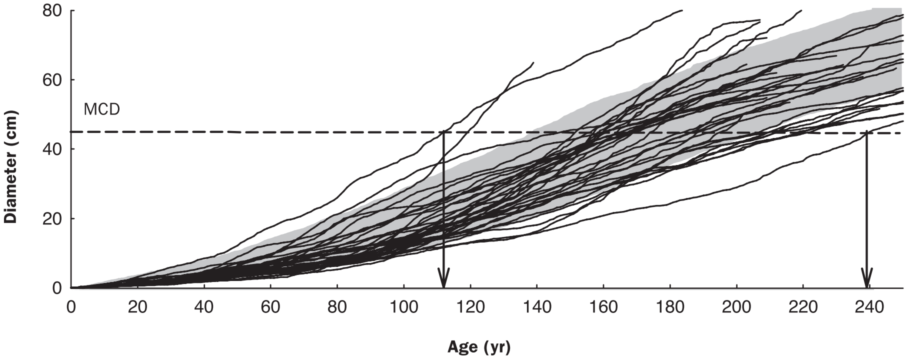
### Timber yield projections

Total timber yield at second harvest was determined by adding harvestable volume from commercial ingrowth to the timber volume at the second harvest from surviving seed trees. These calculations were conducted for a 250-ha area. First, the observed density of har-

(a) *Cedrelinga*



(b) *Clarisia*



(c) *Peltogyne*

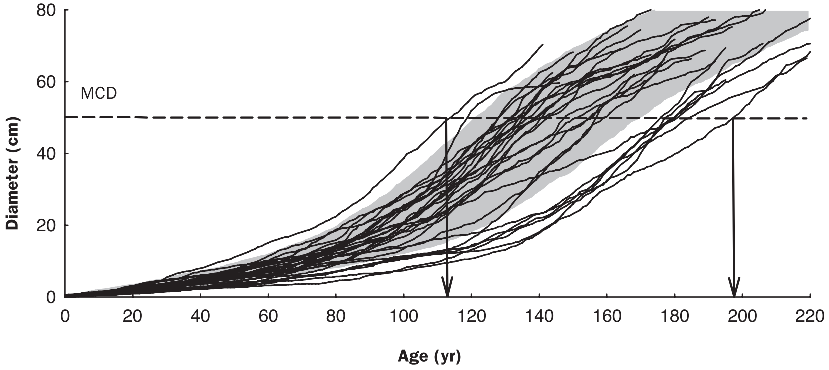


**Fig. 3** Observed and simulated growth trajectories for three Bolivian tree species. Black lines indicate observed growth trajectories of individual trees of harvestable size and the grey area indicates the area in which 95% of the simulated growth trajectories fall. The dashed line represents the minimum cutting diameter (MCD). Arrows indicate the lowest and highest observed age at which trees attained the MCD.

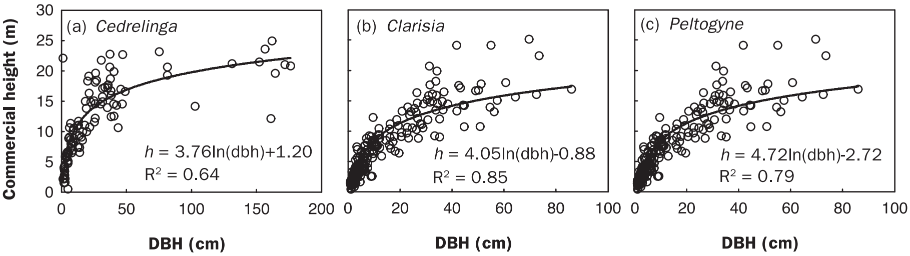


**Fig. 2** Relation between diameter at breast height (dbh) and commercial height for three tropical tree species. Equations with R2 are indicated in the graphs.

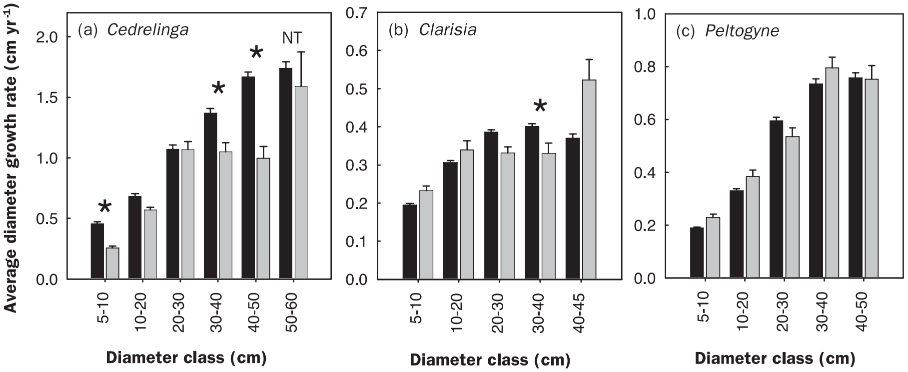


**Fig. 4** Average diameter growth rates for harvestable trees (black bars), and extant trees of all sizes (grey bars) for three tropical tree species in various diameter classes. * indicates a significant difference (Mann-Whitney U-test; $P<0.05$). NT indicates not tested, as growth rates from the same trees were included for both types of growth data. Similarly, one tree was left out for *Cedrelinga* in the 40-50 cm diameter class and for *Clarisia* in the 40-45 cm diameter class, as those were included for both types of growth data. (a) *Cedrelinga*, MCD = 60 cm; (b) *Clarisia*, MCD = 45 cm; (c) *Peltogyne*, MCD = 50 cm.

vestable trees in 250 ha was used to determine initial timber yield. From these trees, 20% was randomly selected as seed tree. Also to these trees an annual mortality rate of 2% was applied. To determine harvestable volume at second harvest, 80% of the seed trees that survived up to the second harvest were included. Second, commercial ingrowth (in $m^3$ $ha^{-1}$) based on simulated growth trajectories from lifetime growth data was expressed per 250 ha. To determine harvestable volume at second harvest resulting from commercial ingrowth, 80% of the commercial ingrowth (in $m^3$ $ha^{-1}$) was added to the harvestable volume from the surviving seed trees. Simulations were repeated 20 times to calculate average values for projected timber yield.

## RESULTS

### Stem density, size distribution and allometric relations

Stem densities varied up to tenfold among species (Fig. 1), with highest densities for *Peltogyne* and lowest for *Cedrelinga*. For all species, population structures showed roughly inverse J-shaped size distributions with relatively more trees in the smaller size classes. This shape suggests that populations are constantly regenerating but with low survival to large size. In *Cedrelinga* relatively more large trees were found compared to the other species (Fig. 1).

The relation between commercial height and dbh was similar for the three species, with 64-85% of the variation in commercial height explained by dbh (Fig. 2).

### Ages of trees at the MCD

Species varied strongly in average age at attaining the MCD. *Cedrelinga* was the fastest-growing species with on average 63 years to reach harvestable size (Fig. 3). *Clarisia* and *Peltogyne* took longer, on average 179 and 150 years to attain the MCD, respectively. Within species, the age at which the MCD was attained varied up to threefold among individual trees. In *Cedrelinga* ages showed strong, threefold, variation (30-107 y; Fig. 3a), while ages at MCD varied somewhat less, twofold, for *Clarisia* (112-241 y) and *Peltogyne* (114-198 y; Fig. 3b,c).

The trial simulations to determine the appropriate time interval of growth data showed the best fit of observed and simulated ages when applying 1-year time intervals (Fig 3). The trial simulations for 2- to 5-year time intervals yielded lower simulated tree ages at MCD than observed. We thus chose to use 1-year time intervals in all growth simulations. Although this resulted in a good match of simulated and observed ages without structural bias, variation in simulated ages was slightly lower than observed (Fig. 3).

### ‘Plot-type growth data’ vs. ‘Lifetime growth data’

Observed growth rates from ring data of trees of harvestable size (lifetime growth data) were compared with the last ten years of growth from extant trees of all sizes (plot-type growth data) to determine whether extant trees had on average lower growth than harvestable trees in the same size class. For *Cedrelinga* growth rates, thus ring widths, obtained from harvestable trees were significantly higher than those of extant trees in three diameter classes: 5-10 cm, 30-40 cm and 40-50 cm diameter (Fig. 4a; Mann-Whitney U-test, $P<0.05$). In the other diameter classes no significant differences were found (Fig. 4a; Mann-Whitney U-test, $P>0.05$). *Clarisia* showed a significant difference in the size class from 30-40 cm only, with higher growth rates for harvestable trees than for small extant trees (Fig. 4b; Mann-Whitney U-test, $P<0.05$). By contrast, growth rates of harvestable trees did not significantly differ from growth rates for small trees in *Peltogyne* (Fig. 4c; Mann-Whitney U-test, $P>0.05$).

## Projected commercial ingrowth

To evaluate the influence of fast juvenile growth on timber volume recuperation, we compared commercial ingrowth from the size classes <MCD between a set of simulated trees based on lifetime growth data and a set of simulated trees from plot-type growth data. Commercial ingrowth differed strongly among species. When using lifetime growth data, commercial ingrowth was highest for *Peltogyne* (2.6 $m^3$ $ha^{-1}$), intermediate for *Cedrelinga* (1.1 $m^3$ $ha^{-1}$) and lowest for *Clarisia* (0.2 $m^3$ $ha^{-1}$) for the 20y-scenario (Fig. 5a-c). The same species ranking in commercial ingrowth was found for the 40y-scenario with a total ingrowth of 4.3 $m^3$ $ha^{-1}$ for *Peltogyne*, 2.4 $m^3$ $ha^{-1}$ for *Cedrelinga* and only 0.5 $m^3$ $ha^{-1}$ for *Clarisia* from the size classes <MCD. Growth rates were highest in *Cedrelinga*, as trees in the 5-10 cm diameter class attained the MCD in 40 years (Fig. 5d). The other two species grew more slowly: *Peltogyne* trees of 10-20 cm diameter were able to attain the MCD in 40 years, while for *Clarisia* this was the case for trees of 20-30 cm dbh (Fig. 5d-f).

For *Cedrelinga* and *Clarisia* projected commercial ingrowth at second harvest was higher when using lifetime growth data than for plot-type growth data for both the 20y- and the 40y-scenarios (Fig. 5). *Peltogyne* showed the opposite pattern. For this species commercial ingrowth of trees <MCD seemed to be somewhat higher when using plot-type growth data than for lifetime growth data (Fig. 5c,f), although differences between the two types of growth data were not significant (Fig. 4). Thus, in two species we indeed found substantially higher projected commercial ingrowth when using lifetime growth data from harvestable trees than when plot-type growth data were used.

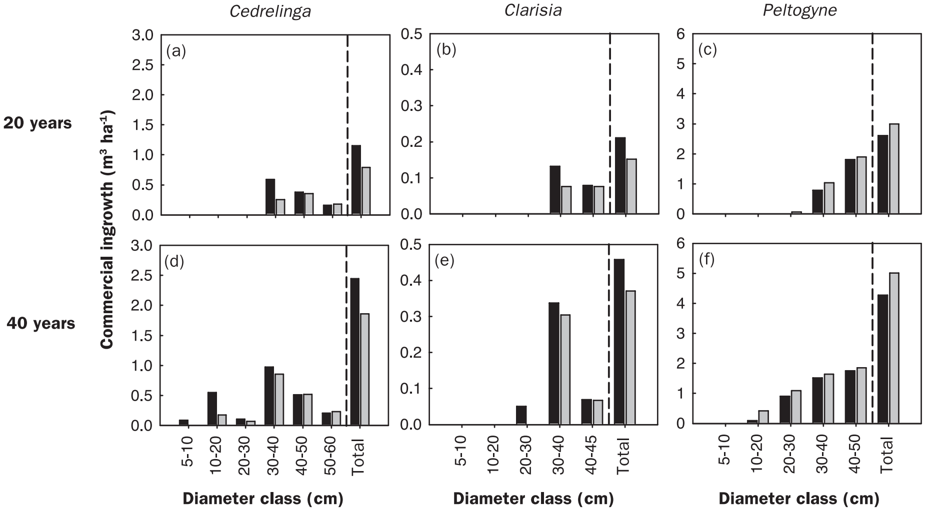


**Fig. 5** Commercial ingrowth expressed in stem volume ($m^3$ $ha^{-1}$) from trees in diameter classes below the minimum cutting diameter to harvestable size using lifetime growth data (black bars) and plot-type growth data (grey bars) for three Bolivian timber species. Values for a second harvest in 20 years and in 40 years after initial harvest are shown. *h*=commercial height, dbh=diameter at breast height.

### Timber yield recuperation

For all species the harvestable timber volume at second harvest was much lower than at initial harvest (Fig. 6). Timber yield recuperation was low for *Cedrelinga* and *Clarisia* with 20% of harvestable volume at initial harvest recuperated after 20 years, and 26-27% when applying a cutting cycle of 40 years. Importantly, a large part of the recuperated timber volume at second harvest, more than 50% for the 20y-scenario, consisted of surviving seed trees for these species (Fig. 6a,b). Thus, commercial ingrowth is very low for these species. For *Cedrelinga* this may be due to the low tree densities in size classes <MCD. In *Clarisia* the low growth rates and low density of trees of 40-50 cm may be causes of low timber volume recuperation. In *Peltogyne* recuperation was higher with 33% and 46% in 20 and 40 years, respectively (Fig. 6c). For *Peltogyne* harvestable volume at second harvest was mainly determined by ingrowth from trees <MCD, whereas the contribution of surviving seed trees to harvestable volume was low compared to the other two species. The higher rate of volume recuperation in *Peltogyne* is probably due to the relatively high tree densities in the diameter classes just below the MCD compared to *Cedrelinga* and *Clarisia*, and higher growth rates than *Clarisia*.

## DISCUSSION

### Simulating tropical timber yield

Overall, simulated ages matched the observed ages from ring data quite well, although variation in simulated ages at the MCD was somewhat lower than in the observed ages of harvested trees (Fig. 3). As the incorporation of variation in growth projections has been shown to increase timber yield (Miina, 1993; Brienen & Zuidema, 2007), we may slightly underestimate recuperation of timber yield. For *Peltogyne* and to some extent for *Clarisia*, the simulated growth trajectories showed slightly lower ages at the MCD compared to the observed trajectories. Thus, this may cause somewhat higher timber yield projections.

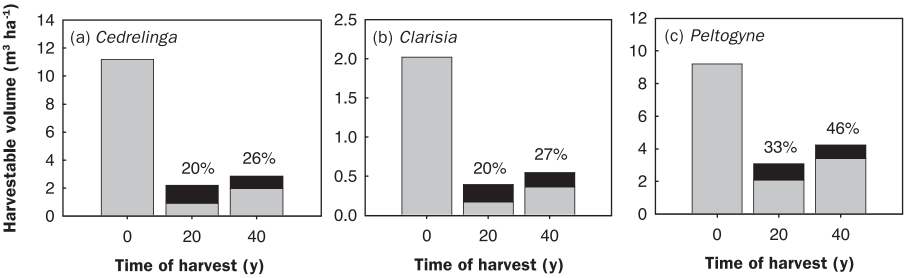


**Fig. 6** Harvestable timber volume per hectare for the initial harvest and for a second harvest 20 or 40 years later for three tropical tree species. The part of the harvestable volume at second harvest which consisted of survived seed trees from initial harvest is indicated in black. Harvestable volume at second harvest is indicated as a percentage from the initial harvest above the bars.

Two other biases may have influenced the results. First, we did not account for the presence of hollow trees in the analysis. For *Cedrelinga*, many harvestable trees showed heart rot (personal observation), which may lead to a lower actual timber yield than projected (cf. Valle *et al.*, 2006). We do not have data on stem quality, but in the Brazilian Amazon 28% of all trees marked for harvest were found to be defective (~50% of all trees; Holmes *et al.*, 2002). Second, we still may underestimate growth rates, as after logging growth rates are known to increase temporarily (Silva *et al.*, 1995; Valle *et al.*, 2006; Peña-Claros *et al.*, 2008a). Thus, this would mean that we might have made a conservative estimate of future timber yield.

In spite of the above-mentioned inaccuracies, we judge that the presented method using lifetime growth data is most accurate in estimating timber yields, as we incorporated realistic growth variation in the simulations and corrected for the juvenile selection effect through including growth rates of trees that reached harvestable size only. We also incorporated autocorrelation in growth projections with plot-type data, which probably enhances accuracy of timber yield projections. In most studies on timber yield projections based on growth data from permanent sample plots variation in growth is not included yet. It is possible to include autocorrelation in timber yield projections based on permanent sample plot data using the method of Brienen and Zuidema (2006b) to improve estimates of future timber yield. Then, annual growth measurements are required, or at least multiple measurements with a fixed time interval.

### Permanent plot data vs. tree-ring data

Most studies on timber yield recuperation used growth projections based on growth data from permanent sample plots (e.g. Condit *et al.*, 1995a; Sist & Ferreira, 2007). This traditional approach in tropical forestry research yields valuable information on growth, recruitment and mortality of tropical forest trees. A disadvantage, however, is the inclusion of many slow-growing, suppressed trees that will not make it to the canopy (cf. Landis & Peart, 2005); Chapter 2). Therefore, future timber yield may be underestimated, as harvestable trees are likely to represent the faster-growing part of the population. To determine the magnitude of this effect we contrasted growth of harvestable volume between lifetime growth data, long-term tree-ring data for harvestable trees, and plot-type growth data, the last ten years for extant trees of all sizes as a proxy for growth data from permanent sample plots. For two out of three species, *Cedrelinga* and *Clarisia*, we found a large difference in commercial ingrowth when using simulated growth trajectories based on lifetime growth data compared to plot-type growth data. Commercial ingrowth was indeed higher when using long-term growth rates from harvestable trees. These results agree with the strong juvenile selection effect in *Cedrelinga*, which lasted until 30 cm (Chapter 2), and may even have an effect at larger sizes. *Clarisia* and *Peltogyne* also showed a juvenile selection effect, but only for the 0-1 cm diameter class (Chapter 2). For *Clarisia*, however, growth rates in the 30-40 cm class were larger for harvestable trees than for smaller extant trees. This suggests the existence of a juvenile selection effect also at larger tree sizes.

Our results confirm the idea that the faster-growing part of the population should be used for growth projections, but up to present this has been suggested particularly for light-demanding species (cf. Baker, 2003; Chapter 2). Here, we showed that for shade-tolerant species such adjustments in growth projections may be required as well. Several studies already presented growth projections using growth rates from the fastest-growers to estimate future timber yield (Condit *et al.*, 1995a; Rondon *et al.*, 2009), and tree ages (O'Brien *et al.*, 1995; Terborgh *et al.*, 1997; Laurance *et al.*, 2004a). So far, it was unclear whether the fastest 10%, 25%, 50% or some other value should be included to obtain reliable estimates of future timber yield. This is likely to differ among species and forest types. To be able to present general recommendations on the percentage of fastest-growers that should be included the two types of growth data should be compared for more species. Here we presented the first comparison for three tropical tree species, but more studies including a larger set of species are needed to determine to which extent the juvenile selection effect influences timber yield estimates in general.

**Low timber volume recuperation**

The observed ages at the minimum cutting diameter were high: on average 63 years for *Cedrelinga*, 150 years for *Peltogyne* and 179 years for *Clarisia* (Fig. 3). These values are comparable to the ages obtained for *Cedrelinga* (61 y, at 50 cm diameter) and *Peltogyne* (135 y) in another study at a different site in Bolivia (Brienen & Zuidema, 2006b). Also in other tropical forests high ages were found at the minimum cutting diameter. For example, *Triplochiton scleroxylon* needed on average 80 years to reach 80 cm in Cameroon (Worbes *et al.*, 2003). In Central Amazonian white-water floodplain forests similar ages at the MCD were observed as for our species: low-density species reached the MCD of 50 cm in an average of 15-67 years, while high-density species needed on average 106-151 years (Schöngart, 2008). The long timespan needed to reach the MCD for most species suggest already that recuperation rates of timber volume will likely be low when short cutting cycles are applied.

Projected timber yields at the second harvest were low: only 20-46% of the volume initially harvested was recuperated at second harvest, 20 or 40 years later (Fig. 6). Timber volume recuperation in 20 years for *Cedrelinga* in our study was comparable to recuperation for *Cedrelinga* in the study of Brienen and Zuidema (2006b). For *Peltogyne* we found a lower percentage, 33% of initial harvestable volume, compared to 61% (Brienen & Zuidema, 2006b), although total harvestable volume was much higher due to higher densities of *Peltogyne* in our study area. Our estimates were slightly higher than a recuperation of 22% after 25 years of the volume harvested at the initial harvest, which was estimated for the Bolivian Amazon based on plot data for three species groups (Dauber *et al.*, 2005). Our results were comparable to those obtained in studies on other species in Neotropical forests (cf. Table 1). Yield estimates at second harvest for individual tree species ranged from 5-61% of initial harvestable volume (Table 1). With the exception of one study in the Brazilian Amazon with 83% of the initial volume recuperated for the total of all commercial species in 30 years (Valle *et al.*, 2007), timber volume recuperation was found to be low (Table 1).

Our projections suggest that for our study species, a cutting cycle of 40 years does not guarantee that timber yields are sustained. To reach sustainable timber yield silvicultural treatments should be applied to increase growth rates of trees <MCD. Recently, silvicultural treatments have been shown to enhance growth of future crop trees (Peña-Claros *et al.*, 2008a; Villegas *et al.*, 2009), and to enhance to some extent successful regeneration of Bolivian timber species (cf. Peña-Claros *et al.*, 2008b; Verwer *et al.*, 2008). Still, it will be hard to obtain timber yields at second and further harvest of the same magnitude as those of the initial harvest. One of the main reasons why this is difficult is that many trees of harvestable size have passed the MCD threshold already since many decades (Brienen & Zuidema, 2007). This is what foresters sometimes call the 'Primary forest premium' (cf. Keller *et al.*, 2007), which cannot be recuperated under relatively short cutting cycles. In subsequent harvests only few very old trees, part of the remaining seed trees, will be available for harvest. It is therefore appropriate to exclude very old (large) trees from yield analyses, or to compare timber yield at second harvest with volume recuperation in subsequent harvests.

### Concluding remarks

Our results suggest that using tree growth data from permanent sample plots in growth simulations may underestimate future timber yield. Tree-ring analysis is a promising tool for forest management, as it provides data on ages of trees at the minimum cutting diameter and long-term growth patterns of trees (cf. Brienen & Zuidema, 2006b). These data can be used to define the degree of autocorrelation that should be included in growth projections, and the strength of the juvenile selection effect for tropical tree species (cf. Chapter 2). General recommendations on accounting for these effects when using permanent plot data should be established, once more information is available on the strength of juvenile selection effect and growth autocorrelation across tropical tree species.

## ACKNOWLEDGEMENTS

Roel Brienen kindly allowed us to use his methodology for incorporating autocorrelation in growth simulations. We are grateful to Mart Vlam for help with the ring measurements and to Claudia Rodríguez for collecting data on tree densities and the relation between dbh and commercial height. We thank Nazareno Martínez, Miguel Cuadiay, Adhemar Saucedo, Jeroen Wiegeraad, Edwin Rodríguez, and many others for help with fieldwork. We are grateful to staff and personnel of PROMAB-UAB for logistic support. Logging company 'Maderera Boliviana Etienne S.A.' is acknowledged for permission to work in their concessions, for providing data on harvestable tree densities and for logistic support. Marielos Peña-Claros provided constructive comments on an earlier version of the manuscript. DMAR was supported by grant W 01.53.2004.047 from the Netherlands Foundation for the Advancement of Tropical Research (WOTRO).

# CHAPTER 6

## Dendroecology in the tropics:

## a review and integrated summary

In this thesis I applied tree-ring analysis to answer questions that require data on long-term tree growth. Worbes (2002) reviewed the history of tropical dendrochronology and formulated three needs for future research in three focal areas. First, tree-ring chronologies used to reconstruct tropical climate should be based on samples from the tropics. Second, studies on tropical forest and population dynamics require the real age of trees and successional stages and, third, management plans for sustainability need real growth data obtained from tree-ring analysis (Worbes, 2002). Here, I focus on the latter two issues. What has tree-ring analysis contributed to the understanding of tropical tree and forest ecology so far, and which questions are still open? In this chapter I give an overview of the achievements in the field of tropical dendroecology and discuss the results of this dissertation.

