Forensic forest ecology

Unraveling the stand history of tropical forests

Mart Vlam

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Unraveling the stand history of tropical forests

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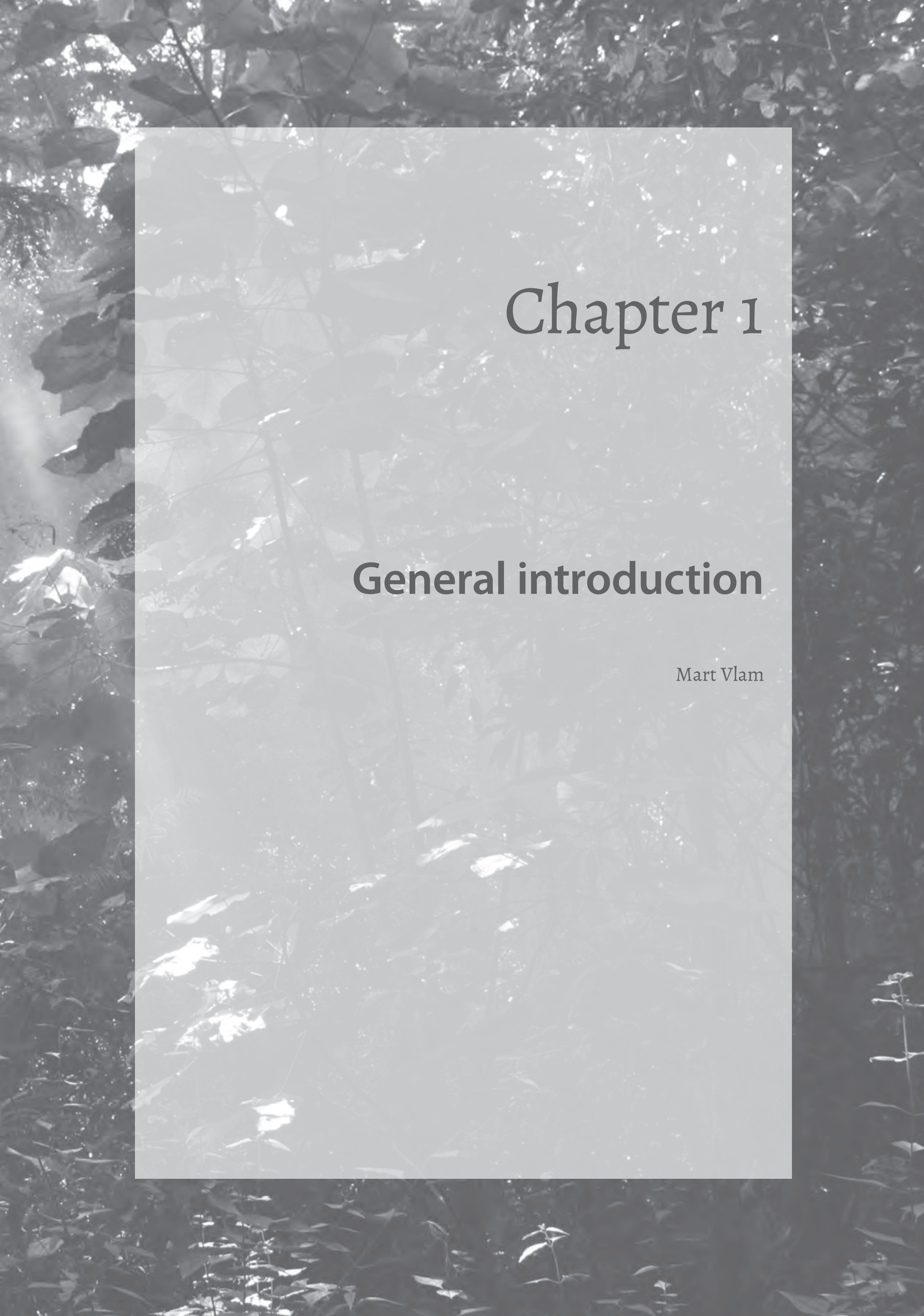


Chapter 1

General introduction

Mart Vlam

Tropical forests and global change

Tropical forests cover only 7% of the land area on earth, but they harbor an estimated half of all the species in the world (Dirzo and Raven 2003). Also tropical forests provide numerous products and services to humankind, for example watershed control, supply of timber, medicine and food (Bonan 2008, Corlett 2011). Furthermore, tropical forests play a key role in the global carbon cycle by storing 25% of carbon in terrestrial ecosystems and accounting for one third of the terrestrial net primary production (Bonan 2008, Lewis et al. 2009b).

Historically tropical forests were seen as relatively stable and undisturbed systems and the focus in studies on forest dynamics has long been on the role of small scale gaps (Denslow 1980, Brokaw 1985). However, the perception of tropical forests as ancient and immutable systems has gradually changed over the past decades, recognizing the fact that tropical forests have long been impacted by large-scale and/or high-intensity natural and human-induced disturbances (Whitmore and Burslem 1998). These disturbances are occasional, spatially extensive canopy disturbances that affect several hectares of forest, but may be heterogeneous in intensity (Whitmore and Burslem 1998, Splechtna et al. 2005, Baker and Bunyavejchewin 2009).

At present tropical forests experience an additional type of disturbance in the form of human-induced change of the climate and atmosphere (Corlett 2011). Over the past two centuries atmospheric CO_2 levels have increased nearly 40% and temperatures around the tropics are rising (IPCC 2007). Because of the crucial role of tropical forests in biodiversity and the global carbon cycle, a better understanding of anthropogenic global change impacts on tropical forest dynamics is much needed (Wright 2005).

Are tropical forest dynamics changing?

Over the past decades remarkable biomass increases of intact rainforest stands in Amazonia (Phillips et al. 1998, Baker et al. 2004) and tropical Africa (Lewis et al. 2009b) have been reported. And tropical forests are also becoming more dynamic, showing increased recruitment and mortality rates (Baker et al. 2004, Lewis et al. 2004, Phillips et al. 2004). These changes in forest dynamics have been related to external drivers, such as increased atmospheric CO_2 levels (Malhi and Phillips 2004, Lewis et al. 2009a) and increasing temperatures (Feeley et al. 2007b). However, it has also been suggested that recovery after past disturbance, may cause similar patterns of forest stand dynamics (Fisher et al. 2008, Chambers et al. 2013). Evidence has been found that tropical forests are occasionally subject to intense canopy disturbances, including multiple-tree blowdowns (Nelson et al. 1994, Vandermeer et al. 2000, Gleason et al. 2008), fire (Baker et al. 2008) and extreme droughts (Slik 2004, Nepstad et al. 2007), just like temperate forests (D'Amato and Orwig 2008). Both global change and recovery after past disturbance may result trends in tropical tree growth and forest biomass at the timescale of decades (Chazdon 2003, Chave et al. 2008).

The conventional way to study long-term tropical forest dynamics has been decadal scale measurements of tree turnover and tree growth in permanent sample plots (e.g., Baker et al. 2004, Clark et al. 2010). However, historical large-scale natural or anthropogenic disturbances that occurred long before the installation of these plots may leave an imprint on present-day stand dynamics (Chai and Tanner 2011) and therefore affect current observations (Chave et al. 2008). This has led to concerns regarding the short temporal scale of most permanent plot studies and the century-long timescale at which changes in forest stand dynamics may occur (Chambers et al. 2013, Zuidema et al. 2013). The century-long life spans of trees and the low return frequency of large-scale disturbances (Kellner and Asner 2009), require reconstruction of stand dynamics at a centennial scale. Long-term tree growth data obtained from tree-ring analyses provides an opportunity to study tropical tree growth and forest dynamics at a century-long time scale (Zuidema et al. 2013).

Tropical tree-ring research

A rapidly developing field

Unlike boreal and temperate forest research, tree-ring research in tropical forests has only recently become a widely recognized discipline (Worbes 2002, Zuidema et al. 2012). The historical underrepresentation of tropical forest systems has mainly been due to the long standing perception that tropical trees do not form annual growth rings (Lieberman et al. 1985, Whitmore 1998). This perception can be traced back to the idea that there is no clear seasonality in the tropics, but also a general lack of awareness of earlier work on tropical tree-ring analysis (Jacoby 1989). At present it is widely recognized that many tropical forests experience an annually returning dry season, resulting in cambial dormancy in trees and annual rings being formed (Worbes 1995).

Various tree-ring studies around the tropics have confirmed the annual nature of tree rings by correlating ring-width and annual climate variability, for example in the Neotropics (Dünisch et al. 2003, Brienen and Zuidema 2005), Africa (Schöngart et al. 2006, Couralet et al. 2010), and Southeast Asia (Buckley et al. 1995, Pumijumnong et al. 1995). Yet, many of these studies were restricted to strongly seasonal tropical (dry) forests (e.g., Brienen et al. 2010a), montane forest species (Buckley et al. 1995) and gymnosperms growing at tropical latitudes (Buckley et al. 1995, Pumijumnong and Wanyaphet 2006, Zuidema et al. 2011). Tree-ring studies describing climate-growth relations of broadleaf lowland tropical tree species are still limited, though they could potentially provide valuable information on the response of tropical trees to projected climate change.

Tropical dendroecology and forest stand dynamics

Dendroecology - the use of tree-rings to study ecological processes – is also a well-established methodology to investigate stand history in boreal and temperate forests (Kuuluvainen et al. 2002, Rubino and McCarthy 2004, Fraver et al. 2008, Simkin and Baker 2008). Age dating of trees in temperate forests has for example revealed recruitment peaks indicative for past canopy disturbance (Cullen et al. 2001, Splechtna et al. 2005). In this way dendroecology has already added considerably to our understanding of long-term stand dynamics of temperate forests.

Tropical dendroecology has developed rapidly over the last decade and important advances in methodology have been made (Rozendaal and Zuidema 2011). Tree-ring analysis has for example been used to describe the age structure of tropical forest stands in Africa and Southeast Asia (Worbes et al. 2003, Baker et al. 2005). Also, tree-ring analysis has been used to describe life time growth patterns of Bolivian trees (Brienen and Zuidema 2006b, Rozendaal et al. 2010b). Furthermore, tree-ring analysis has been used to describe long-term patterns of growth suppression and growth release and to explain species-specific canopy accession strategies (Baker and Bunyavejchewin 2006b, Brienen and Zuidema 2006a). A novel extension of this suppression-release approach was explored by Rozendaal et al. (2011), who used this analysis as a proxy to study long term trends in forest stand dynamics.

Challenges of tropical tree-ring analysis

Despite the possibilities provided by tropical dendroecology, there are limitations to the use of tree-ring analysis in the tropics. First of all, the number of tropical tree species forming visually identifiable rings is limited (Poussart et al. 2004) and a thorough estimate of the prevalence of annual rings in tropical trees is still lacking. Baker et al. (2005) estimated that around one third of the tree species in a seasonal dry evergreen forest of western Thailand formed annual rings. For lowland tropical rainforests (1800-2400 mm of rain per year) the annual nature of rings has been reported for almost 70 species (Zuidema et al. 2012). However, even when trees do form annual rings, the complex wood anatomy of tropical trees may hamper the feasibility of tropical dendrochronology and dendroecology (Stahle 1999). For example false and wedging rings are more commonly observed in tropical than in temperate tree species (Worbes 1995). Also, the high species diversity in tropical forests combined with the limited number of species forming reliable annual rings requires inferences to be made on the wider tree species community. Additionally, a general lack of high quality, long-term climate records for many areas around the tropics is hampering adequate analysis of the relation between tree growth and annual climate variation.

These are some of the challenges faced by tree-ring research in the tropics. However, tree-ring data also provides a unique opportunity to study patterns and processes of tropical forest ecology at new, nearly unexplored, century-long timescales. Tree-ring analysis can therefore shed new light on findings from networks of relatively short-term (i.e. decadal scale) permanent sample plot studies.

Forensic forest ecology

Changing site conditions that occur after removal of (part of) the forest canopy cover, may cause temporally increased recruitment rates of shade-intolerant tree species (Oliver and Larson 1996). Such an event can be witnessed from an irregular age structure of the forests stand, which can be maintained decades or centuries after the disturbance (Lorimer 1980). Analyzing tree age distributions may therefore provide clues on historical events that still affect current stand structure. By looking at the spatial structure of establishment dates of shade-intolerant tree species, we can reconstruct the occurrence of canopy openings through space and time. Spatial analyses of tree ages have been successfully applied in temperate forests to relate the scale of clustering of even-aged trees to the size and distribution of canopy openings formed by past disturbances (Cullen et al. 2001, Rozas 2003, Sánchez Meador et al. 2009). To my knowledge spatial analysis of tree age has never been applied in tropical forests.

In this thesis I combine tree-ring derived population age structures with spatial analysis of tree age. Together with additional data on tree-ring derived growth rates and canopy height measurements a toolbox is created for assessing past forest stand dynamics. The approach I used in this thesis is 'forensic forest ecology': a combination of forensic science – the scientific method of gathering and examining information about the past, with forest ecology – the study of patterns and processes in forests. By combining these two concepts forensic forest ecology emerges, which is aimed to examine information about the past patterns and processes in forests (see also: Wessels 1997). In this thesis I use forensic forest ecology to gather all possible clues, such as tree age and life-time growth rates of trees, to reconstruct historical tropical forest stand dynamics.

Pan-tropical approach

The research presented in this thesis is part of the TROFOCLIM (tropical forests and climate change) project initiated by Dr. Pieter A. Zuidema. The objective of the project was to 'detect, explain and predict long-term climate change effects on tropical tree dynamics' (P.A. Zuidema 2009, *TROFOCLIM project proposal*). The project team consists of one principal investigator (Dr. Pieter A. Zuidema), one postdoc (Dr. Peter Schippers) and three PhD students (Peter Groenendijk MSc, Peter van der Sleen MSc and Mart Vlam MSc). Together this team assembled a tree-ring dataset containing more than 1350 trees belonging to 14 different tree species from three sites in three countries: Bolivia, Cameroon and Thailand. In each country we sampled following the population structure and using an identical sampling scheme. The resulting dataset is larger than any previous dendroecological study in the tropics (e.g., Baker et al. 2005, Rozendaal et al. 2011) and is spanning the three major tropical biomes: the Amazon, Africa and Southeast Asia. The large dataset provides statistical power to test questions and hypotheses on tropical forest stand dynamics and tree regeneration ecology. Additionally, the study design allowed us to address questions on tropical tree ecology and tropical forests stand dynamics at a pan-tropical scale.

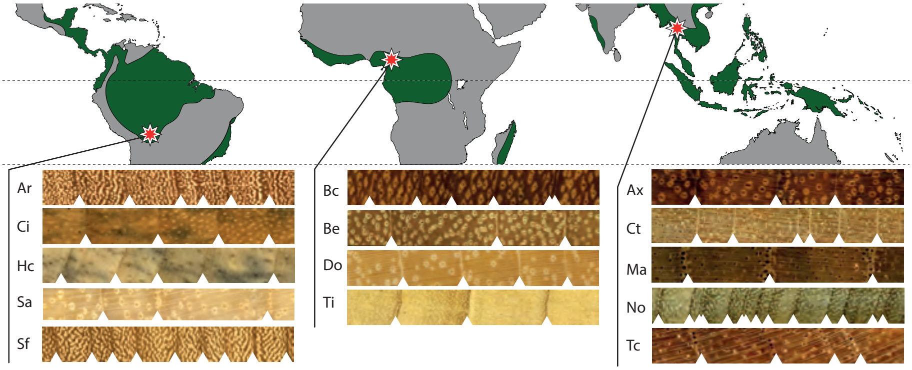


Figure 1.1 Approximate locations of the study areas (top) and wood characteristics of the 14 study species (bottom). The star symbol on the map indicates the approximate location of the study areas in Bolivia, Cameroon and Thailand. White arrows on the wood images indicate tree-ring boundaries. Ar=*Ampelocera ruizii*, Ci=*Cariniana ianeirensis*, Hc=*Hura crepitans*, Sa=*Schizolobium amazonicum*, Sf=*Sweetia fruticosa*, Bc=*Brachystegia cynometroides*, Be=*Brachystegia eurycoma*, Do=*Daniellia ogea*, Ti=*Terminalia ivorensis*, Ax=*Afzelia xylocarpa*, Ct=*Chukrasia tabularis*, Ma=*Melia azedarach*, No=*Neolitsea obtusifolia*, Tc=*Toona ciliata*.

Main objectives

Main objectives of my research project were: (1) To determine the relation between ring width and annual temperature and rainfall variability. Such climate-growth analysis is needed for a better understanding of the potential effect of climate change on tropical tree growth and the carbon balance of tropical forests. (2) To develop methods that combine tree-ring data and spatial analyses to assess the evidence for past large scale canopy disturbances in tropical forests. (3) To reconstruct the disturbance history of tropical forest stands by applying a forensic forest ecology approach. (4) To assess the evidence for long-term alterations in tropical forest dynamics. Such directional changes in tropical forest dynamics may be global change driven, for example by increased atmospheric CO_2 levels, but could also be due to stand development following past disturbance or resulting from natural climate variability.

Study areas and study species

The study was carried out in three tropical forests on three continents: Bolivia, Cameroon and Thailand (Fig. 1.1; Table 1.1). Of my four year PhD project I have in total spent nearly one year in Thailand. Similarly, Peter van der Sleen carried out fieldwork in Bolivia, where he spent nearly two years and Peter Groenendijk spent around one year to collect wood samples in Cameroon. During the course of the project we also made visits to each other's fieldwork sites.

Table 1.1 Characteristics of the study sites in Bolivia, Cameroon and Thailand: elevation (in m above sea level); mean annual rainfall amount; mean annual temperature; Dry season length (months); canopy height (m); tree density (*n* trees ≥10 cm ha^{-1}).

Country	Study area name	Elevation	Rainfall[1]	Temp.[1]	Dry season	Canopy height	Tree density[2]
Bolivia	La Chonta	336 m	1580 mm	24.5 °C	5 mo.	25 m	367
Cameroon	Transformation REEF Cameroon	180 m	~4000 mm	26.7 °C	3 mo.	35 m	492
Thailand	Huai Kha Khaeng	567 m	1470 mm	23.5 °C	6 mo.	31 m	438

[1]Climatological data for Cameroon and Thailand and temperature data for Bolivia were obtained from the KNMI Climate Explorer website (Trouet and Van Oldenborgh 2013). Precipitation data for La Chonta was collected at the sawmill over the period 1993-2006. [2]Tree density data was derived from nearby forest dynamics plots: Bolivia (Peña-Claros et al. 2008a); Cameroon (Chuyong et al. 2004); Thailand (Bunyavejchewin et al. 2009).

Huai Kha Khaeng Thailand

The study area where I worked was situated in the Huai Kha Khaeng Wildlife Sanctuary (HKK), Uthai Thani province, western Thailand, approximately 250 km northwest of Bangkok (15.60 N, 99.20 E). HKK is a protected area of global conservation significance. Both HKK and the adjacent Thung Yai-Naresuan Wildlife Sanctuary are International Man and Biosphere Reserves and together form the main core of Thailand's Western Forest Complex, the largest area of protected forest in continental Southeast Asia. The HKK landscape is characterized by a hilly topography and the soils are highly weathered slightly acidic ultisols (Bunyavejchewin et al. 2009). Mean annual rainfall is around 1473 mm (1993-2001) and the 4-6 month dry season ranges from November to April. Mean annual temperature is 23.5 °C. There is almost no human influence in HKK, except for the Wildlife Sanctuary infrastructure and humans may provide an ignition source for surface fires expanding from agricultural areas around the park (Baker et al. 2008). No logging activities are known to have taken place in the study area. The vegetation in the area is classified as seasonal dry evergreen forest and mixed deciduous forest. A Smithsonian Center for Tropical Forest Science (CTFS) 50-ha forest dynamics plot, installed in 1992, is immediately adjacent to the area we used for our tree-ring study (Fig. 1.1). Mean density of trees ≥10 cm dbh in the 50-ha plot is 438 ha^{-1} and mean density of trees ≥30 cm dbh is 83 ha^{-1} (Bunyavejchewin et al. 2001). Canopy height of the forest is around 30 m, with occasional emergent trees reaching more than 50 m tall. Members of the family Dipterocarpaceae dominate the forest in total basal area; other well-represented families include Annonaceae, Euphorbiaceae and Meliaceae (Bunyavejchewin et al. 2001).

Table 1.2 Characteristics of the 14 study species with their shade-tolerance guild (ST, shade-tolerant; PST, partial shade-tolerant; LLP, long-lived pioneer), leaf phenology (E, evergreen; D, deciduous; BD, brevi-deciduous) and chapters in which they are included.

Country	Species	Family	Ecological guild[1]	Leaf phenology[2]	Chapter
Bolivia	*Ampelocera ruizii*	Ulmaceae	ST	E	5,6
	Cariniana ianeirensis	Lecythidaceae	PST	D	5,6
	Hura crepitans	Euphorbiaceae	PST	D	5,6
	Schizolobium amazonicum	Fabaceae	LLP	D	5,6
	Sweetia fruticosa	Fabaceae	LLP	BD	5,6
Cameroon	*Brachystegia cynometroides*	Fabaceae	PST	D	5,6
	Brachystegia eurycoma	Fabaceae	PST	D	5,6
	Daniellia ogea	Fabaceae	LLP	D	5,6
	Terminalia ivorensis	Combretaceae	LLP	D	5,6
Thailand	*Afzelia xylocarpa*	Fabaceae	LLP	D	2,4,5,6
	Chukrasia tabularis	Meliaceae	PST	BD	2,5,6
	Melia azedarach	Meliaceae	LLP	D	2,3,5,6
	Neolitsea obtusifolia	Lauraceae	ST	E	2,5,6
	Toona ciliata	Meliaceae	LLP	D	2,5,6

[1]Ecological Guilds: Bolivia (Peña-Claros et al. 2008b), Cameroon (Hawthorne 1995), Thailand (Baker et al. 2005) and the definitions are in accordance with (Poorter et al. 2006); [2]Phenology: Bolivia (Mostacedo et al. 2003), Cameroon (Hawthorne 1995, Lemmens et al. 2012), Thailand (Williams et al. 2008).

La Chonta Bolivia

In Bolivia samples were collected in the logging concession ‘La Chonta’ (15.84 S, 62.85 W). The forest in La Chonta is a semi-deciduous moist forest that is transitional between Chiquitano dry forest and moist Amazonian forests (Peña-Claros et al. 2012). Elevation ranges between 298 and 436 m above sea-level. Soils have been classified as relatively fertile ultisols due to human influences. Total annual precipitation in the region is around 1580 mm, with a five month dry season receiving <100 mm precipitation per month from May to September and mean annual temperature is 24.5 °C. Like most of the forests in the Amazon, the area has been selectively logged at low intensity (ca. 1 m^3/ha) for the commercially valuable broad-leaf mahogany (*Swietenia macrophylla*) (Pinard et al. 1999, Gould et al. 2002). This logging took place around 1992, but we have found no direct evidence, for example old skid trails or tree stumps, which indicate logging in our study area. There is, however, abundant evidence for anthropogenic dark earths or 'terra preta' in the area, indicating that the site was inhabited 300-400 years ago (Paz-Rivera and Putz 2009).

Transformation REEF Cameroon

The site in Cameroon (5.25 N, 9.10 E) is a semi-deciduous tropical rainforest of the Guineo-Congolian type. Samples were collected in logging concession 11.001 operated by Transformation REEF Cameroon (TRC). This concession is adjacent to the northwest border of Korup National Park. The forest is locally dominated by groves of Fabaceae-Caesalpinioideae species and other important families in terms of basal area are Euphorbiaceae and Scytopetalaceae (Chuyong et al. 2004). Elevation levels are approximately 100 m above sea-level and soils are sandy and nutrient poor (Chuyong et al. 2004). Mean total annual rainfall is around 4000 mm and mean annual temperature 26.7 °C (Nchanji and Plumptre 2001). The climate is characterized by a distinct three month dry season from December to February with monthly rainfall levels <100 mm. Of the three sites TRC probably has the highest human influence, as several villages are located in directly around the logging concession.

Sample collection

We collected stem discs and increment cores from 14 different tree species. Main criteria for species selection were: (1) Presence of visually identifiable rings and (2) adequate local abundance to reach a target sample size of approximately 100 trees. Together the 14 species represent various families, a variety in leaf phenology characteristics and ecological guilds: from shade-tolerant to very shade-intolerant long-lived pioneers (Table 1.2). We sampled shade-intolerant species, because regeneration events of these species were expected to be a valuable proxy for past canopy disturbance.

Thesis outline

This thesis consists of seven chapters: The introduction (CHAPTER 1), five research chapters (CHAPTERS 2-6) and a general discussion (CHAPTER 7).

In CHAPTER 2 we determine climate sensitivity of broad-leaved tropical tree species. We used tree-ring data from five tree species collected in the study site in HKK western Thailand. A better understanding of climate-growth relations of tropical trees is needed, because climate change effects on growth rates of tropical trees may lead to alterations in carbon cycling of carbon-rich tropical forests.

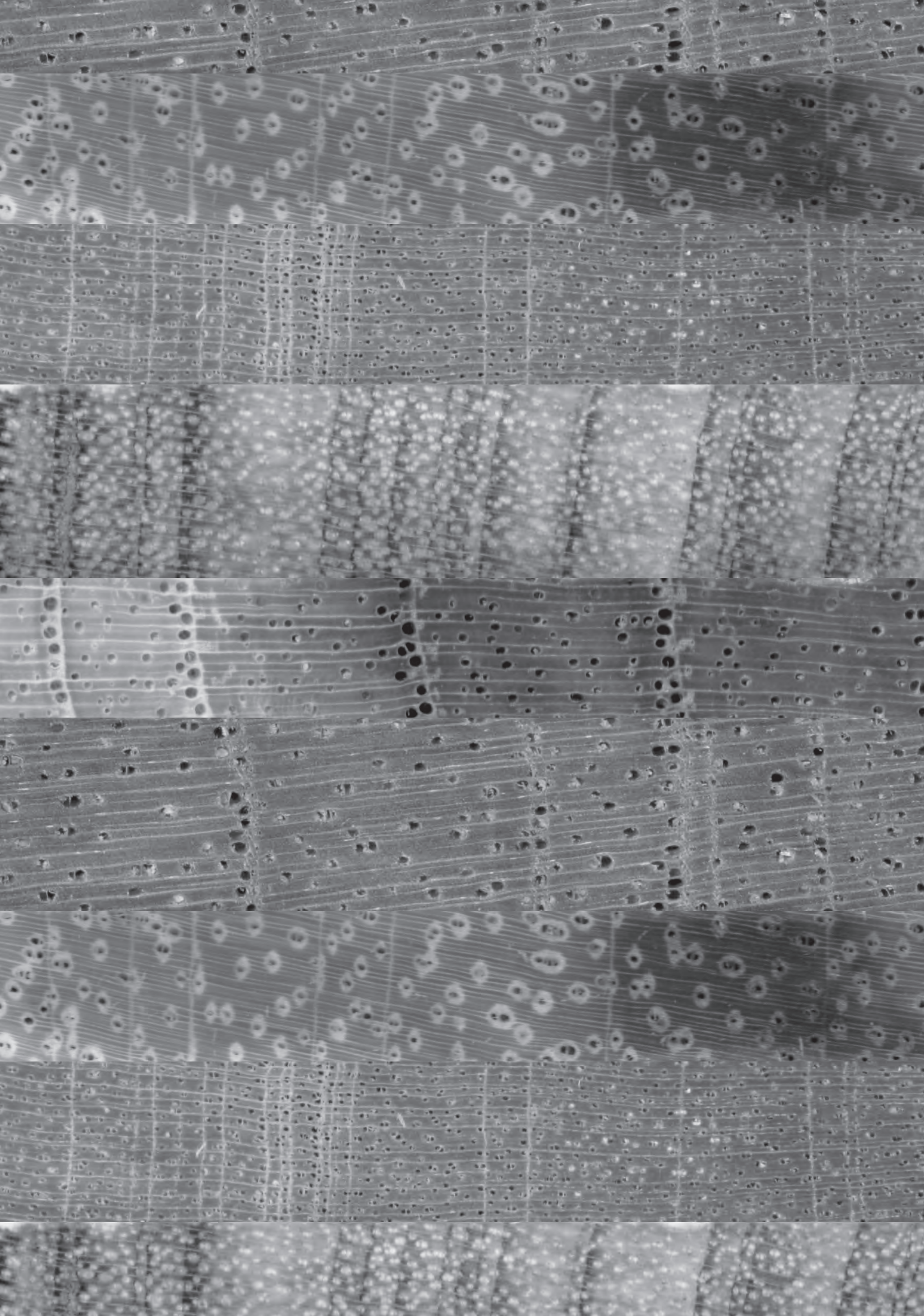
In CHAPTER 3 we examine the potential of combining dendroecological analysis and spatial statistics. This is the first time that this combination of techniques has been used to reconstruct the disturbance history of a tropical forest stand. We used tree-ring-derived age estimates for 70 individuals of the shade-intolerant pioneer species *Melia azedarach* (Meliaceae) and tree locations across a 316-ha study plot in Thailand to identify the timing and spatial extent of past disturbances.

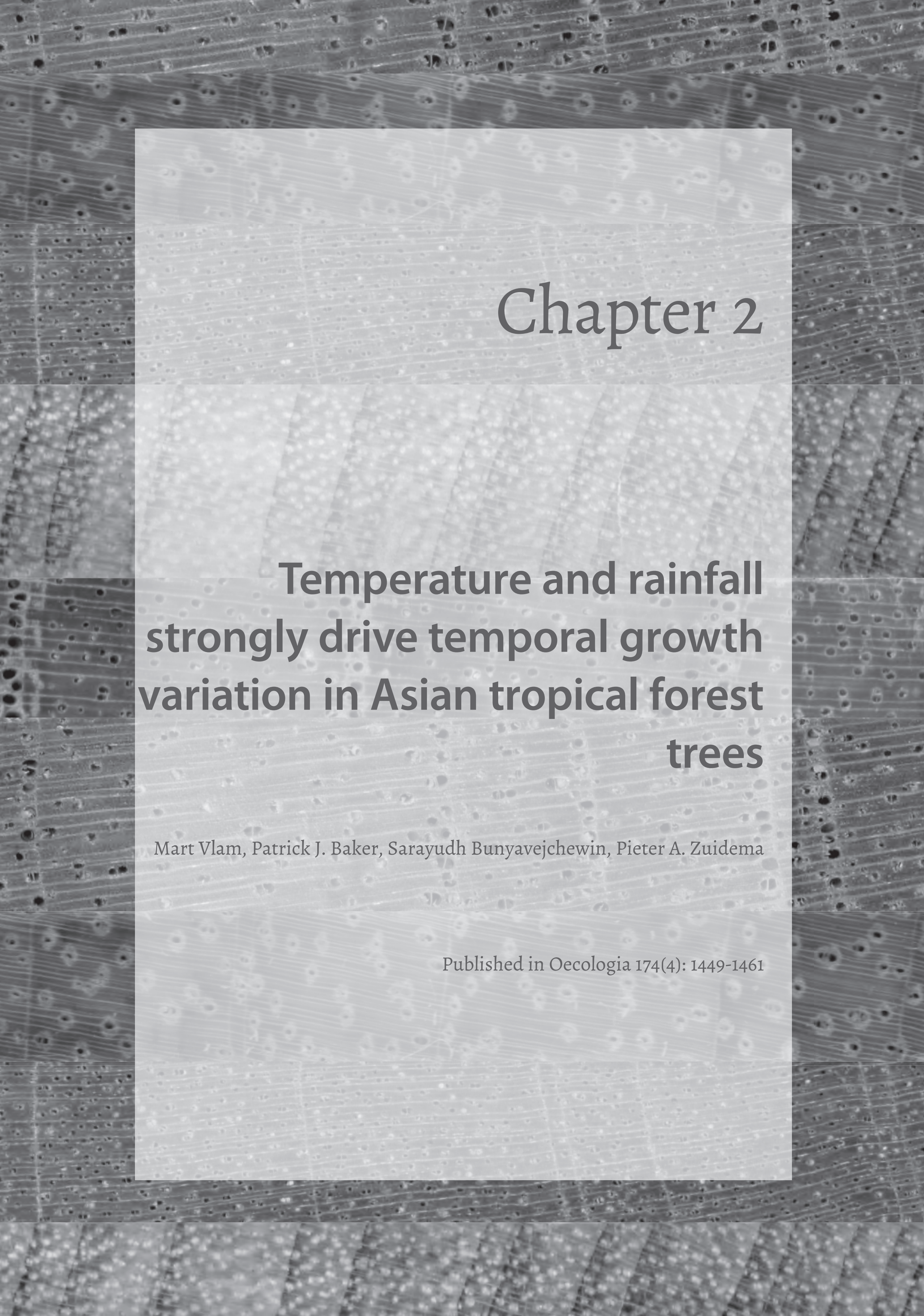
In CHAPTER 4, we use forensic forest ecology to obtain tree ages and reconstruct >200 years of establishment rates in a poorly regenerating population of *Afzelia xylocarpa* (Fabaceae), a shade-intolerant and long-lived canopy tree species. Knowing how, when and where such a tree species regenerates provides insights into the life history characteristics of the species and may identify drivers of forest dynamics in the HKK area in Thailand.

CHAPTER 5 presents a disturbance reconstruction based on tree ring dating of three sites across the tropics. In this chapter tree-ring derived age estimates of all 14 tree species collected at the sites in in Bolivia, Cameroon and Thailand are used.

In CHAPTER 6 we use the occurrence of growth releases recorded in tree-ring series as a proxy for studying forest dynamics over the past centuries. In this chapter we also use the complete dataset of >1350 trees gathered at the three study sites in Bolivia, Cameroon and Thailand.

In CHAPTER 7 the main findings of this thesis are discussed. I present an overview of the most common drivers of large scale disturbance in tropical forests. Then I discuss the applicability of forensic forest ecology in the tropics and my recommendations for further use. I discuss the limitations of tree-ring research for studying tropical forest dynamics. And finally the implications of disturbance-recovery cycles for studying tropical forest responses to global change are discussed.