## Pathways to the canopy

Which trees are able to attain the canopy? Most juvenile tropical trees grow slowly, as light availability in the understorey is low (Chazdon & Fetcher, 1984). Because slow-growing juveniles experience higher mortality rates (Wyckoff & Clark, 2002), they may have a considerably lower chance to attain the canopy compared to the fast-growing individuals (Enright & Hartshorn, 1981; Swaine *et al.*, 1987). This would mean that successful trees have grown faster as juveniles, compared to juvenile trees at this moment in the forest ('juvenile selection effect'). I evaluated the existence of such a juvenile selection effect applying tree-ring analysis for five tropical tree species (Chapter 2). The juvenile growth rates of extant trees over the entire size range of the species were obtained, averaged for narrow size categories and then related to extant diameter. Using this approach, growth rates of extant juvenile trees could be compared with growth rates of trees that made it to the canopy at the time they were young and of the same size (Chapter 2). For three out of five species we found that juvenile growth rates increased with extant tree size, implying that extant large trees had faster juvenile growth than extant juveniles. For the shade-tolerant species *Clarisia*, and *Peltogyne*, only in the diameter class from 0-1 cm diameter this indication for a juvenile selection effect was found. However, in the light-demanding species *Cedrelinga* the effect was stronger, as it was found until 30 cm diameter. Thus, for these three species fast juvenile growth may be essential to reach the canopy, which is in accordance with results for three temperate tree species (Landis & Peart, 2005). These results likely have implications for age projections and modelling tree population dynamics. I discuss these implications in the following paragraphs.

How do tropical trees grow to the canopy? Growth trajectories of canopy trees have been reconstructed with tree-ring analysis to tackle this question (Baker & Bunyavejchewin, 2006; Brienen & Zuidema, 2006a). Although a juvenile selection effect may occur, large variation in the way at which trees attain the canopy has been found both among and within species (Brienen & Zuidema, 2006a; Baker & Bunyavejchewin, 2006). Many researchers hypothesized that juvenile trees of canopy species would require at least one gap event to reach the canopy (e.g. Turner, 2001). Brienen and Zuidema (2006a) indeed found that trees of four non-pioneer species experienced on average 0.8-1.4 releases before attaining the canopy.

Species differed in growth patterns towards the canopy, which suggests that the four non-pioneer species differ in shade tolerance (Brienen & Zuidema, 2006a). Similarly, Baker and Bunyavejchewin (2006) found large differences in canopy accession patterns among species for a seasonal tropical forest in Thailand. The most shade-intolerant species, *Melia azederach*, reached the canopy with constant fast growth, whereas the shade-tolerant *Neolitsea obtusifolia* established mostly in low-light conditions and showed one (or no) release to reach the canopy (Baker & Bunyavejchewin, 2006). So far, only two studies reconstructed lifetime growth patterns, thus general patterns in growth strategies towards the canopy are not known yet. Growth patterns differ strongly among species, as has been shown for a total of nine tropical tree species (Baker & Bunyavejchewin, 2006; Brienen & Zuidema, 2006a). Additionally, growth patterns of species may differ among forest types. Tree-ring studies can play an important role in revealing these growth patterns.

### Volume growth reconstruction of juvenile tropical trees

Growth patterns towards the canopy have been studied mainly in terms of diameter growth, instead of height growth, stem volume growth or biomass growth. In this dissertation I reconstructed stem volume growth, to obtain a more suitable proxy for biomass growth for juveniles of three tropical tree species. Historical rates of volume growth can be quantified from tree-ring analysis at various heights along a tree's stem (cf. Sumida *et al.*, 1997). Growth in stem volume, height and diameter varied strongly among individuals of the same height, probably as a consequence of differences in growth conditions among trees. Among-tree differences in volume growth persisted over height classes, while this was less so for diameter growth and height growth. Thus, shifts in investment in height and diameter growth occurred over time, whereas stem volume growth remained the same (Chapter 4). No correlations between diameter growth and height growth were found in any of the height classes. Even though height growth and diameter growth are unrelated, these results may be consistent with a trade-off between diameter and height growth. A reason for not finding negative (or positive) relations may be the large variation in growth among individual trees within a height class. Van Noordwijk and de Jong (1986) argued that if the total amount of resources which can be invested in two life history traits varies strongly among individuals, positive instead of the expected negative correlations may be observed. Thus, if among-tree differences in volume growth are large, negative correlations between height growth and diameter growth may disappear or change into a positive correlation between height and diameter growth (cf. van Noordwijk & de Jong, 1986). For this reason, we chose to evaluate the relation between volume growth and height growth, rather than relating diameter growth and height growth directly. We found negative correlations between stem volume growth and height growth, for small trees of all species. Thus, trees that grew fast in stem volume invested relatively less in height growth compared to slow-growing trees. Hence, fast juvenile growth is associated with low height growth, suggesting that trees in favourable (light) conditions invest relatively more in stability and crown development than in height growth (Chapter 4).

Thus, the reconstruction of long-term growth in stem volume yielded important information about growth patterns of juvenile tropical trees. Still, to get a complete picture on patterns in biomass growth (and allocation) data on wood density would be needed. Now, wood density is assumed not to vary within trees, and among individuals of a species. However, a radial increase in wood density is known for tropical trees: for six tree species from a seasonally dry forest in Thailand wood density increased with increasing distance from the pith (Nock *et al.*, 2009). Ideally, one would integrate height, diameter, volume and biomass growth of juvenile trees using tree-ring analysis and wood density measurements to get one step closer to a complete reconstruction of biomass growth and an improved understanding of pathways to the canopy in tropical forests.

## Ages of tropical trees

The findings of trees of more than 1000 years old through C14-dating (Chambers *et al.*, 1998), led to an intensive debate about the accuracy of different age estimation methods and the actual occurrence of such old trees (cf. Martínez-Ramos & Alvarez-Buylla, 1998). Probably, the importance of very old trees for carbon cycling has been overstated, as those trees will occur at very low densities in the forest (Martínez-Ramos & Alvarez-Buylla, 1998; Williamson *et al.*, 1999). Tree-ring analysis provides a direct method for age determination. Although also in other studies some very old trees were found using C14-dating (e.g. Kurokawa *et al.*, 2003), tree ages obtained from tree-ring counts appeared to be much lower (maxima from ~400-550 years; e.g. (Worbes & Junk, 1999; Fichtler *et al.*, 2003; Brienen & Zuidema, 2006a).

The use of growth data from permanent sample plots in age projections also resulted in very high estimates, as mostly average growth rates were used with the assumption that all trees eventually reach the canopy (cf. Laurance *et al.*, 2004a). Age estimations from growth models can be much improved by comparing outcomes with observed ages from tree-ring data for the same trees or tree species (Brienen *et al.*, 2006; Chien, 2006; Baker, 2003). In this way, Baker (2003) developed age estimation methods for tropical trees through testing them for tree species with varying shade tolerance in a temperate forest. Two age estimation methods were compared: the crown class method and periodic annual increment (PAI; cf. Condit *et al.*, 1993). The crown class method predicts ages based on the average growth rate for trees in a certain crown class and assumed that a tree made no switches in crown class through ontogeny. This method was found to be most accurate for shade-intolerant species. PAI regression uses average growth rates for all size classes (cf. Condit *et al.*, 1993). This method performed better for shade-tolerant species (Baker, 2003). The methods gave accurate results for tropical tree species as well, although, unexpectedly, the crown class method also gave better results for a shade-tolerant species (Baker *et al.*, 2005). In the crown class method, implicitly, above-average growth rates are used to project tree ages. Applying the crown class method in particular for light-demanding species is consistent with the probably stronger juvenile selection effect – fast-growing juveniles have larger chance to reach the canopy – in these species (Chapter 2). Recently, a new approach for estimating tropical tree ages was presented (Metcalf *et al.*, 2009). In this approach the link between light level and growth was maintained through ontogeny, but results were not verified with ages from tree-ring counts. Results of age projections can be further improved by accounting for autocorrelated growth, which results in higher, more realistic, variation in tree ages (Brienen *et al.*, 2006).

Tree-ring counts may be the most accurate method to determine tree age, as it is a direct method (Martínez-Ramos & Alvarez-Buylla, 1998). However, when a tree grows slow, growth rings can be more difficult to identify and tree age may be underestimated. To evaluate the accuracy of tree age determination from ring counts, C14-bomb peak dating can be applied for trees – or tree rings –, of less than 50 years old (Soliz-Gamboa *et al.*, submitted). Nevertheless, other methods are required for tree species without reliable annual growth rings. C14-dating provides also reasonably accurate ages for trees >350 years old, although it is difficult to determine if a tree is older than 350 years and a disadvantage is the larger dating error (around 50 yr; cf. Martínez-Ramos & Alvarez-Buylla, 1998). The development of age projection methods based on permanent sample plot data, with verification of the accuracy of the method with ring data of species with reliable annual rings, has also large potential.

### Incorporation of autocorrelation in tree growth models

Large variation in growth exists, both among individual trees of a species, and within an individual tree over time (Clark & Clark, 1992). This variation is probably caused by differences in growth conditions among trees and temporal variation in those conditions. Altogether, this may lead to autocorrelated growth, meaning that growth of a tree during one year is related to its growth at the next year, or the following, etc. (Brienen *et al.*, 2006). Strong temporal autocorrelation in tree growth has been observed in permanent sample plot studies (Kohyama & Hara, 1989; Kammesheidt *et al.*, 2003; Clark & Clark, 1992; Grogan & Landis, in press). Traditionally, autocorrelation was not taken into account in tropical tree growth or age projection models, as average growth rates were used (Lieberman & Lieberman, 1985). Some efforts have been done to incorporate autocorrelation in age estimation models (Bullock *et al.*, 2004; Kohyama *et al.*, 2005). Much better estimates for the strength of autocorrelated growth can be derived from tree-ring data. As growth data over the whole lifetime of a tree can be obtained, temporal patterns in growth within trees and the persistence of growth differences among trees over time can be evaluated (cf. Brienen *et al.*, 2006). Growth was found to be strongly autocorrelated in time and differences in growth among trees within a species persisted over long timespans. Thus, fast-growing trees keep growing fast over prolonged time periods, and slow-growing trees continue to do so over long timespans as well. This leads to large variation in age at a certain tree size (Fig. 1; Brienen *et al.*, 2006). When a realistic degree of autocorrelation was incorporated in growth simulations, variation in age estimations became larger and ages agreed with those derived from ring data (Brienen *et al.*, 2006).

Also in population models, variation in growth and the growth history of individuals is usually neglected. For instance, most matrix models for trees do not take into account growth variation between individuals and standard matrix models are not able to accommodate au-

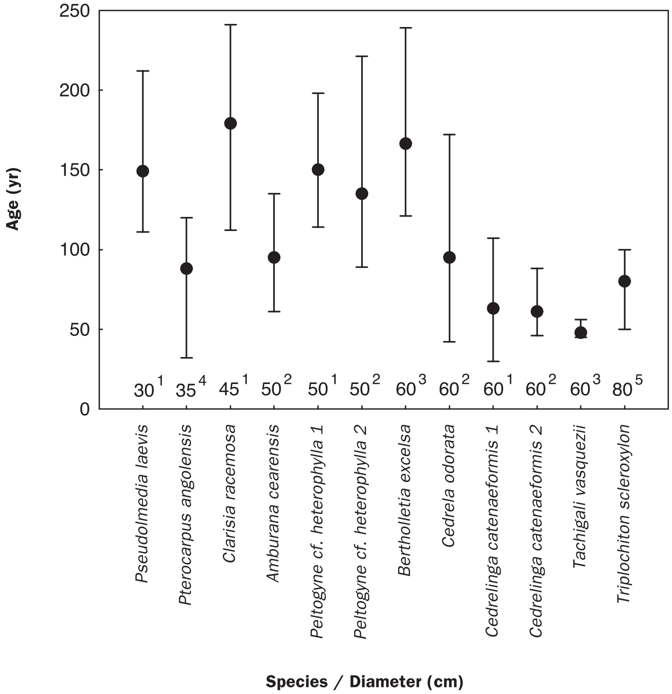


**Fig. 1** Average and range in ages determined through tree-ring counts at a certain tree diameter for various tree species. The numbers in the lower part of the graph indicate the diameter of the tree, superscript numbers indicate the source. [1]This study, [2]Brienen and Zuidema (2006b), [3]Brienen and Zuidema (2006a), [4]Stahle *et al.* (1999), [5]Worbes *et al.* (2003).

tocorrelated growth (Zuidema *et al.*, in press). Recently, Zuidema *et al.* (2009) applied matrix models in which *Cedrela odorata* trees were classified by both age and size, thus explicitly incorporating the growth history of trees. They then evaluated the contribution of persistently fast-growing trees to population growth and found that this was much larger than that of slow growers. If fast growers in general have a larger contribution to population growth, it becomes very important to incorporate autocorrelated growth in population models. Tree-ring analysis can be a valuable tool to obtain information on the strength of autocorrelation, which then can be included into matrix population models or Integral Projection Models.

## Increasing growth over time?

Data from permanent sample plots showed that over the last decades aboveground biomass (Baker *et al.*, 2004), tree growth (Laurance *et al.*, 2004b; Phillips *et al.*, 2008), and stem turnover increased (e.g. Lewis *et al.*, 2004b). Causes of these changes are strongly debated (e.g. Lewis *et al.*, 2004a; Wright, 2005; Chave *et al.*, 2008), and may be due to the increase of atmospheric $CO_2$ (Lewis *et al.*, 2004a). In this dissertation, I applied tree-ring analysis to assess whether tropical tree growth increased over the last centuries (Chapter 2). As I used tree rings, I was able to evaluate such changes over much longer periods of time compared to previous studies that applied permanent plot data. I expressed juvenile growth rates in narrow diameter classes until 30 cm diameter of individuals of five tropical tree species over their entire range of extant tree sizes. This approach allowed relating tree growth to time, and I was therefore able to evaluate whether growth of large extant trees further back in time was larger than recent growth of small extant trees in the same diameter class ('historical growth increase'). For four species we found a historical growth increase. In Cedrela a historical growth increase was found for juveniles of 10-15 cm diameter, for *Clarisia* from 2-4 cm diameter, for *Peltogyne* from 1-3 and 6-8 cm diameter and for *Pseudolmedia* in the diameter categories from 2-8 cm.

The observed patterns of apparently increasing growth rates over time need to be interpreted cautiously. These growth changes might have been (partially) caused by sampling biases (Chapter 2). The reasoning is as follows: suppose that large trees die at a certain size, i.e. that mortality is size-dependent and there is a certain maximum diameter that can be reached. In this case, the trees that are growing persistently fast will reach that diameter at a younger age and therefore die at a younger age, compared to persistent slow-growers. When sampling tree discs at a certain moment in time, the large and old trees that are included in the sample will contain relatively few of the fast-growing trees, and relatively more of the slower-growing part of the population. Thus, when reconstructing historical growth rates based on the tree discs, growth rates in the distant past may appear to be low even though average growth of trees did in reality not change (Sampling bias I). A second sampling bias may occur due to the fact that persistently slow-growing juvenile trees may not have reached the minimum diameter of the trees that were included in the sampling. In that case, this may lead to an overestimation of recent growth rates as a larger share of young trees belongs to the faster-growing part of the population (Sampling bias II). At this moment it is not possible to determine whether these biases have influenced the results outlined in Chapter 2. Nevertheless, it is clear that if such biases occurred, one would have expected to find historical growth increases also for larger diameter classes. This was not the case, as shown in Chapter 2. In all, I cannot rule out some influence of these sampling biases in the results in Chapter 2, but wish to stress that my results are consistent with a response to increased atmospheric $CO_2$. Also in temperate forest stronger historical growth increases have been found for small trees than for large trees (Voelker *et al.*, 2006; Wang *et al.*, 2006).

**Reconstructing the disturbance history of tropical forests**

"Where are all the large trees, if this is a virgin tropical forest?". This question was coined by Hartshorn (1978) in a publication on forest turnover in Costa Rica. The study showed that forest turnover was rather fast, ranging from 80-138 years in the La Selva area, Costa Rica (Hartshorn, 1978). Similar findings were obtained in a tropical forest in French Guiana where 0.64-1.33% of the canopy was opened through gap formation per year (van der Meer & Bongers, 1996). Thus, we may consider tropical forests to be rather dynamic. In temperate forests, tree-ring analysis has been widely applied to reconstruct the disturbance history and historical stand dynamics (Runkle, 1982; Lorimer & Frelich, 1989; Lusk & Smith, 1998). By studying growth patterns, in terms of releases and suppressions and establishment dates of all trees in a certain area, the history of a forest stand can be revealed. Now, as it is possible to apply tree-ring analysis also in tropical forests, similar approaches can be applied to reconstruct historical stand dynamics. Nevertheless, usually not all species do form annual rings, thus some adjustments in the methods may be required.

Some tropical forest studies have applied tree-ring analysis to evaluate forest dynamics. Worbes *et al.* (2003) reconstructed the historical dynamics of a seasonally dry tropical forest in Cameroon in an area of 1 ha, by determining growth rates and ages of trees of nearly all species. The largest trees belonged to long-lived pioneer species, which were usually older than the trees of mature forest species and almost no recruitment of these species was present in the understorey. Mature forest species, in contrast, showed abundant regeneration. In all, the forest was classified as a late secondary forest (Worbes *et al.*, 2003). Similarly, the disturbance history of a seasonal tropical forest in Thailand was reconstructed (Baker *et al.*, 2005), using a combination of tree-ring analysis and age estimations from growth projections (cf. Baker, 2003). The stand structure data showed a single cohort of canopy trees, simulated age distributions showed that the cohort of canopy trees established in the 1800s and showed a peak for the shade-intolerant species in the mid-1900s. Tree-ring analysis provided a more detailed picture: there were peaks in recruitment and growth in the 1910-1920s, 1940-1950s and minor peaks in the late 1800s and 1970s. Tree-ring series of the oldest (*Afzelia xylocarpa*) trees showed elevated growth in the 1850s. Together these results indicate that around 1850 a large, widespread disturbance occurred, followed by a few minor disturbances more recently (Baker *et al.*, 2005). These results show that tropical forest structure and dynamics may indeed be shaped through the occurrence of disturbances at different spatial scales. Although these are a few isolated studies, the implications of their findings may be far reaching, as they show that current species composition and forest structure is the result of transient dynamics and past (major) disturbances.

Tree-ring analysis may also be useful in enhancing the understanding about secondary forest succession. Secondary forest succession is usually studied in chronosequences, a space for time substitution, through comparison of secondary forest stands of different, but known age (e.g. van Breugel *et al.*, 2006; Selaya *et al.*, 2008). Worbes *et al.* (1992) determined the ages of successional stands in floodplain forests by ring counts of the largest trees, but growth patterns were hardly presented. Similarly, an approach was presented to determine ages of secondary forest stands in Mexico, using tree-ring analysis (Brienen *et al.*, 2009a). Annual periodicity of the growth rings could be validated through comparison of ring counts with known stand ages. Ring counts closely matched the stand ages. Nevertheless, in older stands pioneers may already have disappeared, which may lead to errors in reconstructing stand dynamics as for some forests pioneers and non-pioneer species established at the same moment in time and in other stands non-pioneer species established later (Brienen *et al.*, 2009a).

Over the last decades, tropical forests have become more dynamic (Lewis *et al.*, 2004c; Phillips *et al.*, 2004). However, to evaluate patterns and causes of changes in tree turnover, data over much longer periods are required than currently available from permanent sample plots. In Chapter 3 we proposed two methods to detect evidence for long-term changes in tree turnover from tree-ring data for two Bolivian non-pioneer species. First, we checked for synchronization of growth releases in time, to identify possible large-scale disturbances. Second, we related the frequency of growth releases to time with the aim to determine whether the frequency of releases has increased over time. Finally, we calculated the degree of temporal autocorrelation, a measure that is indicative for the temporal changes in growth rates due to canopy dynamics (cf. Brienen *et al.*, 2006). We checked whether the degree of autocorrelation has changed over time. As the occurrence of releases and the strength of autocorrelation may be partly caused by the ontogenetic increase in growth, release frequency and degree of autocorrelation were analyzed based on the residuals from an average relation between tree size and diameter growth.

There was no clear pattern in the occurrence of releases for both species, but the percentage of trees with a release varied somewhat over the past 200-300 years (Chapter 3). We found releases in all time intervals for both species and did not detect a clear clustering of releases at any moment in time in the past centuries. Thus, there were no signs of a large-scale disturbance. Overall, changes in autocorrelation or release frequency were not observed over the last 200-300 years in both species. The exception to this general pattern was the first size category (a 20-y period starting at 0 cm diameter), in which we did find an increase in release frequency over time. This relation is probably the result of the structure of our dataset or of a remaining ontogenetic effect. Due to fast or slow growth of some individuals differences among trees in the strength of the ontogenetic growth increase may remain, as residuals from an average relation between size and growth were used. In all, we found no evidence for a long-term change in tree turnover in the study area over the last two to three centuries (Chapter 3). The proposed methods may be suitable, but causes of the growth patterns should be unravelled and the sampling strategy should be adjusted.

### Importance of unravelling the history of tropical forests

One needs to realize that the current ‘state’ of tropical forests, in terms of structure and dynamics, depends strongly on their history. Thus, the history of tropical forests should be taken into account when quantifying changes in forest structure and dynamics over time (Clark, 2007). For one of the study areas used in this dissertation, La Chonta, evidence for human occupation has been found around 300-400 years ago: remains of pottery have been found and species composition may have been altered (Paz-Rivera & Putz, 2009). These historical patterns may have determined maximum tree ages of trees that we find at this moment. For the species used in this study, *Pseudolmedia laevis*, probably there was no effect as the maximum tree age that we found was 262 years, and most trees >30 cm dbh were between 150 and 200 years old. Additionally, as a historical growth increase was observed in some size classes (Chapter 2), the older trees did probably not establish in high light conditions which might have indicated that they established after a (human-induced) disturbance.

Another important issue to consider is the effect of the timescale on the observed patterns in the dynamics of tree populations. Also here history may play a role and is important to consider. When looking at static data, thus size distributions, population dynamics cannot be inferred (Condit *et al.*, 1998; Feeley *et al.*, 2007b). Nevertheless, although from size distributions as such regeneration status of species cannot be derived, in combination with tree-ring data and careful application of matrix modeling some evaluations can be done (Couralet *et al.*, 2005). Determining the values of vital rates used in matrix models is usually based on a few years of measurements (e.g. Zuidema & Boot, 2002; Chien, 2006). Population growth rates may depend strongly on vital rates, which may lead to extreme estimates of population growth or decline over time as these strongly vary among years.

In this study historical population dynamics on a longer-term timespan play a role in determining whether sampling biases have caused the historical growth increase (cf. Chapter 2). The question that remains is whether mortality is age- or size-dependent or random. To find out whether intrinsically fast- or slow-growers disappeared from the population, growth rates of dead trees can be determined (cf. Henry & Swan, 1974; Dekker *et al.*, 2009). A short-cut may be to evaluate, within species, the relation between longevity (thus, until the moment that they were cut) and growth rate for the large trees that were sampled. In temperate forest, a negative relation between growth and longevity has been shown (Black *et al.*, 2008; Bigler & Veblen, 2009). This would mean that slow-growing trees live longer, which could be an indication for the occurrence of sampling bias I. To obtain insight in possible effects of sampling biases, simulating tree populations with different degrees of size-dependent mortality may help.

### The use of tree rings in forest management issues

To reach a sustainable logging system, data on ages and long-term growth rates of tropical trees are required. Ideally, these growth data should represent the 'lifetime' growth trajectory of a tree, i.e. its growth patterns up to reaching harvestable size. Most growth data from permanent sample plots however, span a very short timespan compared to the lifespan of a tropical tree (cf. Condit, 1995). Tree-ring analysis provides a means to reconstruct growth rates over the entire lifespan of a tree, and the large advantage of this method is that growth rates of the 'successful' trees can be obtained (cf. Chapter 2).

Tree-ring analysis showed that ages at reaching the minimum cutting diameter (MCD) were often high. For example, *Pterocarpus angolensis* needed on average more than 100 years to reach the minimum cutting diameter of 35 cm in various sites in deciduous woodlands in tropical southern Africa (Stahle *et al.*, 1999; Therrell *et al.*, 2007). In Cameroon, *Triplochiton scleroxylon* needed on average 80 years to reach 80 cm (Worbes *et al.*, 2003). In Central Amazonian white-water floodplain forests large variation in ages at the MCD was observed among commercial tree species: low-wood density species reached the MCD of 50 cm in an average of 15-67 years, while high-wood density species needed on average 106-151 years (Schöngart, 2008). Also in moist forests in the Bolivian Amazon, the timespan needed to reach the MCD was long. Average ages at the MCD for five commercial tree species ranged from 61 to 179 years (Brienen & Zuidema, 2006b, Chapter 5). However, one should take into account that within species ages at the MCD may differ strongly across forest types (da Fonseca *et al.*, 2009). *Tabebuia barbata* attained the MCD of 50 cm on average in 117 years in nutrient-rich Amazonian white-water floodplain forest (varzeá), while it took on average 270 years in nutrient-poor black-water floodplain forest (igapó). Similar variation was found for *Vatairea guianensis*: 70 and 162 years to reach the MCD in the várzea and the igapó, respectively (da Fonseca *et al.,* 2009). Thus, management criteria should not be defined only per species, but the forest type should also be taken into account.

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

These studies did not take variation in growth among individual trees into account. Within a species ages at the MCD vary strongly among trees (e.g. Brienen & Zuidema, 2006b; Therrell *et al.*, 2007; Chapter 5). The incorporation of growth variation among and within individual trees may strongly influence the results. Brienen and Zuidema (2006b) applied tree-ring analysis to reconstruct growth rates over the entire lifespan of trees to determine the variation in ages among trees at the moment of attaining the minimum cutting diameter. The observed strength of autocorrelation was incorporated in growth simulation models to be able to simulate tree growth with the same degree of growth variation (cf. Brienen *et al.*, 2006). Harvestable volume for a second cutting cycle in 20 years was much higher, 36-50% of the harvestable volume at initial harvest, when realistic variation in growth was included for four commercial tree species. Nevertheless, recuperated timber volume at second harvest was low, 18-24% of the volume harvested at the initial harvest (Brienen & Zuidema, 2007).

The use of long-term growth data from 'successful' trees, in combination with the inclusion of realistic levels of growth variation, probably provides the most accurate estimations of future timber yield. As most slow-growing trees will not make it to the canopy (Chapter 2, Landis & Peart, 2005), average growth rates obtained from trees of all sizes in permanent sample plots likely underestimate long-term growth of trees that eventually reach harvestable sizes (cf. Sheil, 1995a). In the past, some researchers already recognized this pattern and applied above-average growth rates from permanent sample plot data to estimate timber yield for future harvests (Condit *et al.*, 1995a). Not known is, however, if the use of plot data indeed underestimates timber yield, and, if so, what percentage of the faster-growers should be included in growth projections. To determine the magnitude of this effect growth of trees to harvestable size ('commercial ingrowth') based on growth projections between two types of growth data were contrasted: long-term tree-ring data from harvestable trees ('lifetime growth data') and the last ten years of growth of extant trees over the entire size range ('plot-type growth data') for three tropical tree species (Chapter 5). The latter data type is a proxy for growth data from permanent sample plots. Based on these two types of data tree growth simulations were performed for two scenarios: a second harvest in 20, and in 40 years. A realistic degree of growth autocorrelation was incorporated in the growth projections, for both the lifetime and the plot-type growth data.

Commercial ingrowth was larger when using lifetime growth data than for plot-type growth data for two of the three species. Thus, the faster juvenile growth of trees that reached harvestable size indeed resulted in higher projections of timber yield. In spite of the positive effect of higher juvenile growth on projected timber yield, our simulations showed that the recuperation of timber volume was low. Using lifetime growth data, only 20-33% of the timber volume harvested at the first harvest could be obtained at second harvest after 20 years. For a second harvest after 40 years this was 26-46%.

Based on our results we recommend the use of above-average growth rates in timber yield projections that apply permanent plot data. To determine which percentage of faster-growers should be used in such simulations, it is important that similar analyses are conducted for more species.

## Outlook

Over the last few years, the number of studies in tropical dendroecology rapidly increased and a large step forward was made. The field is clearly and rapidly developing with applications to many important and topical themes: forest ecology, climate change, management and forest succession. Now, all these themes have been addressed in a small set of tropical dendroecology studies. So far, most researchers focused on the reconstruction of historical growth patterns using tree-ring data and the use of these data in growth modelling. More emphasis should be put on unravelling the causes of growth patterns. It is of great importance to reach better understanding of responses of tropical trees to climatic change. First, tree-ring data should be combined with measurements of stable isotopes (e.g. McCarroll & Loader, 2004; Hietz *et al.*, 2005), to unravel the drivers of a historical growth increase. In addition, long-term temporal growth changes should be investigated for more species in different forest types as responses may differ. For instance, also a decrease in growth has been found in some permanent sample plot studies (Feeley *et al.*, 2007c), and tree growth has been found to decrease with increasing temperature (Clark *et al.*, 2003; Clark *et al.*, 2009). Second, the effect of long-term changes in light conditions on tree growth should be quantified to improve the methods for the reconstruction of historical forest dynamics. For instance, through determining species-specific relations between light level and growth rate, threshold values can be established for the detection of suppressions and releases in tree-ring data (cf. Baker & Bunyavejchewin, 2006). Moreover, the effect of tree size should be taken into account.

Tree-ring analysis can strongly contribute to improving our understanding of long-term ecological processes in tropical forests. When combining the above-mentioned approaches, we may gain more insight into the historical development of tropical forests and the mechanisms shaping their dynamics. In the end, this knowledge is much needed in assessing the response of tropical forests to the predicted climate changes in the future.

## ACKNOWLEDGEMENTS

I would like to thank Pieter Zuidema for comments on an earlier version of this chapter.

# RESUMEN EJECUTIVO

## CONTEXTO

### Anillos de crecimiento en el trópico

En el trópico, la formación de anillos anuales de crecimiento ha sido discutida por mucho tiempo (e.g. Lieberman *et al.*, 1985a). La ausencia de anillos anuales de crecimiento ha sido atribuida a la falta de estaciones claramente marcadas. Sin embargo, ya en 1927 se hicieron descripciones de la ocurrencia de anillos anuales de crecimiento en árboles tropicales (Coster 1927; 1928). La formación de anillos anuales en bosques tropicales puede ocurrir en áreas donde los árboles experimentan, anualmente, condiciones ambientales no-favorables que inducen períodos de dormancia del tejido cambial. Por ejemplo, los árboles forman anillos de crecimiento en bosques secos o subhúmedos donde una época seca por año induce dormancia cambial (e.g. Worbes, 1999). También en bosques inundables y en manglares, inundaciones anuales pueden resultar en la formación de anillos anuales (e.g. Schöngart *et al.*, 2002; Dezzeo *et al.*, 2003; Verheyden *et al.*, 2004). Los bosques tropicales secos y los bosques inundables representan gran parte de los trópicos. Por lo tanto, a partir del análisis de anillos de crecimiento de especies de árboles tropicales se pueden esperar contribuciones importantes sobre su crecimiento y ecología.

Los anillos de crecimiento de especies de árboles tropicales son con frecuencia menos distinguibles que en especies de bosques templados, y pueden presentar diversas complicaciones. Fluctuaciones climáticas pueden resultar en la formación de anillos falsos (Priya & Bhat, 1998), redes de anillos (Worbes, 2002) y anillos que carecen de periodicidad anual (Dünisch *et al.*, 2003; Wils *et al.*, 2009; Boninsegna *et al.*, 1989). Por todo lo anterior, es necesario demostrar la naturaleza anual de los anillos de crecimiento. Por ejemplo, mediante el conteo de los anillos de árboles de plantaciones de edad conocida (e.g. Dünisch *et al.*, 2002), por medio del fechado con el análisis del C14 (e.g. Worbes & Junk, 1989; Fichtler *et al.*, 2003), a través del conteo de anillos de crecimiento formados después de haber hecho una herida en el tejido cambial (e.g. Nobuchi *et al.*, 1995; Lisi *et al.*, 2008) o mediante correlaciones entre crecimiento y precipitación anual (e.g. Trouet *et al.*, 2006). En la actualidad, anillos de crecimiento anuales se han confirmado para un número creciente de especies en muchas áreas en el trópico (Baas & Vetter, 1989; Eckstein *et al.*, 1995; Worbes, 2002).

Recientemente, el potencial del análisis de los anillos de crecimiento para responder a preguntas ecológicas que requieren datos de crecimiento a largo plazo empezó a ser explorado. En las últimas décadas, la necesidad de datos confiables sobre las edades y tasas de crecimiento ha sido claramente expresada (Ashton, 1981; Bormann & Berlyn, 1981). Inicialmente, los datos de anillos de crecimiento solo se utilizaron para estudiar la relación entre el crecimiento de árboles y los factores climáticos. Diferentes especies de árboles mostraron diferentes respuestas a la precipitación (e.g. Enquist & Leffler, 2001; Brienen & Zuidema, 2005). El Niño - Oscilación del Sur, parece tener influencia en el crecimiento de los árboles (Schöngart *et al.*, 2004; Brienen *et al.*, 2009b). Segundo, el campo de dendroecología tropical se empezó a desarrollar. El análisis de los anillos de crecimiento es un método directo para determinar la edad de árboles tropicales (Martínez-Ramos & Alvarez-Buylla, 1998;

Worbes & Junk, 1999) y de las tasas de crecimiento durante toda la vida de los mismos. Estos datos de crecimiento fueron utilizados para describir las trayectorias de crecimiento de los árboles al dosel (Baker & Bunyavejchewin, 2006; Brienen & Zuidema, 2006a) y una combinación con otros métodos para estimar edades fue aplicada para reconstruir la historia y la dinámica de un bosque seco estacional en Tailandia (Baker *et al.*, 2005). Recientemente, el análisis de anillos de crecimiento ha sido aplicado también en estudios sobre el manejo sostenible de bosques tropicales (e.g. Brienen & Zuidema, 2006b; Schöngart, 2008). En esta tesis utilizo el análisis de los anillos de crecimiento para responder a preguntas en la ecología de árboles tropicales que requieren datos de crecimiento a largo plazo.

### El camino al dosel

Los bosques tropicales son ecosistemas con una alta diversidad en donde especies arbóreas de diferente historia de vida coexisten. La cantidad de luz es a menudo un factor limitante del crecimiento de los árboles. Solamente 1-2% del total de luz llega al sotobosque (Chazdon & Fetcher, 1984). La apertura de claros en el dosel ocasionada por la caída de árboles aumenta temporalmente la disponibilidad de luz en el sotobosque, resultando en variación espacial y temporal de las condiciones de luz (Canham *et al.*, 1990). Adicionalmente, como la disponibilidad de luz aumenta con la altura en el bosque, existe un fuerte gradiente vertical de luz. Las especies arbóreas ocupan diferentes nichos en el rango de condiciones de luz desde la oscuridad del sotobosque hasta las condiciones de alta luz en claros (Denslow, 1980; Poorter & Arets, 2003). Tradicionalmente, las especies fueron clasificadas como especies pioneras - especies de crecimiento rápido limitadas a crecer en claros, o como especies tolerantes a la sombra - especies de crecimiento lento que completan su ciclo de vida en el sotobosque (Whitmore, 1998). Turner (2001) propuso una clasificación más amplia basada en los requerimientos de luz para regeneración y altura máxima. En la categoría de especies de árboles del dosel generalmente se distinguen especies que regeneran en el sotobosque y en claros (cf. Poorter *et al.*, 2006). Por consiguiente, diferencias en tolerancia a la sombra también pueden ser encontradas entre especies del dosel. Para evaluar estas diferencias se analizó la relación entre altura y posición de la copa de datos estáticos (de parcelas permanentes), como una aproximación del patrón típico de crecimiento al dosel de una especie (Poorter *et al.*, 2005; Sheil *et al.*, 2006).

Para árboles de especies del dosel, es de mayor importancia alcanzar el dosel, para asegurarse la disponibilidad de luz y la posibilidad de reproducirse. En la actualidad, pocos estudios han escrito trayectorias actuales de crecimiento de árboles tropicales al dosel, ya que estos patrones de crecimiento a largo plazo no pueden ser derivados de tasas de crecimiento obtenidas de parcelas permanentes de muestreo. Las parcelas permanentes generalmente no cubren más de 30 años (cf. Clark, 2007), que es un período corto relativo a la duración de vida de un árbol. Por esta razón, trayectorias de crecimiento al dosel fueron estudiadas por medio de proyecciones de crecimiento en base de datos de parcelas permanentes (e.g. Clark & Clark, 1992; Clark & Clark, 2001). Un enfoque más apropiado es la reconstrucción de patrones históricos de crecimiento de árboles individuales mediante la aplicación del análisis de anillos de crecimiento. De esta manera, períodos prolongados de crecimiento lento (‘supresiones’) y períodos prolongados de crecimiento rápido (‘liberaciones’) pueden ser detectados. La presencia de supresiones y liberaciones generalmente se ha atribuido a cambios en los niveles de luz a consecuencia de la apertura y el cierre de claros en el dosel (Nowacki & Abrams, 1997). Recientemente, patrones de crecimiento al dosel de árboles tropicales también fueron reconstruidos por medio del análisis de anillos de crecimiento (Baker & Bunyavejchewin, 2006; Brienen & Zuidema, 2006a). Especies de árboles del dosel difirieron en patrones de crecimiento hasta llegar al dosel, probablemente a causa de diferencias de tolerancia a la sombra entre las especies. Árboles de la mayoría de las especies requirieron en alguna etapa de su desarrollo la presencia de un claro para garantizar el acceso al dosel (Baker & Bunyavejchewin, 2006; Brienen & Zuidema, 2006a). La edad a la que árboles de la misma especie alcanzaron el dosel difirió fuertemente. Por lo tanto, las tasas de crecimiento mostraron una gran variación entre árboles individuales, probablemente causada por gran variación espacial y temporal en condiciones de crecimiento (Brienen & Zuidema, 2006a).

Esta variación tan grande entre árboles también ha sido observada entre árboles juveniles en el bosque (Clark & Clark, 1992), aunque la mayoría de los juveniles tiene el crecimiento suprimido y muestra tasas de crecimiento muy bajas. Una pregunta clave es: ¿Cuáles de estos árboles llegan al dosel? Árboles que crecen lento tienen un riesgo acumulativo de mortalidad más alto (Terborgh *et al.*, 1997; Wyckoff & Clark, 2002), porque necesitan más tiempo para alcanzar el dosel. Esto tendría como consecuencia que solamente se espera que juveniles de alto crecimiento lleguen al dosel (‘efecto de selección juvenil’). Esta hipótesis ha sido planteada frecuentemente (e.g. Enright & Hartshorn, 1981; Swaine *et al.*, 1987), pero no ha sido evaluada para árboles tropicales. Comparando tasas de crecimiento de árboles juveniles en este momento en el bosque con tasas históricas de crecimiento de árboles ‘exitosos’ del dosel cuando eran juveniles, la existencia de un efecto de selección juvenil puede ser evaluada. Landis y Peart (2005) mostraron un efecto de selección juvenil para tres especies de un bosque templado mediante el análisis de los anillos de crecimiento. En esta tesis evalúo si ocurre el efecto de selección juvenil con un enfoque parecido (Capítulo 2).

La mayoría de los estudios sobre crecimiento de árboles tropicales se han enfocado en el crecimiento en diámetro. Estudiando patrones temporales de crecimiento, se asume que el crecimiento en altura muestra patrones similares. La relación estática entre altura y diámetro fue utilizada para comparar patrones de inversión en crecimiento en diámetro y altura entre especies diferentes (e.g. O’Brien *et al.*, 1995; Osunkoya *et al.*, 2007). En la actualidad, un solo estudio evaluó patrones de crecimiento hasta el dosel utilizando datos de crecimiento en altura a largo plazo (16 años; Clark & Clark, 2001), aunque crecimiento en altura es de mayor importancia para llegar al dosel.

En bosques templados se han encontrado fluctuaciones en la inversión en crecimiento en altura relativo al crecimiento en diámetro (e.g. Zenner, 2008). Árboles con crecimiento suprimido crecieron relativamente más en diámetro que en altura (Niklas, 1995; Naidu *et al.*, 1998) y se mostró una relación negativa entre crecimiento en diámetro y altura (Sumida *et al.*, 1997). Coomes y Grubb (1998) evaluaron la relación entre diámetro y altura para juveniles de especies de árboles tropicales utilizando mediciones de crecimiento a corto plazo. Se encontró alta variación en la relación entre diámetro y altura, aunque no hubo diferencias en esta relación entre juveniles que estaban creciendo en claros y en el sotobosque. La falta de diferencias se atribuyó a la historia desconocida del crecimiento de los juveniles (Coomes & Grubb, 1998). Se puede reconstruir también crecimiento en altura a largo plazo utilizando los anillos de crecimiento, porque solamente en la base del tronco se presentan todos los anillos. Por el conteo de los anillos en discos colectados a diferentes alturas en el tronco de un árbol, se puede determinar el tiempo requerido para crecer en largo entre dos discos del tronco (cf. Gutsell & Johnson, 2002). En el capítulo 4 se reconstruye el crecimiento en diámetro, altura y volumen del tronco a largo plazo para tres especies de árboles tropicales.

### Los bosques tropicales están cambiando

Una cantidad creciente de evidencia de parcelas permanentes sugiere que los bosques tropicales están cambiando. La biomasa arriba del suelo (Baker *et al.*, 2004), el crecimiento de los árboles (Laurance *et al.*, 2004b; Phillips *et al.*, 2008) y el recambio de los árboles (Phillips & Gentry, 1994; Lewis *et al.*, 2004b; Phillips *et al.*, 2004) incrementaron en toda la Amazonía durante las últimas décadas. Adicionalmente, se observaron algunos cambios en la composición de especies en los bosques: especies de crecimiento rápido (Laurance *et al.*, 2004b) y lianas se hicieron más abundantes (Phillips *et al.*, 2002). La causa de estos cambios se ha discutido intensivamente (Chambers & Silver, 2004; Lewis *et al.*, 2004a; Wright, 2005; Lewis *et al.*, 2006). El aumento de $CO_2$ en la atmósfera ha sido sugerido como una causa probable de estos cambios (e.g. Lewis *et al.*, 2004a). El aumento en la concentración de $CO_2$ podría estimular el crecimiento, lo que resulta en un aumento en el área basal al nivel de bosque y en el reclutamiento. De la misma manera la densidad de árboles y mortalidad aumentan, lo que significa que ocurre una aceleración en el recambio de los árboles y, por lo tanto, en la dinámica del bosque (Lewis *et al.*, 2004a; Phillips *et al.*, 2008). Sin embargo, otros opinan que por la inclusión de parcelas permanentes en bosques en diferentes estadios de sucesión, el aumento de biomasa podría resultar de las diferencias entre los bosques (Feeley *et al.*, 2007a; Chave *et al.*, 2008; Fisher *et al.*, 2008; pero ver Gloor *et al.*, 2009). Asimismo, el aumento en el crecimiento ha sido cuestionado, porque hay evidencia para tasas reducidas de crecimiento también (Feeley *et al.*, 2007c).

Revelar las causas de estos cambios es de gran importancia, porque los bosques tropicales tienen un papel importante en el ciclo global de carbono (Malhi *et al.*, 2008), y una dinámica acelerada podría causar un cambio desde funcionar como depósito de carbono, a convertirse en una fuente de carbono (cf. Körner, 2004; Phillips *et al.*, 2009). El primer asunto a evaluar es si árboles tropicales individualmente responden al aumento en la concentración de $CO_2$ de la atmósfera. Enriquecimiento artificial de carbono resultó en crecimiento más alto de plántulas de árboles tropicales *in situ* (Würth *et al.*, 1998). Sin embargo, el $CO_2$ atmosférico ha estado aumentando desde la Revolución Industrial, con un aumento fuerte desde 1950 (IPCC, 2007). Se desconoce si los árboles tropicales han respondido a este incremento gradual del $CO_2$, y si árboles de todos los tamaños han tenido una respuesta a este incremento. Para responder a esta pregunta se requieren datos de crecimiento de árboles tropicales a largo plazo. Lloyd y Farquhar (2008) mostraron con un modelo fisiológico que una respuesta es probable para árboles tropicales, sobre todo para árboles que crecen en condiciones de luz baja.

En bosques templados se han llevado a cabo más investigaciones sobre la respuesta de árboles al aumento en la concentración de $CO_2$. Para evaluar la respuesta de los árboles se aplicó el análisis de anillos de crecimiento, lo que facilita la reconstrucción del crecimiento de toda la vida del árbol. Los árboles en bosques templados mostraron un aumento evidente en el crecimiento en los últimos 150 años (e.g. Rolland *et al.*, 1998; Voelker *et al.*, 2006). Corrigiendo para la edad del árbol y comparando la respuesta de árboles pequeños y grandes, se encontró un aumento más notable en el crecimiento de árboles pequeños (Voelker *et al.*, 2006; Wang *et al.*, 2006). Por medio de los anillos de crecimiento se pueden analizar los cambios históricos en el crecimiento de los árboles también en el trópico. En el capítulo 2 exploro cambios a largo plazo en el crecimiento de cinco especies de árboles tropicales.

Adicionalmente, se puede aplicar la medición de los anillos de crecimiento para reconstruir la historia de la dinámica del bosque (cf. Baker *et al.*, 2005). Como un aumento en el recambio de los árboles significa un incremento en la frecuencia de caídas de árboles, y la formación de claros. Podría ser posible observar la formación de claros como períodos de liberación en las series de anillos de los árboles demás. Si el recambio aumentó en el tiempo, se puede esperar mayor frecuencia de liberaciones en el pasado reciente que el pasado lejano. Este tema se explora en el capítulo 3.

## ¿Manejo forestal sostenible?

Para definir criterios para llegar a una industria maderera sostenible de especies de árboles tropicales, se necesitan datos de crecimiento. Sin embargo, datos de crecimiento obtenidos de parcelas permanentes podrán resultar en una subestimación de la futura cosecha de madera. La mayoría de los árboles de crecimiento lento no llegan al dosel y no sobreviven hasta tamaño aprovechable (Landis & Peart, 2005), por eso tasas más altas de crecimiento pueden resultar en estimaciones más sólidas (cf. Condit *et al.*, 1995a). Datos de crecimiento sobre toda la vida de árboles aprovechables, obtenidos por la medición de los anillos de crecimiento, fueron utilizados para evaluar la recuperación del volumen aprovechable de madera después de la primera cosecha (Brienen & Zuidema, 2006b; Brienen & Zuidema, 2007). La ventaja de ese método es que se utilizan tasas de crecimiento de árboles que alcanzaron tamaño aprovechable, y que se incluye la variación temporal del crecimiento en las simulaciones. La inclusión de la autocorrelación en simulaciones de crecimiento resulta en estimaciones más altas, y probablemente más confiables, del volumen de madera que se puede cosechar en el futuro (Miina, 1993; Brienen & Zuidema, 2006b; Brienen & Zuidema, 2007). Todavía se desconoce si la recuperación del volumen maderable es subestimada cuando se utilizan datos de crecimiento obtenidos de parcelas permanentes. Este asunto se evalúa en el capítulo 5.

### Esta tesis

En este estudio colecté datos de anillos de crecimiento de árboles en todo el rango de tamaños de cinco especies de árboles tropicales. Estos datos fueron utilizados para investigar los patrones de crecimiento de árboles tropicales a largo plazo. Primero, la existencia del 'efecto de selección juvenil' fue evaluada con las consecuencias de esto en la proyección del volumen maderable en el futuro. Segundo, evalué los cambios en el tiempo del crecimiento de los árboles y la dinámica del bosque. Finalmente, reconstruí el crecimiento en volumen de juveniles de tres especies de árboles tropicales, para estudiar inversiones en crecimiento en diámetro y altura a largo plazo.

### Específicamente, los objetivos de esta tesis fueron:

- Determinar si solamente árboles juveniles con crecimiento rápido llegan al dosel.
- Evaluar si las tasas de crecimiento juvenil han aumentado en el tiempo.
- Evaluar cambios en la presencia de liberaciones, la frecuencia de liberaciones y el grado de autocorrelación en el crecimiento dentro del árbol en el tiempo.
- Evaluar la relación entre crecimiento en diámetro, altura y volumen del tronco para árboles juveniles tropicales.
- Determinar si existe una relación negativa entre crecimiento en diámetro y altura.
- Analizar las consecuencias de incluir juveniles de crecimiento rápido en la recuperación del volumen maderable en la segunda cosecha.
- Cuantificar el porcentaje del volumen cosechado que se ha recuperado al momento de la segunda cosecha.

## REVISIÓN BIBLIOGRÁFICA Y RESUMEN DE LOS RESULTADOS

### El camino al dosel

La existencia del efecto de selección juvenil fue evaluada mediante el análisis de los anillos de crecimiento para cinco especies de árboles tropicales (Capítulo 2). Las tasas de crecimiento juvenil fueron obtenidas de árboles de todo el rango de tamaños de las especies, expresadas en promedios para categorías estrechas de tamaño y luego relacionadas al diámetro del mismo árbol (tamaño existente). De esa manera, las tasas de crecimiento de juveniles existentes pudieron ser comparadas con las de los árboles del dosel, cuando eran juveniles del mismo tamaño (Capítulo 2). Para tres de las cinco especies encontramos que las tasas de crecimiento juvenil aumentaron con el tamaño existente del árbol, lo que implica que árboles que actualmente están el dosel tuvieron tasas más altas de crecimiento juvenil que los juveniles existentes. Para las especies tolerantes a la sombra, *Clarisia* y *Peltogyne*, solo en la clase diamétrica de 0-1 cm se encontró esta indicación de un efecto de selección juvenil. Sin embargo, en la especie pionera de larga vida *Cedrelinga* el efecto fue mayor, porque ocurrió hasta un diámetro de 30 cm. Por lo tanto, para estas tres especies un crecimiento juvenil rápido podría ser esencial para llegar al dosel, concordante con los resultados para tres especies de bosques templados (Landis & Peart, 2005). Estos resultados tienen probablemente implicaciones en la proyección de edades y los modelos de dinámica de poblaciones de árboles. Las cuales se discuten en los siguientes párrafos.