Chapter 2

Temperature and rainfall strongly drive temporal growth variation in Asian tropical forest trees

Mart Vlam, Patrick J. Baker, Sarayudh Bunyavejchewin, Pieter A. Zuidema

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Abstract

Climate change effects on growth rates of tropical trees may lead to alterations in carbon cycling of carbon-rich tropical forests. However, climate sensitivity of broad-leaved lowland tropical trees is poorly understood. Dendrochronology (tree-ring analysis) provides a powerful tool to study the relation between tropical tree growth and annual climate variability. We aimed to establish climate-growth relations for five annual-ring forming tree species, using ring-width data from 459 canopy and understory trees from a seasonal tropical forest in western Thailand. Based on 183/459 trees, chronologies with total lengths between 29 and 62 years were produced for four out of five species. Bootstrapped correlation analysis revealed that climate-growth responses were similar among these four species. Growth was significantly negatively correlated with current year maximum and minimum temperatures and positively correlated with dry season precipitation levels. Negative correlations between growth and temperature may be attributed to a positive relation between temperature and autotrophic respiration rates. The positive relation between growth and dry season precipitation levels likely reflects the strong water demand during leaf flush. Mixed-effect models yielded results that were consistent across species: a negative effect of current wet season maximum temperatures on growth, but also additive positive effects of for example prior dry season maximum temperatures. Our analyses showed that annual growth variability in tropical trees is determined by a combination of both temperature and precipitation variability. With rising temperature, the predominantly negative relation between temperature and growth may imply decreasing growth rates of tropical trees as a result of global warming.

Keywords: Climate-growth relationship; global change; Thailand; Tree rings; Tropical tree

Introduction

Tropical forests are currently experiencing some of the most rapid rates of warming in recent geological times (Marcott et al. 2013). And not only are temperatures rising around the world, there are indications that temperature anomalies are becoming more frequent (Hansen et al. 2012). The response of tropical forests to global warming may potentially have large impacts on global carbon cycling (Corlett 2011). Warming may reduce leaf-level photosynthesis (Doughty 2011), increase autotrophic respiration rates (Lloyd and Farquhar 2008) and increase evaporative demand (Galbraith et al. 2010), resulting in reduced tree growth. As tropical forests contain one of the largest terrestrial carbon pools (Dixon et al. 1994, Malhi and Grace 2000), it is crucial to understand their response to warming (Clark et al. 2003).

In the absence of *in situ* tree-level warming experiments in the tropics, analysis of temporal tree growth variability in relation to annual climatic variation can be the next best source of information on global warming effects on tropical trees (Brienen et al. 2010a, Clark et al. 2010, Pumijumnong 2012). Repeated diameter measurements of tropical trees has shown that temporal variation in diameter growth was negatively correlated with temperature (Clark et al. 2003, Dong et al. 2012, Clark et al. 2013). However, due to the multi-year census interval of most permanent plot studies (e.g., Dong et al. 2012), the power of correlation analyses is generally low and the multi-year census interval requires an integration of yearly climate parameters over the census interval.

Tropical dendrochronology (tree-ring analysis) can provide long-term, high-resolution tropical tree growth data to complement plot-based repeated diameter measurements (Worbes 1995, Zuidema et al. 2013). Tropical tree species that form reliable annual growth rings provide annual-resolution growth data at multi-decadal to centennial scales, which enhance the detectability of climatic influences on growth variation in tropical trees (Zuidema et al. 2012). Multi-species tree-ring studies on climate-growth relations of broad-leaved trees from moist lowland tropical forests are rare, but studies in the Amazon (Dünisch et al. 2003, Brienen and Zuidema 2005) and West Africa (Schöngart et al. 2006) have shown that temporal variation in growth was positively correlated with total annual precipitation. In lowland tropical forests in Southeast Asia, analysis of the relation between climate and ring width has mainly focused on teak (*Tectona grandis*) (Pumijumnong et al. 1995, Buckley et al. 2007) and only a few examples of other species exist (e.g., Zuidema et al. 2011). Besides the generally low representation of lowland moist tropical forest trees species in climate-growth studies, the focus has traditionally been on precipitation correlations (Jacoby 1989, Rozendaal and Zuidema 2011, Pumijumnong 2012) and effects of temperature anomalies on annual growth variability were often not evaluated (Dünisch et al. 2003, Brienen and Zuidema 2005, Schöngart et al. 2006) or determined non-significant (Couralet et al. 2010). However, whereas there is large uncertainty regarding predicted rainfall changes for the tropics, a clear warming trend across most of the tropics is undisputed (IPCC 2007, Wright et al. 2009).

Here we use tree-ring analyses to evaluate tree growth sensitivity to climatic variation in Southeast Asia. We took tree ring samples from over 450 individuals belonging to five species known to form annual rings (Baker and Bunyavejchewin 2006b). These species represent three different families, vary in leaf phenology and represent several ecological guilds. The availability of >60 years of high quality climate data from a nearby meteorological station allowed us to address questions and hypotheses on the relationship between climate variability and tree growth. Specifically we addressed the following questions: (1) Is tree growth correlated with minimum and maximum temperature? (2) Is tree growth correlated with precipitation? Furthermore we used linear mixed-effects models to assess the relative importance of various seasonal climate indices on standardized diameter growth rates.

Materials and methods

Study area and species

The study area was situated in the Huai Kha Khaeng Wildlife Sanctuary (HKK), Uthai Thani province, western Thailand (15.60 N 99.20 E), approximately 550 m above sea-level. Climate in Huai Kha Khaeng is strictly seasonal with a marked dry season from November to April (Fig. 1a). Mean annual rainfall in HKK is 1473 mm and mean annual temperature is 23.5 °C (Bunyavejchewin et al. 2009). Soils are highly weathered, slightly acidic ultisols and soil textures are sandy loam at the surface and sandy clay-loam in the subsurface horizons (Bunyavejchewin et al. 2009). The vegetation in the area is classified as seasonal dry evergreen and mixed deciduous forest (Bunyavejchewin et al. 2009). Canopy height in the forest is around 30 m, with occasional emergent trees reaching 50 m. Members of the family Dipterocarpaceae dominate the area in total basal area; other well-represented families include Annonaceae, Euphorbiaceae and Meliaceae (Bunyavejchewin et al. 2001).

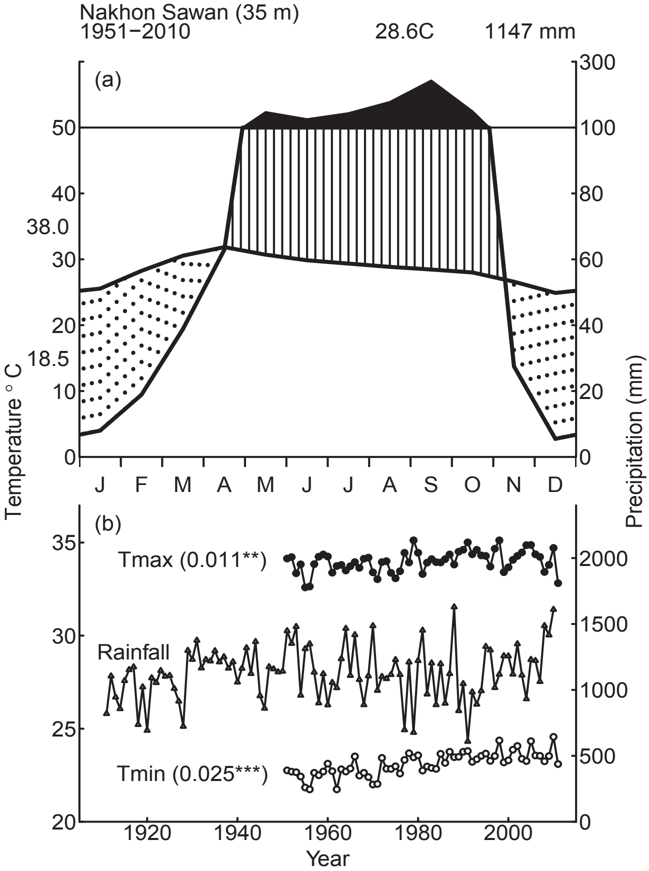

Figure 2.1 (a) Climate diagram for the Nakhon Sawan meteorological station, ~100 km east of the study site. (b) Annual precipitation and temperature observations from the Nakhon Sawan meteorological station. Upper line (T_{max}, filled circles) represents the mean daily maximum temperature, middle line rainfall (triangles) and lower line (T_{min}, open circles) is the mean daily minimum temperature. Linear regression models were fit to the temperature data and regression coefficients are indicated (*,**,*** for $P < 0.05$,0.01 and 0.001 respectively).

We sampled five tree species: *Afzelia xylocarpa* (Kurz) Craib (Fabaceae), *Chukrasia tabularis* A. Juss. (Meliaceae), *Melia azedarach* L. (Meliaceae), *Neolitsea obtusifolia* Merr. (Lauraceae) and *Toona ciliata* M. Roem. (Meliaceae). See Table

2.1 for a summary of the species' characteristics. All five species were known to form annual rings following a cambial wounding experiment over the period 1988-1998 (Baker et al. 2005). *Afzelia, Melia* and *Toona* have a distinctly deciduous leaf phenology, whereas *Chukrasia* is classified as brevi-deciduous and *Neolitsea* is evergreen (Williams et al. 2008). All five species are canopy trees, reaching maximum heights of 30-45 m.

Sampling and measurements

Wood samples for tree-ring analysis were collected from 459 trees during the period between December 2010 and December 2011. All samples were collected within a ~300 ha area of mixed deciduous and seasonal dry evergreen forest. Samples from the locally more abundant species, *Neolitsea* and *Chukrasia,* were mainly collected following a clustered sampling design. These trees were sampled in a 50 m radius around a randomly assigned location in the ~300 ha area that was retrieved using a GPS device (Garmin GPSMAP 60C Sx). Because *Afzelia, Melia* and *Toona* were (locally) rare in the area, these species were sampled more opportunistically, by collecting additional samples from trees that were encountered in the forest. We aimed to gather a random subset of the local population of the five target species, therefore we took samples of all trees >5 cm dbh, irrespective of for example canopy position. At a height of approximately 1 m on the stem, we manually extracted wood cores with a 5.0 mm diameter Suunto (Vantaa, Finland) or a 5.15 mm diameter Haglöf (Långsele, Sweden) increment borer. Depending on the diameter of the tree we used borers with lengths varying between 40 and 70 cm. From trees <40 cm dbh two cores were taken, because the borer would go straight through the tree and we therefore obtained two complete radii per core. From all larger trees we took three cores, because only one complete radius per core was obtained. Taking multiple cores allowed us to measure rings over at least three different radii, thereby correcting for radial variation in diameter increment and facilitating the detection of very narrow and partially missing rings (Stokes and Smiley 1968). Extraction areas were left untreated (Dujesiefken et al. 1999).

The increment cores were glued to wooden mounts and cut perpendicular to the ring boundaries with a large sliding microtome (WSL, Swiss Federal Institute for Forest, Snow and Landscape Research, Switzerland). Digital images (1600 dpi) of the tree cores were obtained using a high-resolution flatbed scanner (Epson Expression 10000 XL) and analyzed in the WinDENDRO program for tree-ring analysis (version 2009b; Regent Instruments Canada Inc.). All tree-ring boundaries were marked manually on the screen by identifying the ring boundaries and measured to the nearest 0.001 mm. Identification of the growth rings, following standard procedures (Worbes and Junk 1989, Worbes 2002), was facilitated by (1) within-ring variations in the size and density of vessels for the ring-porous species *Melia* and *Toona*, (2) bands of marginal parenchyma delineating each ring in *Afzelia* and *Chukrasia* and (3) intra-annual wood-density variation in *Neolitsea* (Fig. S2.1).

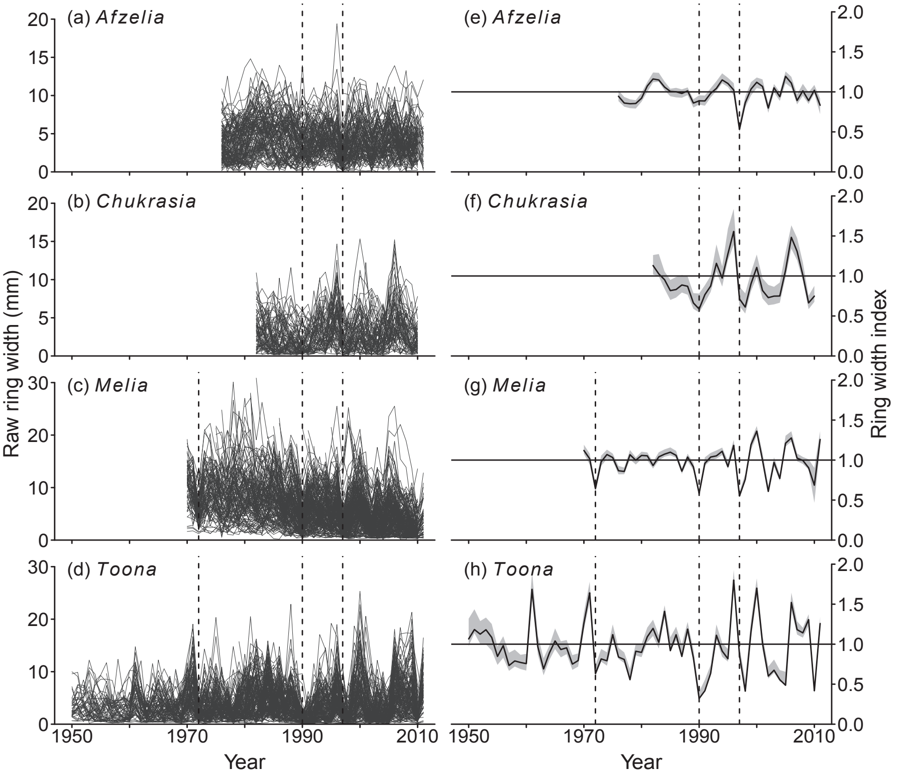

Figure 2.2 (a-d) Raw ring widths of all individual *Afzelia, Chukrasia, Melia* and *Toona* trees that were included in the chronology. (e-h) Chronologies of the study species. Black line represents the mean standardized ring-width index (chronology). Grey area indicates the 95% confidence envelop of the chronology based on 1000 time bootstrap analysis with replacement of individual series. Marker years (1972, 1990 and 1997) were indicated by the vertical dotted lines.

Chronology development

Tree ring data quality was checked by visually crossdating tree ring series in WinDENDRO. For trees sampled during the growing season of 2011, this year was excluded from analysis because this ring did not represent a full growing season. After visually crossdating the tree-ring series, we checked for dating errors using the computer program COFECHA (Holmes 1983). This iterative process of crossdating greatly reduces the number of false and missing rings, both of which are known to occur in tropical species (Worbes 1995). Ring-width series that correlated poorly with the master chronology—for example, due to prolonged growth suppressions—were removed from the dataset prior to chronology development (Pederson et al. 2004). We used the dendrochronology program library in R (dplR; Bunn 2008) to produce species-specific chronologies from the previously selected tree-ring series. Ring-width indices were obtained by detrending the raw ring-width series using a 20-year cubic spline. A 20-year cubic spline was chosen because it showed the best result in removing low-frequency trends (e. g., related to ontogeny and canopy-dynamics), while preserving the high frequency variation in growth. Next all ring-width series were prewhitened using autoregressive modeling to remove any effect of temporal autocorrelation in growth. Upper and lower 95% confidence intervals around the mean chronologies were based on a 1000 bootstrap replicates (Bunn 2008). Residual ring widths after detrending were normally distributed in all species as recommended for climate correlations (Cook et al. 1990).

Table 2.1 Study species characteristics (Nguyen et al. 1996, Nghia 1998, Kalinganire and Pinyopusarek 2000, Williams et al. 2008, LaFrankie 2010).

Species	Family	Light	Leaf habit (months leafless)	Ring structure (ID quality)	Natural distribution range
Afzelia xylocarpa	Fabaceae	Shade intolerant	Deciduous (1.5)	Marginal parenchyma (+)	Mainland Southeast Asia
Chukrasia tabularis	Meliaceae	Shade intolerant; moderately shade tolerant	Evergreen/ brevi-deciduous	Marginal parenchyma (+/-)	South Asia, Southeast Asia
Melia azedarach	Meliaceae	Shade intolerant	Deciduous (2)	Ring porous (++)	South Asia, Southeast Asia, Australia
Neolitsea obtusifolia	Lauraceae	Shade tolerant	Evergreen	Density gradient (-)	Mainland Southeast Asia
Toona ciliata	Meliaceae	Shade intolerant: moderately shade tolerant	Deciduous (0.5)	Ring porous (++)	South Asia, Southeast Asia, Australia

Crossdating of annual growth rings was successful for four out of five species (Fig. 2.2a-d). However, for the non-ring-porous species (*Afzelia*, *Chukrasia*), this lead to the exclusion of a large fraction of trees (>60%) from their respective species-specific chronologies (Table 2.2). Because of high dating uncertainty remaining after attempting to crossdate *Neolitsea* ring-width series, we excluded this species from all further analyses. For the other four species a species-specific chronology was produced (Fig. 2.2e-h). Out of the total sample size the proportion of trees included in the chronology was 38% for *Afzelia*, 27% for *Chukrasia*, 89% for *Melia* and 79% for *Toona* (see Fig. S2.2 for diameter distributions of trees included in the chronologies). In *Afzelia* and *Chukrasia*, false, wedging and generally indistinct rings were frequently observed, especially in periods when growth was suppressed, resulting in higher rejection rates. The resulting chronologies were cut off when the running expressed population signal (EPS) was <0.85 (Wigley et al. 1984, Speer 2010). The EPS is used to assess how well a chronology of a finite number of trees estimates the hypothetical (noise-free) population chronology (Wigley et al. 1984). When the EPS value is <0.85 the chronology starts to be dominated by the individual tree-level signal, rather than the stand level signal and is therefore less useful for climate-growth analysis (Speer 2010).

Table 2.2 Descriptive statistics of the ring-width series. All the statistics displayed concern only those series that were used for the chronology production.

Species	*n* sampled (trees/radii)	*n* chronology (trees/radii)	Time span	*n* years	r^a	ms^b	Rbar.wt[c]	Rbar.bt[d]	EPS[e]
Afzelia	100/341	38/133	1976-2011	36	0.38	0.42	0.45	0.13	0.90
Chukrasia	104/330	28/70	1982-2010	29	0.46	0.57	0.46	0.18	0.88
Melia	90/330	71/252	1970-2011	42	0.48	0.42	0.51	0.20	0.96
Toona	61/220	46/168	1950-2011	62	0.50	0.65	0.64	0.26	0.95

[a] *r* is the mean series intercorrelation of every series with the master chronology as produced by the program COFECHA (Holmes 1983). [b] *ms* is the mean sensitivity, which is a measurement of the year-to-year variability in tree-ring width as produced by the program COFECHA (Holmes 1983). [c] Rbar.wt is the mean of the correlations between series from the same tree. [d] Rbar.bt is the mean interseries correlation between all series from different trees. [e] EPS is the expressed population signal.

Climate data

We used monthly climate data from the Nakhon Sawan meteorological station (15.80N, 100.20E) for the climate-growth analysis. All climate data were obtained from the KNMI Climate Explorer website (Trouet and Van Oldenborgh 2013). The

Nakhon Sawan meteorological station is situated ~100 km east of the sampling area. Because the climate station is situated at a lower elevation, mean yearly temperatures are on average 5 °C higher in Nakhon Sawan and mean annual precipitation 350 mm lower compared to the study site. The temperature dataset from the Nakhon Sawan station was nearly complete for the period 1951-2010 (<0.5% of the data points were missing), monthly precipitation data were missing for <4% of the months (1951-2010). Any missing values were replaced by gridded climate data for the location of the climate station (Trouet and Van Oldenborgh 2013). Significant positive trends in the annual maximum temperature data (0.011 °C, $P < 0.01$) and annual minimum temperatures (0.025 °C, $P < 0.001$) were found (Fig. 2.1b). Because this study did not aim to analyze growth response to long-term climate change, but instead focusses on drivers of annual variability in growth, all climate data was linearly detrended prior to analysis (Fig. 2.1b). Therefore all climate parameters were expressed as deviations from the long-term trend. After detrending we found no evidence for temporal autocorrelation in the climate data.

Climate-growth analysis

All statistical analyses were performed in the R program environment for statistical computing, version 3.0.0 (R Core Team 2013). The climate response of each species was determined by correlating mean standardized ring-width series (chronologies) with monthly climate indices. All monthly correlations were performed using a 24-month window, from January in the prior growing season to December in the current growing season. We included prior year climate variables in the analysis because a lagged effect of climate on tree growth has frequently been found for both temperate and tropical tree species (Pederson et al. 2004, Brienen and Zuidema 2005, Buckley et al. 2007). To test climate-growth relationships, Pearson correlations were calculated using 1000 bootstrapped correlations by random extraction with replacement of values in the climate dataset, following the DENDROCLIM approach (Biondi and Waikul 2004), as applied in the bootRes package in R (Zang and Biondi 2013).

To compare the relative contribution of temperature and rainfall on diameter growth, we used mixed-effects models, with a second order autocorrelation structure and individual trees as a random factor (nlme package in R; Pinheiro et al. 2011). The second order autocorrelation structure was added to the model to account for the effect of growth in year t_{-2} and year t_{-1} on growth in year t_0. A total of four different models was used, because each species was included in a separate model. First, we reduced the number of initial fixed factors to be included in the model by calculating mean 6-month seasonal indices from the monthly precipitation data, minimum- and maximum temperature data. We defined the dry season as November$_{t-1}$ to April$_{to}$ and the wet season as May$_{to}$ to October$_{to}$. In the analysis both the current dry and wet season indices were included as well as prior year dry and wet season indices. This resulted in a total of 12 initial variables to be included as fixed factors in the full model. All seasonal climate variables were linearly detrended prior to analysis and the variance was stabilized. Only standardized diameter growth rates for those trees that were also included in the chronology were used as dependent variables. In this way only those trees that had a strong common signal in growth were used. The full model was subsequently simplified by step-wise removal of the least significant variables and the model with the lowest Akaike's Information Criterion (AIC) value was selected (Zuur et al. 2009).

Results

Tree-ring chronologies

Total chronology lengths ranged from 29 to 62 years (running EPS > 0.85), with the longest chronology spanning the period between 1950 and 2011 for *Toona*. The independently constructed chronologies were significantly positively correlated among all pairs of species (*Pearson r*, $P < 0.05$), except for *Afzelia* and *Toona* ($P < 0.10$). This similarity in year-to-year variation in growth is also expressed by the occurrence of synchronous marker years (years of abnormally low growth) in the chronologies, such as 1972,1990 and 1997 (Fig. 2.2). Both the high correlation among chronologies and the simultaneous occurrence of marker years provides strong evidence for the presence of an external factor driving annual variability in growth. We used the Monsoon Asia Drought Atlas (MADA) data (Cook et al. 2010) as an independent reference chronology to verify dating accuracy of the four chronologies constructed in this study. We found that *Melia* and *Toona* chronologies were highly significantly positively correlated with the MADA chronology ($P < 0.01$), $R^2 = 0.19$ and $R^2 = 0.34$ respectively. However, the *Afzelia* chronology was only marginally correlated with the MADA chronology ($P = 0.07$) and the *Chukrasia* chronology was not significantly correlated with the MADA chronology ($P = 0.36$).

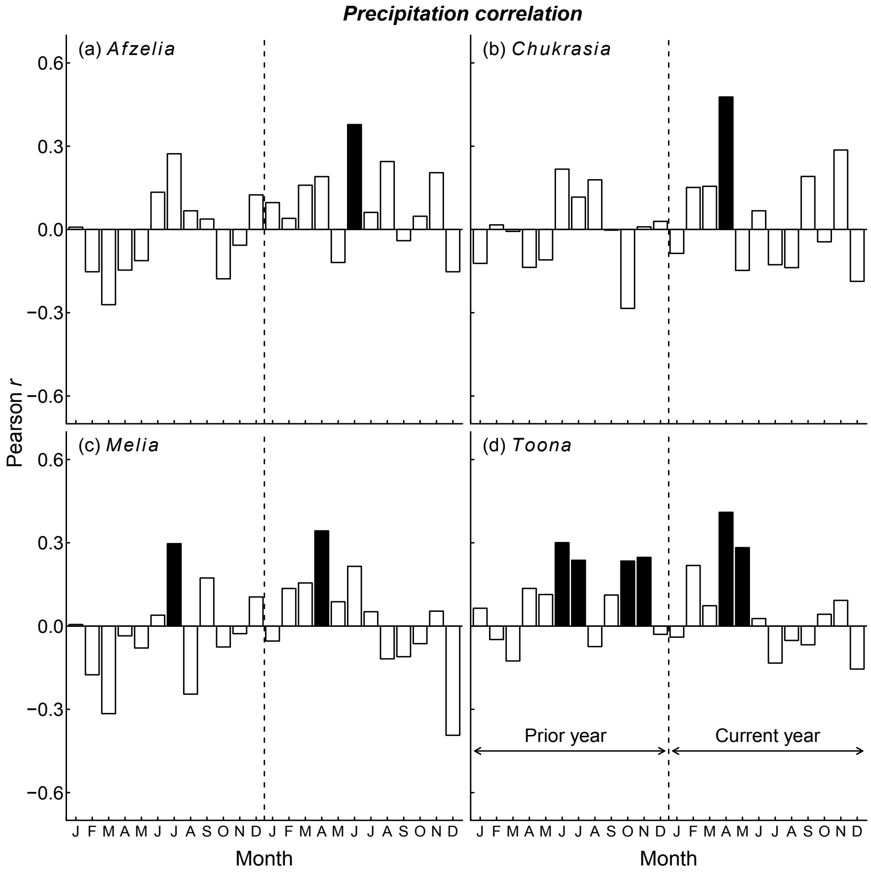

Figure 2.3 Bootstrapped correlation between ring width index and detrended monthly precipitation data from prior January to current December. Solid black bars represent significant correlations at the $P > 0.05$ confidence level.

Correlation between ring width and climate

We started the climate growth analysis by correlating standardized ring-width indices with monthly climate indices of the current and prior year. Significant positive correlations between total monthly precipitation and ring-width index values were found in all species. A significant correlation with current year April precipitation was found in *Chukrasia* and *Toona,* indicating that growth may be positively influenced by early growing season rainfall (Fig. 2.3b,d). *Melia* and *Toona* ring-width indices were also significantly positively influenced by prior year rainfall (Fig. 2.3c,d). We tested the correlation between total current-year precipitation and chronologies of the four species, but this revealed no significant correlations.

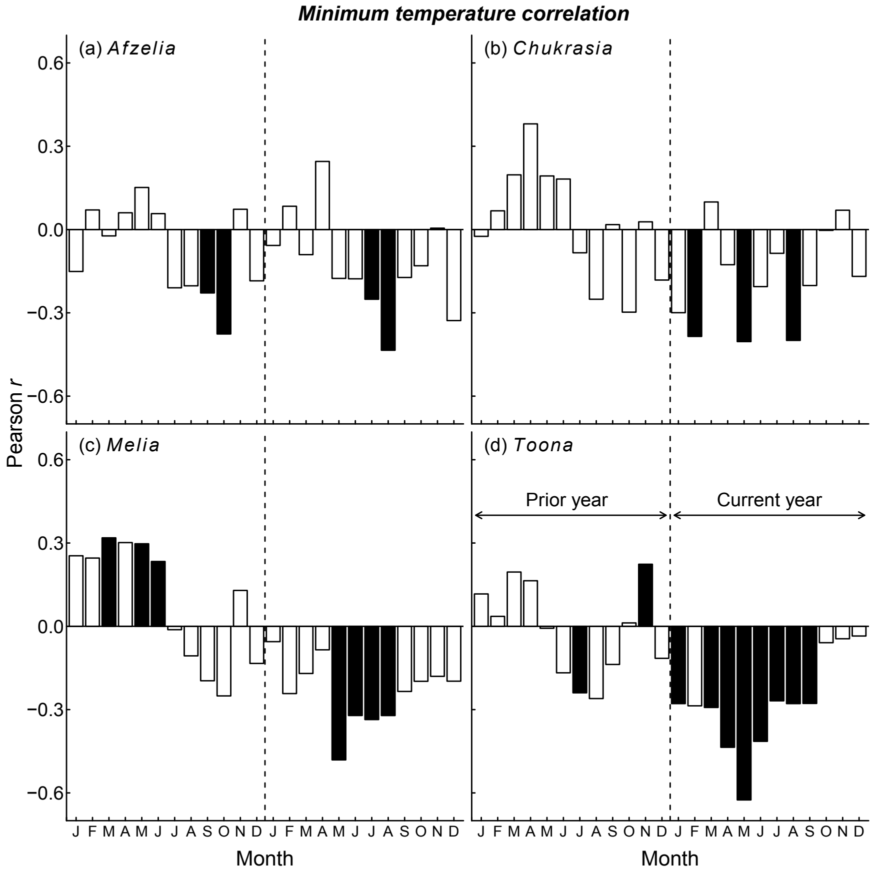

Figure 2.4 Bootstrapped correlation between ring width index and detrended mean monthly minimum temperature data from prior January to current December. Solid black bars represent significant correlations at the $P > 0.05$ confidence level.

Afzelia, *Chukrasia*, *Melia* and *Toona* all showed strong negative correlations with current wet season monthly minimum temperatures (Fig. 2.4). *Chukrasia* and *Toona* also showed significant negative correlations between growth and current dry season minimum temperatures. Positive correlations between growth and minimum temperature of the prior dry season were only found for *Melia* (Fig. 2.4c).

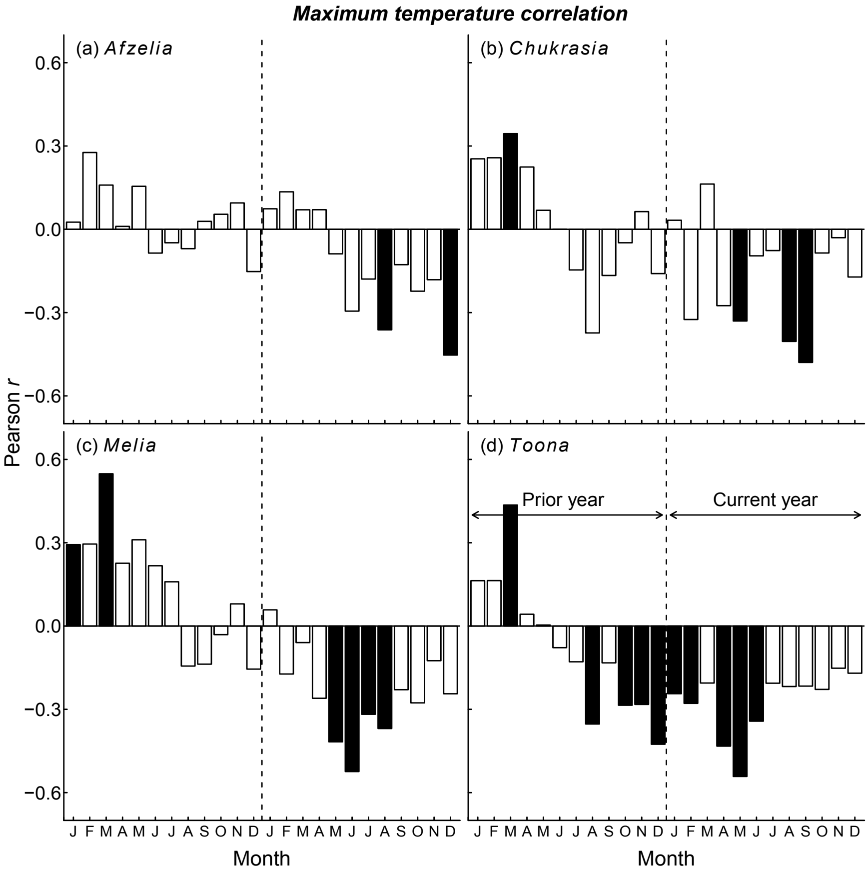

Figure 2.5 Bootstrapped correlation between ring width index and detrended mean monthly maximum temperature data from prior January to current December. Solid black bars represent significant correlations at the $P > 0.05$ confidence level.

When correlating monthly maximum temperatures and growth similar patterns arise as those for monthly minimum temperatures. All four species showed significant negative correlations with current year wet season maximum temperatures (Fig. 2.5). To illustrate the strong synchrony between temperature and growth, we plotted anomalies in current-year wet-season maximum temperature and growth of *Melia* (Fig. 2.6), the species with the strongest temperature-growth correlation (Fig. 2.5c). *Toona* also showed significant negative correlations between growth and current-year dry season maximum temperatures (Fig. 2.5d). In addition, both *Chukrasia, Melia* and *Toona* also showed significant positive correlations between growth and prior dry season monthly maximum temperatures (Fig. 2.5b-d). It is highly unlikely that the significantly negative correlation between mean current year December maximum temperatures and *Afzelia* growth (Fig. 2.5a) has a direct causal relation, because by December the ring has already been completely formed. The significant correlation most likely resulted from temporal autocorrelation in mean monthly maximum temperatures, as it can be seen that the preceding months also show a trend towards negative correlations.

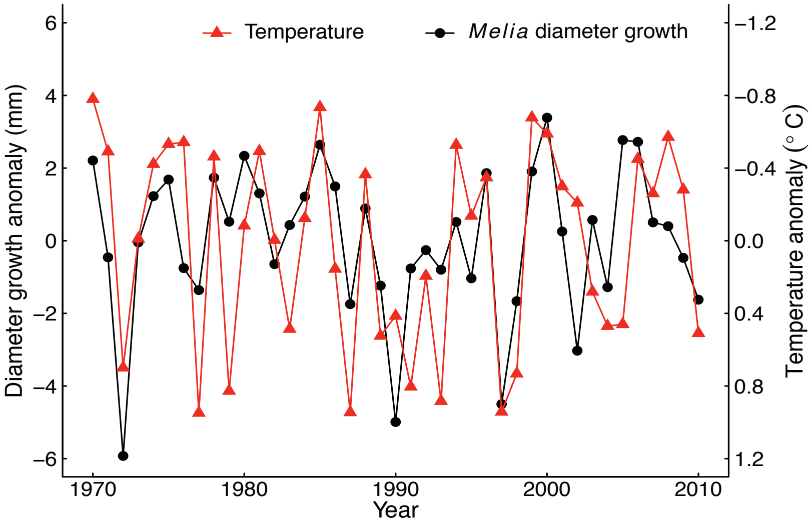

Figure 2.6 An example of the strong synchrony between growth and temperature. Shown are mean annual raw diameter growth anomalies of *Melia* (n = 71) and current-year wet season maximum temperature anomalies for the period 1970-2011. Note that the temperature-axis is inverted.

We used linear mixed-effect models for each species to determine the additive effects of climate on diameter growth (Fig. 2.7). AIC values of the selected models were 0.34-1.98 units lower than that of the model with one-but-lowest AIC value. For *Afzelia* the model explaining diameter growth revealed that current year dry season minimum temperature was positively related with diameter growth, whereas the effect of wet season maximum temperatures was negative (Fig. 2.7a). Prior year dry season maximum temperature had a positive effect on *Afzelia* growth and dry season precipitation, minimum temperature and wet season minimum temperature were all negatively related with *Afzelia* growth.

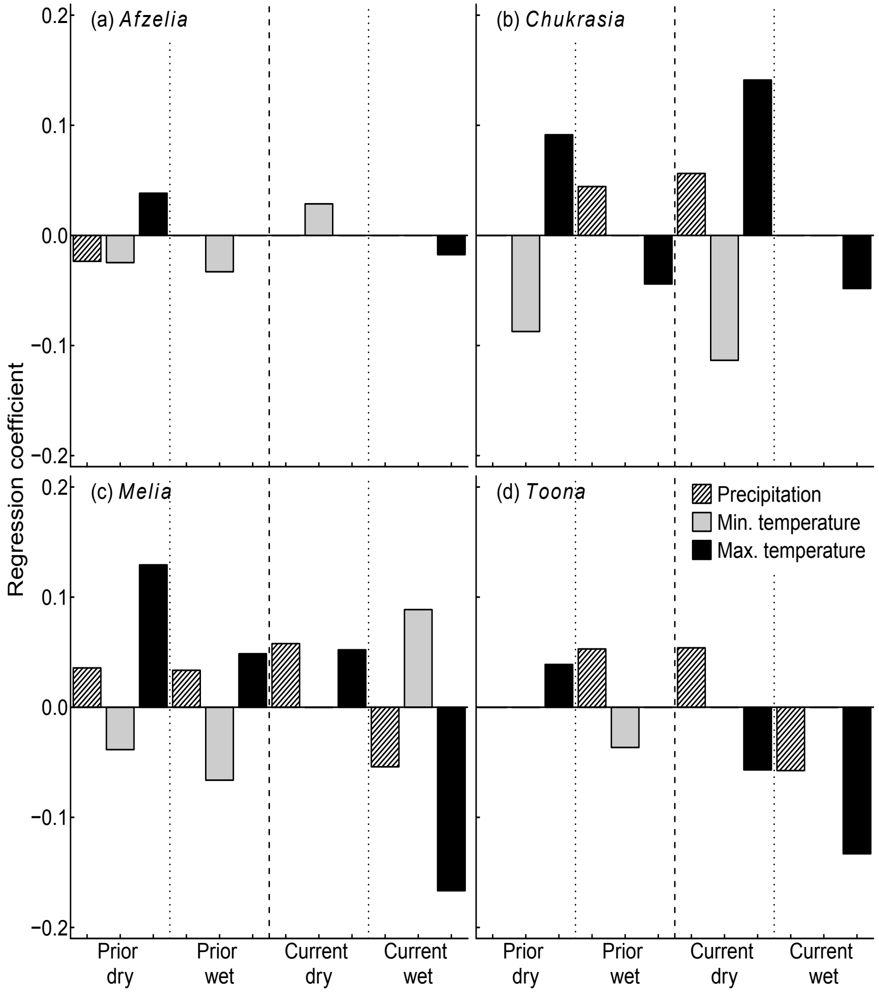

Figure 2.7 Linear mixed-effects model results of the best model explaining mean standardized diameter growth as a function of standardized seasonal climate indices for the current and prior year. *Prior dry* and *prior wet* refer to the six month dry and wet season of the prior year, *current wet* and *current dry* refer to the six month dry and wet season of the current year. Only parameters of the selected model with the lowest AIC value are shown.

Selected models for *Chukrasia, Melia* and *Toona* were relatively similar (Fig. 2.7b,c,d). Current year dry season precipitation was positively related with diameter growth, whereas there was a negative relation between diameter growth and wet season maximum temperatures. Models for *Melia* and *Toona* also included a significant effect of current year wet season precipitation, which was negatively related with diameter growth. *Chukrasia, Melia* and *Toona* showed a positive relation with prior year dry season maximum temperature and prior year wet season precipitation levels. We also selected best fit linear mixed-effects models in which we modeled raw annual diameter growth based on seasonal climate indices (results not presented). By using relations established in these models (modeling raw growth data instead of detrended growth data) we determined that an increase of wet season maximum temperatures with 1 °C was associated with a reduction in mean diameter growth of 0.3 mm for *Afzelia,* 0.9 mm for *Chukrasia,* 2.3 mm for *Toona* and 3.0 mm for *Melia* (see also Fig. 2.6).

Discussion

Species suitability for climate-growth analyses

We showed that *Afzelia, Chukrasia, Melia* and *Toona* rings can be used for climate-growth analysis. Unfortunately, poor crossdating precluded *Neolitsea* from climate-growth analysis, although a cambial wounding experiment has independently demonstrated the annual nature of *Neolitsea* rings (Baker et al. 2005). The frequent association of *Neolitsea* with non-dominant canopy positions, in contrast to the other four species (Vlam, M. *unpublished results*), may have resulted in an overriding effect of local stand dynamics on annual growth variability (Denslow 1980, Druckenbrod et al. 2013) resulting in the more frequent occurrence of false rings. The highly significant correlations of the *Melia* and *Toona* chronologies with the independently constructed MADA-chronology (Cook et al. 2010) further supported our confidence in the dating accuracy of these two species. Unfortunately, *Melia* and *Toona* are relatively short-lived, limiting the establishment of century-long climate-growth relations. The chronology length of *Afzelia* and *Chukrasia* was mainly confined by dating uncertainty and limited crossdating success prior to 1970. For tropical tree species with such complex wood anatomy and high potential for dating errors, tree-ring analyses would ideally be performed on whole stem cross-sections.

We are aware that our study species are a non-random selection and small subset of the most abundant species at our study site. They represent just two families and do not include the most dominant family (Dipterocarpaceae), but they do differ in for example ecological guild and the degree of deciduousness. The number of species fore which tree-ring analyses can be done at a given site will likely increase when recently tested techniques to reconstruct annual growth patterns of (apparently) ring-less species become more accessible (Poussart et al. 2004, Loader et al. 2011).

Climate correlations

Both the correlation analyses and linear mixed-effects models showed that tree growth was strongly driven by climate variability and growth responses were often similar among species. The correlation analysis showed that growth variability in all four species was strongly negatively correlated with current year minimum and maximum temperatures. This finding is similar to that of Clark et al. (2003), who showed that growth rates of trees in an old-growth tropical rain forest in Costa Rica were negatively correlated with current year daily minimum temperatures. Furthermore, Dong et al. (2012) showed that growth anomalies of whole tropical forest stands in Malaysia, Panama and Thailand were negatively correlated with five-year-averaged temperature anomalies. In addition, similar negative effects of temperature on tree growth were found in tropical sites with higher latitude and elevation (e.g., Buckley et al. 2007). The mechanism for a negative relation between temperature and tree growth in the tropics may be through higher temperatures leading to reduced carbon assimilation rates, by having both a direct negative impact on photosynthesis rates (Galbraith et al. 2010) and increasing autotrophic respiration rates (Clark 2007, Feeley et al. 2007b). Maintenance costs of plant tissue increase with higher ambient temperatures (Lloyd and Farquhar 1996). For tropical forests it has been shown that an air temperature increase of 10 °C leads to roughly a doubling of respiration rates (Meir et al. 2008). However, this was contrasted by Doughty (2011) finding little evidence of enhanced respiration rates in an *in situ* warming experiment with tropical trees. It has also been shown for deciduous temperate trees that leaf respiration rates show rapid acclimation to increased air temperature (Lee et al. 2005). Temperature also influences leaf-to-air vapor pressure deficit and tree evapotranspiration rates (Galbraith et al. 2010, Choat et al. 2012). When evaporative demand increases due to higher temperatures, the leaf stomata tend to close to reduce water loss, resulting in lower CO_2-uptake and decreased carbon assimilation rates (Lloyd and Farquhar 2008). Because the majority of annual net primary production of trees in a seasonal forest is concentrated in the months with high rainfall (April-October in HKK), it is likely that growth is most sensitive to temperature variability during this time of the year. And thirdly, temperature is negatively correlated with rainfall (Devall et al. 1995).

Thus, both increased evaporative demand leading to lower carbon assimilation rates, increased respiration costs and reduced precipitation rates during warm years could potentially be driving negative correlations between tree growth and current wet season temperature.

Unlike previously described climate-growth relations for seasonal tropical forests (Dünisch et al. 2003, Brienen and Zuidema 2005, Schöngart et al. 2006, Couralet et al. 2010), the mixed model analysis showed that the relation between growth and temperature were generally stronger than those between growth and precipitation. Weak correlations between single-year drought and tree growth were also found in two large-scale drought experiments in the Amazon (Brando et al. 2008, Metcalfe et al. 2010). Both studies provided evidence that net primary productivity of trees declined during the simulated drought, but this reduction was relatively modest in the first year. But as expected a period of consecutive years with low rainfall, such as the period 1989-1993 in western Thailand, did result in one of the clearest reductions in growth rates among the four species. The positive relation between growth and early growing season precipitation levels has been commonly found in tropical dendrochronological studies (Pumijumnong et al. 1995, Buckley et al. 2007, Rozendaal and Zuidema 2011, Soliz-Gamboa et al. 2011). This strong relation likely reflects the importance of adequate water amounts for the flushing of new leaves (Brando et al. 2008), which occurs around the spring equinox for most species in HKK (Williams et al. 2008). The absence of long-term climate data from the HKK study site forced us to use of data recorded at the Nakhon Sawan meteorological station (~100 km east of HKK) for all climate-growth analyses. Although most of the rainfall during the wet season in HKK originates from the Asian summer monsoon system (Wang and Ho 2002), regional variability in rainfall is comparatively higher than regional variability in temperature. The high local variability in rainfall amounts, combined with a ~100 km distance between to the meteorological station, may have led to an underestimation of the positive growth-precipitation correlations.

Evidence for a lagged climate-growth response is commonly found in dendrochronological investigations across the tropics (e.g., Dünisch et al. 2003, Brienen and Zuidema 2005). Both misdating of the rings and temporal autocorrelation in the growth data have been suggested as methodological causes for observed lagged responses (Soliz-Gamboa et al. 2011). However, temporal autocorrelation in the tree-ring and climate data was low and dating certainty, especially of *Melia* and *Toona,* was high, both were therefore unlikely to have caused the observed lagged responses. Alternatively, physiological pathways leading to lagged climate-growth responses in tropical trees have been suggested but remain poorly investigated so far. In temperate trees the presence of preformed shoots in trees with strong seasonality in leaf formation has been suggested to lead to lagged growth responses because growth for the first flush is set during bud formation in the prior year (Oliver and Larson 1996, Pederson et al. 2004). Also favorable conditions in the current year may promote the formation of reserves, rather than growth in the current year and these reserves can then be used in the beginning of the next growing season (Dünisch et al. 2003, Pederson et al. 2004). For instance, the three deciduous species in our study (*Afzelia*, *Melia* and *Toona*) completely rely on reserve materials for the flushing of new leaves and possibly also for the initial stages of xylem formation (Ohashi et al. 2009). However, we do not understand how prior-year temperatures may have a positive effect on growth in our study species.

Tropical tree growth and climate change

Daily maximum temperatures in western Thailand have been steadily rising over recent decades. The combination of rising temperature and a strong negative relation between diameter growth and current growing season maximum temperatures in all four study species, may indicate that tree growth rates will likely decrease over time. These reduced diameter growth rates may result in a reduced carbon sequestration capacity of the forest as a whole (Brienen et al. 2010a). However, historical growth responses to annual climate variability, e.g., linking past negative growth anomalies with relatively warm years, should not be translated into oversimplified projections of long term growth responses to long term changes in climate (Zuidema et al. 2013). Trees may for example respond to a structural increase in temperatures and drought through physiological acclimation of both photosynthesis and respiration (Galbraith et al. 2010), potentially reducing the long term effect of increased temperature on growth. The negative effect of rising temperatures may also be compensated by a CO_2-fertilization effect (Baker et al. 2004, Lloyd and Farquhar 2008) through a strong increased water-use-efficiency of trees (Hietz et al. 2005, Nock et al. 2011). The extent of this CO_2-fertilization effect on tropical tree growth is the subject of ongoing scientific debate (Körner 2003, Clark 2004, Lloyd and Farquhar 2008, Körner 2009) and requires further in-depth investigation (Zuidema et al. 2013). Analyses of tree rings, climate-growth relations and isotope analyses of tree species from tropical lowland forests can assist in predicting tropical forest dynamics under global change.

Acknowledgments

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Appendix

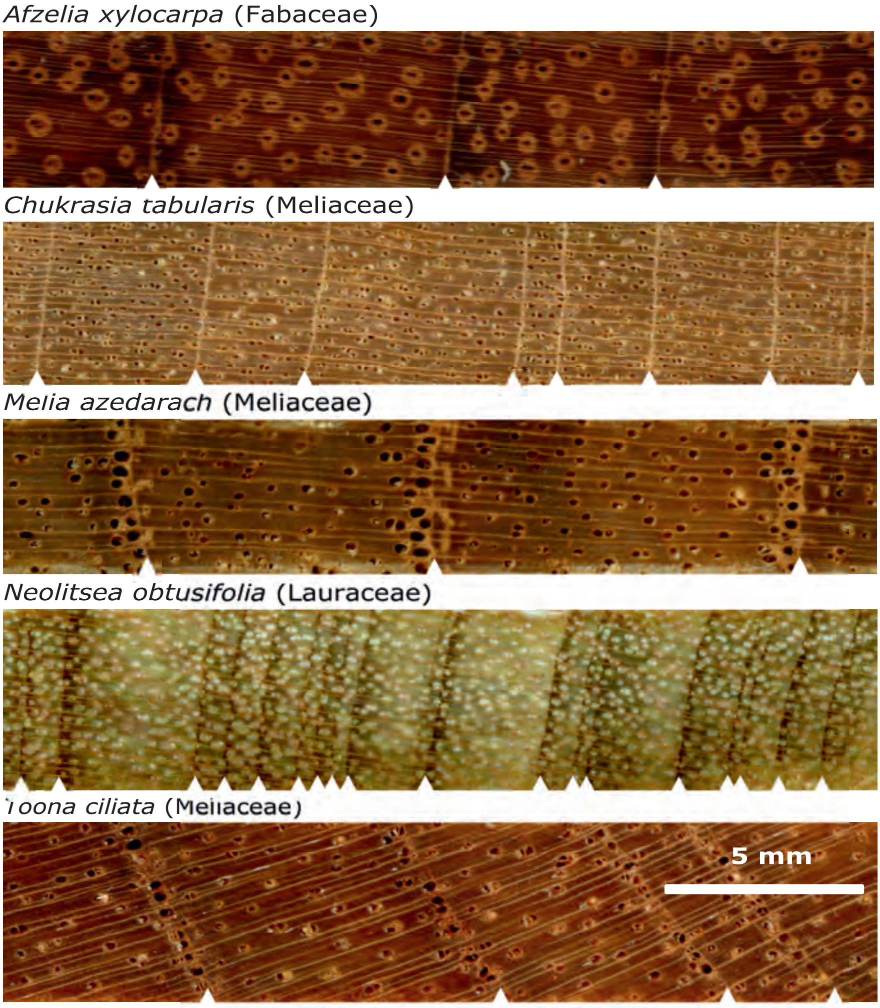


Fig. S2.1 Ring structure of the five study species, direction of growth is from right to left. White arrows indicate ring boundaries.

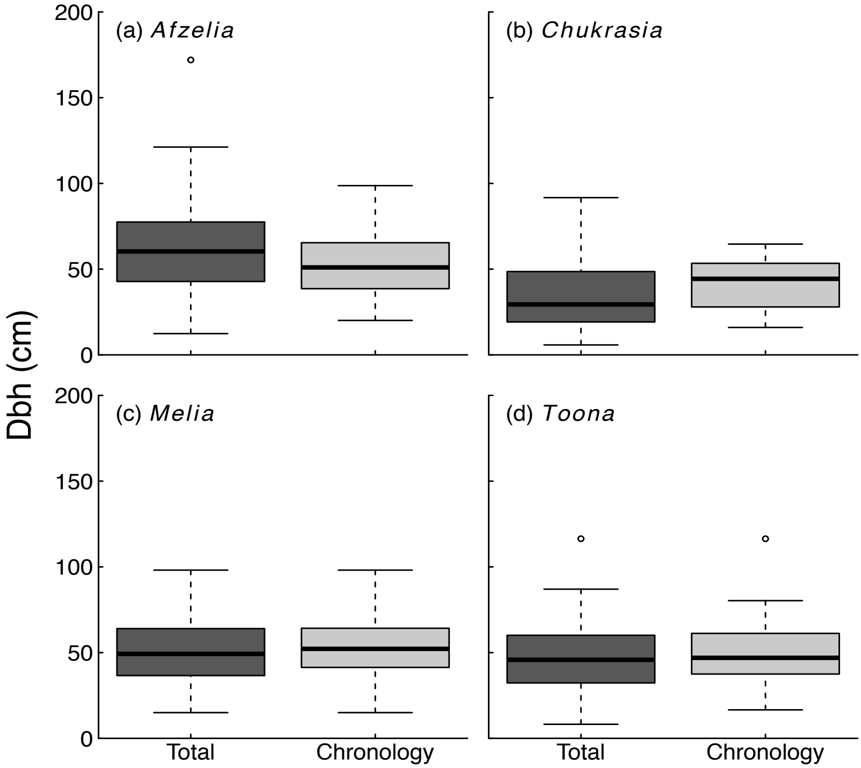
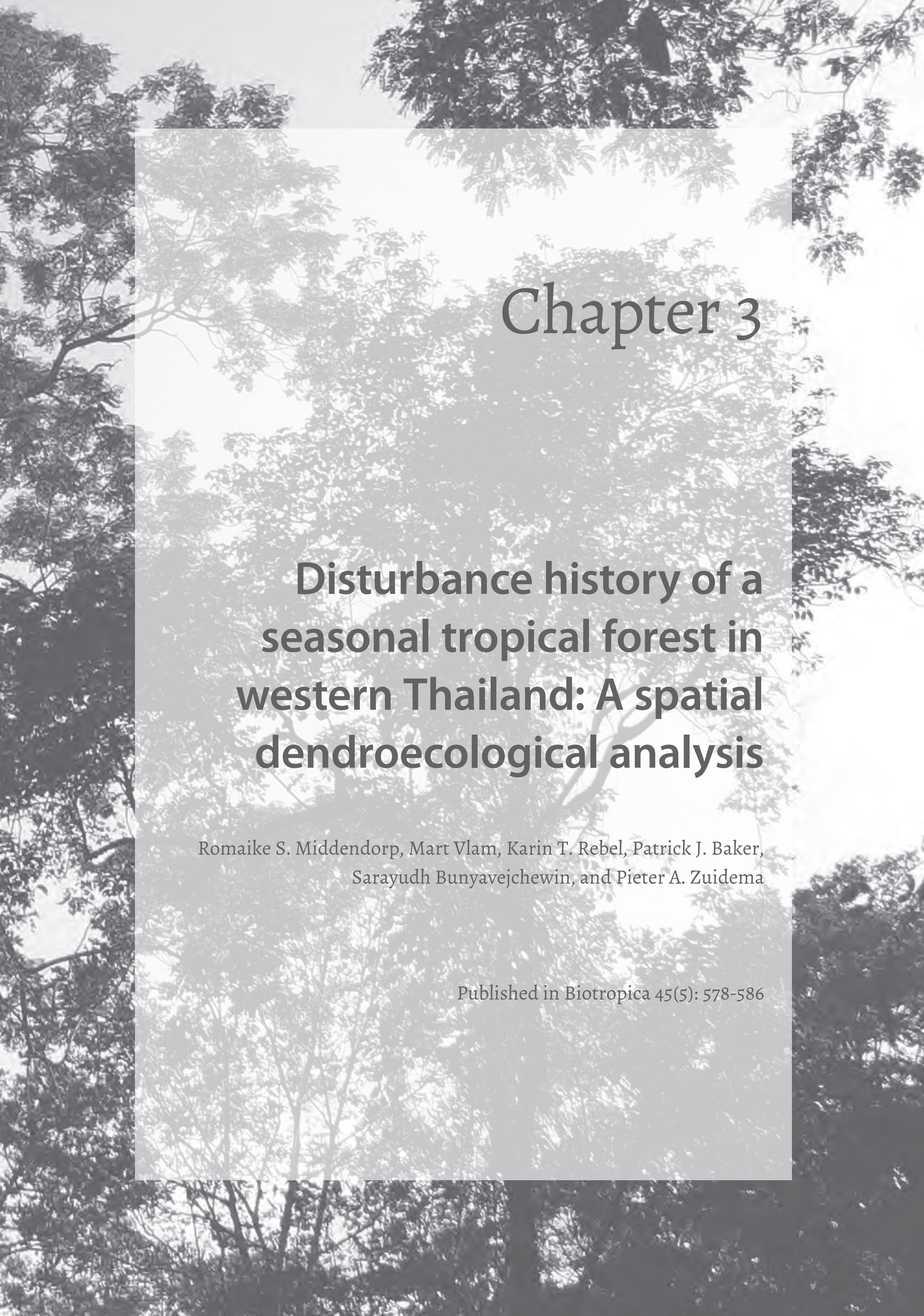


Fig. S2.2 Boxplots showing the dbh distribution of all sampled trees and those trees included in the chronology.



Chapter 3

Disturbance history of a seasonal tropical forest in western Thailand: A spatial dendroecological analysis

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Abstract

Disturbances play an important role in forest dynamics across the globe. Researchers have mainly focused on the temporal context of disturbances but have largely ignored the spatial patterns of tree recruitment they create. Geostatistical tools enable the analysis of spatial patterns and variability in tropical forest disturbance histories. Here, we examine the potential of combining dendroecological analysis and spatial statistics to reconstruct the disturbance history of a seasonal dry evergreen tropical forest plot at the Huai Kha Khaeng Wildlife Sanctuary, western Thailand. We used tree-ring derived age estimates for 70 individuals of the shade-intolerant pioneer species *Melia azedarach* (Meliaceae) and tree locations across a 316-ha study plot to identify the timing and spatial extent of past disturbances. Although the age distribution for *Melia* suggested that regeneration had been continuous over the past 60 year, spatial analyses (mark correlation function and kriging) demonstrated the presence of three spatially discrete age cohorts. Two of these cohorts suggested a severe disturbance ~20 years before present. A third cohort appears to have established ~50 years ago. Using historical records, we conclude that fire disturbance is the most likely disturbance factor affecting HKK. Nevertheless, we do not rule out other disturbance factors. The combined application of tree-ring analysis and spatial statistics as applied in this study could be readily applied to reconstruct disturbance histories in other tropical regions where tree species with annual growth rings are present.

Keywords: Age structure; dendroecology; disturbance history; *Melia azedarach*; Meliaceae; spatial statistics; Thailand; tropical forest.

Introduction

The dynamics of tropical forests have changed in recent decades. Several studies have demonstrated increased tree growth, aboveground biomass, and tree turnover in the past 20 years (e.g., Laurance et al. 2004, Phillips et al. 2008). These trends have mostly been attributed to global change, especially to increasing atmospheric CO_2 concentrations, either through direct carbon fertilization or climate change (e.g., increased temperature) (Lewis et al. 2004, Lewis et al. 2009a). However, others have cautioned that the observed patterns may be occurring as some tropical forests recover from past disturbances (Wright 2005, Feeley et al. 2007a). Under this hypothesis, forests would increase in aboveground biomass as they recover from disturbances in the past (Chave et al. 2008, Chambers et al. 2013). Failure to take these unobserved disturbances into account can lead to biases in estimated mortality and growth rates, potentially leading to overestimations of forest carbon sequestration rates (Chambers et al. 2004, Fisher et al. 2008). It is well known from temperate zone forests that past disturbances influence temporal pattern in forest dynamics (Oliver and Larson 1996), but this historical context is rarely considered in studies of tropical forests.

Recovery from disturbances is a long-term process, although direct observation of forest dynamics typically occurs over relatively short time periods (years to decades, but see also: Condit et al. 1999). The analysis of tree-ring data has proven to be a valuable method to obtain long-term tree growth data and to accurately determine tree ages (Rozendaal and Zuidema 2011). In temperate forests, tree-ring analyses have been applied to reconstruct past disturbances and forest stand dynamics (Lorimer and Frelich 1989, Rentch et al. 2003). An underrepresentation of tropical forest systems in similar studies has mainly been due to the historical perception that tropical trees do not form annual growth rings (e.g., Lieberman et al. 1985). This perception can be traced back to the idea that there is no clear seasonality in the tropics. However, many tropical forests experience an annually returning dry season, resulting in cambial dormancy in trees and annual rings being formed (Worbes 1995). Only recently have the first tree-ring reconstructions been used to study tropical forest dynamics (e.g., Worbes et al. 2003, Rozendaal et al. 2011). Using long-term tree establishment patterns and growth rates, Baker et al. (2005) looked for indications of peaks in tree growth and establishment. Their analyses revealed a complex disturbance history consistent with widespread disturbances of varying intensities over time, but primarily focused on the temporal patterns of recruitment and release. Yet, different types of disturbance are likely to have different spatial signatures. Minor disturbances (e.g., single treefall gaps) result in a small number of trees growing into the canopy, probably rather scattered in the landscape. Major disturbances, on the other hand, are sufficiently severe to ensure that most recruiting trees do not encounter competition from surrounding existing trees (Oliver 1980, Oliver and Larson 1996), likely resulting in larger patches with high density of equally aged trees. Spatial analyses of recruitment ages thus provide useful information on the nature of past disturbances and improve our understanding of the spatial variability in disturbances regimes.

Shade-intolerant pioneer trees establish almost immediately after disturbances that create high-light conditions on the forest floor through canopy tree mortality (Brokaw 1985). This pulse of regeneration is typically short in duration because pioneer species cannot germinate in the shade and growth is severely reduced from even moderate shading. As such, the age, location, and spatial scale of clumping of pioneer tree species can be used to infer the size and distribution of past disturbances (Duncan and Stewart 1991). By looking at the spatial structure of establishment dates of pioneer species, we may be able to follow the formation of canopy openings through time and space, and reconstruct a forest's disturbance history. In temperate regions, spatial statistical analyses of tree ages have been successfully applied to relate the scale of clustering of even-aged trees to the size and distribution of canopy openings formed by past disturbances (Cullen et al. 2001, Rozas 2003, Sánchez Meador et al. 2009). Despite gap dynamics being a long-recognized component of tropical forests, this approach has never been applied in tropical forests.

In this study, we examine the potential of combining tree ring analysis and spatial statistics to reconstruct the disturbance history of a seasonal dry evergreen tropical forest in western Thailand. We analyzed tree-ring samples from the pioneer species *Melia azedarach* (Meliaceae) across a 316-ha area to determine if their spatial distribution was indicative of spatially distinct, age cohorts related to past disturbances. Our specific objectives were to: (1) reconstruct the age distribution of a widespread pioneer tree species over a large area to identify temporal pulses of recruitment; and (2) use spatial analyses to determine if there are spatially discrete groups of trees within each age cohort. We expect that this method will offer useful new insights into tropical forest disturbance history.

Materials and methods

Study area and species selection

We carried out this study in the Huai Kha Khaeng Wildlife Sanctuary (HKK), which is located about 300 km northwest of Bangkok in Uthai Thani province, western Thailand (15°40'N, 99°10'E). HKK and its sister sanctuary Tung Yai-Naresuan were together designated a UNESCO World Heritage Site in 1991. The HKK landscape is dominated by three distinctive forest types common to continental Southeast Asia: seasonal dry evergreen forest (SDEF), mixed deciduous forest, and deciduous dipterocarp forest, of which SDEF is the most species-rich and has the tallest canopy (Bunyavejchewin 1999). Seasonal monsoons form the dominant climatic influence in the area with a rainy season from May to October followed by a dry season from November to April. Mean annual rainfall at the Kapook Kapiang Ranger Station (about 4 km from the study site) was 1427 mm during the period 1983-1993 (Bunyavejchewin et al. 2009). Mean monthly rainfall in the dry season was <100 mm and mean temperatures ranged from 27°C in July to 19°C in January. Figure S3.1 shows a Digital Elevation Model (DEM) of our 316-ha study plot based on inverse distance interpolation of ~20,000 altitude values collected using a GPS-tracker (Garmin GPSMAP 60C Sx). Elevation levels within the plot vary between 490 to 650 meters above mean sea level and a stream runs from north to south through the plot. A Smithsonian Center for Tropical Forest Science (CTFS) 50-ha forest dynamics plot, established in 1992, is immediately adjacent to our study area (Fig. S3.1). There was no evidence in this area of past human activities, such as agriculture or logging (Bunyavejchewin 1999).

The study species, *Melia azedarach* (Meliaceae), is a pioneer tree species that is strongly shade-intolerant (Baker et al. 2005, Williams et al. 2008). Trees of this species depend on high-light conditions for their establishment. Therefore, the presence of this species in the forest is closely linked to past disturbances that created canopy gaps sufficiently large to allow *Melia* seeds to germinate. Furthermore, *Melia* trees are known to form annual growth rings as it is completely deciduous (Williams et al. 2008). The formation of growth rings in *Melia* trees was demonstrated in a cambial wounding experiment at the site (P.J. Baker unpublished results; see also: Baker et al. 2005). Figure S3.2 shows an example of tree ring boundaries in our study species.

Data collection and tree-ring measurements

We collected wood samples from 70 individual *Melia* trees in a 316-ha plot northwest of a 50-ha CTFS forest dynamics plot (Fig. S3.1). Over a period of 5 months, between December 2010 and December 2011, we systematically searched the 316-ha plot for all *Melia* trees >5 cm diameter at breast height (dbh). We used a GPS-tracker to visualize our trails and to verify that the whole area had been covered. We also used the GPS device to record the location of each sample tree to the nearest 5 m. We recorded dbh (1.3 m) and diameter at sampling height for each individual tree. Per individual, we collected two to four cores between 1.0 and 1.3 m above the ground using a 40 cm long, 5.15 mm diameter Suunto (Vantaa, Finland) or Haglöf (Långsele, Sweden) increment borer. Every effort was made to core as close as possible to the pith. Nevertheless, the pith was clearly visible in at least one core for just ~12 percent of the individuals. Sampling was limited to individuals >5 cm dbh to minimize damage to the tree population.

The increment cores were mounted on wooden holders and prepared for visual analysis by cutting them with a large sliding microtome (WSL, Swiss Federal Institute for Forest, Snow and Landscape Research, Switzerland). Cores were scanned at 1600 dpi with a high-resolution digital scanner (Epson Expression 10000XL). We measured annual tree-ring widths in at least three radii per individual, using the WinDENDRO tree-ring image analysis software (v.6.4a, Regent Instruments). Ring-width series within each tree were cross-dated by matching the variation in ring-width patterns, which facilitated the detection of missing and false rings. Additionally, we cross-dated among trees using the program COFECHA (Holmes 1983). The among tree cross-dating of *Melia* ring-width series was relatively straightforward: our chronology contained ~90% of all individuals with a mean series intercorrelation of 0.48 (M. Vlam *unpublished results*).

When all increment cores of an individual missed the pith, we estimated the distance to the pith by the degree of arcing in the oldest visible ring, assuming a circular growth pattern. The number of missing rings was estimated by dividing the missing distance to the pith by the average width of the five oldest visible rings of that sample. We defined tree age as the number of years since an individual tree reached coring height (1.0 to 1.3 m). Based on our field experience and the high growth rates of *Melia*, we expect that the time to reach coring height is only 2-4 years.

Age distribution

We conducted a Hartigans' dip test for unimodality to test the null hypothesis of a unimodal pattern in *Melia* establishment dates (Hartigan and Hartigan 1985). The dip test measures the maximum difference between the empirical age distribution function and the unimodal age distribution function that minimizes the maximum difference, and is appropriate for testing any unimodal against any multimodal pattern (Hartigan and Hartigan 1985). We conducted the dip test using the *diptest* package (Maechler 2011) in the R Software environment version 3.0.0 (R Core Team 2013). The age distribution showed a multimodal pattern if the dip test differed significantly from a unimodal distribution ($P < 0.05$).

Spatial analysis

To establish whether the distribution of sampled tree locations in our plot was random, we described the spatial distribution of *Melia* locations using the *L*-function (Besag 1977), which is the linearized form of the Ripley's *K*-function (Ripley 1977). The *L*-function is based on the second-order analysis of all tree-to-tree distances in a two-dimensional area and characterizes the spatial pattern of tree locations at various distances d. Details on the calculation of the *K*- and *L*-functions can be found elsewhere (Ripley 1977, Venables and Ripley 2002, Illian et al. 2008). We calculated $L(d)$ values for 10 m distance intervals to distances up to half the maximum of the plot dimension (*i.e.,* 1400 m) to reduce errors introduced by edge effects introduced by the unknown pattern of unsampled trees outside our study area (Boots and Getis 1988, Sánchez Meador et al. 2009). To reduce additional bias from edge effects, we applied an isotropic edge correction introduced by Ripley (1988). The *L*-function was plotted as $L(d)-d$, giving a value of 0 under complete spatial randomness. We calculated 95% simulation envelopes obtained from 999 Monte Carlo permutations under the hypothesis of complete spatial randomness (uniform Poisson point process; Baddeley and Turner 2005). If trees are clumped in space, $L(d) > 0$; if trees are regularly dispersed, $L(d) < 0$.