¿Cómo llegan los árboles tropicales al dosel? Trayectorias de crecimiento de árboles del dosel han sido reconstruidas, mediante el análisis de anillos de crecimiento, para responder a esta pregunta (Baker & Bunyavejchewin, 2006; Brienen & Zuidema, 2006a). A pesar de que un efecto de selección juvenil podría haber tenido un efecto, se encontró una gran variación en la manera en la que los árboles crecen al dosel, entre especies y dentro de la misma especie (Brienen & Zuidema, 2006a; Baker & Bunyavejchewin, 2006). Varios investigadores hipotetizaron que árboles juveniles de especies que ocurren en el dosel requerirían por lo menos un claro para poder llegar al dosel (e.g. Turner, 2001). Brienen y Zuidema (2006a) encontraron que árboles de cuatro especies no-pioneras pasan por un promedio de 0.8-1.4 liberaciones antes de llegar al dosel. Las especies difirieron en los patrones de crecimiento hasta el dosel, lo que sugiere que las cuatro especies no-pioneras difieren en tolerancia a la sombra (Brienen & Zuidema, 2006a). Asimismo, Baker y Bunyavejchewin (2006) encontraron grandes diferencias en patrones de crecimiento al dosel entre especies en un bosque estacional tropical en Tailandia. La especie más intolerante a la sombra, *Melia azederach*, alcanzó el dosel mostrando un crecimiento rápido constantemente, mientras árboles de la especie tolerante a la sombra *Neolitsea obtusifolia* se establecieron en condiciones de luz generalmente baja y mostraron la presencia de una (o ninguna) liberación para llegar al dosel (Baker & Bunyavejchewin, 2006). En la actualidad, solamente dos estudios han reconstruido los patrones de crecimiento durante toda la vida de árboles tropicales, por lo tanto patrones generales en estrategias de crecimiento al dosel aun no se conocen. Patrones de crecimiento difirieron fuertemente entre especies, lo que fue mostrado para nueve especies de árboles tropicales en total (Baker & Bunyavejchewin, 2006; Brienen & Zuidema, 2006a). Adicionalmente, patrones de crecimiento de la misma especie podrían variar entre tipos de bosques. La aplicación del análisis de anillos de crecimiento podría tener un importante rol en la revelación de estos patrones de crecimiento.

## RECONSTRUCCIÓN DEL CRECIMIENTO EN VOLUMEN DE ÁRBOLES JUVENILES TROPICALES

El crecimiento en volumen, altura y diámetro difirió fuertemente entre individuos de la misma altura, probablemente como consecuencia de las diferencias en las condiciones del crecimiento entre los árboles. Diferencias en crecimiento entre árboles persistieron en clases de altura, y en el tiempo, aunque las diferencias en crecimiento en diámetro y altura entre los árboles no fueron tan persistentes en el tiempo. Por consiguiente, cambios en la inversión en crecimiento, altura y diámetro ocurrieron en el tiempo, mientras el crecimiento total en volumen se mantuvo invaríale (Capítulo 4). Crecimiento en diámetro y altura no fueron correlacionados en ninguna de las clases de altura. Aunque estos no fueron directamente relacionados, los resultados podrían ser consistentes con una relación negativa entre crecimiento en altura y diámetro. Una de las razones para no haber encontrado relaciones negativas o positivas puede deberse a la gran variación en el crecimiento, entre árboles dentro de una clase de altura. Van Noordwijk y de Jong (1986) sugirieron que si la cantidad total de recursos que pueden ser invertidos varía entre individuos, correlaciones positivas en vez de negativas podrían ser observadas. Por lo tanto, si diferencias en el crecimiento en volumen entre árboles son grandes, correlaciones negativas podrían desaparecer o cambiar a una correlación positiva entre crecimiento en diámetro y altura (cf. van Noordwijk & de Jong, 1986). Por eso, decidimos evaluar la relación entre crecimiento en volumen y altura, en vez de relacionar crecimiento en diámetro y altura directamente. Encontramos correlaciones negativas entre crecimiento en volumen y altura para árboles pequeños de las tres especies. Eso significa que árboles que crecieron rápidamente en volumen invirtieron relativamente menos en crecimiento en altura en comparación con árboles de crecimiento lento de la misma especie. Este resultado sugiere que árboles que crecen en condiciones favorables (en términos de luz) invierten relativamente más en estabilidad y desarrollo de la copa que en crecimiento en altura (Capítulo 4).

En conclusión, la reconstrucción del crecimiento en volumen a largo plazo dio información importante sobre los patrones de crecimiento de árboles juveniles tropicales. Sin embargo, para obtener un mejor conocimiento de los patrones de crecimiento en biomasa se necesitarían datos sobre la densidad de la madera. Se asume que la densidad de madera no varía dentro de un árbol, y entre individuos de una especie. Sin embargo, un incremento radial en densidad de madera fue observada para árboles tropicales: para seis especies de árboles de un bosque seco estacional en Tailandia la densidad de madera aumentó con la distancia de la médula (Nock *et al.*, 2009). Idealmente, se integrarían crecimiento en altura, diámetro, volumen y biomasa de árboles juveniles aplicando el análisis de los anillos de crecimiento y mediciones de la densidad de la madera para realizar la reconstrucción completa de crecimiento en biomasa y obtener mejor entendimiento de trayectorias de crecimiento al dosel de árboles tropicales.

## EDADES DE ÁRBOLES TROPICALES

El descubrimiento de árboles más de 1000 años de edad por medio del fechado de $^{14}$C (Chambers *et al.*, 1998), resultó en un debate intenso sobre la precisión de diferentes métodos de estimación de edades y la ocurrencia actual de árboles tan viejos (cf. Martínez-Ramos & Alvarez-Buylla, 1998). Probablemente se exageró la importancia de árboles viejos para el ciclo de carbono, porque estos árboles ocurrieron en densidades muy bajas en el bosque (Martínez-Ramos & Alvarez-Buylla, 1998; Williamson *et al.*, 1999). El análisis de anillos de crecimiento es un método directo para determinar edades. Aunque también en otros estudios se encontraron algunos árboles muy viejos por medio del fechado de $^{14}$C (e.g. Kurokawa *et al.*, 2003), las edades obtenidas del conteo de los anillos de crecimiento fueron mucho más bajas (máxima de ~400-550 years; e.g. Worbes & Junk, 1999; Fichtler *et al.*, 2003; Brienen & Zuidema, 2006a).

La utilización de datos de crecimiento provenientes de parcelas permanentes también resultó en estimaciones muy altas, porque generalmente se utilizaron tasas promedios de crecimiento así asumiendo que todos los árboles llegarán al dosel finalmente (cf. Laurance *et al.*, 2004a). Estimaciones de edades obtenidas de modelos de crecimiento se pueden mejorar mucho al compararlas con edades observadas por medio del conteo de los anillos para los mismos árboles o para árboles de la misma especie (Brienen *et al.*, 2006; Chien, 2006; Baker, 2003). De esa manera, Baker (2003) desarrolló métodos para estimar edades de árboles tropicales de diferente tolerancia a la sombra a través de probarlos para especies de diferente tolerancia a la sombra en un bosque templado. Se compararon dos métodos para estimar edades: el método de la clase de copa y el de incremento anual periódico (IAP; cf. Condit *et al.*, 1993). El método de la clase de copa predice edades en base de la tasa promedio de crecimiento para árboles de cierta clase de copa, asumiendo que un árbol no cambia de clase de copa durante la ontogenia. Este método fue el más adecuado para especies intolerantes a la sombra. Regresión de IAP (cf. Condit *et al.*, 1993) utiliza el crecimiento promedio para todas las clases de tamaño, este método funcionó mejor para especies tolerantes a la sombra (Baker, 2003). Los métodos también resultaron adecuados para especies de árboles tropicales, aunque, sorprendentemente, el método de la clase de copa también resultó en estimaciones más exactas para especies tolerantes a la sombra (Baker *et al.*, 2005). En el método de la clase de copa, implícitamente, se utilizaron las tasas de crecimiento por encima del promedio. La aplicación del método de la clase de copa para especies intolerantes a la sombra está de acuerdo con, probablemente, un 'efecto de selección juvenil' – juveniles que crecen rápido tienen mayor probabilidad de alcanzar el dosel – más fuerte en estas especies (Capítulo 2). Recientemente, se presentó un nuevo método para estimar edades de árboles tropicales (Metcalf *et al.*, 2009). Este método mantiene la relación entre el nivel de luz y el crecimiento por la ontogenia, pero las estimaciones no fueron comparadas con edades obtenidas del conteo de anillos. Resultados de proyecciones de edades pueden ser mejorados por medio de la inclusión de autocorrelación en el crecimiento, lo que resulta en una mayor variación y una variación más realista de las edades de árboles (Brienen *et al.*, 2006).

El conteo de los anillos de crecimiento podría ser el método más exacto para determinar la edad de un árbol debido a que es un método directo (Martínez-Ramos & Alvarez-Buylla, 1998). Sin embargo, si un árbol crece lentamente, los anillos de crecimiento son más difíciles de distinguir y se podría subestimar la edad del árbol. Para evaluar la precisión de la determinación de la edad utilizando el conteo de los anillos, se puede aplicar el fechado de $^{14}C$ para árboles – o anillos – que tienen menos de cincuenta años a causa de las pruebas nucleares (Soliz-Gamboa *et al.*, submitted). Sin embargo, se requieren otros métodos para aquellos árboles que no forman anillos de crecimiento. El fechado del $^{14}C$ facilita la determinación de las edades con una precisión razonable para árboles de una edad encima de los 350 años, aunque es difícil estimar si un árbol tiene más de 350 años y otra desventaja es el error grande en el fechado (alrededor de 50 años; cf. Martínez-Ramos & Alvarez-Buylla, 1998). El desarrollo de métodos para proyectar edades en base a datos de crecimiento obtenidos de parcelas permanentes, con la verificación de la precisión del método de anillos de crecimiento en especies con anillos anuales confiables, tiene también un gran potencial.

## LA INCORPORACIÓN DE AUTOCORRELACIÓN EN MODELOS DE CRECIMIENTO DE ÁRBOLES

El crecimiento de árboles varía fuertemente, tanto entre individuos de árboles de una misma especie, como dentro del mismo árbol en el tiempo. Esta variación probablemente existe a causa de diferencias en las condiciones de crecimiento entre árboles y variación temporal en estas condiciones. En total, esta variación en condiciones de crecimiento podría resultar en una autocorrelación en el crecimiento, lo que significa que el crecimiento de un árbol en determinado año está relacionado con su crecimiento en el próximo año, o en el siguiente, etc. (Brienen *et al.*, 2006). En estudios de parcelas permanentes se observó una fuerte autocorrelación temporal (Kohyama & Hara, 1989; Kammesheidt *et al.,* 2003; Clark & Clark, 1992; Grogan & Landis, en prensa). Tradicionalmente, la autocorrelación ha sido negada en modelos de crecimiento o de proyección de edades de árboles tropicales, porque se han utilizado tasas promedios de crecimiento (Lieberman & Lieberman, 1985). Se han hecho algunos esfuerzos para incorporar la autocorrelación en los modelos para estimar edades (Bullock *et al.*, 2004; Kohyama *et al.*, 2005). Sin embargo, mejores estimaciones del grado de autocorrelación en el crecimiento pueden ser derivadas de datos de anillos de crecimiento. Como se pueden obtener tasas de crecimiento sobre toda la vida del árbol, los

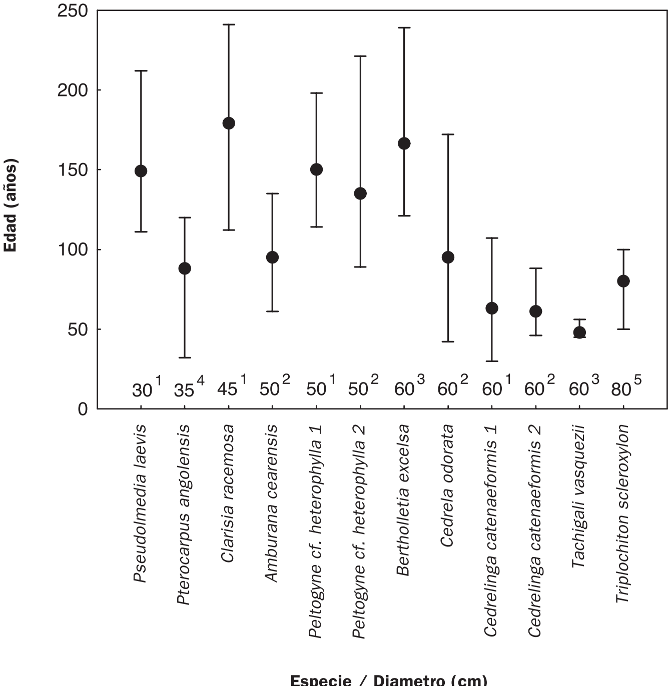


**Fig. 1** Promedio y rango de edades determinadas por medio del conteo de los anillos a cierto diámetro para varias especies de árboles. Los números indican el diámetro de los árboles, los índices superiores indican la fuente. [1]Este estudio, [2]Brienen y Zuidema (2006b), [3]Brienen y Zuidema (2006a), [4]Stahle *et al.* (1999), [5]Worbes *et al.* (2003).

patrones temporales en el crecimiento y la persistencia de diferencias en crecimiento entre árboles pueden ser evaluados en el tiempo (cf. Brienen *et al.*, 2006). El crecimiento mostró fuerte autocorrelación temporal y diferencias entre árboles persistieron por períodos prolongados. Eso significa que árboles que crecen rápido continúan creciendo rápido durante períodos prolongados y árboles de crecimiento lento siguen creciendo lento también por mucho tiempo. Esta autocorrelación en el crecimiento resulta en una variación grande entre árboles comparándolos al mismo tamaño (Fig. 1; Brienen *et al.*, 2006). Si un grado realista de autocorrelación fue incorporado en simulaciones de crecimiento, la variación en las estimaciones de edades se hizo mayor y las edades coincidieron con las obtenidas de datos de anillos de crecimiento (Brienen *et al.*, 2006).

En modelos de poblaciones, la variación en el crecimiento y la historia de crecimiento de individuos también ha sido negada. Por ejemplo, la mayoría de modelos de matrices para árboles no toman en cuenta la variación en el crecimiento entre individuos y en modelos de matrices estándares no se puede incluir crecimiento autocorrelacionado (Zuidema *et al.*, en prensa). Recientemente, Zuidema *et al.* (2009) aplicaron modelos de matrices en los cuales árboles de *Cedrela odorata* fueron clasificados en base de edad y tamaño, así la historia del crecimiento de los árboles fue explícitamente incluida. Luego evaluaron la contribución de los árboles de crecimiento rápido persistente al crecimiento de la población y encontraron que la contribución de árboles de crecimiento rápido fue mucho mayor que la de los árboles de crecimiento lento. Si, en general, árboles que crecen rápido tienen una mayor contribución a la tasa de crecimiento de la población, sería muy importante incorporar la autocorrelación en modelos de poblaciones. El análisis de anillos de crecimiento puede ser una herramienta valiosa para obtener información sobre el grado de autocorrelación, lo que luego puede ser incluido en modelos de matrices o modelos de proyección integral.

## ¿AUMENTÓ EL CRECIMIENTO EN EL TIEMPO?

En esta tesis apliqué el análisis de los anillos de crecimiento para determinar si el crecimiento de árboles tropicales ha aumentado en los últimos siglos (Capítulo 2). Como utilicé anillos de crecimiento, pude evaluar tales cambios sobre períodos de tiempo más largos en comparación con estudios previos que han utilizado datos de crecimiento de parcelas permanentes. Expresé tasas de crecimiento juvenil en clases diámetricas estrechas hasta un diámetro de 30 cm de árboles sobre todo el rango de tamaño existente, para cinco especies de árboles tropicales. De esta manera pude relacionar el crecimiento de árboles con el tiempo y evaluar si el crecimiento de árboles grandes en el pasado fue menor que el crecimiento reciente de árboles pequeños en la misma clase diámetrica ('aumento histórico del crecimiento'). Para cuatro especies encontramos un aumento histórico del crecimiento. En Cedrela un aumento histórico del crecimiento fue encontrado para juveniles de 10-15 cm diámetro, para *Clarisia* de 2-4 cm diámetro, para *Peltogyne* de 1-3 y 6-8 cm diámetro y para *Pseudolmedia* en las clases diamétricas de 2-8 cm.

Estos patrones de crecimiento observados en el tiempo tienen que ser cuidadosamente interpretados. Estos cambios en el crecimiento podrían ser (parcialmente) causados por sesgos en la colección de datos (Capítulo 2). Se razona de la manera siguiente: si se supone que árboles grandes se mueren a cierto diámetro, esto significa que la mortalidad depende del tamaño y que hay cierto diámetro máximo al que un árbol puede llegar. De esa manera, árboles que crecen rápidos de manera persistente, llegarán al diámetro máximo a una menor edad, y por eso se morirían a una menor edad, en comparación con árboles de crecimiento lento persistente. Si se colecta discos a cierto momento en el tiempo, los árboles grandes (y viejos) en el muestreo contendrán pocos árboles de crecimiento rápido, y relativamente un mayor número de árboles de la parte de la población que crece lento. Por lo tanto, en la reconstrucción de tasas históricas de crecimiento en base de los discos colectados, las tasas de crecimiento en el pasado lejano podrán parecer bajas aunque en realidad el crecimiento promedio de los árboles no ha cambiado en el tiempo (sesgo del muestreo I). Otro sesgo del muestreo podría ocurrir por el hecho que árboles juveniles de crecimiento lento todavía no han llegado al diámetro mínimo del muestreo. En este caso, esto podría resultar en una sobreestimación de tasas de crecimiento reciente, porque más de los árboles de baja edad pertenecen en la parte de la población que crece rápido (sesgo del muestreo II). En este momento es imposible determinar si estos sesgos del muestreo influenciaron los resultados presentados en el Capítulo 2. No obstante, es claro que si tales sesgos hubiesen ocurrido, también se habría esperado encontrar un aumento del crecimiento en el tiempo para árboles más grandes. No se puede retrazar del todo cierta influencia de estos sesgos del muestro, pero quisiera indicar que estos resultados están de acuerdo con una respuesta al aumento de la concentración de $CO_2$. También en bosques templados el aumento histórico del crecimiento fue mayor para árboles pequeños (Voelker *et al.*, 2006; Wang *et al.*, 2006).

## LA RECONSTRUCCIÓN DE LA DINÁMICA HISTÓRICA DE BOSQUES TROPICALES

“Si este es un bosque tropical virgen, ¿dónde están todos los árboles grandes?”. Hartshorn (1978) hizo esta pregunta en una publicación sobre el recambio del bosque en Costa Rica. El estudio mostró que el recambio del bosque fue bastante rápido, variando de 80 a 138 años en el área de La Selva en Costa Rica (Hartshorn, 1978). Resultados similares fueron obtenidos en un bosque tropical en la Guayana Francesa donde en torno al 0.64-1.33% del dosel fue abierto mediante la formación de claros anualmente (van der Meer & Bongers, 1996). Por ello, podríamos considerar que los bosques tropicales son dinámicos. En bosques templados el análisis de anillos de crecimiento fue aplicado ampliamente para reconstruir disturbios históricos y la dinámica histórica del bosque (Runkle, 1982; Lorimer & Frelich, 1989; Lusk & Smith, 1998). Estudiando patrones de crecimiento, en términos de liberaciones y supresiones y fechas de establecimiento de todos los árboles en cierta área, la historia de un bosque podría ser revelada. Ahora, como es posible aplicar el análisis de anillos de crecimiento en bosques tropicales también, métodos similares pueden ser aplicados para reconstruir la dinámica histórica del bosque. Sin embargo, generalmente no todas las especies forman anillos de naturaleza anual, por eso algunos ajustes podrían ser requeridos.

Algunos estudios en bosques tropicales aplicaron el análisis de anillos de crecimiento para evaluar la dinámica del bosque. Worbes *et al.* (2003) reconstruyeron la dinámica histórica de un bosque tropical seco en la República de Camerún en un área de una hectárea, determinando las tasas de crecimiento y edades de los árboles de casi todas las especies. Los árboles más grandes fueron de especies pioneras de larga vida. Generalmente, estos árboles fueron más viejos que los árboles de especies tolerantes a la sombra y casi no hubo reclutamiento de estas especies en el sotobosque. Especies tolerantes a la sombra, en cambio, tuvieron regeneración abundante. En total, el bosque fue clasificado como un bosque secundario tardío (Worbes *et al.*, 2003). Comparativamente, la dinámica histórica de un bosque tropical seco en Tailandia fue reconstruida (Baker *et al.*, 2005), utilizando la combinación del análisis de anillos de crecimiento y estimaciones de edades obtenidas de proyecciones de crecimiento (cf. Baker, 2003). La estructura del bosque mostró una cohorte de árboles en el dosel, distribuciones simuladas de edades mostraron que esta cohorte se estableció en los años 1800 y con un pico para las especies intolerantes a la sombra a mediados del siglo veinte. El análisis de anillos de crecimiento resultó en fechas más detalladas: hubieron picos en el establecimiento y crecimiento de árboles en los años 1910-1920, 1940-1950, y picos menores en los años tardíos de 1800 y de los años 1970. Series de anillos de crecimiento de los árboles más viejos (*Afzelia xylocarpa*) mostraron crecimiento elevado en los años de 1850. En conjunto, estos resultados indicaron que alrededor del 1850 ocurrió un disturbio de gran escala, seguido por algunos disturbios pequeños más recientes (Baker *et al.*, 2005). Estos resultados muestran que la estructura y dinámica de bosques tropicales pueden ser determinadas por la ocurrencia de disturbios a diferentes escalas espaciales. Aunque los estudios son pocos, las implicaciones de sus resultados pueden ser de largo alcance, puesto que muestran cómo la composición de especies y la estructura actual del bosque resultan de la dinámica transitoria y de los disturbios históricos.

El análisis de los anillos de crecimiento puede ser también una herramienta útil en el estudio de la sucesión de bosques secundarios. Generalmente, la sucesión de bosque secundario se estudia en cronosecuencias, en las que se sustituye el espacio por tiempo, mediante la comparación de bosques secundarios de edad diferente, pero conocida (e.g. van Breugel *et al.*, 2006; Selaya *et al.*, 2008). Worbes *et al.* (1992) determinaron las edades de bosques secundarios inundables mediante el conteo de los anillos de los árboles del mayor tamaño, pero no presentaron patrones de crecimiento. Del mismo modo, se ha presentado una estrategia para determinar edades de bosques secundarios en México mediante el análisis de los anillos de crecimiento (Brienen *et al.*, 2009a). La periodicidad anual de los anillos de crecimiento podría ser demostrada por la comparación entre el conteo de los anillos y la edad conocida del bosque secundario. Los conteos de los anillos correspondieron con las edades de los bosques. Sin embargo, en bosques más antiguos los árboles pioneros podrían haber desaparecidos ya, lo que podría resultar en errores en la reconstrucción de la dinámica del bosque. En algunos bosques, las especies pioneras y tolerantes a la sombra se establecieron al mismo tiempo, mientras que en otros, las especies tolerantes a la sombra se establecieron más tarde (Brienen *et al.*, 2009a).

Durante las últimas décadas, bosques tropicales se hicieron más dinámicos (Lewis *et al.*, 2004c; Phillips *et al.*, 2004). Sin embargo, para evaluar los patrones y las causas de la modificación del recambio de árboles, se requieren datos de crecimiento a un plazo más largo que los datos disponibles en parcelas permanentes. En el Capítulo 3 propusimos dos métodos para detectar evidencias para cambios en el recambio de árboles utilizando anillos de crecimiento de dos especies bolivianas no-pioneras. Primero, la sincronización de la presencia de liberaciones fue evaluada en el tiempo para identificar disturbios históricos a gran escala. Segundo, relacionamos la frecuencia de liberaciones con el tiempo, con el objetivo de determinar si la frecuencia de árboles con liberaciones aumentó en el tiempo. Finalmente, calculamos el grado de autocorrelación temporal, una medida que indica cambios temporales en tasas de crecimiento a causa de la dinámica del dosel (Brienen *et al.*, 2006). Asimismo, evaluamos si el grado de autocorrelación cambió a lo largo del tiempo. Como la frecuencia de liberaciones puede ser causada parcialmente por un aumento en el crecimiento durante la ontogenia, la frecuencia de liberaciones y grado de autocorrelación fueron analizados en base al crecimiento residual de la relación promedia entre el tamaño del árbol y su crecimiento.