The mark correlation function $k(d)$, introduced by Stoyan (1984), is used in forest ecological studies to describe the spatial correlation of tree properties (*i.e.,* 'marks'), such as tree biomass, diameter, or crown radius, in an observed point pattern given by the discrete locations of trees (Stoyan and Penttinen 2000, Illian et al. 2008, Wälder and Wälder 2008, Law et al. 2009). This function gives a measure of the dependence between the marks of trees for the point process a distance d apart. We used this function to describe the spatial relationship of tree age. For theoretical definitions, we refer to (p. 262; Stoyan and Stoyan 1994)). We applied an isotropic edge correction to reduce bias introduced by edge effects (Ripley 1988). We calculated distributions of *k(d)* under the assumption of a spatially random distribution of ages using 999 Monte Carlo permutations (Baddeley and Turner 2005). We then calculated 95% simulation envelopes for each distance *d* (*d* ranges from 0-1400 m) and compared observed *k(d)* to the these simulated envelopes. If observed *k(d)* values fall within the simulation envelopes, tree age is spatially independent. When *k(d)* is higher than the upper limit of the 95% simulation envelopes, tree ages are clumped in space; while *k(d)* values lower than the lower limit of the 95% simulation envelopes indicate overdispersion of tree age.

Although the spatial distribution of individual trees in our study plot represent a point pattern of discrete points in space, the spatial distribution of tree attributes (e.g., biomass, height, volume, or in our case, tree age) may be considered continuous (Chen et al. 2004). Therefore, the use of kriging techniques to interpret spatial patterns in tree ages is justified. Kriging techniques use a local age estimation of neighboring trees and account for the global age structure (Davis 2002). The global autocorrelation structure is provided by a semi-variogram, which is related to the abovementioned mark correlation function. Semi-variances were calculated over 50-m distance classes.

All spatial analyses were conducted and graphically depicted using the R Software environment version 3.0.0 (R Core Team 2013). We used the following packages: *spatial* (Venables and Ripley 2002); *ncf* (Bjornstad 2013); *spatstat* (Baddeley and Turner 2005); and *gstat* (Pebesma 2004).

Results

Age distribution

We assessed evidence for recruitment pulses of *Melia* based on the age frequency distribution of recruitment decade of all sampled trees in the 316-ha plot (Fig. 3.1). We could not assess recruitment post-2000 due to the minimum sampling diameter of 5 cm dbh. Like many pioneer tree species, *Melia* is relatively short-lived. Mean age of all sampled *Melia* was 35.8 year, with a standard deviation of 13.6 year. However, the oldest individual that we sampled was 121 years old. Because only two out of 70 sampled trees established before 1950 (in 1891 and

1909), we decided to exclude these trees from further spatial analyses as they were statistical outliers and such a low number would unlikely produce meaningful spatial patterns. The Hartigans' dip test showed that the age distribution was unimodal ($P = 0.69$, $n = 70$) and the age data as presented in the age histogram suggest continuous recruitment over the past 60 years.

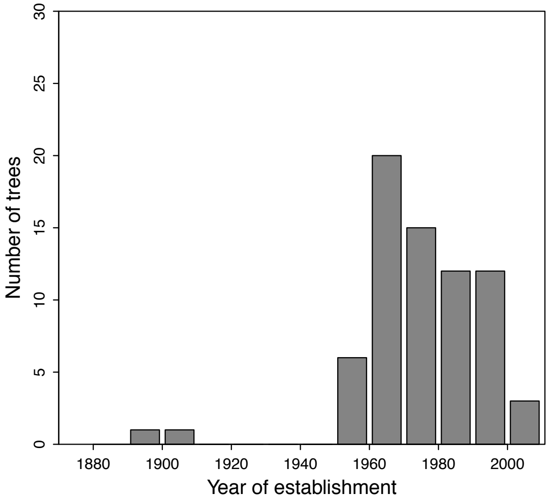

Figure 3.1 Age-frequency distribution for sampled *Melia* trees ($n = 70$) in our 316-ha plot in Huai Kha Khaeng wildlife sanctuary, Thailand. Sampled *Melia* ages ranged from 4 to 121 years. Age distribution of *Melia* trees that established after 1950 was shown to be unimodal ($P = 0.69$, $n = 70$). Recruitment after 2000 could not be assessed because of the minimum sampling diameter of 5 cm.

Spatial distribution of tree locations and ages

We tested whether the spatial distribution of sampled *Melia* tree locations followed the hypothesis of complete spatial randomness, using the Besag's L-function. *Melia* tree locations were significantly clumped at distances up to ~450 m ($P < 0.05$) (Fig. S3.3). At greater distances, *Melia* tree locations were not significantly clumped and showed no consistent pattern.

The mark correlation function revealed departures from complete randomness in the spatial distribution of *Melia* tree ages (Fig. 3.2). Ages appeared to be correlated up to distances of about 450 m and clumps of similarly aged trees were separated by distances of roughly 800-1100 m. We found no significant correlation between tree age and altitude (Spearman, $P = 0.10$, $n = 68$), suggesting that the observed patchy distribution of ages was not related to topography.

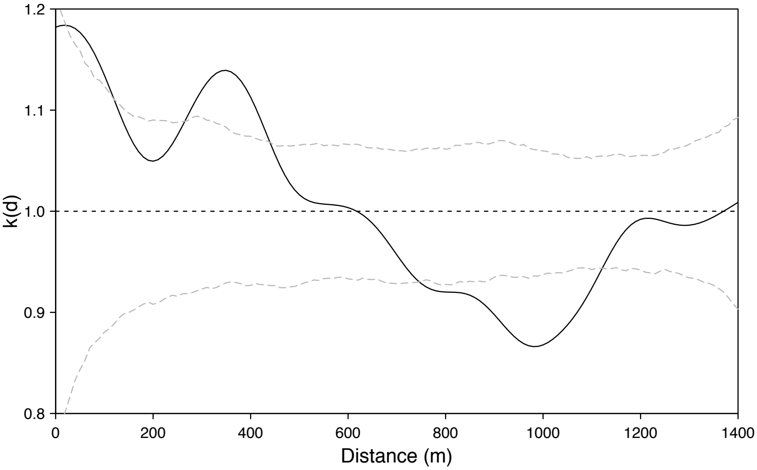

Figure 3.2 Mark correlation function *k(d)* estimated for sampled *Melia* ages over 10 m distance classes to distances up to half the maximum of the plot dimension (*i.e.,* 1400 m) (solid line). Dashed lines are approximate 95% simulation envelopes obtained from 999 Monte Carlo simulations under the hypothesis of complete spatial randomness. Tree ages are: spatially independent if *k(d)* = 1; clumped in space if *k(d)* > 1; and regularly dispersed if *k(d)* < 1.

Spatial interpolation of tree ages

We calculated semi-variances for *Melia* ages over 50 m distance classes as a measure of spatial dependence in *Melia* age in our study plot. A spherical variogram model was fitted through the calculated semi-variances (Fig. S3.4). The semi-variogram model showed that *Melia* ages were spatially dependent until ~800 m, shown by the range of the semi-variogram.

We spatially interpolated *Melia* ages using ordinary kriging based on the variogram model (Fig. S3.4). The resulting surface map showed that all sampled *Melia* trees could be subdivided into three spatially distinct age cohorts throughout our plot, demonstrating a widespread, but diffuse, pattern of synchronous gap formation (Fig. 3.3). The youngest *Melia* cohort was located in the southeast corner of the plot with an average age of 24.5 year and a standard deviation of 10.0 year (*n* = 12). Establishment of this cohort started around 1990. A second spatially distinct age cohort was found in the northwest corner of our plot and had an average age of 24.9 year with a standard deviation of 11.9 year (*n* = 9). This patch most likely recruited around 1985. Finally, a third cohort was located along the northeast to southwest diagonal with an average age of 41.6 year and a standard deviation of 11.1 year (*n* = 47). Recruitment of trees in this third cohort began in the 1960s.

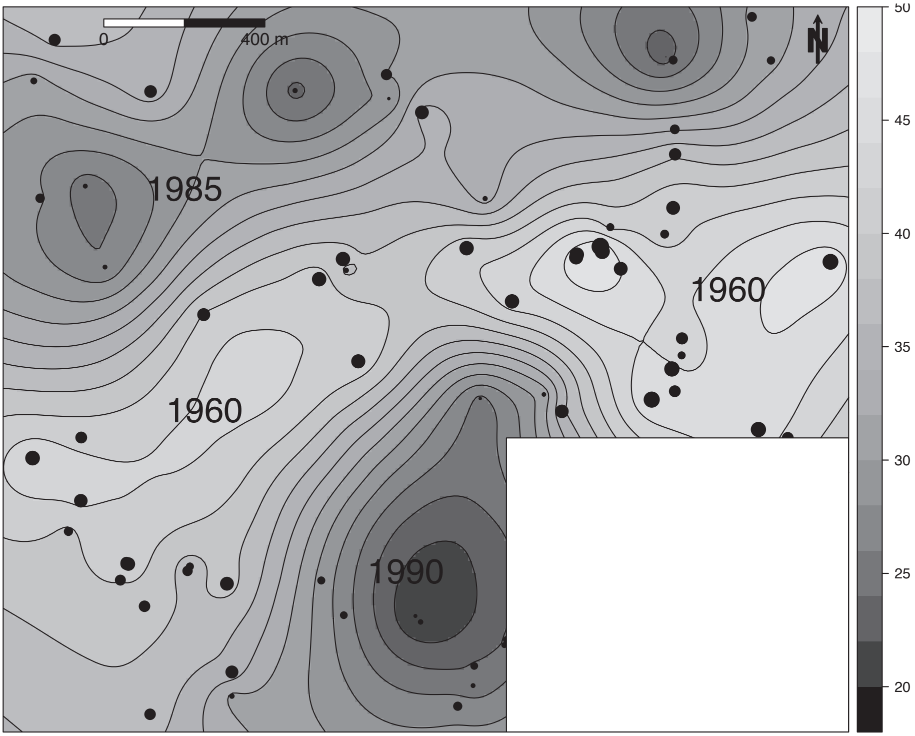

Figure 3.3 Interpolated *Melia* ages in our study plot, based on global ordinary kriging. Grey-scales represent interpolated tree ages, ranging from 4 (dark grey) to 61 (light grey) years. Dots indicate sampled tree locations; dot size corresponds linearly to tree age. Areas with similar ages are delineated by smooth contours. Three spatially distinct cohorts of *Melia* trees can be distinguished that established respectively in 1960, 1985, and 1990. Due to the location of the 50-ha forest dynamics plot in the southeast corner no tree age estimations could be obtained for the area indicated by the white square.

Discussion

Melia recruitment waves and disturbances

To better understand the long-term dynamics of forests, a clear picture of past disturbances is required. Earlier attempts were made to examine long-term community dynamics of tropical forests using tree-ring analyses (Groenendael et al. 1996, Worbes et al. 2003, Rozendaal et al. 2011). Reconstructing historical disturbance regimes of species-rich tropical forests has proven to be a major challenge. To our knowledge, Baker et al. (2005) is the only other study that revealed past disturbances in a tropical forest with the use of long-term establishment patterns, but they made no attempt to include spatial patterns of tree recruitment. New methodological approaches that also account for the spatial pattern of recruitment may offer useful insights on the nature of past disturbances and a better understanding of the spatial variability in disturbances regimes. Here, we demonstrated the potential of combining traditional dendroecological approaches with spatial statistical analyses for reconstructing the disturbance history of a seasonal tropical forest in western Thailand.

We reconstructed the age distribution of a tree species to identify temporal pulses of recruitment similar to Baker et al. (2005). Our tree-ring analyses suggested that *Melia* recruitment was continuous over the past 60 year and showed no indication of distinct age cohorts (Fig. 3.1). However, the spatial analyses of ages revealed a distinct spatial patchiness in *Melia* recruitment and the presence of three spatially discrete age cohorts (Fig. 3.3). Thus, spatial analyses allow detecting spatially explicit recruitment peaks that cannot be inferred from age structures alone.

The distances over which *Melia* ages showed spatial dependency in our study plot were larger (up to ~800 m; Fig. S3.4) than those typically found for pioneer trees in temperate forests (e.g., Wallenius et al. 2002, Rozas 2003). This spatial dependency is indicative of the severity of the disturbances that resulted in the establishment of a new age cohorts in our study area. However, we could not assess patterns in tree age at a fine spatial scale, like in temperate forests (e.g., Splechtna et al. 2005, Sánchez Meador et al. 2009), due to the relative scarcity of *Melia* trees in our study area (<1 tree per 4 ha). In the boreal region of east-central Finland, Wallenius et al. (2002) found spatial dependency at range of 85 m in two old-growth forests, reflecting the distance between three spatially discrete age cohorts of trees that established after three severe fire events. Additionally, the spatial autocorrelation structure of shade-intolerant *Quercus robur* trees in an old-growth beech-oak lowland forest in Northern Spain suggested the presence of spatially distinct age cohorts separated by distances from 22 to 48 m (Rozas 2003). The author showed that several pulses in tree establishment coincided in the 19th century, and that these were related to disturbances (e.g., hurricanes and violent windstorms) resulting in the expansion of existing canopy openings. For studies on disturbance history in temperate regions, researchers often possess high-quality historical records on past natural (e.g., windstorms, fires, droughts) or anthropogenic disturbances (e.g., logging, grazing, agriculture). In tropical forest research, records of past disturbances or climate are often incomplete or absent. This limits the potential to reconstruct tropical disturbance regimes.

The spatial pattern of *Melia* recruitment at our study site is likely indicative for the intensity, severity and type of past disturbances, as in pioneer trees such patterns are closely related to scale and severity of past disturbances (Duncan and Stewart 1991). The most common form of disturbance in tropical forests is created by treefall gaps that result in spatially aggregated, but temporally random, regeneration at a typical scale of ~1 ha (Brokaw 1985). However, one single severe disturbance event can create many tree fall gaps simultaneously across the forest, leading to a diffuse, but widespread, pattern of synchronous gap formation over several hectares (Baker and Bunyavejchewin 2009). The establishment of three spatially distinct *Melia* age cohorts across our study plot suggests such a pattern of diffuse, but synchronous gap formation. We observed one pulse of *Melia* recruitment around 1960 and two *Melia* establishment pulses took place around 1985 and 1990, the last two may have originated from the same disturbance event. We therefore hypothesize that at least two severe past disturbances (*i.e.*, in terms of tree mortality and canopy gap formation) affected forest dynamics at HKK in the past 50 years.

What type of disturbances may have caused the observed *Melia* recruitment patterns? One potential disturbance factor affecting tree establishment at HKK is wind. It is known that wind disturbance plays an important role in determining dynamics in both temperate (Everham and Brokaw 1996) and tropical forests (Nelson et al. 1994, Negrón-Juárez et al. 2010). Windstorms and hurricanes lead to canopy damage and exposure of mineral soils due to uprooted trees, allowing pioneer tree species to regenerate in the resulting gaps (Ashton 1993). In a study by Negrón-Juárez et al. (2010), remote sensing imagery was coupled to field investigations to create a 25-year landscape-scale disturbance chronosequence for old-growth forests in the Central Amazon. The detected disturbances were caused by strong windstorms, which resulted in tree mortality events ranging from small clusters of 6-8 downed trees, to large contiguous blowdowns larger than 30-ha in size (Nelson et al. 1994, Negrón-Juárez et al. 2010). Windstorms are an important disturbance factor at HKK. For example, in 1962 a large cyclone struck Thailand (ADRC 2003), potentially creating the canopy openings that resulted the 1960s *Melia* cohort in our study area. This cyclone has earlier been proposed as an explanation for tree recruitment waves at HKK (Baker et al. 2005). More recently, a ~30-ha block of forest at HKK was blown down by a windstorm in 1987 (Baker et al. 2005). The same windstorm may have led to the regeneration of the two *Melia* age cohorts that we dated to 1985 and 1990.

Another disturbance factor influencing forest dynamics at HKK is fire. A growing number of studies have documented the occurrence of fires in tropical forests and their impacts on forest dynamics (e.g., Leighton and Wirawan 1986, Goldammer 1999, Barlow et al. 2003, Cochrane 2003). Intense El Niño-Southern Oscillation (ENSO) events in 1982-83 and 1997-98 resulted in extreme drought conditions over continental and insular SE Asia that were accompanied by extensive fires throughout the region (Murphy and Lugo 1986, Baker and Bunyavejchewin 2009). Moreover, seasonal tropical forests on the SE Asian continent experience fire relatively frequently due to the Asian monsoon system that generates a dry season of 2-6 months in which little to no rain falls (Baker et al. 2008). In these periods, temperatures on the forest floor increase and relative humidity decreases, making forests more prone to fire. Baker et al. (2008) conducted a study on the impacts of landscape-scale fire in deciduous and evergreen forests at HKK during the 1997-98 ENSO event. While they found that most tree mortality occurred in the smallest size classes, some large canopy trees were killed during the fires and for the ensuing 2-3 months, creating canopy gaps ranging from 25 to 1000 m^2 (Baker et al. 2008). With the onset of the monsoons, several months after the fires, there was a secondary pulse of canopy tree mortality as heavy rains and strong winds knocked over weakened trees (Baker and Bunyavejchewin 2009). Such post-fire mortality may continue for years after low-intensity fires (Barlow et al. 2003). Even though these 1998 fires in HKK were low-intensity (*i.e.*, flame lengths ranging from 5 to 50 cm), they led to diffuse canopy mortality over hundreds of thousands of hectares of forests. This diffuse canopy gap formation pattern that resulted from the 1998 fires is consistent with observed *Melia* recruitment patterns in our study plot. Furthermore, we found physical evidence of trees (both *Melia* and many other species) damaged by fire (e.g., fire scars, charred stumps), especially in the northern parts of our plot. Fire disturbance is therefore also a likely explanation of observed *Melia* recruitment patterns. Unfortunately, no fire data are available for HKK prior to 1992.

A third potential disturbance factor is drought. Severe droughts have a substantial influence on tree mortality in forest canopy species (Leighton and Wirawan 1986). Moreover, we consider the indirect effects monsoonal droughts have on fire occurrence to be of great importance to forest dynamics in terms of tree mortality. Cook et al. (2010) developed a seasonally resolved gridded spatial reconstruction of Asian monsoon drought and pluvials over the past millennium (the Monsoon Asia Drought Atlas) based on tree-ring chronologies spanning the Asian region. They found an intense dry period in the 1960s, consistent with extremely reduced wet-season rainfall inferred from teak chronologies in

Northern Thailand (~300 km from HKK; Pumijumnong et al. 1995). These dates are consistent with the establishment of the *Melia* age cohort we dated to the 1960s. This further supports the idea that the observed *Melia* recruitment patterns may have been the result of drought-induced forest fires.

We have speculated about the potential disturbance types affecting forest dynamics in a seasonal tropical forest in western Thailand. The reconstructed *Melia* establishment patterns suggest that at least two widespread disturbances took place at HKK in the past 60 years. In view of recent research on fire effects across the forest landscape of continental Southeast Asia (Baker et al. 2008, Baker and Bunyavejchewin 2009), we assume that fire is the most likely disturbance factor explaining *Melia* recruitment patterns. Nevertheless, high-quality historical records of disturbances are absent in these regions and other disturbance types, such as wind, cannot be ruled out.

Implications for reconstructing disturbance histories

While the combination of dendroecological and spatial analysis tools, such as the mark correlation function and kriging, proved very useful in our study, we suggest several improvements to our combined methodology. First, we worked on a rather coarse spatial scale as we included on average less than one tree per 4 ha, which reflects the low abundance of *Melia* in this forest. To evaluate gap dynamics on smaller spatial scales, we recommend a sampling design that includes a broader range of pioneer tree species. However, the high species diversity of tropical forests and the relatively limited number of species forming tree rings (Zuidema et al. 2012) make it unlikely that this approach will enable us to study dynamics at the scale of meters, as has been done in temperate forests (e.g., Rogers 1999, Sánchez Meador et al. 2009). It should be taken into account that the identification of spatially distinct cohorts of shade-intolerant trees will be most useful for interpreting disturbance histories. Shade-tolerant trees are not dependent on canopy gap formation for their survival and establishment, and various studies have shown that regeneration of shade-tolerant species is unrelated to past disturbance (Rozas 2003, Song et al. 2011). Therefore, patterns of tree regeneration for shade-tolerant trees may not reflect gap dynamics (Lorimer and Frelich 1989). In addition, shade tolerant species are less likely to form annual growth rings (Baker, P.J., *unpublished data*), limiting their utility for reconstructing historical stand dynamics.

Second, we see an additional application of this methodology. Sudden increases in diameter growth rates that are maintained for some years or decades ('releases') are thought to be the result of canopy gap formation (Rozendaal et al. 2011, Soliz-Gamboa et al. 2012). The use of spatial statistics in the analysis of light-growth relations may allow the temporal variations in growth (Rozendaal et al. 2011) to be interpreted on a spatial scale. In addition, while shade tolerant tree species may not provide evidence of disturbance in their establishment patterns, they are sensitive to abrupt changes in light conditions. As such, spatial patterns of growth release in the few shade tolerant tree species with annual growth rings could be used to supplement establishment patterns in shade intolerant species such as *Melia* (e.g., Baker et al. 2005). This would improve the reconstruction of the complex disturbance histories in tropical forests.

Past disturbances are important drivers of long-term changes in forest structure and growth trends. It is critical that the role of past disturbances in responses to regional and global environmental changes is acknowledged. Tree-ring analyses have the potential to offer great value in the reconstruction of historical stand dynamics in tropical forests. They allow us to gather insights into historical establishment dates without the need to perform long-term monitoring. Combining traditional tree-ring analyses and spatial statistical analyses will allow unraveling the spatial signature of past recruitment events.

Acknowledgements

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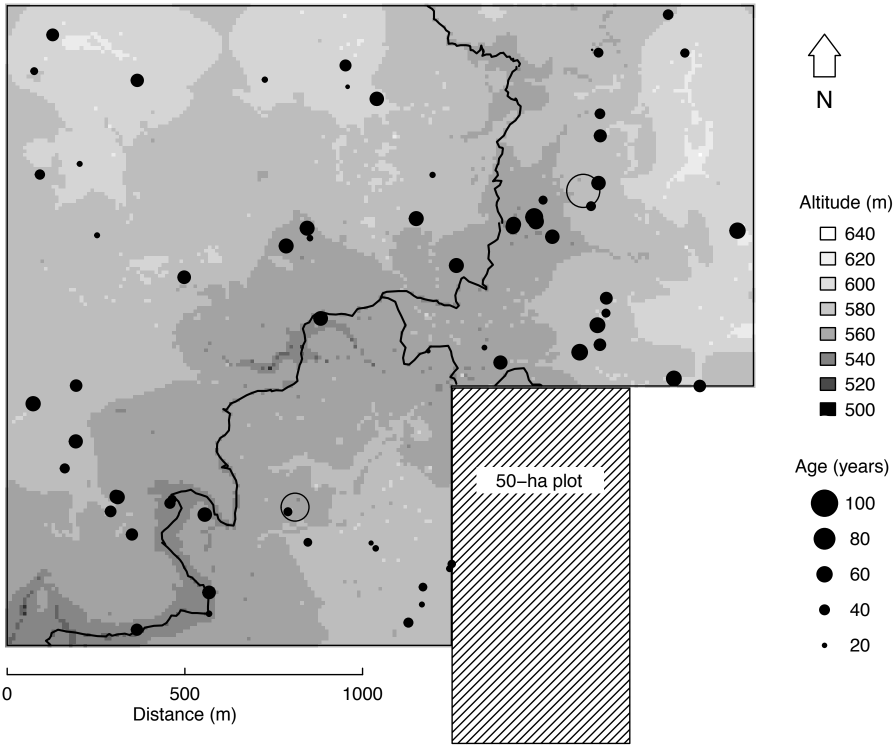


Figure S3.1 Digital Elevation Model (DEM) of the 316-ha study plot in the Huai Kha Khaeng Wildlife Sanctuary showing the locations of all sampled *Melia* trees ($n = 70$). Dot size corresponds to tree age and grey scales indicate varying altitude values. Open circles indicate the two sampled trees older than 100 years that are excluded from spatial analyses. The location of a small river and the adjacent 50-ha forest dynamics plot are shown

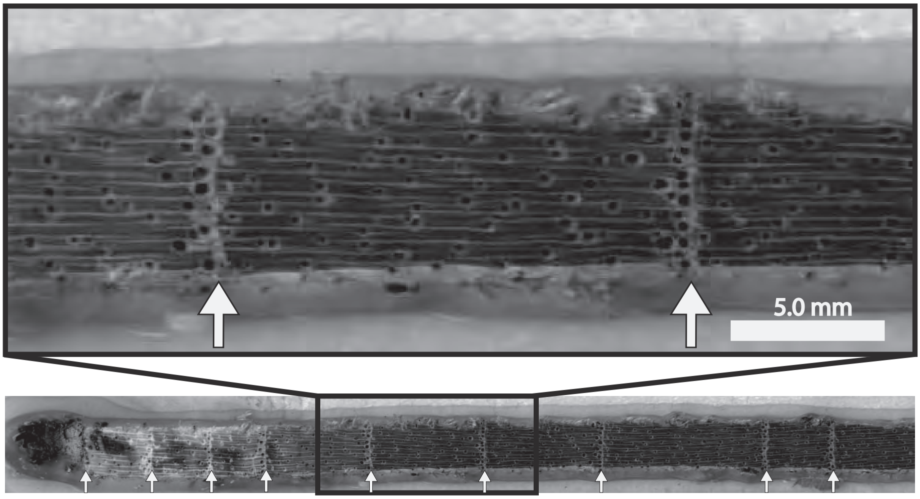


Figure S3.2 Wood structure and growth rings of *Melia azedarach* (Meliaceae). Arrows mark the annual ring boundaries which are easily recognizable due to the large vessels formed early in the growing season. The direction of growth was from right to left.

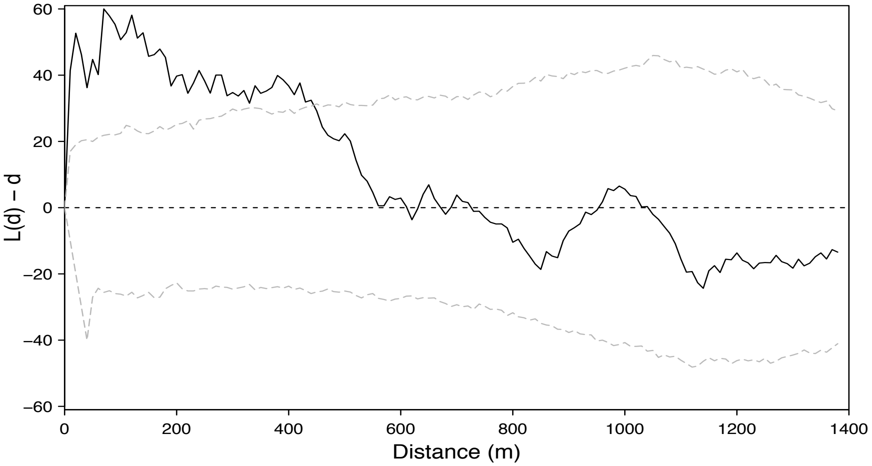


Figure S3.3 Normalized Besag's *L*-function for *Melia* tree locations, calculated over 10 m distance intervals (solid line). Dashed lines are approximate 95% simulation envelopes obtained from 999 Monte Carlo simulations under the hypothesis of complete spatial randomness. The solid line falls within the simulation envelopes for distances greater than 400 m; tree locations are randomly distributed. The solid line falls above the upper simulation envelope for distances between 0-450 m; tree locations are clustered.

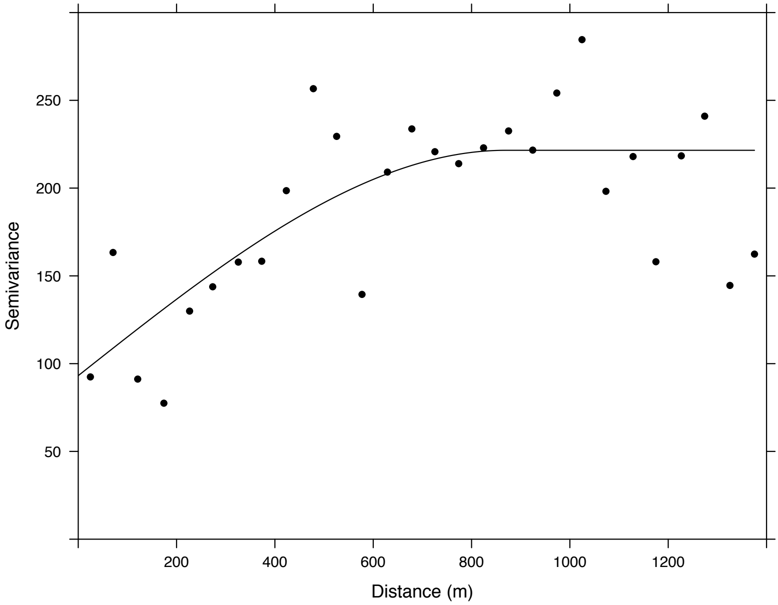
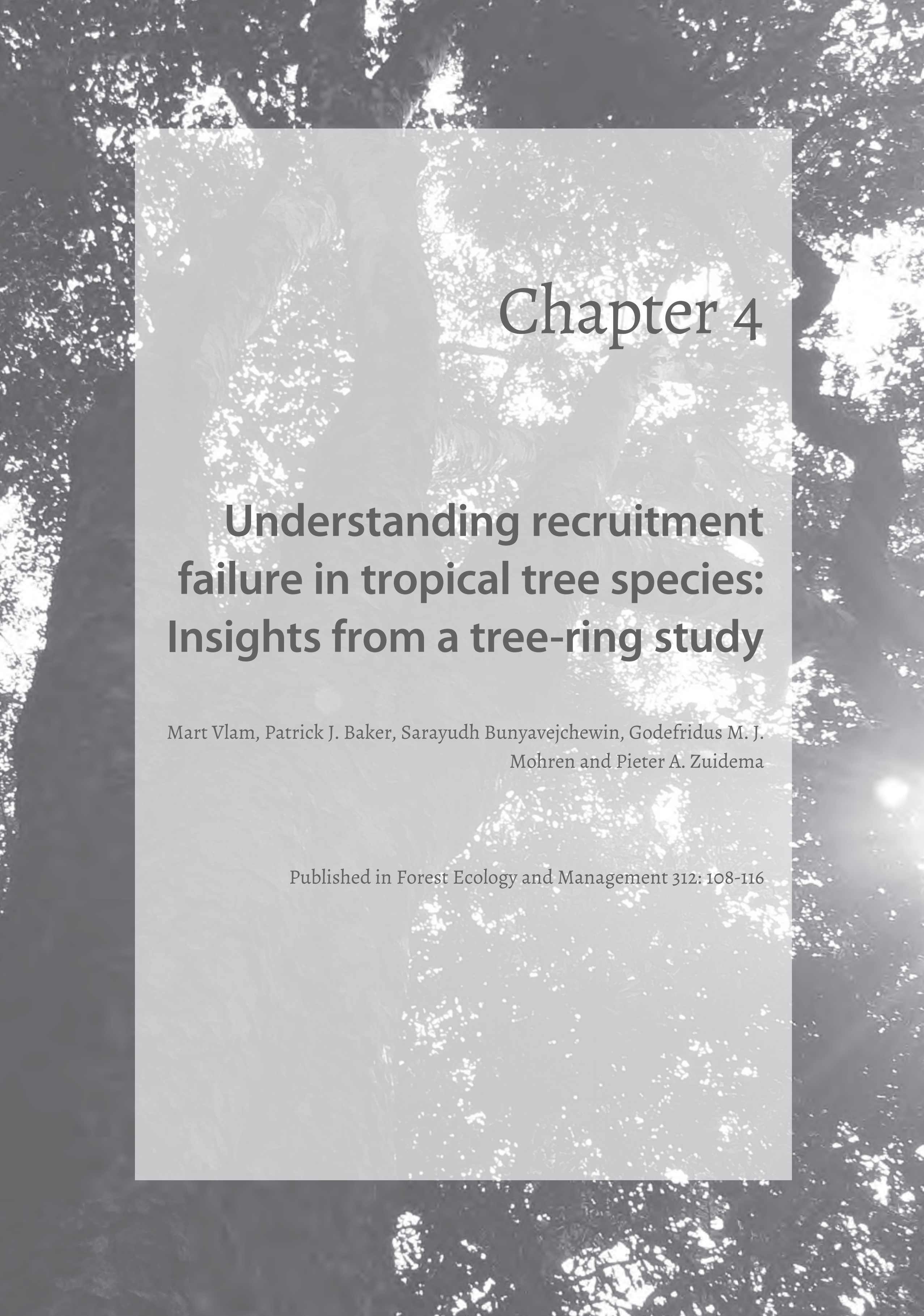


Figure S3.4 Semi-variances calculated over 50 m distance classes for *Melia* tree ages up to half the length of the largest plot dimension. Dots indicate calculated semi-variances; the line represents the calculated theoretical spherical variogram model. The values for the model's *nugget, range,* and *sill* equal ~90, ~820, and ~220 respectively.



Chapter 4

Understanding recruitment failure in tropical tree species: Insights from a tree-ring study

Mart Vlam, Patrick J. Baker, Sarayudh Bunyavejchewin, Godefridus M. J. Mohren and Pieter A. Zuidema

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Abstract

Many tropical tree species have population structures that exhibit strong recruitment failure. While the presence of adult trees indicates that appropriate regeneration conditions occurred in the past, it is often unclear why small individuals are absent. Knowing how, when and where these tree species regenerate provides insights into their life history characteristics. Based on tree age distributions inferences can be made on past forest dynamics and information is obtained that is important for forest management. We used tree-ring analyses to obtain tree ages and reconstruct >200 years of estimated establishment rates in a sparsely regenerating population of *Afzelia xylocarpa* (Fabaceae), a light-demanding and long-lived canopy tree species. We sampled all 85 *Afzelia* trees >5 cm diameter at breast height (dbh) in a 297-ha plot in a seasonal tropical forest in the Huai Kha Khaeng (HKK) Wildlife Sanctuary, western Thailand. The age distribution of the sampled *Afzelia* trees revealed two distinct recruitment peaks centered around 1850 and 1950. The presence of distinct age cohorts provides a strong indication of disturbance-mediated recruitment. Additionally we found three lines of evidence supporting this interpretation. (1) Similarly aged trees were spatially aggregated up to ~500 m, a scale larger than single tree-fall gaps. (2) High juvenile growth rates (5-10 mm dbh year^{-1}) of extant small and large trees indicate that recruitment took place under open conditions. (3) A significant positive correlation between tree age and local canopy height indicates that trees recruited in low-canopy forest patches. Likely causes of these severe canopy disturbances include windstorms and ground fires, which are common in the region. In addition, successful establishment seems to be favored by wetter climate conditions, as the estimated establishment rate was correlated to the Palmer Drought Severity Index (PDSI). Thus, the co-occurrence of canopy disturbance and favorable climatic conditions may provide a window of opportunity for *Afzelia* establishment. Our results indicate that forest patches with occurrence of large *Afzelia* trees have undergone high-severity canopy disturbance prior to establishment, suggesting that these disturbances have shaped forests at HKK. Tree-ring analyses provide a powerful tool to understanding tropical tree establishment patterns. Rare, high-severity canopy disturbances may play a key role in the regeneration of long-lived tropical canopy tree species with recruitment failure, potentially in interaction with climate variability to determine variation in establishment success over decades or centuries.

Keywords: *Afzelia xylocarpa*; age cohort; canopy disturbance; dendroecology; tree regeneration; Thailand

Introduction

Across the tropics the size distribution of many tree species is characterized by the apparent absence of small trees (Swaine and Whitmore 1988, Wright et al. 2003). In West Africa, Poorter et al (1996) described size class distributions for eight large-statured, canopy tree species, of which six did not show the inverse J-shaped distribution expected of a population at equilibrium. In Southeast Asia, Bunyavejchewin et al. (2003) showed that three out of four species in the Dipterocarpaceae family had irregular size distributions, typically lacking individuals in many of the smaller size classes. And in the Brazilian Amazon, Grogan et al. (2008) showed unimodal size distributions for populations of the commercially important mahogany tree (*Swietenia macrophylla*). Although unimodal size distributions may be generated by particular ontogenetic shifts in growth and mortality rates (Bin et al. 2012), they may also be an indication of recruitment limitation (Condit et al. 1998).

This raises questions of how, when and where species with unimodal size distributions regenerate, because without the occasional establishment of new recruits, these populations cannot be viable. Answering these questions is of importance for forest management and tree species conservation. Recruitment limitation is thought to be generated by scarcity of parent trees, limited seed availability and small dispersal distances, as well as establishment limitation, which may be coupled to the occurrence of disturbances (Snook 1996, Clark et al. 1998, Hubbell et al. 1999). In temperate forests, the role of rare and intense disturbances on regeneration of recruitment-limited tree species is well-known. In these forests, tree-ring studies have revealed the presence of discrete age cohorts of light-demanding tree species which were considered a strong indication of recruitment following canopy disturbance (Duncan and Stewart 1991, Splechtna et al. 2005, Jordan et al. 2008), especially if similarly aged trees are spatially aggregated (Rozas 2003). Over the past half century, studies on temperate forest dynamics have demonstrated that rare catastrophic disturbances are ubiquitous and shape forest structure and composition by driving tree recruitment patterns (Oliver & Larson 1996).

In tropical forests, the occurrence of intense disturbances is increasingly well documented (Whitmore and Burslem 1998, Chambers et al. 2013), but the role of intense disturbances in tree recruitment and as a potential mechanism explaining recruitment failure is less well understood. In part this lack of understanding is due to the dominant focus on direct observations at short temporal scales, such as seed trap studies that quantified seed limitation over several years (e.g., Muller-Landau et al. 2008) or censuses showing spatial segregation of seedlings and adult trees (e.g., Gullison et al. 2003). While these studies have been informative, their short temporal scale limits inference of the role of rare events on recruitment of tropical tree species. What is lacking in the study of recruitment limitation of tropical trees is long-term demographic information (Baker et al 2005). Such a century-long temporal scale is required, because the intensive and large-scale disturbances that are hypothesized to induce successful recruitment in tree species showing absence of small trees, are likely to occur at very low frequency (Chambers et al. 2013).

Tropical dendroecology addresses this knowledge gap by revealing the age structure of populations of non-regenerating tree species (Baker et al. 2005, Rozendaal and Zuidema 2011). Not only does dendroecology provide data on ages of trees, ring-width measurements also provide information on historical growth rates of trees (Abrams et al. 1997, Druckenbrod et al. 2013). The method can be used to assess whether growth rates of juvenile trees were high, indicative for establishment in disturbed areas with high light conditions (Landis and Peart 2005, Rozendaal et al. 2010a). Moreover, tree establishment after severe canopy disturbance may be inferred from the spatial segregation between mature trees (e.g., in presently closed-canopy forest) and juvenile trees (e.g., in present low-stature forest) (see Oliver and Larson 1996).

Here we test the hypothesis that episodic recruitment of a tropical tree species with an irregular size distribution is induced by rare, severe canopy disturbance events (Swaine and Whitmore 1988, Poorter et al. 1996, Newbery et al. 2004). We evaluated the regeneration strategy of the light-demanding and IUCN red-listed tropical tree species *Afzelia xylocarpa* (Kurz) Craib (Fabaceae) in western Thailand, where it is currently poorly regenerating (Baker et al. 2005, Baker and Bunyavejchewin 2006b, Bunyavejchewin et al. 2009). We hypothesize that the present-day population is lacking a regeneration niche because establishment is typically induced by occasional, spatially extensive canopy disturbances that affect several hectares of forest, but may be heterogeneous in intensity (Whitmore and Burslem 1998, Splechtna et al. 2005, Baker and Bunyavejchewin 2009). We refer to these events as 'severe canopy disturbances'.

We used data obtained from tree-ring analyses to address four specific questions. 1) Is there evidence for discrete age cohorts? If *Afzelia* relies on occasional large-scale canopy openings for its regeneration, we expect the age distribution to be strongly clustered. 2) Do age cohorts form spatially discrete patches? If regeneration is induced by severe canopy disturbance, we expect similarly aged trees to be spatially aggregated at a scale larger than that of single treefall gaps. 3) Are growth rates of juvenile trees always high in early stages of growth? High diameter growth rates of juveniles are indicative of trees recruiting in open conditions, and if these are found for both old and young trees, this indicates similar recruitment conditions over time. 4) Is forest structure surrounding current young trees different from the forest structure around old trees? We expect that if recruitment depends on canopy disturbance, then younger trees would be associated with low canopy (building phase) forest and older trees with high canopy (mature phase) forest. We use our findings to discuss the regeneration strategy of the study species and the disturbance history of the study site. We also discuss the potential role of severe canopy disturbance in the regeneration of long-lived tropical canopy tree species in general.

Materials and methods

Study area and species

The study area was situated in the Huai Kha Khaeng Wildlife Sanctuary (HKK), Uthai Thani province, western Thailand, around 250 km northwest of Bangkok (15.60 N 99.20 E). HKK is a protected area of global conservation significance. Both HKK and the adjacent Thung Yai-Naresuan Wildlife Sanctuary are International Man and Biosphere Reserves and together form the main core of Thailand's Western Forest Complex, the largest area of protected forest in continental Southeast Asia. The HKK landscape is characterized by a hilly topography. The climate is monsoonal with a rainy season from May to October and a 4-6 month dry season from November to April (Fig. S4.1). Mean annual rainfall is 1473 mm and mean annual temperature is 23.5 °C (Bunyavejchewin et al. 2009). Soils are highly weathered, slightly acidic ultisols and soil textures are sandy loam in the surface and sandy clay-loam in the subsurface horizon (Bunyavejchewin et al. 2009). There is no human influence in HKK, except for the Wildlife Sanctuary infrastructure and as an ignition source for ground fires expanding from agricultural areas around the park (Baker et al. 2008). No logging activities are known to have taken place in our study area. The vegetation in the area is classified as seasonal dry evergreen forest and mixed deciduous forest. A Smithsonian Center for Tropical Forest Science (CTFS) 50-ha forest dynamics plot, installed in 1992, is immediately adjacent to the area we used for our tree-ring study (Fig. 4.1). Mean density of trees ≥10 cm dbh in the 50-ha plot is 438 ha^{-1} and mean density of trees ≥30 cm dbh is 83 ha^{-1} (Bunyavejchewin et al. 2001). Canopy height of the forest is around 30 m, with occasional emergent trees reaching more than 50 m tall. Members of the family Dipterocarpaceae dominate the forest in total basal area; other well-represented families include Annonaceae, Euphorbiaceae and Meliaceae (Bunyavejchewin et al. 2001).

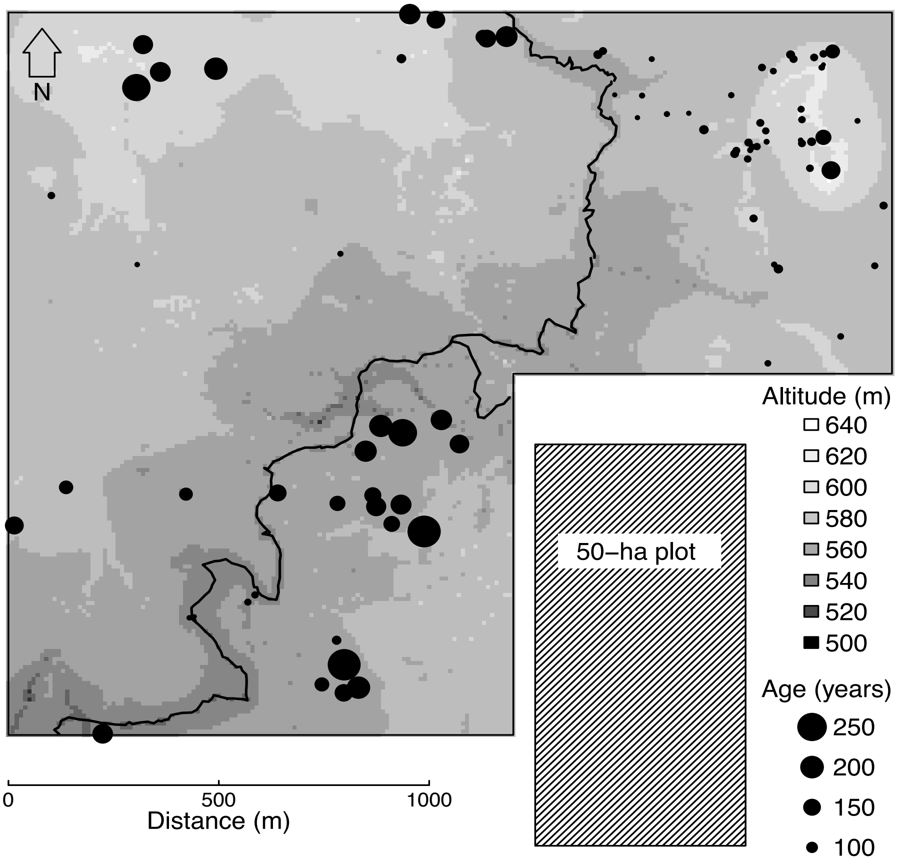


Figure 4.1 Topographic map of the study area in the Huai Kha Khaeng Wildlife Sanctuary showing locations of all *Afzelia* sample trees. Dot size is proportional to tree age. The black line indicates the location of a small stream running through the plot. Location of the adjacent 50-ha forest dynamics plot is also shown.

The study species, *Afzelia xylocarpa* (Kurz) Craib (Fabaceae), is known to form annual rings (Baker et al. 2005). The species is classified as light-demanding (So et al. 2010, Sovu et al. 2010) and in HKK the trees are completely leafless for around 1-2 months in the period from December to February (Williams et al. 2008). Due to loss of habitat and overexploitation for its precious wood the species has been classified as endangered on the IUCN Red List (Nghia 1998). However, in the remote areas of HKK, *Afzelia* is still relatively abundant across the broader landscape. Importantly, though, an earlier survey of the population of *Afzelia* trees in the area revealed an irregular size distribution characterized by many large trees and apparently poor regeneration (Baker et al. 2005). In the 50-ha plot small trees are rare, with only 8 individuals ≤10 cm dbh, compared to a total of 22 trees with a dbh >50 cm (Bunyavejchewin et al. 2009).

Detailed information on *Afzelia* regeneration under natural conditions, especially the seed dispersal mechanism, is scarce. It has been noticed that the large, aril-covered seeds are attractive to a variety of animals and especially gibbons (LaFrankie 2010). This is confirmed by our observations during the fruiting season in August 2011 when we found many fresh *Afzelia* seed pods with tooth marks, presumably from primates. Dispersal of similarly shaped seeds of the African congener, *Afzelia quanzensis*, has been found to be facilitated by primates, squirrels and hornbills (Gathua 2000, Gerhardt and Todd 2009), species groups that are all abundant at HKK. Seeds of *Afzelia* may therefore be dispersed over considerable distance by animals, in which case seed limitation may not be a limiting factor for recruitment.

Sampling and measurements

Our 297-ha ha study site was situated directly northwest of the 50-ha CTFS forest dynamics plot (Fig. 4.1). Wood samples for tree-ring analysis were collected from 85 individual *Afzelia* trees between December 2010 and December 2011. A total of 5 months was spent to thoroughly search the 297-ha area for all *Afzelia* trees >5 cm dbh. We used a GPS-tracker (Garmin GPSMAP 60C Sx) to visualize our trails and to verify that the whole area was covered. Characteristic features, such as early branching, a distinctive flakey bark and presence of large superficial roots greatly facilitate the recognition of the species in the field.

The locations of *Afzelia* trees suitable for coring (i.e., no stem deformities or severe stem rot: <10% of the individuals encountered were not suitable for coring) were GPS-mapped at ~5 m accuracy and the elevation level was recorded.

We measured dbh (1.3 m) and diameter at sampling height of each *Afzelia* tree. Height measurements of all sampled *Afzelia* trees and all taller neighboring trees within 10 m of the sample tree were obtained using a digital hypsometer (Nikon Forestry 550).

At a height of approximately 1 m we manually extracted tree cores with 5.15 mm diameter Suunto (Vantaa, Finland) or Haglöf (Långsele, Sweden) increment borers. Thus, in the following 'tree age' refers to the age since reaching coring height. Depending on the diameter of the tree we used borers with lengths varying between 40 and 70 cm. From trees <40 cm dbh two cores were taken and for all larger individuals we took three cores. Taking multiple cores allowed us to measure rings over at least three complete radii, thereby correcting for radial differences in diameter increment. We only cored trees >5 cm dbh to minimize damage to the juveniles. Core extraction areas were left untreated (Dujesiefken et al. 1999).

The increment cores were glued to wooden holders and cut perpendicular to the ring boundaries with a large sliding microtome (WSL, Switzerland). Digital images (1600 dpi) of the tree cores were acquired using a high-resolution flatbed scanner (Epson Expression 10000 XL) and analyzed in the WinDENDRO program for tree-ring analysis (version 2009b; Regent Instruments Canada Inc.). All tree-ring boundaries, defined by marginal parenchyma bands, were marked manually on the screen and measured to the nearest 0.001 mm. Ring-width series were visually crossdated within trees and then among trees (WinDENDRO). During crossdating the patterns of wide and narrow rings in one tree are matched with those of other trees to improve the dating accuracy of the rings. After crossdating ring-width series were checked for dating errors with the computer program COFECHA (Holmes 1983). As a quality control for the dating accuracy we aimed to produce a species specific tree-ring chronology, which is a record of ring widths representing the stand level signal. First, ring-width series that correlated poorly with the initial chronology—for example, due to prolonged growth suppressions—were removed from the dataset (Pederson et al. 2004). Second, the raw ring-width data was detrended using a 20-year cubic spline to remove all age related trends. Third, the ring-width data was prewhitened using autoregressive modeling to remove any effect of temporal autocorrelation in growth (dplR; Bunn 2008). The resulting chronology was cut off when the running expressed population signal (EPS) was <0.85 (Wigley et al. 1984). The EPS is used to assess how well a chronology of a finite number of trees estimates the hypothetical (noise-free) population chronology and can therefore be used to determine the maximum length of the chronology (Wigley et al. 1984).

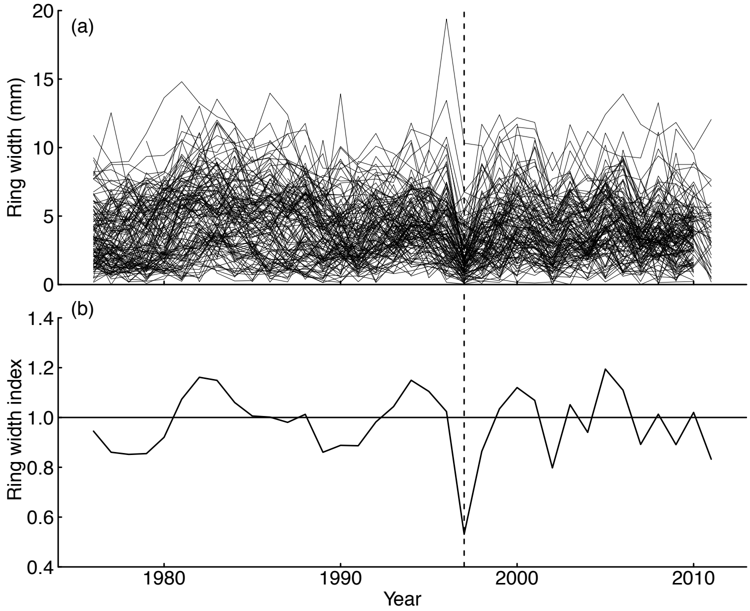


Figure 4.2 Ring widths (a) of all *Afzelia* trees that were included in the species-specific chronology (b). The marker year 1997 is indicated by the dashed line.

The pith was not included in many cores, either due to insufficient borer length or because all coring attempts had failed to include the pith of the tree. The pith was not included in the samples taken for ~75% of the trees (64/85 trees), although the missing distance was >3 cm in only 26% of the cases (22/85 trees) (Fig. S4.2a). If arcing was visible on the cores the missing distance to the pith was estimated by the degree of arcing in the oldest visible ring, assuming a circular growth pattern (Splechtna et al. 2005). If no arcing was visible on the cores we calculated the missing distance to the pith based on the diameter at sample height measured in the field. The missing distance to the pith was then used to estimate the pith dates by dividing the missing radial distance to the pith by the average width of the five oldest visible rings. Because missing distances to the pith lead to some uncertainty around the age estimates we also used an alternative method to obtain age estimates of trees with no pith. Based on all 21 trees that could be pith-dated we constructed a model of age vs. diameter. This model was then used to obtain an alternative estimate of the missing number of rings to the pith and an alternative age distribution.

Data analysis

A digital elevation model of the 297-ha plot was created using an inverse distance weighted interpolation (R gstat package; Pebesma 2004) of ~12,500 individual elevation measurements obtained with the GPS device.

We expected that establishment of new individuals might be related to variability in local climate conditions (Cullen et al. 2001, López et al. 2008, Zimmer and Baker 2009). Therefore we tested the relation between the estimated establishment distribution and the reconstructed Palmer Drought Severity Index (PDSI) for the summer (June-July-August) monsoon season at the location of our study area using the Monsoon Asia Drought Atlas (MADA) (Cook et al. 2010, Trouet and Van Oldenborgh 2013). The PDSI is a measure for soil moisture availability, in which a value of 0 indicates normal moisture conditions, while negative values indicate dry and positive values indicate wet conditions. These PDSI values were derived from a network of more than 300 tree-ring chronologies across the part of Asia that is affected by the summer monsoon system. For each decade in 1700-2000 we calculated the estimated establishment rate and the mean PDSI value. As trees that recruited in the distant past have accumulated a higher mortality risk compared to recent recruits, we calculated the estimated number of established trees per decade z for decade y, $z(y)$, assuming an annual mortality rate of 1%. We calculated $z(y)$ as:

$$z(y) = n_y * \left(\frac{100}{99}\right)^{1990-y}$$

where n_y is the number of trees that survived until the date of sampling and y is the decade of establishment. A generalized linear model (GLM) with Poisson error structure was used to explain variation in z by decadal mean PDSI values.

We assumed that if trees establish in even-aged patches, that the spatial distribution of tree ages should be non-random, with trees of similar age occurring together (Duncan and Stewart 1991, Middendorp et al. 2013). This spatial autocorrelation in tree age was calculated using Moran's *I* coefficient. We used 100 m distance classes and only considered distance classes with more than 15 pairs of neighboring trees. The correlogram was considered globally significant if at least one Moran's *I* coefficient was significant at a Bonferroni-corrected significance level ($P < 0.05/n$), where *n* is the number of distance classes in the correlogram (Fortin et al. 1989). Positive Moran's *I* values indicate that trees over this distance are similarly aged, while negative values indicate dissimilarity in age.

Average growth rates per 10 cm dbh class were calculated for each individual tree to assess the relation between dbh and diameter growth. Growth rates of juvenile trees (<30 cm dbh) were then compared between cohorts. Forest canopy height was estimated by taking the height of the tallest tree within 10 m of the sampled *Afzelia* tree. If no other tree within 10 m from the sampled *Afzelia* tree was taller we estimated forest canopy height as the height of the sample tree. All statistical analyses were performed using the R program for statistical computing, version 2.13.1 (R Development Core Team 2013).

Results

Afzelia xylocarpa was found throughout the 297-ha plot, although spatial variation in tree density was considerable. A large proportion of the trees was located in the northeast corner of the plot, directly north of the 50-ha plot (Fig. 4.1). This forest area was structurally different from the rest of the study area due to the abundance of bamboo clumps of an unidentified species. Patches with older (~150 year) *Afzelia* trees were mainly dominated by large Dipterocarpaceae trees (e.g., *Hopea odorata*, *Vatica harmandiana*).

Table 4.1 Descriptive statistics of the ring-width series used for the chronology of *Afzelia xylocarpa*.

n sampled (trees/radii)	*n* chronology (trees/radii)	Time span	Years	Rbar.wt[a]	Rbar.bt[b]	EPS[c]
100/341	38/133	1976-2011	36	0.45	0.13	0.90

[a] Rbar.wt is the mean of the correlations between series from the same tree; [b] Rbar.bt is the mean interseries correlation between all series from different trees; [c] EPS is the expressed population signal.

Based on crossdated ring-width series of 38 trees (38% of the total) we constructed a standardized chronology (Fig. 4.2). Total chronology length (EPS > 0.85) was 36 years and covered the period between 1976 and 2011 (Table 4.1). The *Afzelia* chronology was marginally positively correlated ($P < 0.07$, Pearson correlation) with the annual resolution PDSI values for the location of our study area. The marginally positive correlation between the chronology and PDSI values indicates that years of high growth in Afzelia were associated with relatively wet years. This is also supported by the occurrence of a marker year (a year with unusually narrow rings) in 1997 when PDSI values were strongly negative.

The size distribution of all *Afzelia* trees in the 297-ha area did not show an inverse J-shaped distribution. The median dbh of trees in this population was 65.4 cm with a standard deviation of 27.5 cm and a range of 12.4 to 172.0 cm. A Kolmogorov-Smirnov (KS) test for normality revealed that the diameter distribution for all 85 sampled *Afzelia* trees was not significantly different from a normal distribution ($P = 0.096$, Fig. 4.3a).

The lack of small-sized individuals in the diameter distribution reflects the absence of recent establishment, only one new *Afzelia* tree had established and survived since 1970 (Fig. 4.3b). More than 90% of the extant *Afzelia* trees in our study plot established during two periods: around 1850 and around 1950 (Fig. 4.3b). Of the 52 trees that established in the age cohort between 1930 and 1970, 67% recruited in the 20 years between 1940 and 1960. The 28 trees that established around the 1850s seem to form a second, though less distinct age cohort (1810-1900). The KS test for normality of the age distribution indicated that this distribution was significantly different from a normal distribution ($P < 0.001$). The alternative age distribution, in which age estimates of trees that did not include the pith were based on mean population growth rates, showed very similar results (Fig. S4.3). This alternative age distribution was also significantly different from a normal distribution ($P < 0.001$). Because the trees in the 1850s cohort have experienced 100 years of additional mortality risk compared with the 1950s cohort, the estimated number of established trees was probably much higher in that cohort. Indeed, the distribution of estimated establishment rate per decade, z, contained two cohorts of roughly equal size. The 1950s cohort consisted of an estimated 79 trees, vs. 52 extant trees, whereas the 1850s cohort was estimated to have consisted of 117 trees instead of the 28 extant trees (Fig. S4.4).

We were interested in the potential role of regional climate variability in explaining decadal variation in estimated establishment rate, z. We therefore related *z* to the PDSI values for western Thailand (Fig. 4.3b). We found a significant ($P < 0.001$) positive relationship between 10-year mean PDSI values and estimated establishment rate. For instance, the onset of the second recruitment pulse (~1940), was associated with a period of unusually wet years (annual PDSI > 0) between 1938 and 1956 (Fig. 4.3b).

The correlogram revealed a significant spatial structure in the distribution of tree ages, with positive Moran's *I* coefficients at distances <500 m and negative coefficients at distances >700 m (Fig. S4.5). This reflected a patchy distribution of similarly aged trees at the scale of 0-25 hectares, with trees in the 1950s cohort clumped in a ~25 ha area in the northeast of the plot. Trees belonging to the 1850 cohort are primarily grouped in 3-4 smaller clumps (~5 ha) in the southeast corner and upper northern section of the study area (Fig. 4.1). The significantly negative values of the Moran's *I* coefficient at larger distances (750-1500 m) indicated that patches of similarly aged trees were spatially segregated. We found no relationship between sample tree age and elevation suggesting that topography was no causal factor in the observed patchy distribution of ages (Spearman rank correlation, $P > 0.8$).

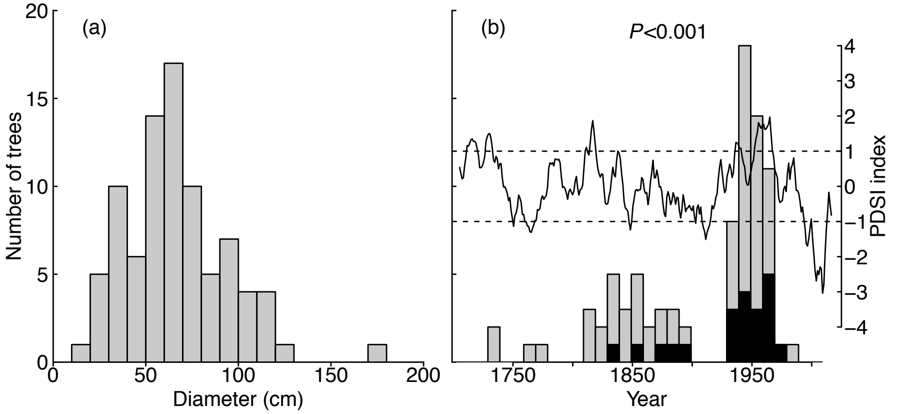


Figure 4.3 Diameter distribution in number of individual trees per 10 cm dbh class (a) and age distribution (b) for *Afzelia*. The age distribution is shown as the decadal establishment rate of the extant trees. Dark grey bars represent ages of those individuals for which the pith was included in at least one of the samples ($n = 21$). Light-grey bars represent those individuals for which the pith was not included in any of the samples ($n = 64$). The black line represents a 10 year running mean of reconstructed Palmer Drought Severity Index (PDSI) values of the regional summer monsoon. Positive PDSI values indicate wet conditions; negative values indicate dry conditions. A generalized linear model (GLM) was used to determine the relation between estimated establishment frequency and mean PDSI values, *P*-value of the model fit is indicated.

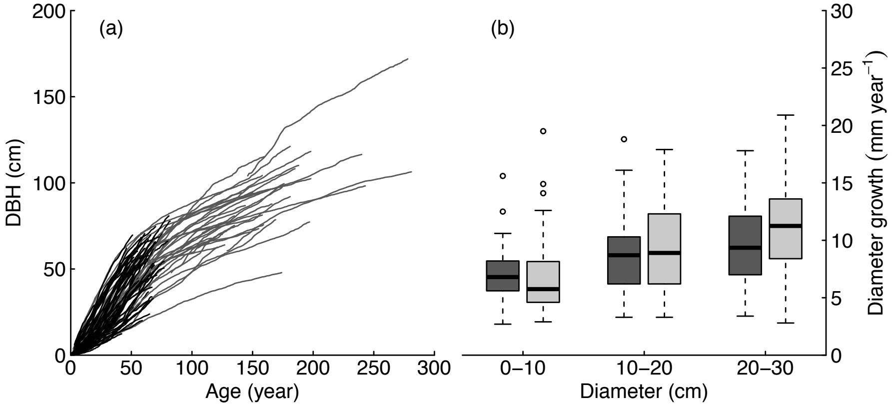


Figure 4.4 Growth trajectories of all 85 sample trees (a) and boxplots of diameter growth in three size classes (b). (a) Black lines represent individuals that established after 1900, grey lines represent individuals that established prior to1900. (b) Boxplots were colored dark grey for trees that established before 1900 and light grey for trees that established after 1900. No significant differences in growth rates of trees among any of the size classes were present (Wilcoxon rank-sum test, $P > 0.05$).

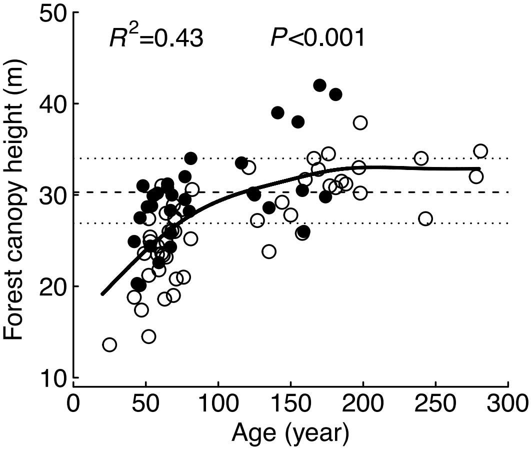


Figure 4.5 Relationship between current canopy height and *Afzelia* tree age. Filled circles represent situations in which neighbor trees were taller and open circles represent those situations in which the sampled *Afzelia* tree itself was the tallest tree. The dashed line indicates median canopy height in the study area (30.3 m) and the dotted lines indicate the 25th and 75th percentiles (26.9 m and 34.0 m). The black line represents a fitted generalized additive model (GAM) response curve with a single smoothing parameter, R^2 and P-value of the model fit is indicated.

The growth pattern of *Afzelia* was characterized by a rapid increase in diameter growth just after establishment followed by a decrease over time. Mean diameter growth of juvenile *Afzelia* trees (5-30 cm dbh) was 7.5 ± 4.3 mm year^{-1}

(standard deviation). On average, growth of *Afzelia* reached its maximum of ~10 mm year^{-1} for trees in the 30-40 cm dbh class and then declined to ~3.0 mm year^{-1} for the biggest trees (>80 cm dbh). Variation in growth rates was high (2-20 mm year^{-1}) resulting in variable growth trajectories (Fig. 4.4a). We found no evidence that trees that established before 1900 had different median growth rates than trees that established in the 20th century. For each size class (0-10, 10-20, 20-30 cm) we compared median growth rates of trees that established before 1900 with trees that established after 1900 (Fig. 4.4b). We found no significant differences in growth rates of trees among any of the size classes (Wilcoxon rank-sum test, $P > 0.05$).

We expected that younger trees would be associated with more recently disturbed forest and that older trees would be predominantly found in more mature forest. We used estimated canopy height as a proxy for stand development stage (Fig. 4.5) and found a positive relation between tree age and forest canopy height ($P < 0.001$, generalized additive model (GAM) with one smoothing parameter). Because the estimated canopy height was often the height of the focal individual we performed a second regression in which we only used canopy heights that were based on trees other than the focal tree. This revealed a similarly positive relation between tree age and forest canopy height ($P < 0.001$).

Discussion

We hypothesized that the lack of recruitment in *Afzelia* is due to the sporadic occurrence of severe canopy disturbance events. Based on tree-ring dating we found a bimodal age structure in which similarly aged trees were spatially aggregated, showing evidence of episodic recruitment. The high juvenile growth rates in the past and the present, and the association of young trees with building-phase forest suggest that recruitment peaks were initiated by large canopy openings. This suggests that the process of disturbance-mediated recruitment limitation is not limited to temperate forests and may also play a role in tropical forests.