No hubo un patrón claro en la ocurrencia de liberaciones para ambas especies, sin embargo observamos alguna variación en el porcentaje de árboles con una liberación sobre los 200-300 años pasados (Capítulo 3). Las liberaciones fueron detectadas en todos los períodos y no se observó una sincronización en el tiempo durante los últimos siglos. Por lo tanto, no hubo señales de un disturbio pasado a gran escala. En total, cambios en el grado de autocorrelación o la frecuencia de liberaciones en el tiempo no fueron observados durante los últimos 200-300 años para ambas especies. La excepción fue la primera clase de tamaño (un período de 20 años empezando a 0 cm diámetro), en la cual encontramos un aumento en la frecuencia de liberaciones en el tiempo. Esta relación puede deberse a la estructura de la base de datos o a un efecto restante de ontogenia. Debido al crecimiento rápido o lento de algunos individuos, las diferencias entre árboles a causa del efecto de la ontogenia pueden mantenerse, ya que se utilizó el crecimiento residual como la relación promedio entre tamaño y crecimiento. En general, no encontramos evidencias para un cambio en el recambio de árboles durante los últimos dos, incluso tres siglos (Capítulo 3). Los métodos propuestos pueden ser adecuados, sin embargo, las causas de los patrones de crecimiento deben seguir siendo estudiadas y el muestreo debería que ser reajustado.

## LA IMPORTANCIA DE REVELAR LA HISTORIA DE BOSQUES TROPICALES

Es necesario darse cuenta que el ‘estado’ actual de los bosques tropicales, en términos de estructura y dinámica, depende fuertemente de su historia. Por consiguiente, se debe tomar en cuenta la historia de los bosques tropicales para cuantificar cambios en la estructura y dinámica del bosque a lo largo del tiempo (Clark, 2007). Para una de las áreas de estudio de esta tesis, La Chonta, se encontraron evidencias de la ocupación de seres humanos alrededor de 300-400 años atrás: fueron encontrados restos de cerámica y se piensa que la composición de especies podría estar alterada (Paz-Rivera & Putz, 2009). Dichos patrones históricos podrían haber determinado las edades máximas de los árboles que encontramos en este momento. Para la especies incluida en este estudio, *Pseudolmedia laevis*, probablemente no hubo un efecto, ya encontramos una edad máxima de 262 años, y la mayoría de los árboles de >30 cm diámetro tenían entre 150 y 200 años. Adicionalmente, ya que se encontró un aumento histórico del crecimiento en algunas clases diámetricas (Capítulo 2), los árboles de mayor edad probablemente no se establecieron en condiciones de alta luz. Esto podría haber indicado que los árboles se establecieran después de un disturbio inducido por seres humanos.

Otro asunto importante a considerar es el efecto de la escala de tiempo en los patrones de la dinámica de poblaciones de árboles. La historia también puede tener un rol y es importante tomarla en consideración. No se puede derivar la dinámica poblacional de datos estáticos de la estructura de la población (Condit *et al.*, 1998; Feeley *et al.*, 2007b). No obstante, aunque no se pueden derivar patrones de regeneración de una especie de su estructura poblacional, en combinación con datos de anillos de crecimiento y aplicación cuidadosa de modelos de matrices se pueden hacer algunas evaluaciones (Couralet *et al.*, 2005). Generalmente, los valores de las tasas de vida a utilizar en modelos de matrices fueron basados en solamente pocos años de mediciones (e.g. Zuidema & Boot, 2002; Chien, 2006). La tasa de crecimiento de la población es muy dependiente de las tasas de vida, lo que podría resultar en crecimiento extremo o una disminución extrema de la población sobre el tiempo, por que estos varían fuertemente entre años.

En este estudio la dinámica histórica de la población tiene un rol en determinar si sesgos en el muestreo causaron el incremento histórico del crecimiento (cf. Capítulo 2). La pregunta que queda es si la mortalidad es dependiente de la edad, dependiente del tamaño o aleatoria. Para determinar si árboles de crecimiento rápido o lento desaparecieron de la población, se podrían evaluar las tasas de crecimiento de árboles muertos (cf. Henry & Swan, 1974; Dekker *et al.*, 2009). Otra opción podría ser la evaluación, dentro de una especie, de la relación entre la longevidad (hasta el momento que los árboles fueron cortados) y la edad para los árboles grandes en la base de datos. En bosques templados, una relación negativa entre el crecimiento y la longevidad fue mostrada (Black *et al.*, 2008; Bigler & Veblen, 2009). Esto significaría que los árboles de crecimiento lento viven más largos, lo que podría indicar la ocurrencia del sesgo en el muestro I. Para entender posibles efectos de sesgos en el muestreo, se necesita ejecutar simulaciones de poblaciones de árboles con diferentes grados de dependencia del tamaño en las tasas de mortalidad.

## LA APLICACIÓN DE ANILLOS DE CRECIMIENTO EN EL MANEJO FORESTAL

El análisis de anillos de crecimiento mostró que edades fueron altas al momento de llegar al diámetro mínimo de corta (DMC). Por ejemplo, *Pterocarpus angolensis*, necesitó un promedio de más que 100 años para llegar al diámetro mínimo de corta de 35 cm en varios sitios en bosques secos en la parte tropical del sur de Africa (Stahle *et al.*, 1999; Therrell *et al.*, 2007). En la República de Cámerun, *Triplochiton scleroxylon* necesitó un promedio de 80 años para llegar a un diámetro de 80 cm. En bosques inundables en la parte central de la Amazonía gran variación en edades al DMC fue observada entre especies de árboles comerciales: especies de baja densidad de madera llegaron al MDC de 50 cm en un promedio de 15-67 años, aunque especies de alta densidad de madera necesitaron un promedio de

106-151 años (Schöngart, 2008). También en bosques subhúmedos en la Amazonía Boliviana, el tiempo requerido para llegar al DMC fue largo. Edades promedias al DMC para cinco especies comerciales variaron de 61 hasta 179 años (Brienen & Zuidema, 2006b, Capítulo 5). Sin embargo, se debe tomar en cuenta que dentro de una especies las edades pueden diferir mucho entre tipos de bosques (da Fonseca *et al.*, 2009). *Tabebuia barbata* llegó el DMC de 50 cm en un promedio de 117 años en un bosque inundable de alta concentración de nutrientes (varzeá), mientras en un bosque inundable de baja concentración de nutrientes (igapó) la misma especie necesitó un promedio de 270 años para llegar al dosel. Variación similar fue encontrada para *Vatairea guianensis*, 70 y 162 años para llegar al DMC, en la várzea y el igapó, respectivamente (da Fonseca *et al.*, 2009). Por eso, criterios para el manejo no deberían ser definidos solamente por especie, sino también se necesita tomar en cuenta el tipo de bosque.

Aunque las edades la diámetro mínimo de corta dan una idea de las tasas de crecimiento a largo plazo y, así, del tiempo requerido para la recuperación del volumen maderable, se requieren proyecciones de crecimiento. Para determinar el DMC adecuado y el largo del ciclo de corta para sostener el volumen aprovechable de madera, generalmente se calculó el promedio de las trayectorias de crecimiento de árboles para obtener el patrón típico de crecimiento de una especie (Schöngart *et al.*, 2007; Schöngart, 2008). En la várzea el DMC estimado varió de 47-70 cm para especies de diferente tolerancia a la sombra, tal como el largo estimado del ciclo de corta varió de 3-32 años (Schöngart, 2008; da Fonseca *et al.*, 2009). Estos resultados ilustran que se necesitan criterios específicos para el manejo de cada especie.

Sin embargo, estos estudios no tomaron la variación en crecimiento entre árboles en cuenta. Dentro de una especies las edades al DMC variaron entre árboles (e.g. Brienen & Zuidema, 2006b; Therrell *et al.*, 2007; Capítulo 5). La incorporación de variación en el crecimiento entre y dentro de indiviuos de árboles podría tener influencia en los resultados. Brienen and Zuidema (2006b) aplicaron el análisis de anillos de crecimiento para reconstruir tasas de crecimiento sobre toda la vida de los árboles para determinar la variación en edades entre árboles al llegar al DMC. El grado observado de autocorrelación fue incorporado en modelos de simulación del crecimiento para poder simular el crecimiento de árboles incluyendo el mismo grado de autocorrelación (cf. Brienen *et al.*, 2006).

El volumen aprovechable para la segunda cosecha después de 20 años fue mucho más alto, 36-50% del volumen aprovechable en la cosecha inicial, cuando un grado realista de variación en el crecimiento fue incluido para cuatro especies comerciales. Sin embargo, el volumen recuperado en la segunda cosecha fue baja, 18-24% del volumen aprovechable inicial (Brienen & Zuidema, 2007).

Por lo tanto, utilizar tasas de crecimiento a largo plazo de árboles que alcanzaron el dosel, en combinación con un grado realista de autocorrelación incluido, resulta probablemente en las estimaciones más exactas del volumen aprovechable en el futuro. Como la mayoría de los árboles de crecimiento lento no llega al dosel (Capítulo 2, Landis & Peart, 2005), tasas promedias de crecimiento de árboles de todos los tamaños podrían resultar en una subestimación del crecimiento de los árboles que llegan al diámetro mínimo de corta (cf.

Sheil, 1995a). En el pasado, algunos investigadores ya reconocieron este fenómeno y aplicaron tasas de crecimiento de encima del promedio de datos de parcelas permanentes para estimar el volumen aprovechable en futuras cosechas (Condit *et al.*, 1995a). Se desconoce si la aplicación de datos de crecimiento de parcelas permanentes subestima la recuperación del volumen aprovechable, y de ser así, que porcentaje de los árboles que crecen más rápido tendría que ser incluido. Para determinar la magnitud de este efecto el crecimiento de árboles menores del diámetro mínimo de corta hasta llegar diámetro mínimo de corta fue proyectado. Dos tipos de datos fueron comparados: datos de crecimiento provenientes de anillos de crecimiento sobre toda la vida de árboles aprovechables y el crecimiento de los últimos diez años de árboles existentes del todo el rango de tamaños para tres especies de árboles tropicales (Capítulo 5). El último tipo de datos es una aproximación para datos de crecimiento provenientes de parcelas permanentes. En base de estos dos tipos de datos simulaciones de crecimiento fueron ejecutadas para dos escenarios: una segunda cosecha después de 20, y una después de 40 años. Un grado realista de autocorrelación fue incorporado en las simulaciones para ambos tipos de datos de crecimiento.

El volumen aprovechable de árboles que alcanzaron el diámetro mínimo de corta fue mayor utilizando datos de crecimiento sobre toda la vida de árboles aprovechables que para los últimos diez años de crecimiento de árboles de todos los tamaños para dos de las tres especies. De hecho, el crecimiento juvenil más rápido de los árboles que llegaron al tamaño aprovechable resultó en proyecciones más altas de volumen aprovechable. A pesar del efecto positivo de crecimiento juvenil rápido en el volumen aprovechable proyectado, nuestras proyecciones mostraron que la recuperación del volumen maderable fue baja. Utilizando datos de crecimiento sobre toda la vida de árboles aprovechables, solamente 20-33% del volumen aprovechado en la primera cosecha se pude aprovechar después de 20 años. Similarmente, se pude aprovechar 26-46% en una segunda cosecha después de 40 años.

En base a nuestros resultados recomendamos utilizar tasas de crecimiento encima del promedio en proyecciones basadas en datos de crecimiento provenientes de parcelas permanentes. Para determinar que porcentaje de los árboles de rápido crecimiento se debería utilizar en aquellas simulaciones, es importante ejecutar análisis similares para más especies.

## DIRECCIONES FUTURAS

En los últimos años el número de estudios en el campo de dendroecología tropical aumentó rápidamente y se hizo un gran paso adelante. El campo está desarrollándose rápidamente con muchas aplicaciones en varios temas importantes: la ecología de bosques, el cambio climático, el manejo forestal y el proceso de la sucesión de los bosques. Actualmente, todos de estos temas han sido tocados en algunos estudios de dendroecología tropical. La mayoría de los investigadores se concentró en la reconstrucción de patrones históricos de crecimiento en base de datos de anillos de crecimiento y la aplicación de estos datos en modelos de crecimiento. Sin embargo, se necesita un mayor esfuerzo en revelar los factores que causan los patrones de crecimiento. Es de gran importancia llegar a mejor entendimiento sobre las respuestas de árboles tropicales al cambio climático. Primero, se tendría que combinar datos de anillos de crecimiento con mediciones de isótopos estables (e.g. McCarroll & Loader, 2004; Hietz *et al.*, 2005), para revelar las causas del aumento histórico del crecimiento. Adicionalmente, cambios en el crecimiento en el tiempo a largo plazo necesitan a ser investigados para más especies en diferentes tipos de bosque, ya que las respuestas podrían variar. También se encontró una reducción del crecimiento en el tiempo en algunos estudios de parcelas permanentes (Feeley *et al.*, 2007c), y el crecimiento de árboles podría disminuir con un aumento de la temperatura (Clark *et al.*, 2003; Clark *et al.*, 2009). Segundo, el efecto de cambios a largo plazo en condiciones de luz tendría que ser cuantificado para mejorar los métodos de reconstruir la dinámica histórica del bosque. Por ejemplo, determinando la relación específica entre el nivel de luz y la tasa de crecimiento por especie, se puede establecer líneas directrices para la detección de supresiones y liberaciones en datos de anillos de crecimiento (cf. Baker & Bunyavejchewin, 2006). Además se necesita tomar en cuenta el efecto del tamaño del árbol.

El análisis de anillos de crecimiento puede contribuir significativamente al entendimiento sobre procesos ecológicos a largo plazo en los bosques tropicales. Cuando se combinan los métodos indicados arriba, podríamos adquirir mayor comprensión del desarrollo histórico de los bosques tropicales y los mecanismos que determinan su dinámica. Al final, este conocimiento es muy importante en estimar la respuesta de los bosques tropicales a los cambios climáticos predichos para el futuro.

## AGRADECIMIENTOS

Gracias a Pieter Zuidema por los comentarios en el texto original en inglés. La versión en español fue corregida por Claudia Soliz-Gamboa y Maria Paula Balcázar.

# SAMENVATTING

## ACHTERGROND

Lang heeft men gedacht dat tropische bomen geen jaarringen vormden, omdat sterke seizoensverschillen in de tropen over het algemeen ontbreken. Toch vormen veel bomen jaarringen in gebieden waar jaarlijks de groeiomstandigheden gedurende een bepaalde periode minder geschikt zijn. Jaarringen komen voor in gebieden met één uitgesproken droog seizoen per jaar en in overstromingsbossen waar hoge waterniveaus tijdens één bepaalde tijd van het jaar de boomgroei onderdrukken. Dit betekent dat ook in de tropen jaarringmetingen een belangrijke bijdrage aan ons inzicht in boomgroei en bosecologie kunnen leveren. In deze dissertatie wordt jaarringanalyse toegepast om ecologische vragen op te lossen die alleen met groeigegevens over een lange tijdsperiode beantwoord kunnen worden.

In vijf tropische boomsoorten in Bolivia heb ik jaarringen van bomen van allerlei groottes gemeten. Deze gegevens heb ik gebruikt om groeipatronen over lange tijdsperioden te bekijken. Ten eerste heb ik onderzocht of alleen snelgroeiende jonge bomen het kronendak halen en wat voor gevolgen dit heeft voor het voorspellen van de toekomstige houtopbrengst. Ten tweede heb ik onderzocht of er aanwijzingen voor veranderingen in de groeisnelheden van tropische bomen en in bosdynamiek over de tijd waren. Daarnaast heb ik de investeringspatronen in hoogte- en diametergroei van jonge bomen bekeken door de groei in stamvolume over het hele leven van de boom met behulp van zijn jaarringen te reconstrueren.

## WELKE BOMEN HALEN HET KRONENDAK?

Voor tropische bomen is het van groot belang om het kronendak te bereiken en zich op die manier te verzekeren van de beschikbaarheid van voldoende licht en de mogelijkheid om zich voort te planten. In het onderbos groeien de meeste jonge bomen echter langzaam door gebrek aan licht. De vraag is dan welke jonge bomen uiteindelijk overleven en het kronendak halen. Langzaam groeiende bomen bouwen over een langere tijd een mortaliteitsrisico op en hebben, doordat ze langere tijd in het onderbos doorbrengen, ook een hogere kans op beschadiging door vallende takken en bomen. Dit zou kunnen betekenen dat alleen snelgroeiende jonge bomen uiteindelijk het kronendak bereiken. In deze dissertatie wordt deze hypothese voor het eerst op een directe manier getoetst voor tropische bomen. Groeigegevens uit permanente plots beslaan vaak niet meer dan enkele decennia. Het meten van de jaarringen geeft echter wel de mogelijkheid het hele groeitraject van een boom naar het kronendak te beschrijven. Met jaarringen is het mogelijk om te evalueren of alleen de snelle groeiers het kronendak halen: het schept de mogelijkheid om groeisnelheden van de jonge bomen van nu te vergelijken met de groeisnelheden van bomen in het kronendak op het moment dat ze nog jong waren.

Voor drie van de vijf soorten nam de juveniele groeisnelheid toe met de grootte van de boom op dit moment. Dit geeft aan dat de grote bomen van nu hard groeiden toen ze jong waren vergeleken met de jonge bomen van nu. Dit effect was het sterkst voor een lichtminnende boomsoort, hoewel twee schaduwtolerante soorten, hetzij minder sterk, het ook lieten zien. Dit bevestigt dat alleen snelgroeiende jonge bomen in staat zijn het kronendak te halen en dit is eerder ook al voor bomen in gematigde bossen gevonden. Dit heeft gevolgen voor de methoden die gebruikt worden voor het schatten van leeftijden van tropische bomen en voor het modelleren van hun populatiedynamica. Sommige onderzoekers verwachtten dit effect al en gebruikten alleen de groeigegevens van de sneller groeiende bomen om houtvolumes te berekenen en leeftijden van bomen te schatten.

## HET GEBRUIK VAN JAARRINGEN VOOR DE RECONSTRUCTIE VAN GROEI IN STAMVOLUME

In de meeste studies over de groei van tropische bomen beperkte men zich tot het meten van diametergroei, omdat het moeilijker is om de hoogtegroei van grotere bomen nauwkeurig te meten. Door alleen de diametergroei te meten, neemt men indirect aan dat de hoogtegroei van een boom met de diametergroei correspondeert. Om investeringen in hoogte- en diametergroei tussen soorten te vergelijken werden per boomsoort vaste relaties tussen hoogte en diameter bepaald. Door de jaarringen van een boom te meten kan echter ook de hoogtegroei gereconstrueerd worden. Aan de basis van de boom zijn alle ringen aanwezig. Door de jaarringen te tellen op verschillende hoogten in de boom kan de tijd, die een boom nodig heeft om door de hoogte-intervallen heen te groeien, bepaald worden. Groei in zowel stamvolume, hoogte, als diameter varieerde sterk tussen bomen van dezelfde hoogte, wat waarschijnlijk door verschillende groeiomstandigheden veroorzaakt wordt. Verschillen in volumegroei tussen bomen hielden stand over verscheidene klassen in boomhoogte en dus over lange tijd, terwijl dit voor diameter- en hoogtegroei in mindere mate zo was. Dit betekent dat volumegroei niet veel varieerde over de tijd, maar dat bomen wel de mate van investeren in hoogte- en diametergroei over de tijd kunnen variëren. Er was geen relatie tussen hoogte- en diametergroei in de verschillende hoogteklassen. Dit zou een gevolg van grote verschillen in groeiomstandigheden tussen de bomen kunnen zijn. Wel werd er voor kleine bomen een negatieve relatie tussen volumegroei en hoogtegroei gevonden. Boompjes die snel in volume groeiden, groeiden relatief veel in de dikte, terwijl langzaam groeiende boompjes meer in de hoogte groeiden. Deze resultaten suggereren dat boompjes die hard groeien, en dus onder goede omstandigheden staan, relatief meer in stevigheid en ontwikkeling van de kroon investeren, dan in hoogtegroei.

## VERANDERINGEN IN TROPISCHE BOSSEN

Tropische bossen zijn aan het veranderen. Groeigegevens uit permanente proefvlakken laten zien dat over de afgelopen decennia groei, bovengrondse biomassa en bosdynamiek in tropische bossen zijn toegenomen. Nog steeds is er een stevig debat gaande over de oorzaak van deze veranderingen. Gesuggereerd wordt dat deze veranderingen het gevolg zijn van klimaatsverandering, en wel de toename in de $CO_2$-concentratie in de atmosfeer, hoewel anderen menen dat deze veranderingen het gevolg zijn van het feit dat deze proefvlakken in bossen in verschillende stadia van successie zijn uitgezet. Het is van groot belang om de oorzaken van deze veranderingen in kaart te brengen, omdat tropische bossen een belangrijke rol in de wereldwijde koolstofcyclus spelen. Een eerste vraag is of individuele, tropische bomen reageren op de verhoging van de $CO_2$-concentratie in de atmosfeer in de afgelopen 150 jaar. Jaarringgegevens kunnen helpen om te bepalen of er over de afgelopen 150 jaar een historische groeitoename heeft plaatsgevonden. Naast het reconstrueren van historische boomgroei, kunnen jaarringen ook gebruikt worden om een idee van de bosdynamiek in het verleden te krijgen. Een toename in bosdynamiek betekent dat er meer openingen in het kronendak gevormd worden doordat bomen omvallen. In de jaarringmetingen kunnen deze gebeurtenissen als een tijdelijke, sterke toename in groei teruggevonden worden. Als er over de tijd een toename in het aantal bomen met dit soort groeispurts wordt gevonden, zouden we dat als een aanwijzing voor een toename in bosdynamiek kunnen beschouwen.

Om te bepalen of groeisnelheden met het verloop van de tijd zijn toegenomen, vergeleek ik de huidige groei van jonge bomen met de groeisnelheden van oude bomen toen ze nog jong waren. Dit werd gedaan door groeisnelheden in smalle diameterklassen in te delen en binnen deze diameterklassen groei aan tijd te relateren. Voor vier van de vijf soorten werd er voor kleine bomen een historische groeitoename gevonden. Deze groeitoename moet voorzichtig geïnterpreteerd worden, omdat deze ook (gedeeltelijk) door de structuur van de dataset veroorzaakt kan zijn. De redenering gaat als volgt: stel dat grote bomen doodgaan bij het bereiken van een zekere maximumdiameter, dat mortaliteit dus grootteafhankelijk is. In dat geval zullen de bomen die snel groeien en dit over lange tijd volhouden, op een jongere leeftijd doodgaan dan de bomen die langzaam groeien. Als er dan op een zeker moment schijven van bomen verzameld worden, dan zijn de snelle groeiers al doodgegaan en worden er alleen relatief langzame groeiers meegenomen. Verder terug in de tijd zullen de gemeten groeisnelheden dan relatief laag zijn. Daarnaast kan het zijn dat, als er vanaf een bepaalde minimumdiameter bomen meegenomen worden, de langzamere groeiers deze minimumdiameter op het moment dat de schijven verzameld worden nog niet gehaald hebben. Dit zou dan betekenen dat de recentere groei op de snelst groeiende bomen gebaseerd is. Eén van deze effecten, of de combinatie van beide, kan betekenen dat we een groeitoename met de tijd waarnemen, terwijl in werkelijkheid de groeisnelheden niet veranderd zijn. Hoewel deze effecten een rol gespeeld kunnen hebben, zijn deze waarschijnlijk niet de bepalende factoren geweest. In dat geval zouden we ook een groeitoename met de tijd voor grotere bomen verwachten. Dit betekent dat de resultaten met de veronderstelde stimulering van de groei door de verhoogde $CO_2$-concentratie in overeenstemming zijn. Ook in gematigde bossen is er een sterkere groeitoename voor kleine bomen gevonden.

Ik presenteer twee methoden om veranderingen in bosdynamiek met het verloop van tijd te bestuderen. Een toename in bosdynamiek met de tijd houdt in dat er relatief meer openingen in het kronendak gevormd worden. De vorming van een opening in het kronendak door bijvoorbeeld het omvallen van een boom, betekent dat er tijdelijk meer licht voor de overgebleven bomen beschikbaar is. Deze bomen kunnen daardoor gedurende een periode harder groeien. Eerst ben ik nagegaan of er in het verleden een grootschalige verstoring had plaatsgevonden, door te bepalen of er in een bepaalde tijdsperiode relatief veel bomen groeispurts vertoonden. In dat geval zou er een verandering in bosdynamiek waargenomen kunnen worden doordat het bos herstellende is van een verstoring. Daarna heb ik het voorkomen van groeispurts bij een bepaalde boomgrootte met de tijd bekeken, door zowel de jonge als de oude bomen te evalueren. Als tweede methode berekende ik de sterkte van autocorrelatie in groei en bepaalde hiervoor ook of er veranderingen met de tijd plaatsvonden. Autocorrelatie in groei betekent dat de groei in een jaar sterk overeenkomt met de groei in het volgende jaar. De sterkte van de autocorrelatie in groei geeft een idee over veranderingen in de mate van geslotenheid van het kronendak over die tijdsperiode. Het voorkomen van groeispurts en de sterkte van de autocorrelatie kunnen gedeeltelijk door de toename in groei met toenemende boomgrootte veroorzaakt worden. Om deze reden heb ik de groeisnelheden gecorrigeerd voor de gemiddelde relatie tussen boomgrootte en groeisnelheid.