Age cohorts

In studies on tree regeneration in temperate forests, the presence of discrete age cohorts in tree populations is considered a strong indication of past severe canopy disturbance (Cullen et al. 2001, Splechtna et al. 2005). In our study species we found evidence of two age cohorts. In contrast to most temperate forest studies, in which age cohorts are usually narrow, our age cohorts were rather broad with the oldest one spanning nearly a century. Given that forests in our study area are strongly light-limited and *Afzelia* is a shade-intolerant species (see below), we did not expect to find such broad age cohorts. There are several potential methodological explanations for this pattern. First, counting and measuring growth rings of *Afzelia*, and rings of tropical tree species in general, can be difficult due to the occurrence of missing and false rings (Worbes 1995). Although growth rings of *Afzelia* are distinctly annual (Baker et al. 2005) and among-tree crossdating was successful, ring identification errors likely occurred and have accumulated towards earlier dates. Second, the majority uncertainty most likely resulted from the missing distance to the pith on cores of ~70% of our sampled trees. For these samples, we estimated the number of missing rings to the pith both by extrapolating growth rates based on the five oldest visible rings and modelling growth rates based on 21 individuals that did include the pith in one of the samples. As the trees in the older cohort were larger, the estimated number of missing rings per tree in the 1850s cohort was higher (median = 12 rings), compared to the estimated number of missing rings per tree in the 1950s cohort (median = 2 rings). Third, the observed age variation may also have resulted from variation in time to reach coring height (~1 m). We estimated that this error would be comparatively small because initial height growth of *Afzelia* juveniles is generally high (So et al. 2010). Although the above factors were almost certainly responsible for part of the age variation in the two cohorts, we cannot rule out the possibility that the broad age cohorts reflect recruitment conditions occurring during a period of several years or decades.

Afzelia regeneration strategy

In general the presence of distinct age cohorts provides a strong indication of disturbance-mediated recruitment. We found three additional lines of evidence which support this interpretation for *Afzelia*. (1) We hypothesized that age cohorts of trees would form spatially discrete patches if recruitment had initiated after severe canopy disturbance (Snook 1996, Rozas 2003). Similarly aged trees were indeed aggregated in patches larger than those typically formed by single treefall gaps. This clustering of ages is unlikely under a scenario of for example dispersal limitation (Hubbell et al. 1999), or an association with edaphic factors (e.g., Potts et al. 2002, John et al. 2007), because this only predicts spatial aggregation of individuals of a species, not of individuals of a certain age. (2) We also expected to find high juvenile growth rates indicative of recruitment under very open conditions, similar to those that occur after a severe disturbance. As expected growth rates of juvenile trees (<30 cm dbh) are high, typically 5 to 10 mm year^{-1}, which is comparable to the shade-intolerant pioneer species *Melia azedarach* (~10 mm year^{-1}) and considerably higher than the 2.4 ± 2.6 mm year^{-1} mean growth rate for trees <30 cm dbh (n = ~28,000) in the 50-ha forest dynamics plot (Bunyavejchewin, S. & Baker, P. J. unpublished data). (3) Our fourth research question was whether forest structure surrounding current young trees would be different from the forest structure around old trees. We found a significant positive correlation between tree age and canopy height suggesting that *Afzelia* regeneration is associated with younger, more recently disturbed forest patches. In a situation in which this species regenerated in mature forest, where juveniles occur under a canopy of adults, such a canopy-age relation would not have been found. The preference of young *Afzelia* for disturbed forest patches is further supported by studies in which *Afzelia* regeneration was found to be favored by high light conditions after logging (Kaewkrom et al. 2005, Sovu et al. 2010).

A small share (~10%) of *Afzelia* trees in our study occurred as solitary individuals. These trees tend to be somewhat smaller and younger than the *Afzelia* trees in the surrounding forest, though no clear pattern arises. Young trees that were not in close proximity to other *Afzelia* trees were all in exposed, high-light environments, such as along the stream running through the plot. High light has likely contributed to their establishment success, although increased establishment success may also have resulted from the lower fire risk and intensity in more open vegetation patches. The last observed case of successful establishment of an individual >5 cm dbh occurred around 1987 and was of a solitary individual that recruited in an exposed area along the stream.

Recruitment success: canopy disturbance and climate stochasticity

The evidence pointed out above suggests that successful establishment of Afzelia requires canopy disturbance, but what type of canopy disturbance? In the seasonal tropical forests of continental Southeast Asia the most common types of intense disturbance are wind storms, fires and droughts (Ashton 1993). All three disturbance types have likely shaped the forest structure of HKK over the past few centuries (Bunyavejchewin et al. 2003) and indications for canopy disturbance in HKK have been found before (Baker et al. 2005, Middendorp et al. 2013). In

Thailand heavy winds are mainly associated with the rainy season, resulting in stem breakage and uprooting of large trees (Marod et al. 2004). Windfall would usually result in a diffuse pattern of small and large canopy gaps, increasing understory light levels (Oliver and Larson 1996, D'Amato and Orwig 2008). Large amounts of woody debris after windfall may also increase fire susceptibility of the forest in the following dry season. Low-intensity ground fires of anthropogenic origin occurred nearly every year somewhere within HKK in the past two decades (Baker et al. 2008). Sanctuary wide fires are less common and occur only once every 3-10 years in HKK (Baker et al. 2008). These more widespread fires are possibly associated with intense ENSO events and may increase in intensity after windfall has increased fuel loads (Bunyavejchewin et al. 2009, Wanthongchai et al. 2011). In HKK low- intensity ground fires have been observed to lead to extensive mortality of canopy trees (Baker et al. 2008). But extensive mortality of canopy trees may also be induced by prolonged droughts (Nepstad et al. 2007). So, either canopy damage by a windstorm, ground fire or drought, or a combination of windfall and more intense ground fires may have resulted in an increased openness of the forest canopy around 1850 and 1950. Evidence for the dating of these disturbance events is also consistent with earlier findings from an adjacent study site (Baker et al. 2005).

Our analyses of climate data suggests that disturbance is not the only factor determining Afzelia recruitment, as recruitment rates seem to be higher during wetter periods, particularly during the 20th century. Marod et al. (2004) have shown that drought and fire are major bottlenecks for seedling survival in seasonal tropical forests of Southeast Asia. Since 1980 western Thailand has been characterized by strong negative deviations in PDSI values (Cook et al. 2010) and very poor Afzelia recruitment in our study area. These droughts may have indirectly hampered recruitment through increased probability of ground fire incidence (Baker et al. 2008). In the first years after germination Afzelia seedlings are very prone to ground fires, although they possess the ability to resprout (So et al. 2010). Fire exclusion from the forest area of regenerating trees in the first years might therefore be critical for seedlings to escape the life stage most susceptible to dieback after fire (Grogan et al. 2010). In 1991- 1992, 1998 and 2004 ground fires passed through the area of the study site (Baker et al. 2008, Bunyavejchewin et al. 2009) and there is no evidence of recruitment of Afzelia during this period.

While we lack direct observation of natural regeneration of Afzelia, our results do suggest that severe canopy disturbance followed by relatively wet conditions provide a window of opportunity for successful recruitment of this species (see also Brown and Wu 2005). Such a wet spell combined with the high light conditions that follows a severe canopy disturbance would allow seedlings to grow rapidly in height and girth, and quickly escape the small size classes susceptible to fire-induced mortality.

Episodic recruitment in tropical tree species

We have provided evidence that severe canopy disturbance and climate stochasticity may play a key role in the episodic regeneration of a long-lived tropical tree species. Other long-lived, poorly regenerating tropical canopy tree species may possess similar strategies of episodic recruitment (Poorter et al. 1996, Gullison et al. 2003) and their size distribution may obscure an underlying pattern of discrete age cohorts. Such episodic recruitment, in combination with a high observed maximum age, may indicate that a population that appears to lack regeneration is not actually in an 'unhealthy' state (Condit et al. 1998). As long as severe disturbances cause occasional wide-spread canopy loss, populations of these tree species will be able to regenerate naturally, thereby sustaining their populations. This observation could have significant implications for the conservation of other IUCN Red List tree species that possess similar life history strategies as Afzelia. If regeneration depends on rare disturbance events, possibly in combination with a climate anomaly, it may take decades before protected populations start to regenerate and grow.

Our findings of patchy and episodic recruitment of Afzelia provide evidence of severe canopy disturbances at our study site. The forest patches containing old Afzelia trees in parts of our study area point to severe canopy disturbances that occurred some 60 and 160 years ago, probably in concert with relatively wet conditions that enhanced seedling survival. The interaction of past disturbances and climatic fluctuations has likely shaped the patchwork mosaic of structurally and floristically distinct forest types that are common in western Thailand (Bunyavejchewin et al. 2001). Such localized, severe disturbance events caused by windfall, ground fire or climate anomalies can be found across the tropics (Ashton 1993, Foster et al. 1999, Burslem et al. 2000, Chave et al. 2008) and likely shape forest dynamics and tree regeneration (Newbery et al. 2013).

Tree-ring analysis provides a powerful tool for studying regeneration dynamics of tropical tree species with recruitment failure. Annual-ring producing tropical tree species offer the possibility to identify recruitment peaks in the population structure and reconstruct historical growth rates. Using the tree-ring approach we were able to assess a bimodal age structure that would otherwise have been obscured by a unimodal diameter distribution. Our findings provide evidence that severe canopy disturbances and climate stochasticity have played a key role in the regeneration of a long-lived tropical tree species.

Acknowledgements

We thank the European Research Council (ERC, grant #242955) for providing financial support for this study. The National Research Council Thailand (NRCT) and the Department of National Parks (DNP) provided permission for accessing the Huai Kha Khaeng Wildlife Sanctuary and the collection of wood samples. Field staff of the Huai Kha Khaeng forest dynamics plot provided logistical support and assistance with species identification in the field. Somboon Kiratiprayoon provided invaluable support in arranging the conditions for our fieldwork.

Appendix

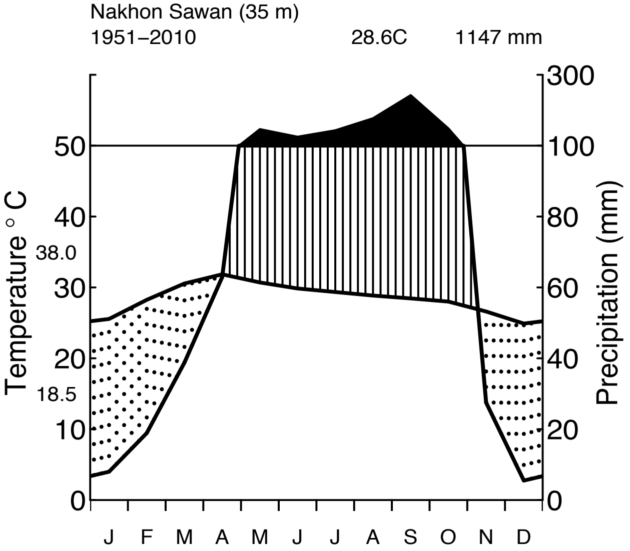


Figure S4.1 Climate diagram for the Nakhon Sawan meteorological station, ~100 km east of the study site. All meteorological data were obtained from the KNMI Climate Explorer website (climexp.knmi.nl; Trouet and Van Oldenborgh 2013)

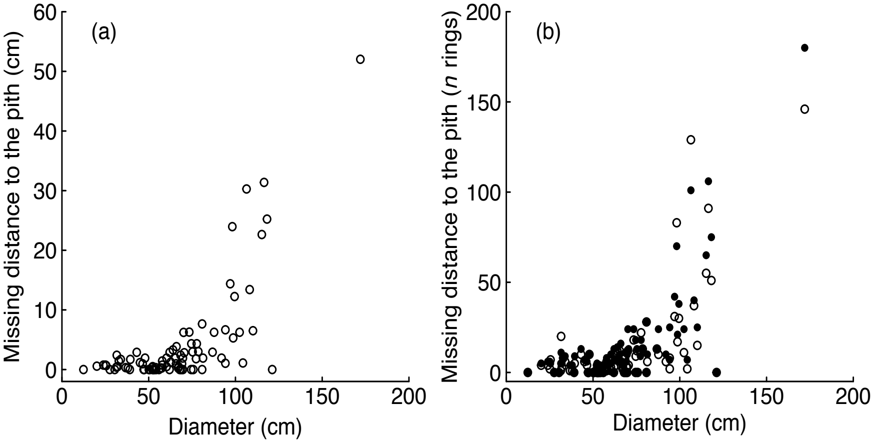


Figure S4.2 Relation between diameter and missing distance to the pith in cm (a) and number of rings (b). (b) Open symbols represent estimated number of rings based on average width of the five oldest visible rings. Closed symbols represent estimated number of rings based on modeled growth rates for those trees that did include the pith in one of the samples.

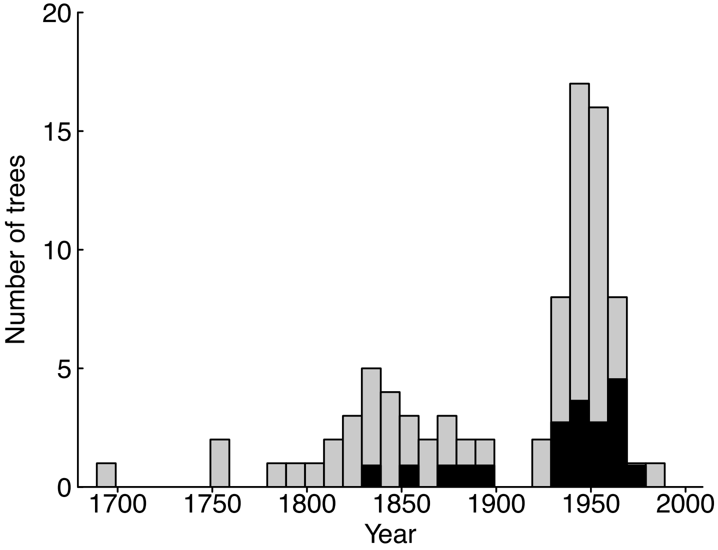


Figure S4.3 Alternative age distribution based on modeled growth rates of the 21 trees that did include the pith. Black bars represent ages of those individuals for which the pith was included in at least one of the samples (*n* = 21). Light-grey bars represent those individuals for which the pith was not included in any of the samples (*n* = 64).

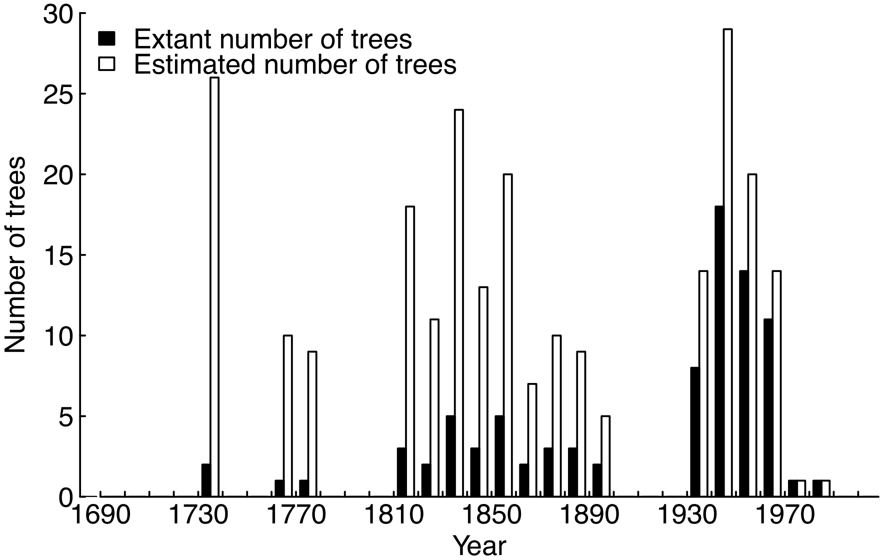


Figure S4.4 Establishment distribution of the extant trees (white bars) and estimated establishment distribution (black bars). The estimated establishment distribution was based on the age distribution of the extant trees, assuming a constant mortality rate of 1% year^{-1}.

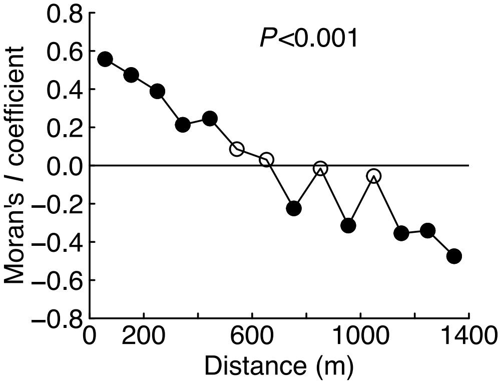
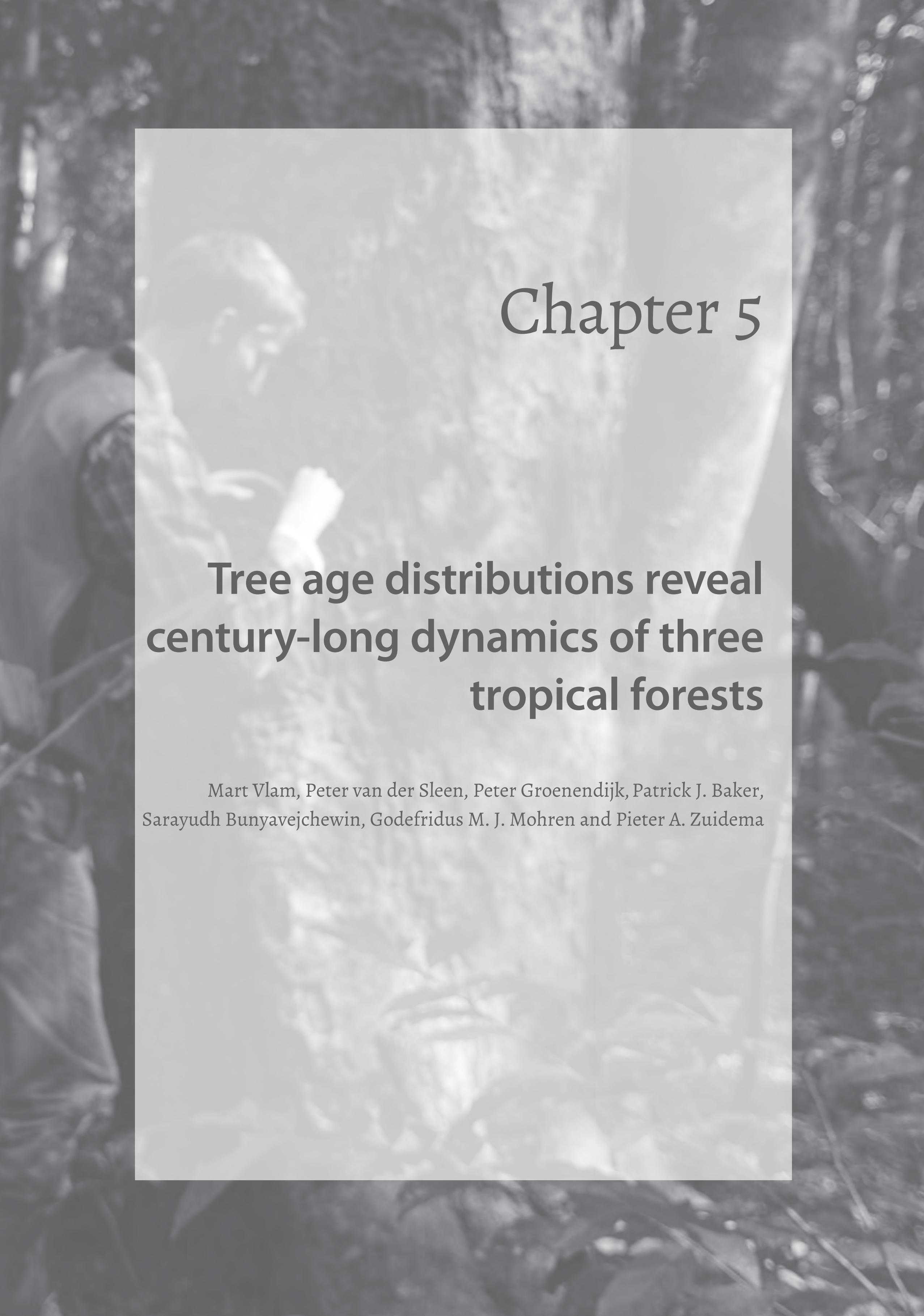


Figure S4.5 Correlogram of *Afzelia* age distribution in the 297-ha plot. Filled dots indicate significant Moran's *I* coefficient values, open dots are non-significant values. The *P*-value refers to the Bonferroni-corrected (*P*/*n*) global significance of the correlogram.



Chapter 5

Tree age distributions reveal century-long dynamics of three tropical forests

Mart Vlam, Peter van der Sleen, Peter Groenendijk, Patrick J. Baker,
Sarayudh Bunyavejchewin, Godefridus M. J. Mohren and Pieter A. Zuidema

Abstract

Tropical forests have long been seen as relatively stable systems that are subject to only minor fluctuations caused by small scale canopy gap dynamics. This assumption is contrasted by remarkable increases in tree growth and forest biomass reported from remeasurements of tree diameter in permanent sample plots in intact tropical forest stands. This observed increase in productivity has been attributed to increased resource availability, i.e. elevated atmospheric CO_2 levels. However, it is has also been suggested that biomass increases may result from stand development following past disturbance. These contrasting hypotheses on observed change in tropical forests demand for a better understanding of long-term tropical forest dynamics and for insights into the disturbance history of tropical forest stands. Tree-ring analysis provides a unique tool to study regeneration dynamics of trees at a century-long timescale. We analyzed population age distributions and spatial maps of tree ages of 14 species for evidence of severe canopy disturbance. Research was conducted in tropical forests in Bolivia, Cameroon and Thailand. In large plots we sampled ~100 trees per 4-5 tree-ring producing species. The resulting age distributions were used to investigate temporal and spatial patterns in tree regeneration. We found evidence for irregular regeneration rates in all sites and strongly reduced regeneration rates for the past 20-80 years in Cameroon and Thailand. In Bolivia we found near constant regeneration rates of four species and a marked regeneration pulse of one long-lived pioneer species. Evidence for spatial clustering in tree age was limited, although in Thailand ages of two long-lived pioneer species were significantly clustered at a multi-hectare scale, indicating a recruitment pulse following a multi-hectare disturbance event. In all three sites we have found evidence for century-long changes in the regeneration patterns of pioneer species. The occurrence of past large-scale and/or high-intensity disturbances, due to fire, windthrow or anthropogenic disturbance provide the most plausible explanation for the observed patterns. This study supports the hypothesis that long-term dynamics of tropical forests are driven by disturbance-recovery cycles, rather than by continuous, small scale regeneration. Stand development patterns following past disturbance may generate trends of increasing forest biomass that cannot be distinguished from those generated by external growth stimulation.

Keywords: dendroecology; recruitment failure ; tree age distribution; tree regeneration; tree-rings

Introduction

Historically tropical forests were regarded as relatively stable systems mainly driven by small scale gap dynamics (Denslow 1980, Brokaw 1985). However, the perception of tropical forests as untouched ecosystems has gradually changed over the past decades, recognizing the fact that tropical forests have long been impacted by severe natural and human-induced disturbances (Whitmore and Burslem 1998), just like temperate forests (Oliver 1980). We refer here to severe canopy disturbance events that are spatially extensive, affecting at least several hectares of forest, though potentially heterogeneous in intensity (Whitmore and Burslem 1998, Splechtna et al. 2005, Baker and Bunyavejchewin 2009). The role of past severe disturbances in long-term stand development of tropical forests has gained renewed attention in the light of recently reported trends in tropical forest dynamics (Chave et al. 2008, Gloor et al. 2009).

Over the past decades changes in tropical forest biomass and tropical tree growth have been reported (Phillips et al. 1998) and these changes were attributed to external drivers, such as increased atmospheric CO_2 (Malhi and Phillips 2004, Lewis et al. 2009a) and increasing temperatures (Feeley et al. 2007b). However, it has also been suggested that recovery after past disturbance, may result in very similar patterns of tree growth and forest biomass (Fisher et al. 2008, Chambers et al. 2013). Evidence shows that that tropical forests are occasionally subject to severe canopy disturbances, including multiple-tree blowdowns (Nelson et al. 1994, Vandermeer et al. 2000, Gleason et al. 2008), fire (Baker et al. 2008) and extreme droughts (Slik 2004, Nepstad et al. 2007), just like temperate forests (D'Amato and Orwig 2008). The recovery process after severe canopy disturbance is characterized by well-defined stages in stand development that to a certain extant can be anticipated (Oliver and Larson 1996).

The difficulty in disentangling causes of observed changes in tropical forests is that both a hypothesized CO_2-fertilization effect and recovery from past disturbance are characterized by a gradual increase in forest stand biomass (Chazdon 2003, Chave et al. 2008). At present, tropical forest stand dynamics are primarily studied using remeasurements of tree diameter in permanent sample plots over a maximum three decades (e.g., Baker et al. 2004, Clark et al. 2010). However, natural or anthropogenic disturbances in the past, long before the plots were installed, may leave a lasting legacy on tropical forest composition, structure and dynamics (Chai and Tanner 2011). Therefore, a better understanding of tropical forest stand dynamics at the timescale of centuries is much needed (Zuidema et al. 2013).

In boreal and temperate forests, dendroecology - the use of tree-rings to study ecological processes - is a well-established methodology to investigate stand history (Kuuluvainen et al. 2002, Rubino and McCarthy 2004, Fraver et al. 2008, Simkin and Baker 2008). When recruitment and mortality rates are constant (Fig. 5.1a), the expected age distribution of a tree population has a 'reversed-J' shape (Fig. 5.1d; Agren and Zackrisson 1990, Westphal et al. 2006). But changing conditions, e.g., after a severe canopy disturbance, may cause temporally increased recruitment rates of pioneer tree species, resulting in an irregular age distribution (Lorimer 1980). Systematic dating of establishment years of whole tree populations in temperate forests has revealed recruitment peaks reflecting past canopy disturbances (Cullen et al. 2001, Splechtna et al. 2005). Additionally, the legacy of past disturbance has been inferred from spatial aggregation of similarly aged trees at large, multi-hectare, scales (Duncan and Stewart 1991, Rozas 2003, Sánchez Meador et al. 2009).

Here we provide a spatiotemporal reconstruction of tree establishment rates in three tropical forest sites on three continents. We used age distributions of shade-intolerant tree species to assess century-long changes in tree regeneration rates. Forests at all three sites are classified as primary forests, but have likely been impacted by large-scale and/or high-intensity disturbances in the past. At the site in Bolivia anthropogenic soils with abundant fragments of pottery have been found (Paz-Rivera and Putz 2009). In Cameroon local human population density has likely been variable (Malhi et al. 2013) and, like other African rain forests, the area may have been significantly impacted by human activity in the relatively recent past (White and Oates 1999). In Thailand both windfall (Marod et al. 1999) and fire (Baker et al. 2008) are occasionally recurring (natural) disturbances.

We examined: (1) Whether tree regeneration rates have changed over the past one to two centuries; and (2) if similarly aged trees were spatially aggregated. Finally, we discuss the potential effect of changes in tree regeneration on observed long-term trends in tropical tree growth and forest biomass.

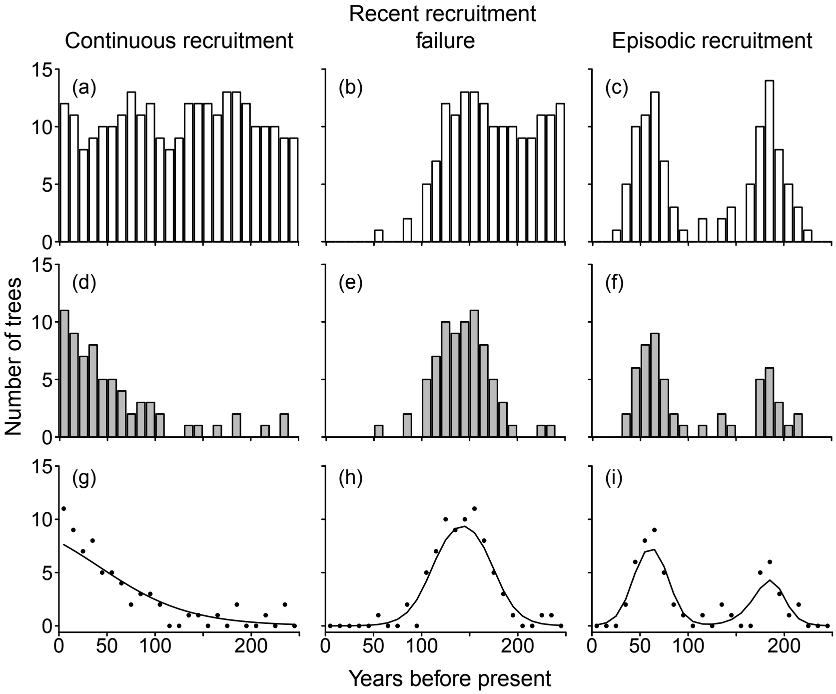


Figure 5.1 Hypothetical recruitment rates (top panels), the resulting current age distribution (mid panels) and age distribution model fit (bottom panels). We used three hypothetical recruitment patterns: continuous recruitment (a), recent recruitment failure (b) and episodic recruitment (c). As a result of an assumed constant mortality rate of 1% year^{-1}, the extant age distribution has less individuals in the older age classes (d-f). We used a set of seven logistic regression functions to describe the age distribution and the best model fit was based on the AICc-value.

Materials and Methods

Study area and species

The study was carried out in three countries: Bolivia, Cameroon and Thailand (Fig. 5.2). In Bolivia samples were collected in the logging concession 'La Chonta' (15.84 S, 62.85 W). The forest in La Chonta is a semi-deciduous moist forest that is transitional between Chiquitano dry forest and moist Amazonian forests (Peña-Claros et al. 2012). Elevation ranges between 298 and 436 m above sea-level. Soils have been classified as relatively fertile ultisols due to human influences. Total annual precipitation in the region is around 1580 mm, with a five month dry season receiving <100 mm precipitation per month from May to September and mean annual temperature is 24.5 °C. Like most of the forests in the Amazon the area has been selectively logged at low intensity (ca. 1 m^3/ha) for the commercially valuable broad-leaf mahogany (*Swietenia macrophylla*) (Pinard et al. 1999, Gould et al. 2002). This logging took place around 1992, but we have found no direct evidence, e.g., old skid trails or tree stumps, that indicate logging in our study area. But, there is abundant evidence for anthropogenic dark earths or 'terra preta' in the area, indicating that the sites was inhabited 300-400 years ago (Paz-Rivera and Putz 2009).

Table 5.1 Characteristics of the 14 study species, their shade-tolerance guild (ST, shade-tolerant; PST, partial shade-tolerant; LLP, long-lived pioneer).

Country	Species	Family	Ecological guild[1]	Wood density[2] (kg/m^3)	Leaf phenology[3]
Bolivia	*Ampelocera ruizii*	Ulmaceae	ST	760	E
	Cariniana ianeirensis	Lecythidaceae	PST	370	D
	Hura crepitans	Euphorbiaceae	PST	400	D
	Schizolobium amazonicum	Fabaceae	LLP	390	D
	Sweetia fruticosa	Fabaceae	LLP	820	BD
Cameroon	*Brachystegia cynometroides*	Fabaceae	PST	620	D
	Brachystegia eurycoma	Fabaceae	PST	620	D
	Daniellia ogea	Fabaceae	LLP	550	D
	Terminalia ivorensis	Combretaceae	LLP	500	D
Thailand	*Afzelia xylocarpa*	Fabaceae	LLP	820	D
	Chukrasia tabularis	Meliaceae	PST	630	BD
	Melia azedarach	Meliaceae	LLP	480	D
	Neolitsea obtusifolia	Lauraceae	ST	850	E
	Toona ciliata	Meliaceae	LLP	470	D

[1] Ecological Guilds: Bolivia (Peña-Claros et al. 2008b), Cameroon (Hawthorne 1995), Thailand (Baker et al. 2005) and the definitions are in accordance with (Poorter et al. 2006); [2] Wood density: Bolivia (M. van de Sande, *unpublished results*), Cameroon (CIRAD Forestry Department 2008, Lemmens et al. 2012), Thailand (Nock et al. 2009). [3] Leaf phenology: Bolivia (Mostacedo et al. 2003), Cameroon (Hawthorne 1995, Lemmens et al. 2012), Thailand (Williams et al. 2008).

The site in Cameroon (5.25 N, 9.10 E) is a semi-deciduous tropical rainforest of the Guineo-Congolian type. Samples were collected in logging concession 11.001 operated by Transformation REEF Cameroon (TRC). This concession is adjacent to the northwest border of Korup National Park. The forest is locally dominated by groves of Fabaceae-Caesalpinioideae species and other important families in terms of basal area are Euphorbiaceae and Scytopetalaceae

(Chuyong et al. 2004). Elevation levels are approximately 100 m above sea-level and soils are sandy and nutrient poor (Chuyong et al. 2004). Mean total annual rainfall is around 4000 mm and mean annual temperature 26.7 °C (Nchanji and Plumptre 2001). The climate is characterized by a distinct three month dry season from December to February with monthly rainfall levels <100 mm. Of the three sites TRC probably has the highest human influence, as several villages are located in directly around the logging concession.

The third site is situated in the Huai Kha Khaeng Wildlife Sanctuary (HKK), Thailand (15.60 N, 99.20 E). The site at HKK is a semi-deciduous tropical moist forest and dominated by trees in the Annonaceae and Dipterocarpaceae family. Altitudes in HKK vary between 490 and 650 m above sea-level and the soils are highly weathered slightly acidic ultisols (Bunyavejchewin et al. 2009). Mean annual rainfall is around 1473 mm (1993-2001) and the 4-6 month dry season ranges from November to April. Mean annual temperature is 23.5 °C. There is no human influence in HKK, except for the Wildlife Sanctuary infrastructure and agricultural areas around the park providing a potential ignition source for surface fires (Baker et al. 2008). No logging activities are known to have taken place in the study area.

We collected stem discs and increment cores from 14 different tree species (for a full list of the species, see: Table 5.1). At each site we collected samples from two to three long-lived pioneer species and two (partial) shade-tolerant species (Table 5.1). For convenience, we will refer to all species by their genus names, except for the two *Brachystegia* species. Primary criteria for species selection were primarily the presence of clearly identifiable annual rings and secondly adequate local abundance enabling a sample size of approximately 100 trees. The 14 species represent various families, a variety in leaf phenology characteristics and ecological guilds: from shade-tolerant to shade-intolerant long-lived pioneer (Table 5.1).