Er was geen duidelijk patroon in de tijd in het voorkomen van groeispurts, dus was er geen aanwijzing voor een grootschalige verstoring. Over het algemeen heb ik geen veranderingen over de tijd in het voorkomen van groeispurts en de sterkte van autocorrelatie gevonden. Alleen voor de kleinste grootteklasse (een periode van twintig jaar startend bij een diameter van 0 cm) werd er een toename in het aantal bomen met groeispurts over de tijd gevonden. Deze toename is waarschijnlijk toch nog toe te schrijven aan een overgebleven effect van de toename in groei met de boomgrootte. Ik gecorrigeerde met de gemiddelde relatie, maar van boom tot boom zal de sterkte van de toename verschillen. Dus vond ik geen aanwijzing voor een verandering in bosdynamiek over de afgelopen 200-300 jaar. De gepresenteerde methoden zouden een bijdrage aan het bestuderen van dergelijke veranderingen kunnen leveren, maar de oorzaken achter de groeipatronen moeten uitgezocht worden.

## IS HOUTKAP DUURZAAM?

Kennis over groeisnelheden van tropische bomen is ook nodig om tot richtlijnen voor duurzame houtkap te komen. Groeisnelheden uit permanente proefvlakken kunnen tot een onderschatting van de toekomstige houtopbrengst leiden, omdat de meeste langzaam groeiende jonge bomen het kronendak niet halen. Het gebruik van groeisnelheden over het hele leven van bomen die wel de minimale grootte bereiken om gekapt te kunnen worden, leidt waarschijnlijk tot betrouwbaardere schattingen. Het is nog niet bekend of de hergroei van het houtvolume na de eerste oogst inderdaad wordt onderschat wanneer groeisnelheden van bomen uit permanente proefvlakken gebruikt worden. Om de grootte van dit effect te bepalen, heb ik groeisimulaties op basis van ringgegevens van grote bomen en een maat voor groeigegevens uit permanente proefvlakken vergeleken. De laatste tien ringbreedtes, die overeenkomen met de laatste tien jaar groei, van bomen van allerlei groottes gebruikte ik als een benadering voor groeisnelheden uit permanente proefvlakken. Op basis van deze twee soorten groeigegevens heb ik groeisimulaties uitgevoerd om het houtvolume te bepalen dat in de tweede kapcyclus, na 20 of 40 jaar, geoogst kan worden. Ik heb een realistische mate van autocorrelatie in groei in de simulatiemodellen ingebouwd. Wanneer ringgegevens van grote bomen werden gebruikt, vond ik voor twee van de drie boomsoorten een groter houtvolume bestaand uit kleine bomen die in 20 of 40 jaar oogstbare grootte bereiken. Dus de relatief snelle groei van oogstbare bomen toen ze jong waren leverde inderdaad hogere schattingen van het te oogsten houtvolume in de toekomst op. Ondanks de hogere schattingen gebaseerd op ringgegevens van grote bomen, was de schatting van de totale houtopbrengst in de tweede kapcyclus laag. Voor een tweede oogst 20 jaar na kap was dit 20-33% van het houtvolume dat in de eerste kap geoogst werd. Zelfs voor een tweede kap, die pas na 40 jaar zou worden uitgevoerd, waren de percentages laag: slechts 26-46% voor de drie boomsoorten.

Naar aanleiding van de resultaten kan ik inderdaad aanbevelen om in groeimodellen bovengemiddelde groeisnelheden te gebruiken. Het is belangrijk om een dergelijke vergelijking voor meer boomsoorten te maken om aanbevelingen te kunnen doen over het exacte percentage van de snellere groeiers dat in simulaties gebruikt zou moeten worden.

## TOEKOMSTPERSPECTIEF

Tot nu toe was het onderzoek in de tropische dendro-ecologie voornamelijk gericht op het reconstrueren van historische groeipatronen door het meten van jaarringen en het gebruik van deze gegevens in groeimodellen. Er zou een grotere nadruk op het verklaren van de oorzaken van de waargenomen groeipatronen moeten worden gelegd. Stabiele isotopen ($^{14}$C en $^{18}$O) zouden gebruikt kunnen worden om meer inzicht in de factoren die boomgroei beïnvloeden te krijgen. Daarnaast is het belangrijk om na te gaan wat de reactie van een boom op veranderingen in de hoeveelheid licht is en of dit inderdaad sterke veranderingen in groei veroorzaakt. Op deze manier kunnen methodes voor het reconstrueren van bosdynamiek verbeterd worden.

Het bestuderen van jaarringen van tropische bomen kan een grote bijdrage leveren aan het inzicht in de werking van ecologische processen op de lange termijn in tropische bossen. Wanneer er meer bekend wordt over de oorzaken van de geobserveerde groeipatronen, krijgen we meer inzicht in de historische ontwikkeling van tropische bossen en in de verschillende mechanismen die de bosdynamiek bepalen. Deze kennis is hard nodig om te kunnen voorspellen hoe tropische bossen op de toekomstige klimaatsveranderingen zullen reageren.

# REFERENCES

**Aiba M, Nakashizuka T. 2007.** Differences in the dry-mass cost of sapling vertical growth among 56 woody species co-occurring in a Bornean tropical rain forest. *Functional Ecology* **21:** 41-49.

**Arets EJMM. 2005.** *Long-term responses of populations and communities of trees to selective logging in tropical rain forests in Guyana.* PhD thesis, Utrecht University, Utrecht, the Netherlands. Tropenbos-Guyana series 13, Tropenbos-Guyana Programme, Tropenbos International, the Netherlands.

**Ashton PS. 1981.** The need for information regarding tree age and growth in tropical forests. In: Bormann FH, Berlyn G, eds. *Age and growth rate of tropical trees; new directions for research.* Yale University: School of Forestry and Environmental Studies. Bulletin No. 94, 3-6.

**Baas P, Vetter RE. 1989.** Growth rings in tropical trees. *IAWA Bulletin* **10:** 95-174.

**Baker PJ. 2003.** Tree age estimation for the tropics: a test from the southern Appalachians. *Ecological Applications* **13:** 1718-1732.

**Baker PJ, Bunyavejchewin S. 2006.** Suppression, release and canopy recruitment in five tree species from a seasonal tropical forest in western Thailand. *Journal of Tropical Ecology* **22:** 521-529.

**Baker PJ, Bunyavejchewin S, Oliver CD, Ashton PS. 2005.** Disturbance history and historical stand dynamics of a seasonal tropical forest in western Thailand. *Ecological Monographs* **75:** 317-343.

**Baker TR, Burslem DFRP, Swaine MD. 2003.** Associations between tree growth, soil fertility and water availability at and regional scales in Ghanian tropical rain forest. *Journal of Tropical Ecology* **19:** 109-125.

**Baker TR, Phillips OL, Malhi Y, Almeida S, Arroyo L, Di Fiore A, Erwin T, Higuchi N, Killeen TJ, Laurance SG, Laurance WF, Lewis SL, Monteagudo A, Neill DA, Vargas PN, Pitman NCA, Silva JNM, Martínez RV. 2004.** Increasing biomass in Amazonian forest plots. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **359:** 353-365.

**Bebber DP, Thomas SC, Cole WG, Balsillie D. 2004.** Diameter increment in mature eastern white pine *Pinus strobus* L. following partial harvest of old-growth stands in Ontario, Canada. *Trees-Structure and Function* **18:** 29-34.

**Bevilacqua E, Puttock D, Blake TJ, Burgess D. 2005.** Long-term differential stem growth responses in mature eastern white pine following release from competition. *Canadian Journal of Forest Research* **35:** 511-520.

**Bigler C, Veblen TT. 2009.** Increased early growth rates decrease longevities of conifers in subalpine forests. *Oikos* **118:** 1130-1138.

**Black BA, Abrams MD. 2003.** Use of boundary-line growth patterns as a basis for dendroecological release criteria. *Ecological Applications* **13:** 1733-1749.

**Black BA, Abrams MD, Rentch JS, Gould PJ. 2009.** Properties of boundary-line release criteria in North American tree species. *Annals of Forest Science* **66**.

**Black BA, Colbert JJ, Pederson N. 2008.** Relationships between radial growth rates and lifespan within North American tree species. *Ecoscience* **15:** 349-357.

**Bongers F, Sterck FJ. 1998.** Architecture and development in rain forest trees: responses to light variation. In: Newbery MD, Prins HHT, Brown ND, eds. *Dynamics of tropical communities.* Oxford: Blackwell Scientific Press, 125-162.

**Boninsegna JA, Villalba R, Amarilla L, Ocampo J. 1989.** Studies on tree rings, growth-rates and age-size relationships of tropical tree species in Misiones, Argentina. *IAWA Bulletin* **10:** 161-169.

**Bonser SP, Aarssen LW. 1994.** Plastic allometry in young sugar maple (*Acer saccharum*): adaptive responses to light availability. *American Journal of Botany* **81:** 400-406.

**Bormann FH, Berlyn G. 1981.** *Age and growth rate of tropical trees: new directions for research.* New Haven: Yale University: School of Forestry and Environmental Studies. Bulletin No. 94.

**Bouriaud O, Breda N, Dupouey JL, Granier A. 2005.** Is ring width a reliable proxy for stem-biomass increment? A case study in European beech. *Canadian Journal of Forest Research* **35:** 2920-2933.

**Brienen RJW, Lebrija-Trejos E, van Breugel M, Peréz-García EA, Bongers F, Meave JA, Martínez-Ramos M. 2009a.** The potential of tree rings for the study of forest succession in southern Mexico. *Biotropica* **41:** 186-195.

**Brienen RJW, Lebrija-Trejos E, Zuidema PA, Martínez-Ramos M. 2009b.** Climate-growth analysis for a Mexican dry forest tree shows strong impact of sea surface temperatures and predicts future growth declines. *Global Change Biology.* doi: 10.1111/j.1365-2486.2009.02059.x

**Brienen RJW, Zuidema PA. 2005.** Relating tree growth to rainfall in Bolivian rain forests: a test for six species using tree ring analysis. *Oecologia* **146:** 1-12.

**Brienen RJW, Zuidema PA. 2006a.** Lifetime growth patterns and ages of Bolivian rain forest trees obtained by tree ring analysis. *Journal of Ecology* **94:** 481-493.

**Brienen RJW, Zuidema PA. 2006b.** The use of tree rings in tropical forest management: projecting timber yields of four Bolivian tree species. *Forest Ecology and Management* **226:** 256-267.

**Brienen RJW, Zuidema PA. 2007.** Incorporating persistent tree growth differences increases estimates of tropical timber yield. *Frontiers in Ecology and the Environment* **5:** 302-306.

**Brienen RJW, Zuidema PA, During HJ. 2006.** Autocorrelated growth of tropical forest trees: unraveling patterns and quantifying consequences. *Forest Ecology and Management* **237:** 179-190.

**Bullock SH, Turner RM, Hastings JR, Escoto-Rodríguez M, Lopez ZRA, Rodríguez-Navarro JL. 2004.** Variance of size-age curves: bootstrapping with autocorrelation. *Ecology* **85:** 2114-2117.

**Canham CD, Denslow JS, Platt WJ, Runkle JR, Spies TA, White PS. 1990.** Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Canadian Journal of Forest Research* **20:** 620-631.

**Carmean WH. 1972.** Site index curves for upland oaks in the Central States. *Forest Science* **18:** 102-120.

**Chambers JQ, Higuchi N, Schimel JP. 1998.** Ancient trees in Amazonia. *Nature* **39:** 135-136.

**Chambers JQ, Silver WL. 2004.** Some aspects of ecophysiological and biogeochemical responses of tropical forests to atmospheric change. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **359:** 463-476.

**Chave J, Andalo C, Brown S, Cairns MA, Chambers JQ, Eamus D, Folster H, Fromard F, Higuchi N, Kira T, Lescure JP, Nelson BW, Ogawa H, Puig H, Riera B, Yamakura T. 2005.** Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* **145:** 87-99.

**Chave J, Condit R, Muller-Landau HC, Thomas SC, Ashton PS, Bunyavejchewin S, Co LL, Dattaraja HS, Davies SJ, Esufali S, Ewango CEN, Feeley KJ, Foster RB, Gunatilleke N, Gunatilleke S, Hall P, Hart TB, Hernandez C, Hubbell SP, Itoh A, Kiratiprayoon S, LaFrankie JV, de Lao SL, Makana JR, Noor MNS, Kassim AR, Samper C, Sukumar R, Suresh HS, Tan S, Thompson J, Tongco MDC, Valencia R, Vallejo M, Villa G, Yamakura T, Zimmerman JK, Losos EC. 2008.** Assessing evidence for a pervasive alteration in tropical tree communities. *PLOS Biology* **6:** 455-462.

**Chave J, Muller-Landau HC, Baker TR, Easdale TA, Ter Steege H, Webb CO. 2006.** Regional and phylogenetic variation of wood density across 2456 neotropical tree species. *Ecological Applications* **16:** 2356-2367.

**Chazdon RL, Fetcher N. 1984.** Light environments of tropical forests. In: Medina E, Mooney HA, Vasques-Yanes C, eds. *Physiological ecology of plants of the wet tropics.* W. Junk, The Hague, The Netherlands, 27-36.

**Chien PD. 2006.** *Demography of threatened tree species in Vietnam.* PhD-thesis, Utrecht University.

**Clark DA. 2007.** Detecting tropical forests' responses to global climatic and atmospheric change: Current challenges and a way forward. *Biotropica* **39:** 4-19.

**Clark DA, Clark DB. 1992.** Life-history diversity of canopy and emergent trees in a neotropical rain-forest. *Ecological Monographs* **62:** 315-344.

**Clark DA, Clark DB. 1999.** Assessing the growth of tropical rain forest trees: Issues for forest modeling and management. *Ecological Applications* **9:** 981-997.

**Clark DA, Clark DB. 2001.** Getting to the canopy: Tree height growth in a neotropical rain forest. *Ecology* **82:** 1460-1472.

**Clark DA, Piper SC, Keeling CD, Clark DB. 2003.** Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984-2000. *Proceedings of the National Academy of Sciences of the United States of America* **100:** 5852-5857.

**Clark DB, Clark DA. 1991.** The impact of physical damage on canopy tree regeneration in tropical rain-forest. *Journal of Ecology* **79:** 447-457.

**Clark DB, Clark DA, Oberbauer SF. 2009.** Annual wood production in a tropical rain forest in NE Costa Rica linked to climatic variation but not to increasing $CO_2$. *Global Change Biology.* doi: 10.1111/j.1365-2486.2009.02004.x

**Claveau Y, Messier C, Comeau PG, Coates KD. 2002.** Growth and crown morphological responses of boreal conifer seedlings and saplings with contrasting shade tolerance to a gradient of light and height. *Canadian Journal of Forest Research* **32:** 458-468.

**Collet C, Chenost C. 2006.** Using competition and light estimates to predict diameter and height growth of naturally regenerated beech seedlings growing under changing canopy conditions. *Forestry* **79:** 489-502.

**Condit R. 1995.** Research in large, long-term tropical forest plots. T*rends in Ecology & Evolution* **10:** 18-22.

**Condit R, Hubbel SP, Foster RB. 1993.** Identifying fast-growing native trees from the neotropics using data from a large, permanent census plot. *Forest Ecology and Management* **62:** 123-143.

**Condit R, Hubbel SP, Foster RB. 1995a.** Demography and harvest potential of Latin American timber species: data from a large, permanent plot in Panama. *Journal of Tropical Forest Science* **7:** 599-622.

**Condit R, Hubbel SP, Foster RB. 1995b.** Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. *Ecological Monographs* **65:** 419-439.

**Condit R, Sukumar R, Hubbell SP, Foster RB. 1998.** Predicting population trends from size distributions: A direct test in a tropical tree community. *American Naturalist* **152:** 495-509.

**Coomes DA, Grubb PJ. 1998.** A comparison of 12 tree species of Amazonian caatinga using growth rates in gaps and understorey, and allometric relationships. *Functional Ecology* **12:** 426-435.

**Coster C. 1927.** Zur Anatomie und Physiologie der Zuwachszonen und Jahresbildung in den Tropen. *Annales du Jardin Botanique de Buitenzorg* **37:** 49-160.

**Coster C. 1928.** Zur Anatomie und Physiologie der Zuwachszonen und Jahresbildung in den Tropen. *Annales du Jardin Botanique de Buitenzorg* **38:** 1-144.

**Couralet C, Sass-Klaassen U, Sterck F, Bekele T, Zuidema PA. 2005.** Combining dendrochronology and matrix modelling in demographic studies: an evaluation for *Juniperus procera* in Ethiopia. *Forest Ecology and Management* **216:** 317-330.

**da Fonseca SF, Piedade MTF, Schöngart J. 2009.** Wood growth of *Tabebuia barbata* (E. Mey.) Sandwith (Bignoniaceae) and *Vatairea guianensis* Aubl. (Fabaceae) in Central Amazonian black-water (igapó) and white-water (varzea) floodplain forests. *Trees-Structure and Function* **23:** 127-134.

**Dauber E. 2003.** Modelo de simulación para evaluar las posibilidades de cosecha en el primer y segundo ciclo de corta en bosques tropicales de Bolivia. Documento Técnico #128. Proyecto BOLFOR. Santa Cruz, Bolivia.

**Dauber E, Fredericksen TS, Peña-Claros M. 2005.** Sustainability of timber harvesting in Bolivian tropical forests. F*orest Ecology and Management* **214:** 294-304.

**Dekker M, Sass-Klaassen U, den Ouden J, Goedhart PW. 2009.** The effect of canopy position on growth and mortality in mixed sapling communities during self-thinning. *European Journal of Forest Research* **128:** 455-466.

**Denslow JS. 1980.** Gap partitioning among tropical rain forest trees. *Biotropica* **12:** 47-55.

**Dezzeo N, Worbes M, Ishii I, Herrera R. 2003.** Annual tree rings revealed by radiocarbon dating in seasonally flooded forest of the Mapire River, a tributary of the lower Orinoco River, Venezuela. *Plant Ecology* **168:** 165-175.

**Dünisch O, Bauch J, Gasparotto L. 2002.** Formation of increment zones and intraannual growth dynamics in the xylem of *Swietenia macrophylla*, *Carapa guianensis*, and *Cedrela odorata* (Meliaceae). *IAWA Journal* **23:** 101-119.

**Dünisch O, Montoia VR, Bauch J. 2003.** Dendroecological investigations on S*wietenia macrophylla* King and *Cedrela odorata* L. (Meliaceae) in the central Amazon. *Trees-Structure and Function* **17:** 244-250.

**Dyer ME, Bailey RL. 1987.** A test of six methods for estimating true heights from stem analysis data. *Forest Science* **33:** 3-13.

**Eckstein D, Sass U, Baas P. 1995.** Growth periodicity in tropical trees. *IAWA Journal* **16:** 325-442.

**Enquist BJ, Leffler AJ. 2001.** Long-term tree ring chronologies from sympatric tropical dry-forest trees: individualistic responses to climatic variation. *Journal of Tropical Ecology* **17:** 41-60.

**Enright NJ, Hartshorn GS. 1981.** The demography of tree species in undisturbed tropical rainforest. In: Bormann FH, Berlyn G, eds. *Age and growth rate of tropical trees; new directions for research.* Yale university: School of Forestry and Environmental Studies. Bulletin No. 94, 107-119.

**Feeley KJ, Davies SJ, Ashton PS, Bunyavejchewin S, Supardi MNN, Kassim AR, Tan S, Chave J. 2007a.** The role of gap phase processes in the biomass dynamics of tropical forests. *Proceedings of the Royal Society B-Biological Sciences* **274:** 2857-2864.

**Feeley KJ, Davies SJ, Noor MNS, Kassim AR, Tan S. 2007b.** Do current stem size distributions predict future population changes? An empirical test of intraspecific patterns in tropical trees at two spatial scales. *Journal of Tropical Ecology* **23:** 191-198.

**Feeley KJ, Wright SJ, Supardi MNN, Kassim AR, Davies SJ. 2007c.** Decelerating growth in tropical forest trees. *Ecology Letters* **10:** 461-469.

**Fichtler E, Clark DA, Worbes M. 2003.** Age and long-term growth of trees in an old-growth tropical rain forest, based on analyses of tree rings and C-14. *Biotropica* **35:** 306-317.

**Finegan B, Camacho M, Zamora N. 1999.** Diameter increment patterns among 106 tree species in a logged and silviculturally treated Costa Rican rain forest. *Forest Ecology and Management* **121:** 159-176.

**Fisher JI, Hurtt GC, Thomas RQ, Chambers JQ. 2008.** Clustered disturbances lead to bias in large-scale estimates based on forest sample plots. *Ecology Letters* **11:** 554-563.

**Fredericksen TS, Putz FE, Pattie P, Pariona W, Peña-Claros M. 2003.** Sustainable forestry in Bolivia - beyond planning logging. *Journal of Forestry* **101:** 37-40.

**Gloor M, Phillips OL, Lloyd JJ, Lewis SL, Malhi Y, Baker TR, López-González G, Peacock J, Almeida S, de Oliveira ACA, Alvarez E, Amaral I, Arroyo L, Aymard G, Bánki O, Blanc L, Bonal D, Brando P, Chao KJ, Chave J, Davila N, Erwin T, Silva J, Di Fiore A, Feldpausch TR, Freitas A, Herrera R, Higuchi N, Honorio E, Jiménez E, Killeen T, Laurance W, Mendoza C, Monteagudo A, Andrade A, Neill D, Nepstad D, Vargas PN, Peñuela MC, Cruz AP, Prieto A, Pitman N, Quesada C, Salomão R, Silveira M, Schwarz M, Stropp J, Ramírez F, Ramírez H, Rudas A, ter Steege H, Silva N, Torres A, Terborgh J, Vásquez R, van der Heijden G. 2009.** Does the disturbance hypothesis explain the biomass increase in basin-wide Amazon forest plot data? *Global Change Biology* **15:** 2418-2430.

**Gourlet-Fleury S, Comu G, Jesel S, Dessard H, Jourget JG, Blanc L, Picard N. 2005.** Using models to predict recovery and assess tree species vulnerability in logged tropical forests: a case study from French Guiana. *Forest Ecology and Management* **209:** 69-86.

**Grogan J, Jennings SB, Landis RM, Schulze M, Baima AMV, Lopes JDA, Norghauer JM, Oliveira LR, Pantoja F, Pinto D, Silva JNM, Vidal E, Zimmerman BL. 2008.** What loggers leave behind: impacts on big-leaf mahogany (*Swietenia macrophylla*) commercial populations and potential for post-logging recovery in the Brazilian Amazon. *Forest Ecology and Management* **255:** 269-281.

**Grogan J, Landis RM. in press.** Growth history and crown vine coverage are principal factors influencing growth and mortality rates of big-leaf mahogany *Swietenia macrophylla* in Brazil. *Journal of Applied Ecology.* doi: 10.1111/j.1365-2664.2009.01720.x

**Gutsell SL, Johnson EA. 2002.** Accurately ageing trees and examining their height-growth rates: implications for interpreting forest dynamics. *Journal of Ecology* **90:** 153-166.

**Hall P, Ashton PS, Condit R, Manokaran N, Hubbell SP. 1998.** Signal and noise in sampling tropical forest structure and dynamics. In: Dallmeier F, Comiskey JA, eds. *Forest biodiversity research, monitoring and modeling: conceptual background and old world case studies.* Paris: UNESCO/Parthenon Publishing Group, 63-77.

**Hara T, Kimura M, Kikuzawa K. 1991.** Growth patterns of tree height and stem diameter in populations *Abies veitchii*, *A. mariesii* and *Betula ermanii*. *Journal of Ecology* **79:** 1085-1098.

**Hartshorn GS. 1978.** Tree falls and tropical forest dynamics. In: Tomlinson PB, Zimmermann MH, eds. *Tropical Trees as Living Systems.* Cambridge: Cambridge University Press, 617-638.

**Henry HAL, Aarssen LW. 1999.** The interpretation of stem diameter-height allometry in trees: biomechanical constraints, neighbour effects, or biased regressions? *Ecology Letters* **2:** 89-97.

**Henry JD, Swan JMA. 1974.** Reconstructing forest history from live and dead plant material: an approach to the study of forest succession in southwest New Hampshire. *Ecology* **55:** 783.

**Hietz P, Wanek W, Dünisch O. 2005.** Long-term trends in cellulose delta C-13 and water-use efficiency of tropical *Cedrela* and *Swietenia* from Brazil. *Tree Physiology* **25:** 745-752.

**Holmes TP, Blate GM, Zweede JC, Pereira R, Barreto P, Boltz F, Bauch R. 2002.** Financial and ecological indicators of reduced impact logging performance in the eastern Amazon. *Forest Ecology and Management* **163:** 93-110.

**Ikonen VP, Kellomaki S, Vaisanen H, Peltola H. 2006.** Modelling the distribution of diameter growth along the stem in Scots pine. *Trees-Structure and Function* **20:** 391-402.

**IPCC. 2007.** Synthesis report.

**Jaffe MJ, Forbes S. 1993.** Thigmomorphogenesis: the effect of mechanical perturbation on plants. *Plant Growth Regulation* **12:** 313-324.

**Johnson SE, Abrams MD. 2009.** Basal area increment trends across age classes for two long-lived tree species in the eastern U.S. In: Kaczka, R., Malik, I., Owczarek, P., Gärtner, H., Helle, G., and Heinrich, I. eds. In: *TRACE - Tree Rings in Archeaology, Climatology and Ecology.* Volume 7. Scientific Technical Report STR 09/03. Potsdam, Germany: GFZ Potsdam, 127-134.

**Kammesheidt L, Dagang AA, Schwarzwaller W, Weidelt HJ. 2003.** Growth patterns of dipterocarps in treated and untreated plots. *Forest Ecology and Management* 174: 437-445.

**Kammesheidt L, Kohler P, Huth A. 2001.** Sustainable timber harvesting in Venezuela: a modelling approach. *Journal of Applied Ecology* **38:** 756-770.

**Keller M, Asner GP, Blate G, McGlocklin J, Merry F, Peña-Claros M, Zweede J. 2007.** Timber production in selectively logged tropical forests in South America. *Frontiers in Ecology and the Environment* **5:** 213-216.

**Kerstiens G. 2001.** Meta-analysis of the interaction between shade-tolerance, light environment and growth response of woody species to elevated $CO_2$. *Acta Oecologica* **22:** 61-69.

**Killeen TJ, García E. E, Beck SG. 1993**. Guía de árboles de Bolivia. Quipus S.R.L., La Paz, Bolivia.

**King DA. 1994.** Influence of light level on the growth and morphology of saplings in a Panamanian forest. *American Journal of Botany* **81:** 948-957.

**King DA, Leigh EG, Condit R, Foster RB, Hubbel SP. 1997.** Relationships between branch spacing, growth rate and light in tropical forest saplings. *Functional Ecology* **11:** 627-635.

**King DA. 1986.** Tree form, height growth, and susceptibility to wind damage in *Acer Saccharum*. *Ecology* **67:** 980-990.

**Kobe RK, Pacala SW, Silander JA, Canham CD. 1995.** Juvenile tree survivorship as a component of shade tolerance. *Ecological Applications* **5:** 517-532.

**Kohyama T, Hara T. 1989.** Frequency-distribution of tree growth-rate in natural forest stands. *Annals of Botany* **64:** 47-57.

**Kohyama T, Hotta M. 1990.** Significance of allometry in tropical saplings. *Functional Ecology* **4:** 515-521.

**Kohyama T, Kubo T, Macklin E. 2005.** Effect of autocorrelation on apparent growth rate variation in forest tree census data and an alternative distribution function of tree growth data. *Ecological Research* **20:** 11-16.

**Kooyman RM, Westoby M. 2009.** Costs of height gain in rainforest saplings: main-stem scaling, functional traits and strategy variation across 75 species. *Annals of Botany* **104:** 987-993.

**Körner C. 2004.** Through enhanced tree dynamics carbon dioxide enrichment may cause tropical forests to lose carbon. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **359:** 493-498.

**Korning J, Balslev H. 1994.** Growth rates and mortality patterns of tropical lowland tree species and the relation to forest structure in Amazonian Ecuador. *Journal of Tropical Ecology* **10:** 151-166.

**Kurokawa H, Yoshida T, Nakamura T, Lai J, Nakashizuka T. 2003.** The age of tropical rain-forest canopy species, Borneo ironwood (*Eusideroxylon zwageri*), determined by $^{14}$C dating. *Journal of Tropical Ecology* **19:** 1-7.

**Landis RM, Peart DR. 2005.** Early performance predicts canopy attainment across life histories in subalpine forest trees. *Ecology* **86:** 63-72.

**Larson PR. 1963.** Stem form development of forest trees. *Forest Science Monograph* **5:** 1-42.

**Laurance SG, Laurance WF, Henrique EMN, Andrade A, Fearnside PM, Expedito RGR, Condit R. 2009.** Long-term variation in Amazon forest dynamics. *Journal of Vegetation Science* **20:** 323-333.

**Laurance WF, Nascimento HEM, Laurance SG, Condit R, D'Angelo S, Andrade A. 2004a.** Inferred longevity of Amazonian rainforest trees based on a long-term demographic study. *Forest Ecology and Management* **190:** 131-143.

**Laurance WF, Oliveira AA, Laurance SG, Condit R, Nascimento HEM, Sanchez-Thorin AC, Lovejoy TE, Andrade A, D'Angelo S, Ribeiro JE, Dick CW. 2004b.** Pervasive alteration of tree communities in undisturbed Amazonian forests. *Nature* **428:** 171-175.

**Lewis SL, Malhi Y, Phillips OL. 2004a.** Fingerprinting the impacts of global change on tropical forests. P*hilosophical Transactions of the Royal Society of London Series B-Biological Sciences* **359:** 437-462.

**Lewis SL, Phillips OL, Baker TR, Lloyd J, Malhi Y, Almeida S, Higuchi N, Laurance WF, Neill DA, Silva JNM, Terborgh J, Lezama AT, Martínez RV, Brown S, Chave J, Kuebler C, Vargas PN, Vinceti B. 2004b.** Concerted changes in tropical forest structure and dynamics: evidence from 50 South American long-term plots. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **359:** 421-436.

**Lewis SL, Phillips OL, Sheil D, Vinceti B, Baker TR, Brown S, Graham AW, Higuchi N, Hilbert DW, Laurance WF, Lejoly J, Malhi Y, Monteagudo A, Vargas PN, Sonke B, Supardi N, Terborgh JW, Martínez RV. 2004c.** Tropical forest tree mortality, recruitment and turnover rates: calculation, interpretation and comparison when census intervals vary. *Journal of Ecology* **92:** 929-944.

**Lewis SL, Phillips OL, Baker TR. 2006.** Impacts of global atmospheric change on tropical forests. *Trends in Ecology & Evolution* **21:** 173-174.

**Lieberman D, Lieberman M, Hartshorn GS, Peralta R. 1985a.** Growth rates and age-size relationships of tropical wet forest trees in Costa Rica. *Journal of Tropical Ecology* **1:** 97-109.

**Lieberman D, Lieberman M, Peralta R, Hartshorn GS. 1985b.** Mortality patterns and stand turnover rates in a wet tropical forest in Costa Rica. *Journal of Ecology* **73:** 915-924.

**Lieberman M, Lieberman D. 1985.** Simulation of growth curves from periodic increment data. *Ecology* **66:** 632-635.

**Lisi CS, Tomazello M, Botosso PC, Roig FA, Maria VRB, Ferreira-Fedele L, Voigt ARA. 2008.** Tree-ring formation, radial increment periodicity, and phenology of tree species from a seasonal semi-deciduous forest in southeast Brazil. *IAWA Journal* **29:** 189-207.

**Lloyd J, Farquhar GD. 2008.** Effects of rising temperatures and [$CO_2$] on the physiology of tropical forest trees. *Philosophical Transactions of the Royal Society B-Biological Sciences* **363:** 1811-1817.

**Lorimer CG, Frelich LE. 1989.** A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. *Canadian Journal of Forest Research* **19:** 651-663.

**Lorimer CG, Frelich LE, Nordheim EV. 1988.** Estimating gap probabilities for canopy trees. *Ecology* **69:** 778-785.

**Lusk CH, Smith B. 1998.** Life history differences and tree species coexistence in an old-growth New Zealand rain forest. *Ecology* **79:** 795-806.

**Malhi Y, Roberts JT, Betts RA, Killeen TJ, Li WH, Nobre CA. 2008.** Climate change, deforestation, and the fate of the Amazon. *Science* **319:** 169-172.

**Malhi Y, Wright J. 2004.** Spatial patterns and recent trends in the climate of tropical rainforest regions. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **359:** 311-329.

**Martínez-Ramos M, Alvarez-Buylla ER. 1998.** How old are tropical rain forest trees? *Trends in Plant Science* **3:** 400-405.

**McCarroll D, Loader NJ. 2004.** Stable isotopes in tree rings. *Quaternary Science Reviews* **23:** 771-801.

**Metcalf CJ, Horvitz CC, Tuljapurkar S, Clark DA. 2009.** A time to grow and a time to die: a new way to analyze the dynamics of size, light, age, and death of tropical trees. *Ecology* **90:** 2766-2778.

**Miina J. 1993.** Residual variation in diameter growth in a stand of Scots pine and Norway spruce. *Forest Ecology and Management* **58:** 111-128.

**Naidu SL, DeLucia EH, Thomas RB. 1998.** Contrasting patterns of biomass allocation in dominant and suppressed loblolly pine. *Canadian Journal of Forest Research* **28:** 1116-1124.

**Niklas KJ. 1995.** Size-dependent allometry of tree height, diameter and trunk-taper. *Annals of Botany* **75:** 217-227.

**Nilsson U, Albrektson A. 1993.** Productivity of needles and allocation of growth in young scots pine trees of different competitive status. *Forest Ecology and Management* **62:** 173-187.

**Nobuchi T, Ogata Y, Siripatanadilok S. 1995.** Seasonal characteristics of wood formation in *Hopea odorata* and *Shorea henryana*. *IAWA Journal* **16:** 361-369.

**Nock CA, Geihofer D, Grabner M, Baker PJ, Bunyavejchewin S, Hietz P. 2009.** Wood density and its radial variation in six canopy tree species differing in shade-tolerance in western Thailand. *Annals of Botany* **104:** 297-306.

**Nowacki GJ, Abrams MD. 1997.** Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. *Ecological Monographs* **67:** 225-249.

**O'Brien ST, Hubbel SP, Spiro P, Condit R, Foster RB. 1995.** Diameter, height, crown, and age relationships in 8 neotropical tree species. *Ecology* **76:** 1926-1939.

**Osunkoya OO, Omar-Ali K, Amit N, Dayan J, Daud DS, Sheng TK. 2007.** Comparative height-crown allometry and mechanical design in 22 tree species of Kuala Belalong rainforest, Brunei, Borneo. *American Journal of Botany* **94:** 1951-1962.

**Pacala SW, Canham CD, Saponara J, Silander JA, Kobe RK, Ribbens E. 1996.** Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecological Monographs* **66:** 1-43.

**Pacala SW, Canham CD, Silander JA, Kobe RK. 1994.** Sapling growth as a function of resources in a north temperate forest. *Canadian Journal of Forest Research* **24:** 2172-2183.

**Paciorek CJ, Condit R, Hubbel SP, Foster RB. 2000.** The demographics of resprouting in tree and shrub species of a moist tropical forest. *Journal of Ecology* **88:** 765-777.

**Paz-Rivera C, Putz FE. 2009.** Anthropogenic soils and tree distributions in a lowland forest in Bolivia. *Biotropica.* doi: 10.1111/j.1744-7429.2009.00521.x

**Pearce D, Putz FE, Vanclay JK. 2003.** Sustainable forestry in the tropics: panacea or folly? *Forest Ecology and Management* **172:** 229-247.

**Peña-Claros M, Fredericksen TS, Alarcon A, Blate GM, Choque U, Leano C, Licona JC, Mostacedo B, Pariona W, Villegas Z, Putz FE. 2008a.** Beyond reduced-impact logging: silvicultural treatments to increase growth rates of tropical trees. *Forest Ecology and Management* **256:** 1458-1467.

**Peña-Claros M, Peters EM, Justiniano MJ, Bongers F, Blate GM, Fredericksen TS, Putz FE. 2008b.** Regeneration of commercial tree species following silvicultural treatments in a moist tropical forest. *Forest Ecology and Management* **255:** 1283-1293.

**Phillips OL, Aragão LEOC, Lewis SL, Fisher JB, Lloyd J, López-González G, Malhi Y, Monteagudo A, Peacock J, Quesada CA, van der Heijden G, Almeida S, Amaral I, Arroyo L, Aymard G, Baker TR, Bánki O, Blanc L, Bonal D, Brando P, Chave J, de Oliveira ACA, Cardozo ND, Czimczik CI, Feldpausch TR, Freitas MA, Gloor E, Higuchi N, Jiménez E, Lloyd G, Meir P, Mendoza C, Morel A, Neill DA, Nepstad D, Patiño S, Peñuela MC, Prieto A, Ramírez F, Schwarz M, Silva J, Silveira M, Thomas AS, ter Steege H, Stropp J, Vásquez R, Zelazowski P, Dávila EA, Andelman S, Andrade A, Chao KJ, Erwin T, Di Fiore A, Honorio E, Keeling H, Killeen TJ, Laurance WF, Cruz AP, Pitman NCA, Vargas PN, Ramírez-Angulo H, Rudas A, Salamão R, Silva N, Terborgh J, Torres-Lezama A. 2009.** Drought sensitivity of the Amazon rainforest. *Science* **323:** 1344-1347.

**Phillips OL, Baker TR, Arroyo L, Higuchi N, Killeen TJ, Laurance WF, Lewis SL, Lloyd J, Malhi Y, Monteagudo A, Neill DA, Vargas PN, Silva JNM, Terborgh J, Martínez RV, Alexiades M, Almeida S, Brown S, Chave J, Comiskey JA, Czimczik CI, Di Fiore A, Erwin T, Kuebler C, Laurance SG, Nascimento HEM, Olivier J, Palacios W, Patiño S, Pitman NCA, Quesada CA, Saldias M, Lezama AT, Vinceti B. 2004.** Pattern and process in Amazon tree turnover, 1976-2001. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **359:** 381-407.

**Phillips OL, Gentry AH. 1994.** Increasing turnover through time in tropical forests. *Science* **263:** 954-958.

**Phillips OL, Lewis SL, Baker TR, Chao KJ, Higuchi N. 2008.** The changing Amazon forest. *Philosophical Transactions of the Royal Society B-Biological Sciences* **363:** 1819-1827.

**Phillips OL, Martínez RV, Arroyo L, Baker TR, Killeen T, Lewis SL, Malhi Y, Mendoza AM, Neill D, Vargas PN, Alexiades M, Ceron C, Di Fiore A, Erwin T, Jardim A, Palacios W, Saldias M, Vinceti B. 2002.** Increasing dominance of large lianas in Amazonian forests. *Nature* **418:** 770-774.

**Picard N, Yalibanda Y, Namkosserena S, Baya F. 2008.** Estimating the stock recovery rate using matrix models. *Forest Ecology and Management* **255:** 3597-3605.

**Poorter L, Arets EJMM. 2003.** Light environment and tree strategies in a Bolivian tropical moist forest: an evaluation of the light partitioning hypothesis. *Plant Ecology* **166:** 295-306.

**Poorter L, Bongers F, Sterck F, Woll H. 2005.** Beyond the regeneration phase: differentiation of height-light growth trajectories among tropical tree species. *Journal of Ecology* **93:** 256-267.

**Poorter L, Bongers L, Bongers F. 2006.** Architecture of 54 moist-forest tree species: Traits, trade-offs, and functional groups. *Ecology* **87:** 1289-1301.

**Poorter L, Boot RGA, Hayashida-Oliver Y, Leigue J, Peña-Claros M, Zuidema PA. 2001.** Estructura y dinámica de un bosque húmedo tropical en el norte de la Amazonía Boliviana. PROMAB. Informe técnico No. 2.

**Poorter L, Werger MJA. 1999.** Light environment, sapling architecture, and leaf display in six rain forest tree species. *American Journal of Botany* **86:** 1464-1473.

**Priya PB, Bhat KM. 1998.** False ring formation in teak (*Tectona grandis* Lf) and the influence of environmental factors. *Forest Ecology and Management* **108:** 215-222.

**Rentch JS, Fajvan MA, Hicks RR. 2003.** Spatial and temporal disturbance characteristics of oak-dominated old-growth stands in the central hardwood forest region. *Forest Science* **49:** 778-789.

**Rice RE, Gullison RE, Reid JW. 1997.** Can sustainable management save tropical forests? *Scientific American* **276:** 44-49.

**Rolland C, Petitcolas V, Michalet R. 1998.** Changes in radial tree growth for *Picea abies*, *Larix decidua*, *Pinus cembra* and *Pinus uncinata* near the alpine timberline since 1750. *Trees* **13:** 40-53.

**Rondon XJ, Gorchov DL, Noble RB. 2009.** Projection of tree growth and timber volume following strip clear-cutting in the Peruvian Amazon. *Forest Ecology and Management* **257:** 588-599.

**Rubino DL, McCarthy BC. 2004.** Comparative analysis of dendroecological methods to assess disturbance events. *Dendrochronologia* **21:** 97-115.

**Runkle JR. 1982.** Patterns of disturbance in some old-growth mesic forest of eastern north America. *Ecology* **63:** 1533-1546.

**Schmitt J, Wulff RD. 1993.** Light spectral quality, phytochrome and plant competition. *Trends in Ecology & Evolution* **8:** 47-51.

**Schöngart J. 2008.** Growth-Oriented Logging (GOL): A new concept towards sustainable forest management in Central Amazonian várzea floodplains. *Forest Ecology and Management* **256:** 46-58.

**Schöngart J, Junk WJ, Piedade MTF, Ayres JM, Huttermann A, Worbes M. 2004.** Teleconnection between tree growth in the Amazonian floodplains and the El Niño-Southern Oscillation effect. *Global Change Biology* **10:** 683-692.

**Schöngart J, Piedade MTF, Ludwigshausen S, Worbes M. 2002.** Phenology and stem-growth periodicity of tree species in Amazonian floodplain forests. *Journal of Tropical Ecology* **18:** 1-17.

**Schöngart J, Wittmann F, Worbes M, Piedade MTF, Krambeck HJ, Junk WJ. 2007.** Management criteria for *Ficus insipida* Willd. (Moraceae) in Amazonian white-water floodplain forests defined by tree-ring analysis. *Annals of Forest Science* **64:** 657-664.

**Schulze M, Grogan J, Uhl C, Lentini M, Vidal E. 2008a.** Evaluating ipê (*Tabebuia*, *Bignoniaceae*) logging in Amazonia: sustainable management or catalyst for forest degradation? *Biological Conservation* **141:** 2071-2085.

**Schulze M, Grogan J, Landis RM, Vidal E. 2008b.** How rare is too rare to harvest? Management challenges posed by timber species occurring at low densities in the Brazilian Amazon. *Forest Ecology and Management* **256:** 1443-1457.

**Selaya NG, Oomen RJ, Netten JJC, Werger MJA, Anten NPR. 2008.** Biomass allocation and leaf life span in relation to light interception by tropical forest plants during the first years of secondary succession. *Journal of Ecology* **96:** 1211-1221.

**Sheil D. 1995a.** A critique of permament plot methods and analysis with examples from Budongo-forest, Uganda. *Forest Ecology and Management* **77:** 11-34.

**Sheil D. 1995b.** Evaluating turnover in tropical forests. *Science* **268:** 894.

**Sheil D, May RM. 1996.** Mortality and recruitment rate evaluations in heterogeneous tropical forests. *Journal of Ecology* **84:** 91-100.

**Sheil D, Salim A, Chave JR, Vanclay J, Hawthorne WD. 2006.** Illumination-size relationships of 109 coexisting tropical forest tree species. *Journal of Ecology* **94:** 494-507.

**Silva JNM, de Carvalho JOP, Lopes JDA, de Almeida BF, Costa DHM, de Oliveira LC, Vanclay JK, Skovsgaard JP. 1995.** Growth and yield of a tropical rain-forest in the Brazilian Amazon 13 years after logging. *Forest Ecology and Management* **71:** 267-274.

**Sist P, Ferreira FN. 2007.** Sustainability of reduced-impact logging in the Eastern Amazon. *Forest Ecology and Management* **243:** 199-209.

**Sist P, Picard N, Gourlet-Fleury S. 2003.** Sustainable cutting cycle and yields in a lowland mixed dipterocarp forest of Borneo. *Annals of Forest Science* **60:** 803-814.

**Smith H. 1982.** Light quality, photoperception, and plant strategy. *Annual Review of Plant Physiology* **33:** 481-518.

**Soliz-Gamboa CC, Rozendaal DMA, Ceccantini G, Angyalossy V, van der Borg K, Zuidema PA. submitted.** Evaluating the annual nature of juvenile rings in Bolivian tropical rainforest trees.

**Soulé PT, Knapp PA. 2006.** Radial growth rate increases in naturally occurring ponderosa pine trees: a late-20th century $CO_2$ fertilization effect? *New Phytologist* **171:** 379-390.

**Stahle DW, Mushove PT, Cleaveland MK, Roig FA, Haynes GA. 1999.** Management implications of annual growth rings in *Pterocarpus angolensis* from Zimbabwe. *Forest Ecology and Management* **124:** 217-229.

**Sterck F, Martínez-Ramos M, Dyer-Leal G, Rodríguez-Velazquez J, Poorter L. 2003.** The consequences of crown traits for the growth and survival of tree saplings in a Mexican lowland rainforest. *Functional Ecology* **17:** 194-200.

**Sterck FJ, Bongers F. 1998.** Ontogenetic changes in size, allometry, and mechanical design of tropical rain forest trees. *American Journal of Botany* **85:** 266-272.

**Sterck FJ, Bongers F, Newbery DM. 2001.** Tree architecture in a Bornean lowland rain forest: intraspecific and interspecific patterns. *Plant Ecology* **153:** 279-292.

**Sumida A, Ito H, Isagi Y. 1997.** Trade-off between height growth and stem diameter growth for an evergreen oak, *Quercus glauca*, in a mixed hardwood forest. *Functional Ecology* **11:** 300-309.

**Swaine MD, Hall JB, Alexander IJ. 1987.** Tree population dynamics at Kade Ghana (1968-1982). *Journal of Tropical Ecology* **3:** 331-345.

**Takahashi K, Seino T, Kohyama T. 2001.** Responses to canopy openings in architectural development of saplings in eight deciduous broadleaved tree species. *Canadian Journal of Forest Research* **31:** 1336-1347.

**Terborgh J, Flores C, Mueller P, Davenport L. 1997.** Estimating the ages of successional stands of tropical trees from growth increments. *Journal of Tropical Ecology* **13:** 833-856.

**Therrell MD, Stahle DW, Mukelabai MA, Shugart HH. 2007.** Age, and radial growth dynamics of *Pterocarpus angolensis* in southern Africa. *Forest Ecology and Management* **244:** 24-31.

**Toledo M, Poorter L, Peña-Claros M, Leaño C, Bongers F. 2008.** Diferencias, en las características edáficas y la estructura del bosque, de cuatro ecoregiones forestales de Bolivia. *Revista Boliviana de Ecología y Conservación Ambiental* **24:** 11-26.

**Trouet V, Coppin P, Beeckman H. 2006.** Annual growth ring patterns in *Brachystegia spiciformis* reveal influence of precipitation on tree growth. *Biotropica* **38:** 375-382.

**Turner IM. 2001.** *The ecology of trees in the tropical rainforest.* New York: Cambridge University Press.

**Valle D, Phillips P, Vidal E, Schulze M, Grogan J, Sales M, van Gardingen P. 2007.** Adaptation of a spatially explicit individual tree-based growth and yield model and long-term comparison between reduced-impact and conventional logging in eastern Amazonia, Brazil. *Forest Ecology and Management* **243:** 187-198.

**Valle D, Schulze M, Vidal E, Grogan J, Sales M. 2006.** Identifying bias in stand-level growth and yield estimations: a case study in eastern Brazilian Amazonia. *Forest Ecology and Management* **236:** 127-135.

**van Breugel M, Martínez-Ramos M, Bongers F. 2006.** Community dynamics during early secondary succession in Mexican tropical rain forests. *Journal of Tropical Ecology* **22:** 663-674.

**van Gardingen PR, Valle D, Thompson I. 2006.** Evaluation of yield regulation options for primary forest in Tapajos National Forest, Brazil. *Forest Ecology and Management* **231:** 184-195.

**van Noordwijk AJ, de Jong G. 1986.** Acquisition and allocation of resources: their influence on variation in life history tactics. T*he American Naturalist* **128:** 137-142.