Field sampling

All wood samples were collected over a period of two years between May 2010 and May 2012. The majority of samples were collected following a clustered sampling design, in which trees were sampled in a 50 m radius around a randomly assigned location. Total areas in which trees were sampled following the clustered sampling design ranged from 144 ha in Cameroon, to 272 ha Bolivia and 296 ha in Thailand. We aimed to sample roughly 500 trees per study area, divided equally over study species. However, due to rarity of some target species, the full sample size could not always be achieved within the framework of this sampling scheme. Species for which no adequate sample size could be achieved within the standardised sampling design, were sampled more opportunistically by collecting additional samples from trees that were encountered in the forest. This resulted in clustered sampling of the more abundant species, which were all species in Bolivia, the two *Brachystegia* species in Cameroon and *Chukrasia* and *Neolitsea* in Thailand (Fig. S5.3). For all the other species every individual that was encountered in the plot was sampled.

The locations of all sample trees were GPS-mapped (Garmin GPSMAP 60C Sx) and we measured dbh (1.3 m) and diameter at sampling height of each sample tree. Height measurements of all sampled trees and all taller neighboring trees within 10 m of each target tree were obtained using a digital hypsometer (Nikon Forestry 550). In the logging concessions in Bolivia and Cameroon a large fraction of the samples were collected as stem discs from recently felled trees. All other samples were collected using an Suunto (Vantaa, Finland) or Haglöf (Långsele, Sweden) increment borer. At a height of approximately 1 m we manually extracted tree cores with a diameter of ~5 mm. Therefore, in the following 'tree age' and 'year of establishment' always refer to the moment since reaching sampling height. Depending on the diameter of the tree we used borers with lengths varying between 40 and 70 cm. From trees <40 cm dbh two cores were taken, because the borer would go straight through the tree and two radii per core were obtained. For all larger individuals we took three cores, because only one radius per core was obtained. Collecting multiple cores and stem discs allowed us to measure rings over at least three complete radii, thereby correcting for radial differences in diameter increment. We only cored trees >5 cm to minimize damage to the juveniles. Sampling of *Ampelocera* trees was restricted to individuals <65 cm dbh because larger individuals were too hard to be cored and no stem discs could be collected because this species was not commercially logged in the area.

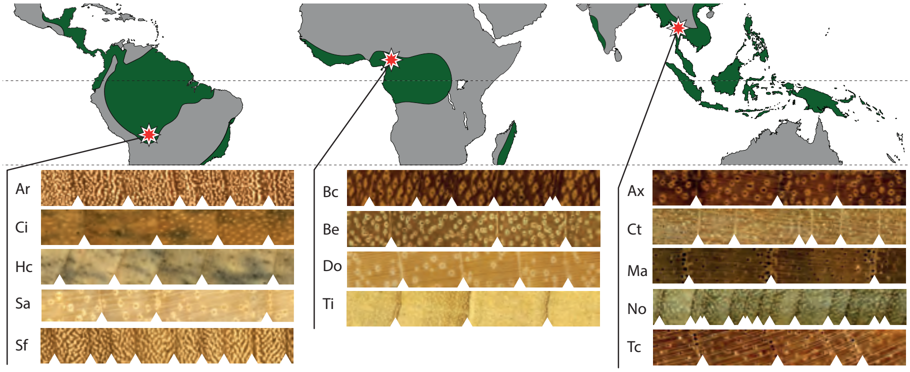


Figure 5.2 Study area (top) and wood characteristics of the 14 study species (bottom). Approximate location of the study areas is indicated by the star symbol. White arrows indicate tree-ring boundaries. Ar=*Ampelocera ruizii*, Ci=*Cariniana ianeirensis*, Hc=*Hura crepitans*, Sa=*Schizolobium amazonicum*, Sf=*Sweetia fruticosa*, Bc=*Brachystegia cynometroides*, Be=*Brachystegia eurycoma*, Do=*Daniellia ogea*, Ti=*Terminalia ivorensis*, Ax=*Afzelia xylocarpa*, Ct=*Chukrasia tabularis*, Ma=*Melia azedarach*, No=*Neolitsea obtusifolia*, Tc=*Toona ciliata*.

Tree-ring measurements

Increment cores were glued to wooden mounts and cut perpendicular to the ring boundaries with a large sliding microtome (WSL; Swiss Federal Institute for Forest, Snow and Landscape Research, Switzerland). Stem discs were sanded with progressively finer sand paper. Digital images (1600 dpi) of the tree cores and stem discs were acquired using a high-resolution flatbed scanner (Epson Expression 10000 XL) and analyzed in the WinDENDRO program for tree-ring analysis (version 2009b; Regent Instruments Canada Inc.). Tree-ring boundaries were marked manually on the screen and measured to the nearest 0.001 mm (for ring structures see: Fig. 5.2). Approximately 10% of the samples were measured to the nearest 0.01 mm using a LINTAB 5 measurement device and TSAP software (Rinntech). All ring-width series were first visually crossdated within trees and then among trees. Afterwards series were checked for dating errors with the computer program COFECHA (Holmes 1983). If the pith was not included in any of the samples taken from a tree, the distance to the pith was estimated by the degree of arcing in the oldest visible ring, assuming a circular growth pattern (cf. Splechtna et al. 2005). If no arcing was visible on the cores we calculated the missing distance to the pith based on the diameter at sample height measured in the field. The missing distance to the pith was then used to estimate the pith dates by dividing the missing radial distance to the pith by the average width of the five oldest visible rings.

The annual character of the rings was verified by various means. For four Bolivian species, *Ampelocera, Cariniana, Hura* and *Sweetia,* scars in the wood produced by a fire were used to prove the annual nature of the rings (Brienen and Zuidema 2003, Lopez et al. 2012). The annual nature of *Schizolobium* rings was determined by counting rings of trees of known age in a plantation forest ~200 km from the study area (*P. van der Sleen, unpublished results*). To verify dating accuracy of three Cameroonian tree species we used the bomb-peak dating method (Worbes and Junk 1989). This revealed that dating accuracy of *B. eurycoma* and *Daniellia* rings was high, but dating accuracy of *B. cynometroides* rings revealed a mean error of around 10% (Fig. S5.1). This dating error in *B. cynometroides* was presumably caused by the erroneous interpretation of false rings, which led to a general underestimation of *B. cynometroides* ages. The annual nature of *Terminalia* rings was proven by a cambial wounding experiment (Detienne et al. 1998). For all five Thai species the annual nature of the rings was also proven by a cambial wounding experiment in HKK (Baker et al. 2005). The annual growth periodicity was further proven by correlating *Afzelia, Chukrasia, Melia* and *Toona* tree-ring chronologies with seasonal climate data (Vlam et al. 2014b).

Data analysis

We produced age distributions of all species to detect irregularities in recruitment rates. For all 14 species population age distributions were produced using 10-year age classes. Because sampling was limited to trees >5 cm dbh, we calculated the number of years it took trees to reach 5 cm dbh. Per species we produced an 'age at 5 cm dbh distribution' and we took the 75th percentile as a threshold value for all further analysis. For example out of the 91 *Ampelocera* trees in this study 75% had reached 5 cm dbh in ≤26 years. So, for *Ampelocera* all analysis of age distributions was restricted to age classes >26 years.

To quantify the relation between tree age and counts of the number of trees per age class we used a hierarchical set of seven models (Huisman et al. 1993, Jansen and Oksanen 2013). In this analysis age classes were used, such that in all species the age distribution spanned at least 10 classes. In 11 out of 14 species theses age classes were set at the standard 10 years. However, this age class was not suitable for some of the faster growing and more short-lived species. For these species we used smaller age classes. In *Ampelocera* and *Melia,* counts per 5-year age class were used, and in *Schizolobium* counts per 2-year age class were used.

Table 5.2 Results of measurements and analyses for the 14 study species. Number of trees included in this study (*n*); maximum adult stature (H_{max}); maximum adult diameter (dbh_{max}); maximum age (Age_{max}); modal age (Age_{mod}); mean juvenile (<20 cm dbh) growth rate (JG_{mean}); years to 5 cm dbh; shape of the age distribution (*Age-shape*): exponential decrease (ED), logistic decrease (LD), unimodal (UM); Range of spatial clustering (*SC*).

Country	Species	*n*	H_{max} (m)	dbh_{max} (cm)	Age_{max} (yr)	Age_{mod} (yr)	JG_{mean} (mm yr^{-1})	>5 cm dbh (yr)	*Age-shape*	*SC* (m)
Bolivia	*Ampelocera ruizii**	91	22.0	65.0	82	42	4.2	26	LD	500
	Cariniana ianeirensis	98	37.4	125.0	170	50	4.6	17	LD	*ns*
	Hura crepitans	96	34.0	216.0	163	13	8.2	11	ED	*ns*
	Schizolobium amazonicum	87	28.6	58.8	23	14	23.5	4	UM	*ns*
	Sweetia fruticosa	96	27.0	71.5	220	55	3.2	26	ED	*ns*
Cameroon	*Brachystegia cynometroides*	111	55.0	155.0	200	107	3.6	27	UM	*ns*
	Brachystegia eurycoma	125	50.0	181.0	190	87	3.2	36	UM	*ns*
	Daniellia ogea	98	51.0	158.0	282	100	2.8	36	UM	*na*
	Terminalia ivorensis	62	44.0	220.0	188	134	14.1	7	UM	*na*
Thailand	*Afzelia xylocarpa*	100	37.9	172.0	281	58	6.6	13	UM	>1000
	Chukrasia tabularis	104	40.8	91.7	267	80	3.9	23	UM	*ns*
	Melia azedarach	90	41.0	98.1	121	50	19.5	4	UM	500
	Neolitsea obtusifolia	104	34.4	70.4	136	88	2.6	32	UM	*ns*
	Toona ciliata	61	43.0	116.4	210	65	6.3	10	UM	*ns*

* Sampling of *Ampelocera* trees was restricted to individuals <65 cm dbh.

The seven models are logistic regression functions of increasing complexity which are traditionally used to relate species presence or abundance to environmental variables. In our case these models were used to relate density per age class to the age data, using maximum likelihood estimation. The simplest model that sufficiently explained the observed age pattern was selected based on the Akaike Information Criterion corrected for small datasets (AICc) (Jansen and Oksanen 2013). If best fit models were either a straight line, exponential decrease or logistic decrease, we determined that recruitment rates had been relatively constant over time (Fig. 5.1g; exponential decrease). If selected models were unimodal shaped (two model types), we determined that there was evidence for recent recruitment failure (Fig. 5.1h), but no evidence for episodic recruitment. Only a best model fit with a bimodal shape (two model types) would indicate a significantly bimodal age distribution and was determined an indication for episodic recruitment (Fig. 5.1i). The analysis of age distributions was always restricted to complete age classes for which ≥75% of the trees had reached the minimum sampling diameter of 5cm.

To analyze spatial patterns in tree age and create maps we used geostatistical tools. Although spatial distribution of individual trees in our study plot represent a point pattern of discrete points in space, the spatial distribution of tree attributes, in this case tree age, may be considered continuous (Chen et al. 2004, Dimov et al. 2005, Robinson and Hamann 2011). Therefore, the use of kriging techniques to interpret spatial patterns in tree ages can be justified (cf. Middendorp et al. 2013). The global autocorrelation structure is provided by a semi-variogram. Semi-variances were calculated over 50 m distance classes by the formula:

$$\bar{\gamma}(r) = \frac{1}{2n_r} \sum_{\|y_\beta - y_\alpha\| = r} (Z(y_\beta) - Z(y_\alpha))^2$$

where is the semivariance estimator, is the inter-point difference, is the number of pairs () separated by vector , and are the locations of points and , and and are the values at the measurement locations. For each species the semivariance values were calculated and a model variogram was fitted. For visualisation of the age clustering we used grids with 10x10 m raster cells of the total area of the study plot. Due to insufficient sample sizes no spatial maps could be produced for *Daniellia* and *Terminalia* in the plot in Cameroon. All statistical and spatial analyses were conducted and graphically depicted using the R Software environment version 3.0.0 (R Core Team 2013). We used the following packages: *sp* (Bivand et al. 2008); *gstat* (Pebesma 2004) and *eHOF* (Jansen and Oksanen 2013).

Results

Age distributions

The age distributions of the 14 study species are shown in Figure 5.3. Of the 12 long-lived pioneer and partial shade-tolerant species, nine show irregular age distributions. In particular, the tree populations in Cameroon and Thailand show a marked absence of young (<50 year old) trees.

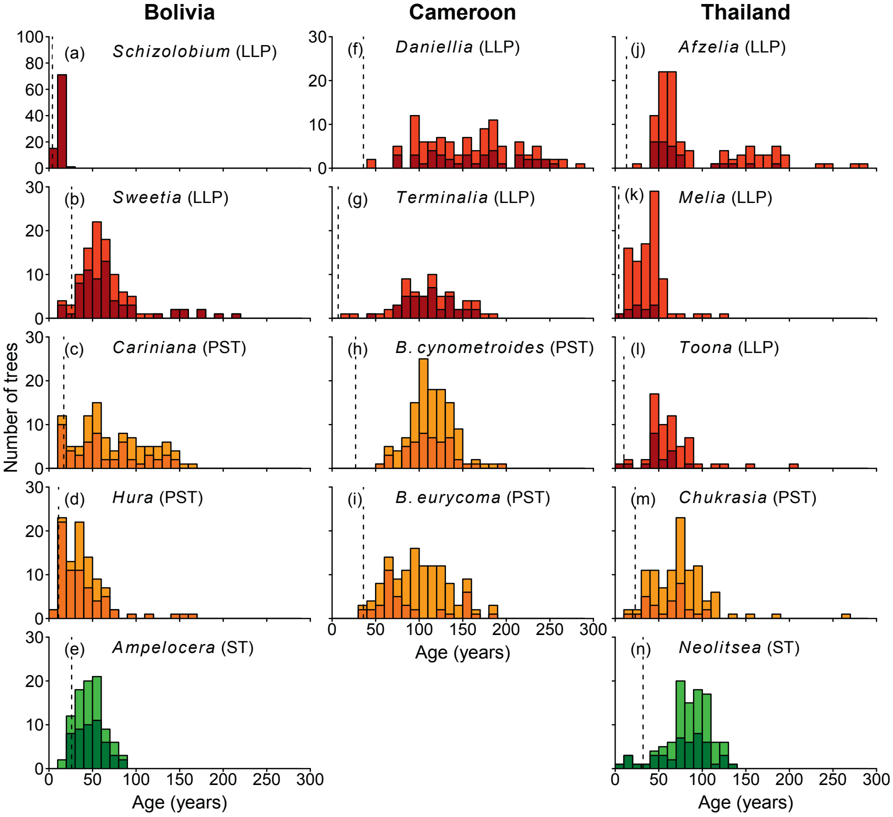


Figure 5.3 Age histograms for the 14 study species. Dashed line indicates the age at which >75% of the individuals in our dataset had reached 5 cm dbh (minimum sampling size used in this study). Shade-tolerance guild is indicated: ST, shade-tolerant (green bars); PST, partial shade-tolerant (orange bars); LLP, long-lived pioneer (red bars). Dark colored bars represent ages of those individuals for which the pith was included in at least one of the samples. Lighter colored bars represent those individuals for which the pith was not included in any of the samples.

In Bolivia, age distributions of four species, both long-lived pioneers and (partial) shade-tolerants, were best described by exponential and logistic decrease functions, indicating relatively continuous recruitment rates over the past century

(Fig. 5.4b-e). Only the age distribution of the long-lived pioneer *Schizolobium* was indicative of an irregular regeneration pattern (Fig. 5.4a). All these trees have established in the late 1990s, with mean year of establishment 1998.

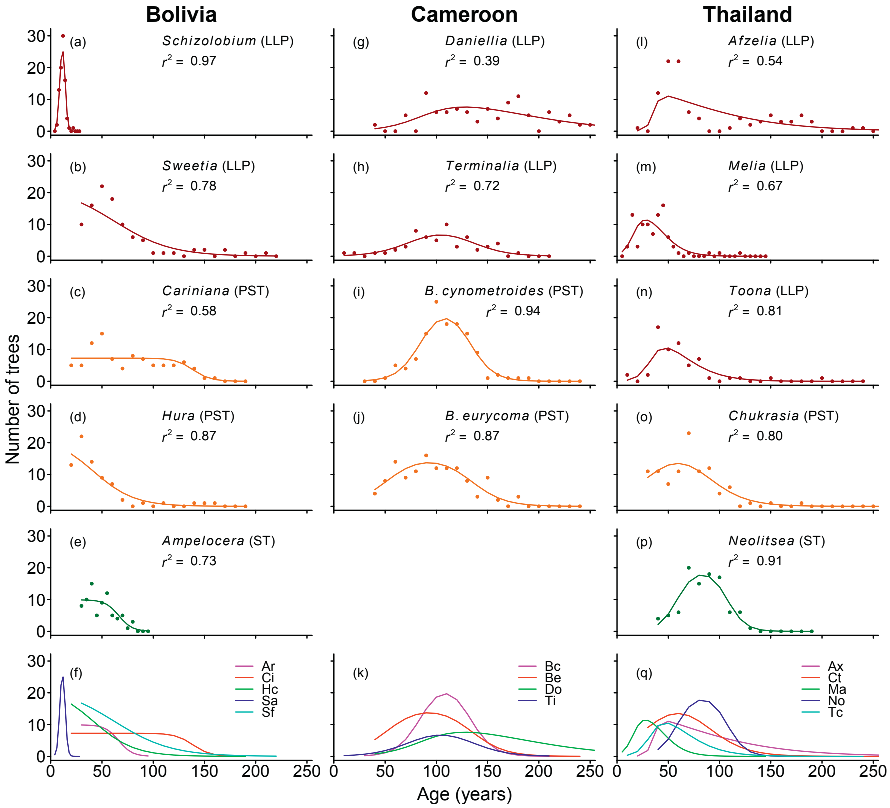


Figure 5.4 Observed (dots) and predicted (line) age distributions for the 14 study species. The line represents the best-fit model based on the AICc-value. The r^2-values shown in the graphs are calculated as the square of the *Pearson* correlation between the observed and predicted values. Except for the bottom panels, the shade-tolerance guild is indicated: ST, shade-tolerant (green); PST, partial shade-tolerant (orange); LLP, long-lived pioneer (red).

In Cameroon population age distribution of the long-lived pioneer *Daniellia* and *Terminalia* were best described by unimodal functions. Both of these species have had almost no successful regeneration over the past 70 years (Fig. 5.4g,h). The age distribution of *Daniellia* was relatively flat (Fig. 5.4g), compared to the other three species, but this seems to result from the comparatively high maximum age (Table 5.2). The age distributions of the two partial shade-tolerant species, *B. cynometroides* and *B. eurycoma*, were relatively similar to each other with a large cohort of trees ~100 years old (Fig. 5.4i,j). Regeneration of *B. cynometroides* was completely absent for the past 50 years and *B. eurycoma* did not show any regeneration over the past 30 years.

Age distributions of all Thai species were best described by unimodal functions. In Thailand the age distribution of the long-lived pioneer *Afzelia* resembles a bi-modal structure, with two recruitment events that occurred around 60 and 160 years ago (Fig. 5.3j); however, this bi-modal shape was not confirmed by the model fitting (Fig. 5.4l). We found evidence for recent recruitment failure in all Thai species, but the period of low recruitment was variable per species. For the long-lived pioneers *Afzelia* and *Toona*, recruitment was almost completely absent for the past 40 years. The partial shade-tolerant *Chukrasia* showed reduced recruitment rates over the past 30 years. Recruitment rates for the shorter-lived shade-intolerant *Melia* was reduced only over the past ~15 years. The shade-tolerant *Neolitsea* showed the longest period of strong recruitment failure: ~70 years (Fig. 5.3n).

Spatial structure in tree age

For 12 out of 14 species we analyzed the spatial structure in tree age in the three study plots (Table 5.2). In Bolivia tree age appeared to be randomly dispersed over the 272 ha sample plot in all species, except for the shade-tolerant *Ampelocera*. Older *Ampelocera* trees were mainly concentrated in the north-eastern half of the plot (Fig. 5.5a). These older trees seem to form a spatially distinct cohort of which mean age is approximately 20 years higher than the mean age of the trees in the southwest corner of the plot. Although age of the other Bolivian species did not show significant spatial clustering we noticed that older *Cariniana*, *Hura* and *Sweetia* trees were present in the northeast corner, whereas they were absent in the southeast corner associated with the young *Ampelocera* trees (Fig. S5.3). Schizolobium showed a strong peak in recruitment but no spatial aggregation of tree ages. In Cameroon only two of the four species were represented with a sufficiently large sample to test spatial dependence in tree age within the 144-ha plot. For these two partial shade-tolerant species, *B. cynometroides* and *B. eurycoma*, we found no evidence that age was significantly clustered in space (Fig. S5.3). In Thailand the shade-intolerant species *Afzelia* and *Melia* both showed spatial clustering of tree age (Fig. 5.5b,c). The semivariogram (Fig. S5.4) revealed that this spatial clustering was especially strong in *Afzelia* with a range of >1000 m. Most of the *Afzelia* trees in the younger age cohort (mean age ~60 years) were situated in the north-eastern part of the study plot (Fig. 5.5b), whereas the older trees occurred in two clusters in the west of the plot. Older Melia trees (mean age ~50 years) formed a band from the south-west corner of the plot to the north-east corner (Fig. 5.5c). This band of older *Melia* trees is also partial overlapping with the patch of younger *Afzelia* trees (Fig. 5.5b,c). We did not find any evidence of spatial clustering of the partial shade-tolerant *Chukrasia,* the shade-tolerant *Neolitsea* or the long-lived pioneer *Toona*.

Discussion

To our knowledge this is the first study that investigates regeneration rates of tropical tree species at centennial timescales and for large (140-300 ha) areas. We found evidence for recent recruitment failure of long-lived pioneer tree species at each site. Especially in Cameroon and Thailand a large fraction of the species showed virtually no recruitment in the past 20-80 years.

Age dating accuracy

By using tree-ring dating we were able to directly assess tree-age distributions, instead of using less direct diameter distributions. Dendroecological studies in temperate and boreal forests have long reported clear indications for episodic recruitment and prolonged recruitment failure of tree populations (e.g., Agren and Zackrisson 1990). Only relatively recently has the field of dendroecology been extended to the tropics and evidence for episodic or irregular regeneration of tropical tree species has been found in this region (e.g., Baker et al. 2005, Vlam et al. 2014a).

The annual nature of the rings of all 14 study species was previously established in several ways (see methods section). Nevertheless counting and measuring growth rings of tropical tree species can be difficult due to the occurrence of missing and false rings (Worbes 1995). First, such ring identification errors have likely occurred in this study and any dating errors have been accumulated towards earlier dates (i.e. older trees). Secondly, additional uncertainty resulted from the missing distance to the pith in a considerable fraction (54%) of our tree-ring samples. For these samples, we estimated the number of missing rings to the pith by extrapolating growth rates based on the five oldest visible rings (cf. Splechtna et al. 2005). And thirdly, some age variation may also have resulted from variation in time to reach sampling height (~1 m). This combination of dating issues has likely resulted in a spread in tree ages around their actual age; a spread that unfortunately we were not able to quantify. In general this age spreading will obscure patterns of episodic recruitment. Therefore our observations of recent recruitment failure in many species are probably conservative estimates of the actual pattern. On the other hand, wide age distributions of tree species with shade-intolerant juveniles may also reflect prolonged enhanced recruitment conditions following past disturbance (Oliver and Larson 1996, Vlam et al. 2014a), or regeneration in scattered canopy gaps that were formed over an extensive time period (Baker et al. 2005).

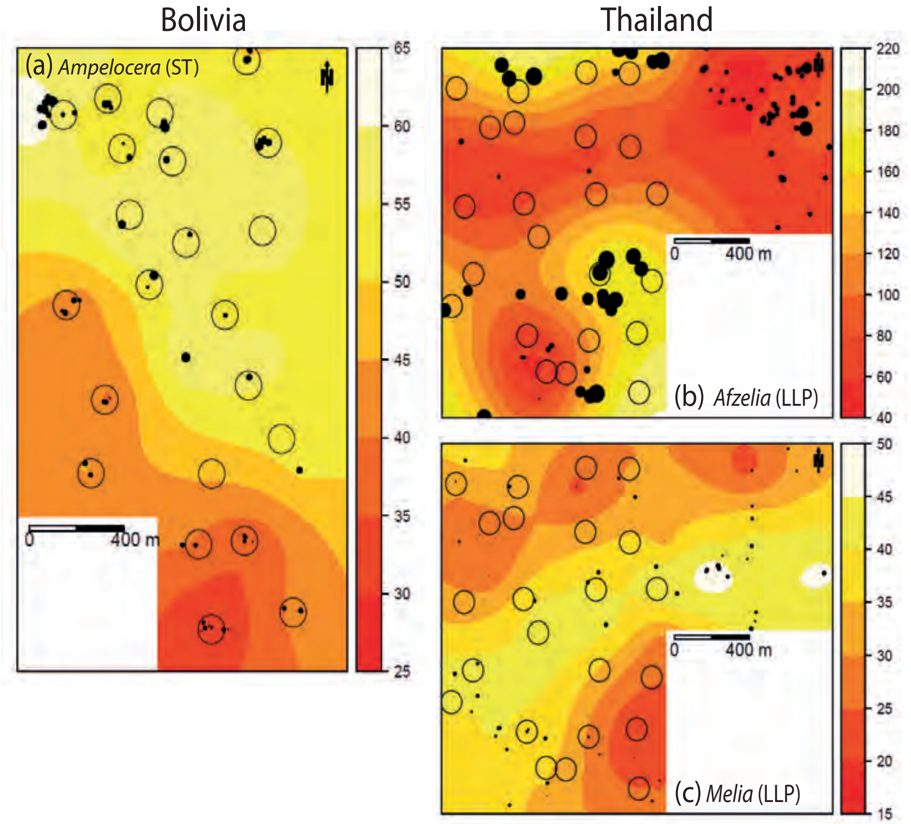


Figure 5.5 Kriging maps for the three study species for which a significant spatial structure in tree age was found. Black dots indicate the location of the sampled trees, dot size is relative to tree age. Open circles indicate the location of the 50m radius random sampling plots.

Site evidence for disturbance

In all sites we found evidence for pulses of tree regeneration that could be associated with large-scale and/or high-intensity disturbance events. In this section we discuss the disturbance factors most likely explaining the patterns found.

Bolivia

We have several indications that canopy disturbances have affected the forest stand at the site in Bolivia. The recent recruitment pulse of the shade-intolerant *Schizolobium* in Bolivia is for example indicative for a canopy disturbance. This was likely a disturbance with a diffuse character, because it did not appear to result in the mortality of all canopy trees, as can be inferred from the ages of the other four study species in the area. The population of *Schizolobium* trees likely reflects an age cohort that established in the late 1990s, because we found no tree >23 years old. We estimated that it is highly unlikely that 23 years is close to the maximum age of *Schizolobium*, because the largest tree in our dataset ($n = 87$) had a dbh of 59 cm (Fig. S5.2), whereas in a nearby permanent sample plot *Schizolobium* trees >100 cm dbh have been found. The recruitment pulse of *Schizolobium* in the late 1990s likely resulted from a wildfire that occurred across an estimated 1×10^6 ha of forest in La Chonta towards the end of the dry season in 1995 (Pinard et al. 1999, Lopez et al. 2012). The fire originated from pasture fires set to rejuvenate forage for cattle (Pinard et al. 1999). Recently, Baker et al. (2008) demonstrated that low-intensity fires can generate a widespread pulse of forest gap formation across a similar seasonal tropical landscape in western Thailand.

The widespread character of the fires in La Chonta may also explain the lack of spatial clustering in tree ages of long-lived shade-intolerant species at the study site. In their study Pinard et al. (1999) found that ca. 40% of the trees were killed by the 1995 fire, but with a much larger impact on small trees (saplings) than on large canopy trees. If these wildfires create widespread pulses of synchronous gap formation no spatial clustering of tree age of shade-intolerant tree species would be expected at a hectare level. The spatial pattern of tree age for the shade-tolerant *Ampelocera*, can hardly be attributed to clustered regeneration following canopy disturbance, because disturbance is not a perquisite for successful establishment of shade-tolerant tree species (Duncan and Stewart 1991). Therefore we have no satisfactory explanation for the spatial pattern in tree age of this species.

There is abundant evidence, including charcoal and pottery fragments, indicating that local human population densities in La Chonta were historically high (Paz-Rivera and Putz 2009). Abandonment of former farmlands and settlement may have favored establishment of shade-intolerant tree species. However, population decline must have started >330 years ago (Paz-Rivera and Putz 2009), which outdates by far the oldest tree that we found. Therefore, age distributions of our study species do not reflect this initial period of forest recovery that may have occurred. However, past disturbances may have a long lasting effect on tree species composition (Chai and Tanner 2011). Additionally the recent recruitment peak of the highly shade-intolerant *Schizolobium* and continuous recruitment rates of the other shade-intolerant species indicate that large-scale disturbances leading to a diffuse pattern of gap formation, e.g., fire or drought, are relatively common in the area.

Cameroon

The evidence for recent (>50 years) recruitment failure of all four species from Cameroon was very clear. It provides indications for a change in regeneration conditions of the study species over recent decades. *Terminalia* is a long-lived pioneer species and an indicator species for secondary forest stands (Lemmens et al. 2012). Successful establishment of such species is dependent on large canopy openings generating adequate light-levels at the forest floor (Newbery et al. 2013). The lack of recruitment of Terminalia in the past ~70 years indicates that such high-light levels have not occurred in the study area over this period. The three other study species are classified as either partial shade-tolerant or shade-intolerant (Hawthorne 1995). Given the shade-intolerant nature of the juveniles of all four Cameroonian study species, their past regeneration success was likely related higher light-levels at the forest floor over a period 150-100 years ago.

Currently, the dense and homogenous canopy of mainly Caesalpinioideae species is likely creating strong shading of the forest understory. This dark understory is the most likely cause for the observed low recruitment rates of the four study species, because their seedlings all require some canopy opening to survive. Our findings are consistent with earlier observations on the dominance of non-regenerating long-lived pioneer canopy species in West African forests (Newbery and Gartlan 1996, Poorter et al. 1996). An alternative explanation for the observed recent recruitment failure of the study species may be a lack of large vertebrate seed dispersers. It has been shown that high levels of defaunation in West-African forests may lead to regeneration failure of animal-dispersed tree species (Blake et al. 2009, Effiom et al. 2013). However, all four Cameroonian species are primarily dispersed by wind (*Daniellia* and *Terminalia*) or pod ejection (*Brachystegia* species) (Hawthorne 1995, Effiom et al. 2013). It is therefore unlikely that defaunation has played a major role in recent recruitment failure of these species.

Unlike the sites in Bolivia and Thailand, large-scale disturbances caused by widespread fires are unlikely in the Cameroonian site, because of the high precipitation amounts (4000 mm) and relatively short dry season (~ 3 months). Windthrow has been reported to flatten areas of up to 1 ha in the nearby Korup National Park, but the origin of these winds is unknown (Chuyong et al. 2004). Drought and/or human activity are therefore the most likely drivers of canopy disturbance at this site. In their study (Newbery et al. 2004) related establishment of the large canopy tree *Microberlinia bisulcata* (Fabaceae) in the neighboring Korup National Park to periods of intense drought around 1820-1830 and 1870-1895. The latter period roughly coincides with the period of highest tree establishment found in this study. These 19th century droughts may therefore have resulted in a period of scattered canopy disturbance, due to drought induced tree mortality (cf. Phillips et al. 2009), that favored the establishment of shade-intolerant species. However, there are also indications for human occupation of what now seem pristine forests in West and Central Africa, providing an alternative explanation for past large-scale disturbance (Malhi et al. 2013). This past human occupation was inferred from soil layers under West African forests containing charcoal and pottery fragments (White and Oates 1999, Denham et al. 2007). As in Bolivia, the sudden abandonment of agricultural fields may have induced the establishment success of shade-intolerant tree species at the Cameroonian site, although we lack any direct evidence on charcoal or pottery fragments from our study site.

Thailand

High past regeneration rates of long-lived pioneer tree species such as *Afzelia*, *Melia* and *Toona* are an indication for past canopy disturbance in HKK and the spatial clustering in tree ages two of these species is further evidence for severe canopy disturbances (Rozas 2003). The 1950s recruitment pulse of *Afzelia* was synchronous with the establishment of nearly all *Toona* individuals in the area. Later establishment of the shade-intolerant *Melia*, which recruited well into the late 1980s, is evidence for additional canopy disturbance. Intense windstorms that infrequently pass through the region are among the most likely causes of canopy disturbance in HKK (Baker et al. 2005). Windthrow may have caused the large canopy openings that were required for the recruitment of some of the long-lived pioneer species, such as *Toona* and *Afzelia*. Although classified as shade-tolerant, the age distribution of *Neolitsea* suggests that these trees have established over the same period as the long-lived pioneer species.

Besides wind, fire is also an important disturbance in HKK. Fires occurred nearly every year somewhere within HKK in the past two decades and Sanctuary-wide fires are known to have occurred in 1991, 1994, 1998 and 2004. The 1998 fires, which were associated with an intense El Niño-Southern Oscillation event, were the largest fires at HKK in the past 30 years (Baker et al. 2008, Johnson and Dearden 2009). The presence of fires and subsequent canopy gaps may explain the more recent establishment success of *Melia*. The high juvenile growth rates of *Melia* allow it to quickly escape the fire-prone stages of development. Juveniles of *Afzelia* are noticeably susceptible to understory fires (So et al. 2010) and successful regeneration may therefore require a period of low fire frequency. It was shown earlier that regeneration of *Afzelia* in HKK was positively associated with relatively wet climatological conditions in HKK, which may reduce the occurrence and intensity of forest fires (Vlam et al. 2014a). There is also some concern that the decreasing time interval between recurrent fires in HKK may lead to impoverishment of the tree species diversity in the seasonal evergreen forest (Johnson and Dearden 2009). This is especially true when the time required to escape the fire-prone stages of development becomes longer than the mean interval length between two consecutive fires. However, a direct link between tree species population structures in HKK and fire tolerance (bark thickness) was not found (Baker and Bunyavejchewin 2006a). Therefore, a more plausible explanation for recent recruitment failure in HKK, in particular of long-lived pioneer and partial shade-tolerant species, is the absence of severe canopy disturbance in the past ~40 years.