**van Rheenen HMPJB. 2005.** *The role of seed trees and seedling regeneration for species maintenance in logged-over forests - a study in the Bolivian Amazon rainforest.* PhD thesis, Utrecht University, Utrecht, the Netherlands. PROMAB Scientific Series 9.

**van der Meer PJ, Bongers F. 1996.** Formation and closure of canopy gaps in the rain forest at Nouragues, French Guiana. *Vegetatio* **126:** 167-179.

**Verheyden A, Kairo JG, Beeckman H, Koedam N. 2004.** Growth rings, growth ring formation and age determination in the mangrove *Rhizophora mucronata*. *Annals of Botany* **94:** 59-66.

**Verwer C, Peña-Claros M, van der Staak D, Ohlson-Kiehn K, Sterck FJ. 2008.** Silviculture enhances the recovery of overexploited mahogany *Swietenia macrophylla*. *Journal of Applied Ecology* **45:** 1770-1779.

**Villegas Z, Peña-Claros M, Mostacedo B, Alarcón A, Licona JC, Leaño C, Pariona W, Choque U. 2009.** Silvicultural treatments enhance growth rates of future crop trees in a tropical dry forest. *Forest Ecology and Management* **258:** 971-977.

**Voelker SL, Muzika RM, Guyette RP, Stambaugh MC. 2006.** Historical $CO_2$ growth enhancement declines with age in *Quercus* and *Pinus*. *Ecological Monographs* **76:** 549-564.

**Wang GG, Chhin S, Bauerle WL. 2006.** Effect of natural atmospheric $CO_2$ fertilization suggested by open-grown white spruce in a dry environment. *Global Change Biology* **12:** 601-610.

**Weiner J, Thomas SC. 1992.** Competition and allometry in 3 species of annual plants. *Ecology* **73:** 648-656.

**Whitmore TC. 1998.** *An introduction to tropical rain forests.* New York: Oxford University Press.

**Williamson GB, Eldik TV, Delamonica P, Laurance WF. 1999.** How many millenarians in Amazonia? Sizing the ages of large trees. *Trends in Plant Science* **4:** 387.

**Wils THG, Robertson I, Eshetu Z, Sass-Klaassen UGW, Koprowski M. 2009.** Periodicity of growth rings in *Juniperus procera* from Ethiopia inferred from crossdating and radiocarbon dating. *Dendrochronologia* **27:** 45-58.

**Worbes M. 1999.** Annual growth rings, rainfall-dependent growth and long-term growth patterns of tropical trees from the Caparo Forest Reserve in Venezuela. *Journal of Ecology* **87:** 391-403.

**Worbes M. 2002.** One hundred years of tree-ring research in the tropics- a brief history and an outlook to future challenges. *Dendrochronologia* **20:** 217-231.

**Worbes M, Junk WJ. 1989.** Dating tropical trees by means of C-14 from bomb tests. *Ecology* **70:** 503-507.

**Worbes M, Junk WJ. 1999.** How old are tropical trees? The persistence of a myth. *IAWA Journal* **20:** 255-260.

**Worbes M, Klinge H, Revilla JD, Martius C. 1992.** On the dynamics, floristic subdivision, and geographical distribution of várzea forests in Central Amazonia. J*ournal of Vegetation Science* **3:** 553-564.

**Worbes M, Staschel R, Roloff A, Junk WJ. 2003.** Tree ring analysis reveals age structure, dynamics and wood production of a natural forest stand in Cameroon. *Forest Ecology and Management* **173:** 105-123.

**Wright SJ. 2005.** Tropical forests in a changing environment. *Trends in Ecology & Evolution* **20:** 553-560.

**Würth MKR, Winter K, Körner C. 1998.** In situ responses to elevated $CO_2$ in tropical forest understorey plants. *Functional Ecology* **12:** 886-895.

**Wyckoff PH, Clark JS. 2002.** The relation between growth and mortality for seven co-occurring tree species in the southern Appalachian Mountains. *Journal of Ecology* **90:** 604-615.

**Zarin DJ, Schulze MD, Vidal E, Lentini M. 2007.** Beyond reaping the first harvest: management objectives for timber production in the Brazilian Amazon. *Conservation Biology* **21:** 916-925.

**Zenner EK. 2008.** Short-term changes in *Pinus strobus* sapling height/diameter ratios following partial release: testing the acclimative stem-form development hypothesis. *Canadian Journal of Forest Research* **38:** 181-189.

**Zuidema PA, Boot RGA. 2002.** Demography of the Brazil nut tree (*Bertholletia excelsa*) in the Bolivian Amazon: impact of seed extraction on recruitment and population dynamics. *Journal of Tropical Ecology* **18:** 1-31.

**Zuidema PA, Brienen RJW, During HJ, Güneralp B. 2009.** Do persistently fast-growing juveniles contribute disproportionately to population growth? A new analysis tool for matrix models and its application to rainforest trees. *American Naturalist* **174:** 709-719.

**Zuidema PA, Jongejans E, Chien PD, During HJ, Schieving F. in press.** Integral Projection Models for trees: a new parameterization method and a validation of model output. *Journal of Ecology.*

# DANKWOORD
# ACKNOWLEDGEMENTS
# AGRADECIMIENTOS

De afgelopen vier jaar zijn omgevlogen! En bijna niet te geloven, maar het boekje ligt er nu echt. Het is niet altijd makkelijk geweest, maar ik ben tevreden met het resultaat (hoewel ik wel eens wat anders geroepen heb…)! Veel mensen hebben op de een of andere manier bijgedragen aan het tot stand komen van dit boekje en daarvoor wil ik al diegenen heel hartelijk danken.

Vier jaar geleden stapte ik op het vliegtuig naar Bolivia, op weg naar een groot avontuur! De eerste maanden bracht ik mijn tijd door in Santa Cruz, fijn om daar weer terug te komen. Los primeros meses pasé en Santa Cruz para iniciar el proyecto. Quiero agradecer a Marielos y Bonifacio por su ayuda en establecer los contactos con las empresas y la ayuda en obtener el permiso para cortar árboles, ¡lo que tomó en Santa Cruz dos semanas solamente! ¡Gracias! Daarnaast wil ik Lourens en Marielos bedanken voor alle hulp en goede suggesties. Bedankt dat jullie je huis aan mij 'uitleenden' voor twee maanden en voor de gastvrijheid als ik weer eens een paar dagen als een gek door Santa Cruz kwam rennen voor al de regelkarweitjes om daarna naar Riberalta of naar Nederland te vliegen! Marlene, gracias por la ayuda en buscarme mi primera casa en Santa Cruz. A todos trabajando en el IBIF: Alfredo, Ari, Bonifacio, Carlos, Claudio, Emma, Juan-Carlos, Geovana, Karina, Laly, Lars, Lourens, Marielos, Marisol, Marlene, Martijn, Vincent, Zulma, ¡gracias por toda la ayuda y la amistad! Los juegos de frisbee a las cinco de la tarde en la cancha de la Superintendencia fueron inolvidables…

Debo mucho a Don Eugenio ("ya, ahora vamos a machetear una pica, tumbamos los palos, y sacamos los anillos", ¡imagínate los gestos correspondientes!). El me ayudó con el trabajo de campo en La Chonta, trabajamos duro, en la época de lluvia, con treinta centímetros de barro en el camino… Gracias a José Chuviña y Don Wicho también. Lars, ook bedankt, dat ik tijdens een veldreisje ook meekon naar La Chonta. En jammer dat we op dezelfde dag en tijd onze proefschriften verdedigen, helaas… Don Eugenio también lijó los discos en la carpintería de la Universidad Gabriel Rene Moreno (UAGRM). De la UAGRM quiero agradecer al ing. José Angulo y el ing. Cerrogrande. Gracias por la ayuda, el permiso para trabajar en la universidad y la posibilidad de guardar madera.

Daarna verhuisde ik naar Riberalta, een rustig stadje aan de Rio Beni en de Rio Madre de Dios, vlakbij de grens met Brazilië. Prachtig, een heel andere wereld, en het wende snel om alleen per vliegtuig uit mijn woonplaats weg te kunnen! Met Claudia begon daar het grote werk: contact leggen met de houtkapbedrijven, met PROMAB en de universiteit, en verder moesten we alles logistiek gezien aan de gang te krijgen. Al momento de llegar a Riberalta por primera vez, el pueblo ya me gustó. ¡Tanta tranquilidad! El trabajo de campo fue siempre un desafío, pero todo salió bien, gracias a todos que nos ayudaron. Siempre fuimos un equipo grande, mejor conocido como 'los Cascos Azules':

Adhemar ("¡Hola amiguito!"), Nazareno ("solo los perros duermen de día"), Miguel ("jefita…."), Samuel (el motosierrista, cuando estábamos sacando un disco de morado, una especie de madera muy dura, salió una cantidad inmensa de 'petoabejas'…: "el trabajo no es tan grave, pero esos bichos…."), Eloy ("¿Dana, porque me haces esto??"), Edmundo (no hablaba mucho, pero sabía mucho de los árboles), Don Victor, Efraim (alias 'lycra', porque comía tanto que su estomago pareció hecho de 'lycra'), Nilson, Raul y Maggy.

Pasábamos la mayoría del tiempo en el famoso 'Patujusal', en Los Indios. Compartíamos el campamento durante el día con millones de 'petoabejas' y durante la noche con legiones de 'compadres'. A los compadres, había que tratarles como amigos. Si los llamaríamos 'sepes', perderíamos todo el campamento... Llegamos a cierto tipo de acuerdo: al final perdimos solamente algunas carpas, un poco de ropa, y algunos kilos de arroz y lentejas...

Colectábamos muchos discos de todas formas y tamaños. Teníamos 'el gato', 'la mariposa', y todos los tipos de aves. Y 'el caballo', que tenía mala fama, por su tamaño tuvimos que volver el día siguiente. Transportábamos los discos de todas maneras posibles: en bici, en moto, en carro, en avión, en flota, en skidder y en camión. ¡Todavía me acuerdo la cara llena de sorpresa del carpintero cuando llegamos con un camión lleno de discos para que les cortaran los aletones (sino, no entraban bajo del microscopio de la medidora)! Muchísimas gracias a Nazareno y Miguel, especialmente. Ellos trabajaron durante un año y medio para nosotras, tiempo completo, tanto en el campo, como en Riberalta. En Riberalta, ellos lijaron todos los discos, un trabajo muy duro. Y siempre han ayudado en solucionar problemas, de cualquier tipo.

En PROMAB-UAB quisiera agradecer a Armelinda Zonta por todo su apoyo en asuntos logísticos. Sobre todo por la ayuda, en cooperación con Vanesa, en el tramite del permiso para cortar árboles. También gracias a Adhemar, Lilian y Carla por el apoyo.

Edwin Rodríguez A. tenía toda la paciencia para medir los discos de almendrillo amarillo, ¡muy bien hecho! Felicidades con la finalización tu tesis todavía. Gracias por la amistad, y toda la ayuda en el campo y en Riberalta. Y la gran historia sobre 'pie de coco'. Gracias a Claudia Rodríguez R. por hacer el trabajo de los transectos. Ook vanuit Nederland kwamen er studenten om het praktische werk voor hun stage te doen binnen onze onderzoeksprojecten. Daan, hartelijk dank voor het werk dat je verzet hebt, al viel het leventje in Riberalta je niet altijd mee. Jeroen (alias 'Yogurt'), het was even wennen, maar daarna was je praktisch een Riberalteño. Jij ook bedankt voor het werk dat je gedaan hebt. En Mart, jij werkte met Claudia samen, ook bedankt voor je bijdrage!

La vida en Riberalta fue tranquila. Al inicio del proyecto: gracias, José Carlos, por poder compartir la casa por un rato. Siempre tomamos un café en la oficina con todos de PROMAB, los de Forlive y los estudiantes. Agradezco a todos: Alberto, Carmelo, Claribel, Edgar, Edwin, Huanger, Mario, Vincent y Nolvia y sus hijos, Walter, las cosas que compartimos: los churrascos, las fiestas y los viajes a Tumi! Pero los karaokes no me gustaron tanto... Gracias al equipo de frontón también: Edgar especialmente (¡el más fanático!), Alberto, José Torrico (ay, ¡muy fanático también!), Jeroen y Mart. También gracias a los visitantes de Forlive, entre todos Jessica, Rik y Karol, por haber compartido un poco de la vida en Riberalta. Gracias, Nazareno, por darme clases de manejar moto, y claro, había que pasar 'el semáforo' y el examen fue 'dar una vuelta por la plaza'. Mario y Walter, gracias por la amistad.

And then, I want to thank one person in special. Claudia, we shared much of our time over the past few years. Although it was not always easy to work together, and to live together in

Riberalta for almost two years, I enjoyed it very much. I learned a lot from you about dendrochronology. It was good that we could discuss the work, and deal with the changes and the disappointments in the project together. And I am still surprised that, in the end, everything worked out in some way: we did it! Thanks for everything, and good luck in finishing your thesis the coming months!

I also want to thank your parents for everything they did: Carmen e Eduardo, gracias por la hospitalidad, siempre cuando pasé por La Paz. Y por haber pasado Navidad dos años seguidos con ustedes. También quiero agradecerles por toda la ayuda logística. Siempre llegaron cajas con materiales y comida en avión desde La Paz: lámparas, hasta una pulidora entera, y, claro, queso... y mucho más. Increíble. ¡Muchas gracias!

Terug in Nederland begon het grote werk: het analyseren van de data en het schrijven. Ten eerste wil ik Marinus bedanken voor de kans die ik gekregen heb. En als er zaken waren die geregeld moesten worden, gebeurde dat altijd uiterst efficiënt en snel. Ook op de stukken tekst kwam altijd snel commentaar, met af en toe de vraag of ik even kon uitleggen wat ik bedoelde, dan zou je het wel even opschrijven op een begrijpelijke manier... Hartelijk dank!
Pieter, jij was nauw betrokken bij het hele onderzoeksproces. Dat was dan ook moeilijk te voorkomen met de niet aflatende stroom, erg lange e-mails vanuit Bolivia... Dank voor je geduld, het beantwoorden van al die e-mails, alle discussies over de resultaten en voor het meerdere malen bekijken van al mijn pogingen tot het schrijven van leesbare teksten. Ik heb veel geleerd de afgelopen vier jaar, bedankt daarvoor!

Ook Roel en Heinjo hebben in grote mate bijgedragen aan hoofdstukken in dit proefschrift. Roel, bedankt voor je suggesties over het ringenwerk toen ik als AIO begon. Je hebt veel bijgedragen aan het tweede hoofdstuk, niet alleen alle data van *Cedrela*, maar ook je ideeën over de sampling biases. Dank voor het ter sprake brengen van deze ideeën, ik heb veel waardering daarvoor. Ook de methodologie van de groeisimulaties uit hoofdstuk 5 was van jou afkomstig. Dankjewel! Heinjo, bedankt voor je nuchtere, kritische blik op alle zaken en de discussies: vooral over het hoogte- en diametergroeiverhaal en de definitie van releases. Altijd kwam er uit een puntenwolk wel weer een patroon naar boven! Ook Niels en Marielos hebben hoofdstukken uit dit proefschrift kritisch doorgelezen, veel dank daarvoor. Ute, bedankt voor de discussies over de ringen, en Feike voor de suggesties voor het berekenen van volumegroei.

I started my PhD in the Plant Ecology Group, in the meantime I came back from Bolivia in the Plant Ecology and Biodiversity Group, and I finished my thesis in the Ecology and Biodiversity Group. Quite some changes over the last four years. A lot of people were part of the group, at least at some stage. It was very nice to work in a group with such a variety of research topics. I tried to include all of you: Arjen (sorry, I did not kill the guppies on purpose), Bas, Bas, Betty, Binh, Bjorn, Boacheng, Boudewijn, Chien, Claudia, David, Feike, Galia, Gerrit, Gerrit, Hans, Henri, Heinjo, Jan, Joost, Jos, Judith, Juliana, Karlijn, Liang, Maria Paula, Mariet, Marijke (we always agreed on the tropical temperatures in our room!), Marinus, Mario, Marja, Merel, Niels, Olaf, Onno, Paddy, Paul, Peter, Pieter, Roel, Ronald, Roy, Sander, Sandra, Shouli, Sonja, Suzanne, Sylvia, Tiep, Toshi, Walter, Wang, Yuki, Yun and Yusuke (was nice to have you as an officemate!). Thanks for the good time! Ook wil ik graag Bertus (o.a. voor het redden van mijn laptop door het Boliviaanse stof onder de aan/uit-knop te verwijderen), Martie, Natasja en Piet bedanken voor de logistieke ondersteuning. En Henri, voor de hulp met de ringen in Utrecht.

Een woord van dank aan mijn familie en vrienden. Dank voor alle steun en goede raad (die meteen weer in de wind geslagen werd natuurlijk…) en sorry dat ik er soms enigszins gestresst bijliep de laatste tijd. Ik krijg het nu echt minder druk, en zal inderdaad (ja, het staat er echt) eens op vakantie gaan binnenkort!

Demian, ik vond het erg leuk dat je langskwam in Riberalta, en dat we de tijd hadden om een paar weken rond te reizen door Bolivia. Door jouw (duizenden?) prachtige foto's heeft de rest van de familie ook een aardig idee van het Boliviaanse wereldje gekregen.

Tonnie, heel veel dank voor het vormgeven van dit boekje! Dat was een flinke klus. Het ziet er prachtig uit.

Met een harde schijf vol muziek was het in Riberalta absoluut geen punt om de wereld eens een jaartje door een microscoop te bekijken! Ik had dan wel een Boliviaanse viool van tropisch hardhout, die het trouwens best goed deed, toch is het erg fijn om weer echt muziek te maken nu. Dank aan alle muzikanten, en vooral de Zoro's natuurlijk.

# CURRICULUM VITAE

Danaë Rozendaal was born on the 18th of August 1981 in Amsterdam, the Netherlands. In 1999 she obtained her high school degree at the Gymnasium Camphusianum in Gorinchem. In the same year she started her Biology studies at Utrecht University. During her studies she specialized in tropical ecology and conducted two research projects. The first project was carried out in the group of Plant Systematics at Utrecht University. With the use of a phylogeny she reconstructed the evolution of *Eperua* (Fabaceae), linked to pollination ecology, distribution and habitat ecology. She conducted fieldwork in Suriname and Guyana during six weeks. In her second research project at the Plant Ecology Group, Utrecht University, she studied functional leaf traits of 39 Bolivian moist forest tree species, differing in shade and drought tolerance. For this project she worked during six months in Bolivia. In October 2005 she started as a PhD-student at the Plant Ecology group (now Ecology and Biodiversity Group) to work on tree rings of Bolivian trees to evaluate long-term growth patterns. She spent two years in Santa Cruz and Riberalta, Bolivia, to conduct the fieldwork and tree-ring measurements.

## PUBLICATIONS

**Poorter L, Rozendaal DMA. 2008.** Leaf size and leaf display of thirty-eight tropical tree species. *Oecologia* **158:** 35-46.

**Rozendaal DMA, Hurtado VH, Poorter L. 2006.** Plasticity in leaf traits of 38 tropical tree species in response to light; relationships with light demand and adult stature. Functional *Ecology* **20:** 207-216.

**Rozendaal DMA, Brienen RJW, Soliz-Gamboa CC, Zuidema PA. in press.** Tropical tree rings reveal preferential survival of fast-growing juveniles and increased juvenile growth rates over time. *New Phytologist.* doi: 10.1111/j.1469-8137.2009.03109.x

## PROMAB PUBLICATIONS

### Scientific Series

1. **Poorter L. 1998.** Seedling growth of Bolivian rain forest tree species in relation to light and water availability. PhD thesis, Utrecht University. 195 pp.
2. **Zuidema PA. 2000.** Demography of exploited tree species in the Bolivian Amazon. PhD thesis, Utrecht University. 240 pp.
3. **Peña-Claros M. 2001.** Secondary forest succession - Processes affecting the regeneration of Bolivian tree species. PhD thesis, Utrecht University. 170 pp.
4. **Bojanic Helbingen A. 2001.** Balance is beautiful: assessing sustainable development in the rain forest of the Bolivian Amazon. PhD thesis, Utrecht University. 256 pp.
5. **Henkemans AB. 2002.** Tranquilidad and hardship in the forest: livelihoods and perceptions of Camba forest dwellers in the northern Bolivian Amazon. PhD thesis, Utrecht University. 285 pp.
6. **Zuidema PA. 2003.** Ecology and management of the Brazil nut tree (*Bertholletia excelsa*). 112 pp.
7. **Henkemans AB. 2003.** Tranquilidad y sufrimiento en el bosque. Recursos de sostento y percepciones de los Cambas en el bosque de la Amazonía Boliviana. Spanish translation of PhD thesis. 97 pp.
8. **Bojanic Helbingen A. 2003.** El balance es lo hermoso: el desarrollo sustentable y los bosques de la Amazonía Boliviana. Spanish translation of PhD thesis. 129 pp.
9. **van Rheenen HMPJB. 2005.** The role of seed trees and seedling regeneration for species maintenance in logged-over forests - a study in the Bolivian Amazon rainforest. PhD thesis, Utrecht University. 142 pp.
10. **Brienen RJW. 2005.** Tree rings in the tropics: a study on growth and ages of Bolivian rain forest trees. PhD thesis, Utrecht University. 142 pp.
11. **Selaya NG. 2007.** Sprinting, climbing and persisting: light interception and carbon gain in a secondary tropical forest succession. PhD thesis, Utrecht University. 158 pp.
12. **Rozendaal DMA. 2010.** Looking backwards: using tree rings to evaluate long-term growth patterns of Bolivian forest trees. PhD thesis, Utrecht University. 152 pp.

## Technical Series

1. **Peña M, Zuidema PA, Zonta A, Goncalves A, Chapi G. 2001.** Producción de palmito: limitaciones del manejo sostenible de poblaciones naturales de Asai (*Euterpe precatoria*) y el potencial de cultivo de embe (*Bactris gasipaes*) como fuente alternativa. PROMAB/IPHAE, Bolivia. 47 pp.
2. **Poorter L, Boot RGA, Hayashida Y, Leigue J, Peña M, Zuidema PA. 2001.** Estructura y dinámica de un bosque húmedo tropical en el norte de la Amazonía Boliviana. PROMAB, Bolivia. 54 pp.
3. **Poorter L. (Editor) 2003.** Investigaciones ecológicas, forestales y socioeconómicas en el norte de la Amazonía Boliviana. PROMAB, Bolivia. 141 pp.
4. **Santibañez JL. 2003.** Evaluación de la cacería por castañeros, y su impacto sobre la fauna silvestre en una barraca castañera del norte de Bolivia. 39 pp.
5. **Murakami S, Boot R, Leigue Gomez J, Llanque O, Zuidema PA. 2003.** Madera residual en un bosque aprovechado en el norte de Bolivia: Evaluación de seis especies. PROMAB, Bolivia, 13 pp.
6. **van Rheenen J, Boot R, Zuidema PA, Werger M, Ulloa M, Wieringa N, Vos V, Guardia S. 2003.** Regeneración natural de árboles maderables en un bosque aprovechado en la Amazonía Boliviana: Resultados de estudios y sus implicancias para el manejo sostenible. PROMAB, Bolivia, 27 pp.
7. **Brienen R, Zuidema PA. 2003.** Anillos de crecimiento de árboles maderables en Bolivia: Su potencial para el manejo de bosques y una guía metodológica. PROMAB/IGEMA, Bolivia, 33 pp.
8. **Brienen R, Zuidema PA, Leigue Gomez J. 2003.** Recuperación del volumen de madera bajo diferentes ciclos de corta: Resultados de simulaciones para seis especies maderables en el Norte de Bolivia. PROMAB, Bolivia, 32 pp.

These publications can be obtained free of charge from www.promab.org. Recent information on PROMAB publications can be found at www.promab.org.

To reach better understanding of tropical forest dynamics long-term data on tree growth are required. Tree-ring analysis provides the opportunity to obtain ages and growth rates over the entire lifespan of tropical trees. This PhD thesis reports on the use of tree-ring analysis for reconstructing long-term growth patterns of trees in tropical forests in Bolivia. Tree-ring data of trees over the entire size range were collected for five tropical tree species. These data were used to evaluate whether only fast-growing juvenile trees attain the canopy ('juvenile selection effect'). The consequence of such a juvenile selection effect on projected timber yield recuperation was evaluated. Second, changes in tree growth and forest dynamics over time were assessed. Last, historical stem volume growth of juvenile trees was reconstructed to study long-term investments in stem diameter and height growth.

Universiteit Utrecht

Prince
Bernhard
Chair

PROMAB
Asociación Programa de Manejo de Bosques de la Amazonia Boliviana
HERENCIA UAB UAP IPHAE

NWO
Netherlands Organisation for Scientific Research