Tropical forest disturbance

In all three sites we have found evidence for long-term changes in the regeneration patterns of shade-intolerant species. These changes in regeneration patterns suggest changes in forest stand structure that have occurred over the past 100-200 years. In the two drier sites, Bolivia and Thailand, regeneration of shade-intolerant tree species was likely related to canopy openings created by historical fire events. Although multiple hectare windthrow events also provide a possible mechanism for past canopy disturbance (Nelson et al. 1994, Negrón-Juárez et al.

2010), in particular for the site in Thailand (Ashton 1993, Baker et al. 2005). An absence of severe canopy disturbance provides the most plausible mechanism for recent (40-70 year) regeneration failure of canopy tree species across the sites in Cameroon and Thailand. This study shows that long-term dynamics of tropical forests are heavily impacted by rare large-scale and/or intensity disturbances. Earlier findings in 'pristine' tropical forests, such as irregular tree-diameter distributions (Poorter et al. 1996, Bunyavejchewin et al. 2003) and the dominance of long-lived, shade-intolerant tree species in the forest canopy (Newbery et al. 2013), are consistent with this legacy of past canopy disturbance.

Based on tree-age distributions and spatial statistics we were able to obtain a proxy for long- term tree regeneration patterns and the occurrence of canopy disturbances at each site. Long-term forest stand development patterns due to past disturbance may generate increasing trends in forest biomass that cannot be distinguished from those generated by external growth stimulation. This study also supports the hypothesis that long-term forest dynamics are driven not only by small-scale disturbances resulting from single treefall gaps, but also by large-scale and/or high-intensity disturbances.

Acknowledgements

This study was financially supported by the European Research Council (ERC, grant #242955). We thank Somboon Kiratiprayoon for making arrangements for fieldwork and assistance in the permit procedure in Thailand. We thank the National Research Council of Thailand the Department of National Parks, Wildlife and Plant Conservation for granting permission to carry out fieldwork in the Huai Kha Khaeng Wildlife Sanctuary. We thank the personnel of the logging companies Transformation REEF Cameroon and La Chonta Ltd. Bolivia. We acknowledge Roberto Quevedo of the Carrera Forestal UAGRM Bolivia and Martin Tchamba of the Forestry department, University of Dschang, Cameroon for their contribution. We all thank students and fieldwork staff for their valuable contribution to this project.

Appendix

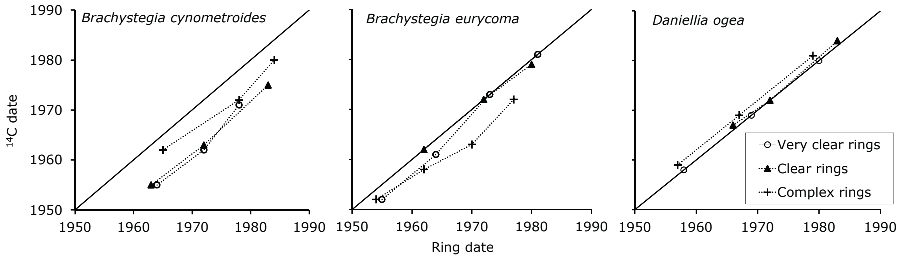


Figure S5.1 14C bomb-peak dating confirms annual ring formation in three species from Cameroon, but also points to dating errors in two species (Groenendijk et al. 2014). We tested whether ring based age estimations matched well (within 1 year margin of error) with 14C based age estimations. We used three different types of samples: tree discs with *very clear* rings (open circles); increment cores with *clear* rings (closed triangles) and cores with *complex* rings (crosses), e.g., with suppressions or strong wedging rings.

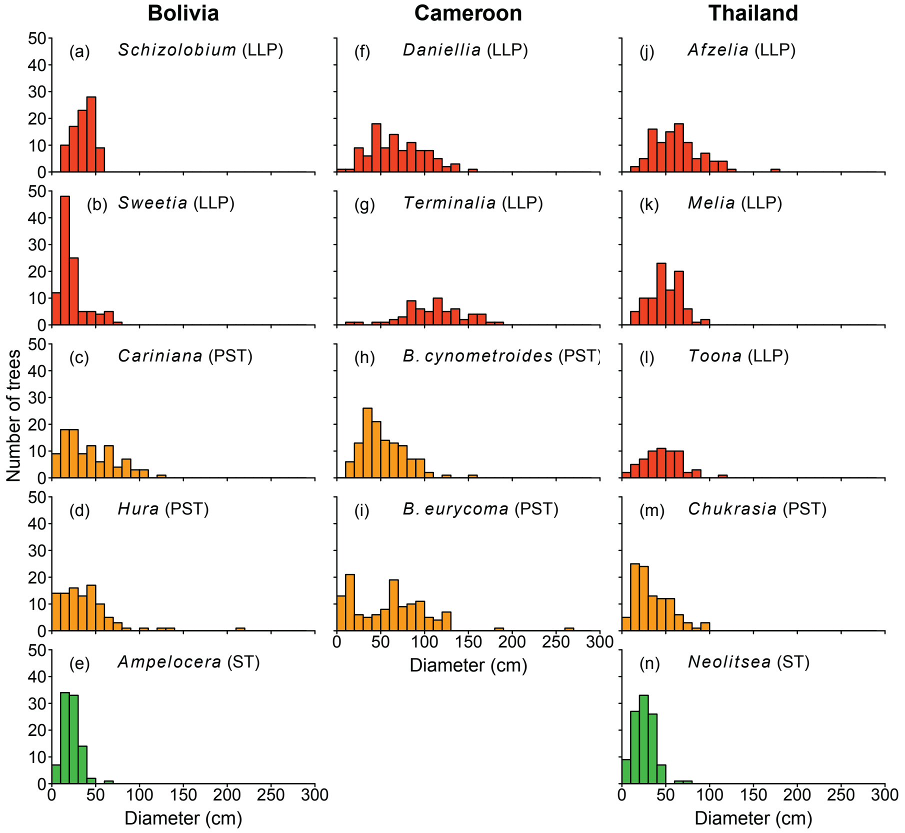


Figure S5.2 Diameter distributions for the 14 study species. Shade-tolerance guild is indicated: ST, shade-tolerant (green bars); PST, partial shade-tolerant (orange bars); LLP, long-lived pioneer (red bars).

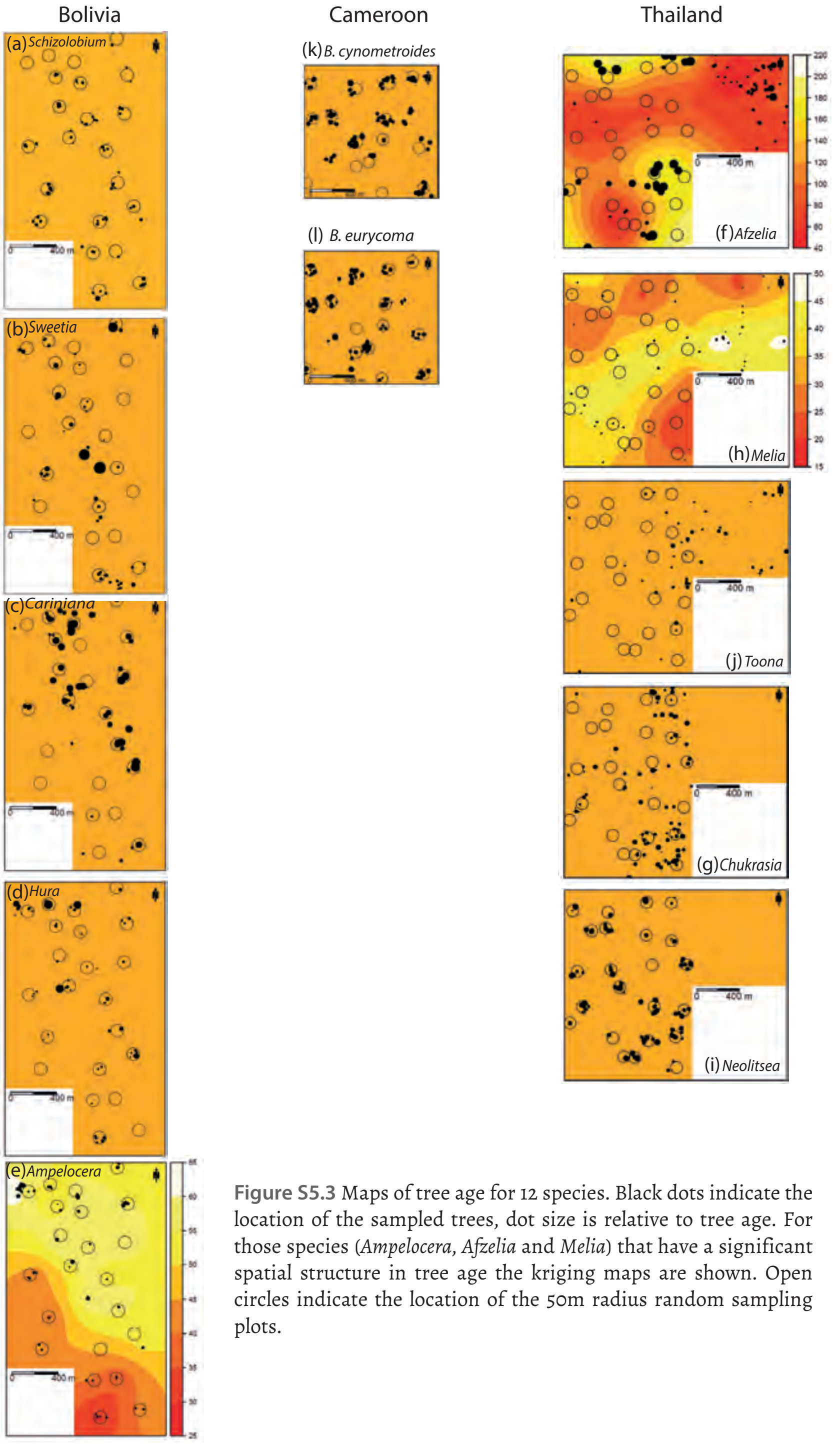


Figure S5.3 Maps of tree age for 12 species. Black dots indicate the location of the sampled trees, dot size is relative to tree age. For those species (*Ampelocera, Afzelia* and *Melia*) that have a significant spatial structure in tree age the kriging maps are shown. Open circles indicate the location of the 50m radius random sampling plots.

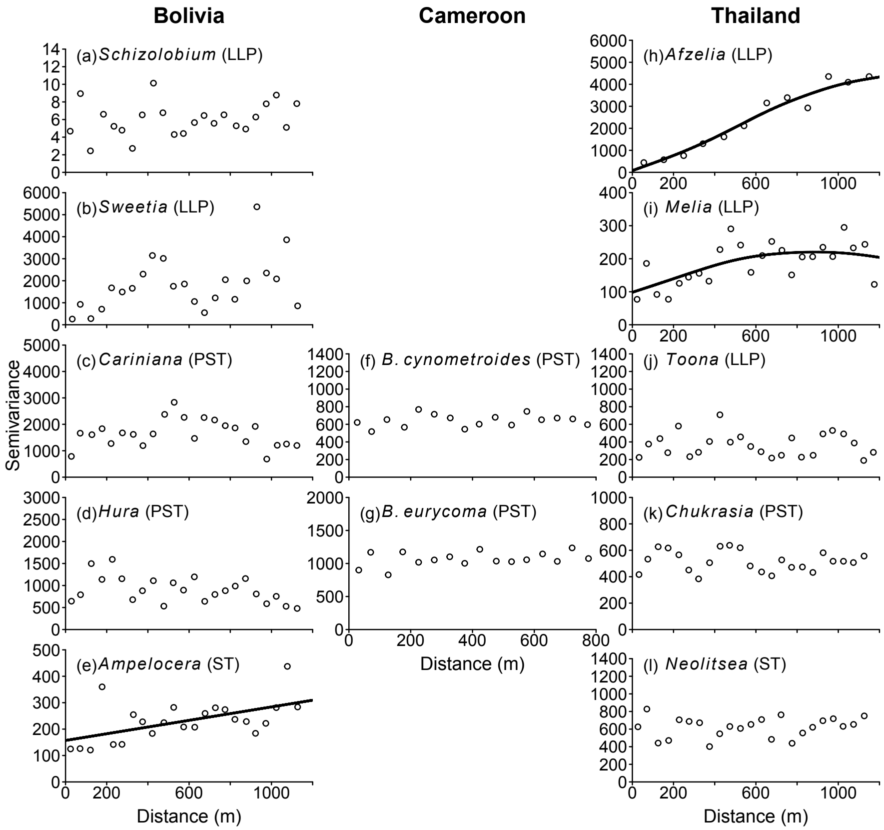
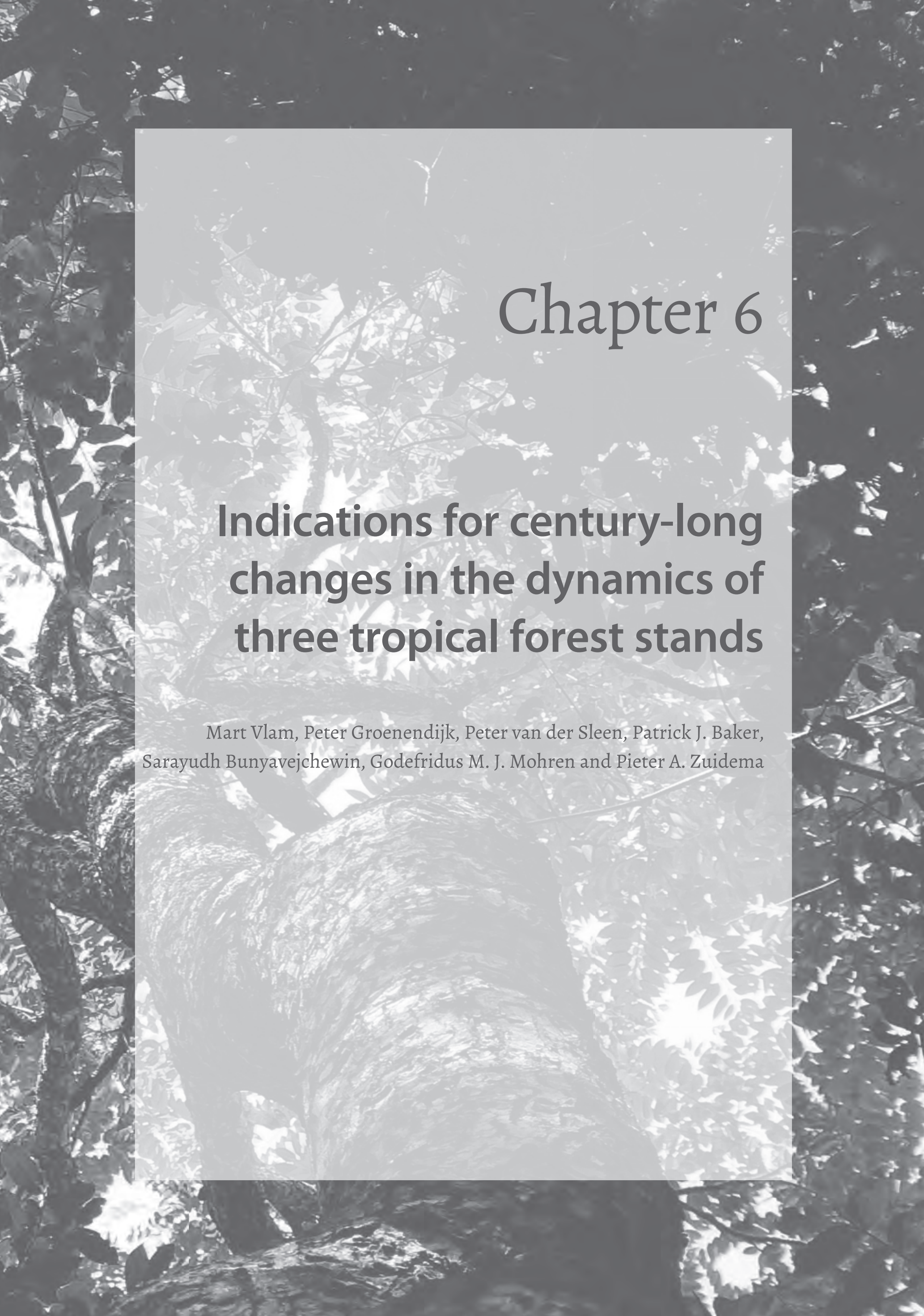


Figure S5.4 Semivariograms for 12 species, the semivariance is indicated by the open circles. For those species with significant spatial structure in age, the model fit is shown (black line). Shade-tolerance guild is indicated: ST, shade-tolerant; PST, partial shade-tolerant; LLP, long-lived pioneer.



Chapter 6

Indications for century-long changes in the dynamics of three tropical forest stands

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Sarayudh Bunyavejchewin, Godefridus M. J. Mohren and Pieter A. Zuidema

Abstract

Over the past decades indications for significant changes in dynamics of seemingly intact tropical forests stands have been found. These findings have mainly been reported from permanent sample plots in which remeasurements of tree diameter were used for a maximum of three decades. However, this approach largely ignores the century-long life spans of trees and the long time scale at which natural fluctuations in stand dynamics as a result of past disturbances may occur. We used a century-long tree-ring dataset of >1250 trees representing 14 species from three sites in Bolivia, Cameroon and Thailand. Most of these species were estimated to respond strongly to changes in light availability by a so called growth 'release'. We assessed tree-ring series for the occurrence of growth releases that were sustained ≥5 years and used these as a proxy for historical canopy gap formation. The binomial data on growth releases was then analyzed using a generalized linear mixed model (GLMM). In total we counted 858 release events over the period 1746-2002. GLMM-analysis showed that species specific trends in release frequency were predominantly negative or absent. When analyzing the trends for the individuals sites we found significant decreasing trends for the sites in Bolivia and Cameroon and no trend for the site in Thailand. However, after including climate variability in the GLMM a significant positive trend in release frequency for the site in Thailand emerged. When analyzing the trend across the sites we found evidence for a significant decrease in the frequency of growth releases over the past ~250 years. In general the pattern across the three sites indicated decreasing release frequency over time, which is indicative for a trend of decreasing gap formation and increasing canopy density. These results are consistent with short term observations of Australian tropical forests, but contrasting with permanent plot studies from the Neotropics. Our findings suggest that occasional disturbances, both natural and anthropogenic, and natural climate variability are key drivers of long-term tropical forest dynamics. These drivers may obscure changes in tropical forest dynamics on shorter time scales that are caused by global change.

Keywords: Bolivia; Cameroon; Growth release; Thailand; tree rings; canopy gaps

Introduction

Tropical forests contain roughly 25-50% of the global carbon stored in terrestrial biomass (Bonan 2008, Lewis et al. 2009b). Any change in carbon cycling of tropical forests will therefore have strong consequences for the global carbon cycle (Clark 2007). Over the past decades forest monitoring plots have reported significant increases in aboveground biomass (Phillips et al. 1998, Baker et al. 2004, Lewis et al. 2009b) and increasing recruitment and mortality rates (Baker et al. 2004, Lewis et al. 2004, Phillips et al. 2004, Laurance et al. 2009) of seemingly intact tropical forest stands. Other networks of long term forest monitoring plots showed a relation between growth an climate variability but no recent changes in tree growth rates (Clark et al. 2010), or opposite trends of declining growth rates (Feeley et al. 2007b) and decreasing stem density (Murphy et al. 2013).

There is uncertainty about the causes for these observed changes, although global change has been identified as potential driver (Phillips et al. 2004). Enhanced forest productivity as a result of increased resource availability, e.g., rising atmospheric CO_2 concentrations and increased nitrogen deposition, may lead to higher tree growth and turnover rates (Malhi and Phillips 2004, Hietz et al. 2011). Although detrimental effects of increased temperatures have also been identified (Corlett 2011). But, more importantly, concerns have risen about the experimental design used for studying tropical forest dynamics (Fisher et al. 2008, Gloor et al. 2009, Chambers et al. 2013). Until now trends in tropical forest stand dynamics have predominantly been studied using remeasurements of tree diameter in networks of relatively small (1 ha) permanent sample plots (e.g., Baker et al. 2004). However, the century-long life spans of trees and the long-time scale at which natural fluctuations in stand dynamics occur as a result of past disturbances, call for testing the hypothesis of altered tropical forest dynamics at a similar century-long timescale (Nelson 2005, Chambers et al. 2013). Dendroecology - using tree-rings to study ecological processes - provides an opportunity to gather long-term data on tropical tree growth to complement plot-based repeated diameter measurements (Zuidema et al. 2013).

If forest dynamics have gradually changed over time we expect that this will be reflected by altered rates of canopy gap formation. In tropical forests death of a nearby tree will be followed by a growth response of saplings in and around the canopy opening (Brokaw 1985). This growth response is recorded as a sustained increase in ring widths from the long term mean growth rate, which is referred to in dendroecology as a 'release' (Nowacki and Abrams 1997). Tree-ring studies in temperate forests have already established the clear relation between past canopy disturbance and the occurrence of growth releases in the remaining trees (Canham 1985, Druckenbrod et al. 2013). Indications for a similar link between gap formation an releases in tree saplings have also been found in tropical forests (Soliz-Gamboa et al. 2012). Additionally, studies in the tropics have revealed a relation between favorable climate and the occurrence of a growth release, showing that water availability may be a dominant driver of long-term tree growth variability (Brienen et al. 2010b). In this study growth releases observed in individual tropical trees were used as a proxy for canopy gap formation. If forest canopy gap dynamics have significantly changed over the past centuries, we would expect to find significant trends in the number of growth releases over time. Based on the developmental stages of temperate forests as described by Oliver (1980), such trends in the occurrence of canopy gap formation may be related with forest stand development following past disturbance.

Recently two studies have used tree-ring data to investigate forest dynamics at a century-long timescale (Rozendaal et al. 2011, Druckenbrod et al. 2013). We took advantage of these recent methodological developments to improve our calculations of growth releases, for example by applying rigorous standardization techniques and applying appropriate release criteria. To test the hypothesis on accelerated forest dynamics we use a 'pan-tropical' dataset containing >200 years of tree-ring data on ~1300 trees. This dataset included 14 species, which were primarily selected for the formation of reliable annual rings and adequate local abundance. Furthermore they represent various ecological guilds; from long-lived pioneers to shade-tolerant species. All tree-ring samples were collected in large (150-300 ha) areas of contiguous 'old-growth' tropical forest, following an identical sampling design. The principal aim of this setup was to gather a sample set that would be representative for the forest stand in general. We have two research questions. (1) Do we find evidence for a significant change in the frequency of growth releases over time? (2) Does climate explain some of the long-term variation in release frequency?

Materials and methods

Study area and species

The study was carried out in three sites on three continents: Bolivia, Cameroon and Thailand (Fig. 6.1). In Bolivia samples were collected in the logging concession 'La Chonta' (15.84 S, 62.85 W). The forest in La Chonta is a semi-deciduous moist forest that is transitional between Chiquitano dry forest and moist Amazonian forests (Peña-Claros et al. 2012). Elevation ranges between 298 and 436 m above sea-level. Soils have been classified as relatively fertile ultisols due to human influences. Total annual precipitation in the region is around 1580 mm, with a five month dry season receiving <100 mm precipitation per month from May to September and mean annual temperature is 24.5 °C. Like many forests in the Amazon the area has been selectively logged at low intensity (ca. 1 m3/ha) for the commercially valuable broad-leaf mahogany (*Swietenia macrophylla;* (Pinard et al. 1999, Gould et al. 2002). This logging took place around 1992, but we have found no direct evidence, e.g., old skid trails or tree stumps, that indicate logging in our study area. There is abundant evidence for anthropogenic dark earths or 'terra preta' in the area, indicating that the site was inhabited 300-400 years ago (Paz-Rivera and Putz 2009).

The site in Cameroon (5.25 N, 9.10 E) is a semi-deciduous tropical rainforest of the Guineo-Congolian type. Samples were collected in logging concession 11.001 operated by Transformation REEF Cameroon (TRC). This concession is adjacent to the northwest border of Korup National Park. The forest is locally dominated by groves of Fabaceae-Caesalpinioideae species and other important families in terms of basal area are Euphorbiaceae and Scytopetalaceae (Chuyong et al. 2004). Elevation levels are approximately 100 m above sea-level and soils are sandy and nutrient poor (Chuyong et al. 2004). Mean total annual rainfall is around 4000 mm and mean annual temperature 26.7 °C (Nchanji and Plumptre 2001). The climate is characterized by a distinct three month dry season from December to February with monthly rainfall levels <100 mm. Of the three sites TRC probably has the highest human influence, as several villages are located in directly around the logging concession.

The third study site is situated in the Huai Kha Khaeng Wildlife Sanctuary (HKK), Thailand (15.60 N, 99.20 E). The site at HKK is a semi-deciduous tropical moist forest and dominated by trees in the Annonaceae and Dipterocarpaceae family. Altitudes in HKK vary between 490 and 650 m above sea-level and the soils are highly weathered slightly acidic ultisols (Bunyavejchewin et al. 2009). Mean annual rainfall is around 1473 mm (1993-2001) and the 4-6 month dry season ranges from November to April. Mean annual temperature is 23.5 °C. There is no human influence in HKK, except for the Wildlife Sanctuary infrastructure and as an ignition source for surface fires expanding from agricultural areas around the park (Baker et al. 2008). No logging activities are known to have taken place in the study area.

Table 6.1 Characteristics of the 14 study species; their ecological guild (ST, shade-tolerant; PST, partial shade-tolerant; LLP, long-lived pioneer), leaf phenology (D, deciduous; E, evergreen; BD, brevi-deciduous) and age at 27 cm dbh ± **SD.**

Country	Species	Family	Ecological guild[1]	Leaf phenology[2]	Age @ 27cm (years)
Bolivia	*Ampelocera ruizii*	Ulmaceae	ST	E	47.1 ± 15.2
	Cariniana ianeirensis	Lecythidaceae	PST	D	53.5 ± 10.3
	Hura crepitans	Euphorbiaceae	PST	D	30.3 ± 7.8
	Schizolobium amazonicum	Fabaceae	LLP	D	9.8 ± 3.1
	Sweetia fruticosa	Fabaceae	LLP	BD	65.3 ± 18.3
Cameroon	*Brachystegia cynometroides*	Fabaceae	PST	D	68.3 ± 24.1
	Brachystegia eurycoma	Fabaceae	PST	D	62.4 ± 19.1
	Daniellia ogea	Fabaceae	LLP	D	89.0 ± 23.0
	Terminalia ivorensis	Combretaceae	LLP	D	20.8 ± 12.4
Thailand	*Afzelia xylocarpa*	Fabaceae	LLP	D	37.3 ± 12.0
	Chukrasia tabularis	Meliaceae	PST	BD	54.7 ± 17.0
	Melia azedarach	Meliaceae	LLP	D	15.0 ± 5.1
	Neolitsea obtusifolia	Lauraceae	ST	E	81.1 ± 16.3
	Toona ciliata	Meliaceae	LLP	D	39.5 ± 20.2

[1] Ecological Guilds: Bolivia (Peña-Claros et al. 2008b), Cameroon (Hawthorne 1995), Thailand (Baker et al. 2005) and the definitions are in accordance with (Poorter et al. 2006); [2] Leaf phenology: Bolivia (Mostacedo et al. 2003), Cameroon (Hawthorne 1995, Lemmens et al. 2012), Thailand (Williams et al. 2008).

Field sampling

In the Bolivian and Thai site we sampled five different tree species. In Cameroon four species were selected for sampling. For a full list of the species see Table 6.1. Species selection was primarily based on the presence of clearly identifiable annual growth rings and local abundance. The 14 species represent various families, a variety in leaf phenology and functional groups: from shade-tolerant to highly shade-intolerant. For convenience, we will refer to all species by their genus names, except for the two *Brachystegia* species.

All wood samples for tree-ring analysis were collected over a period of two years between May 2010 and May 2012. The majority of samples were collected following a clustered sampling design, in which all trees of target species >5 cm dbh were sampled in a 50 m radius around a randomly assigned location. Total areas in which trees were sampled following the clustered sampling design ranged from 144 ha in Cameroon to 272 ha Bolivia and 296 ha in Thailand. We aimed to sample roughly 500 trees per study area, divided equally over previously selected target species. Species for which no adequate sample size could be achieved in this way, were sampled more opportunistically by collecting additional samples from trees that were encountered in the forest. We measured dbh (1.3 m) and diameter at sampling height of each sample tree. In the logging concessions in Bolivia and Cameroon a large fraction of the samples were collected as stem discs from recently felled trees. All other samples were collected using an Suunto (Vantaa, Finland) or Haglöf (Långsele, Sweden) increment borer. At a height of approximately 1 m we manually extracted tree cores with a diameter of ~5 mm. Depending on the diameter of the tree we used borers with lengths varying between 40 and 70 cm. From trees <40 cm dbh two cores were taken, because the borer would go straight through the tree and two radii per core were obtained. For all larger individuals we took three cores, because only one radius per core was obtained. Taking multiple cores and stem discs allowed us to measure rings over at least three complete radii, thereby correcting for radial differences in diameter increment.

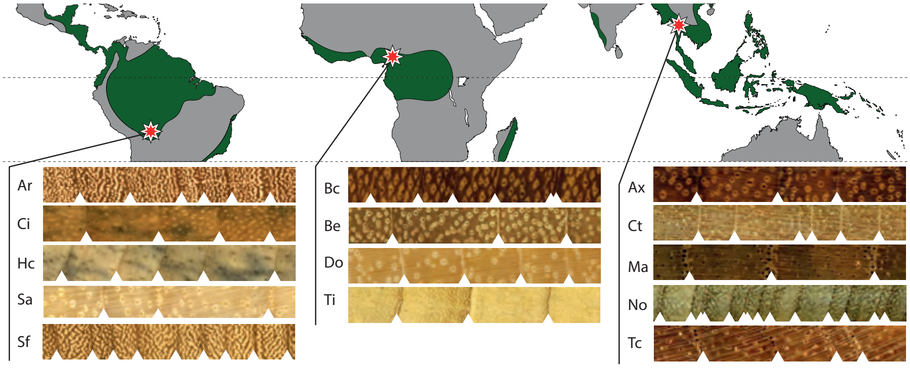


Figure 6.1 Study area (top) and wood characteristics of the 14 study species (bottom). Approximate location of the study areas is indicated by the star symbol. White arrows indicate tree-ring boundaries. Ar=Ampelocera ruizii, Ci=Cariniana ianeirensis, Hc=Hura crepitans, Sa=Schizolobium amazonicum, Sf=Sweetia fruticosa, Bc=Brachystegia cynometroides, Be=Brachystegia eurycoma, Do=Daniellia ogea, Ti=Terminalia ivorensis, Ax=Afzelia xylocarpa, Ct=Chukrasia tabularis, Ma=Melia azedarach, No=Neolitsea obtusifolia, Tc=Toona ciliata.

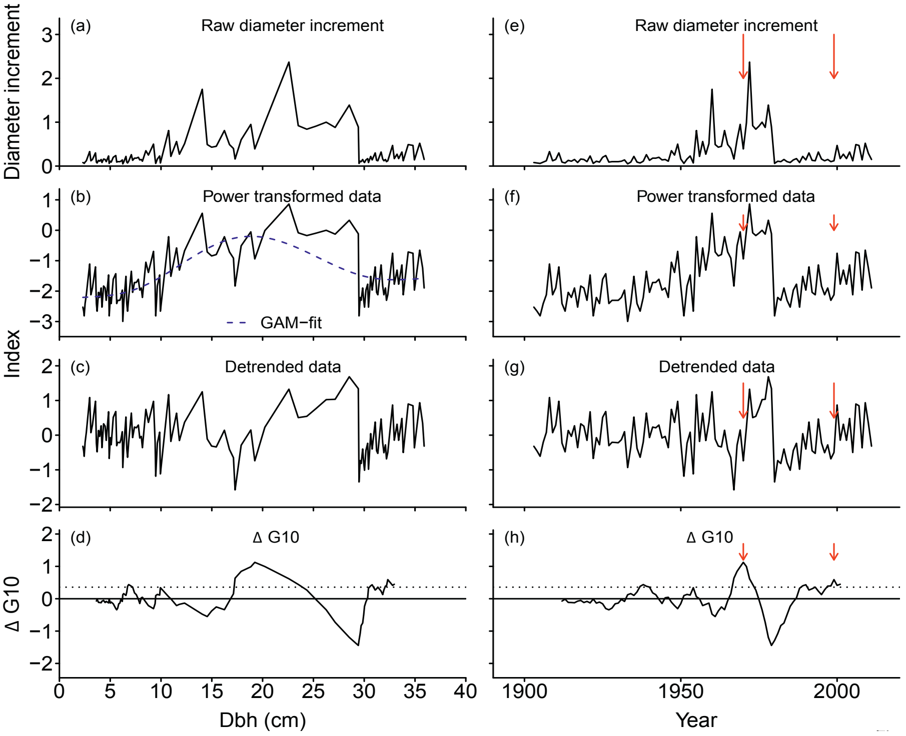


Figure 6.2 Illustration of the techniques used to identify growth releases. The curves represent growth rates of one individual *Daniellia ogea* tree. Graphs on the left show raw and standardized diameter increment vs. diameter, graphs on the right express diameter increment per year. Dashed line shows the GAM-fit used to remove age related shifts in growth rate. Arrows indicate years of release. The two bottom graphs show relative growth change.

Tree-ring measurements

The increment cores were glued to wooden mounts and cut perpendicular to the ring boundaries with a large sliding microtome (WSL; Swiss Federal Institute for Forest, Snow and Landscape Research, Switzerland). Stem disks were sanded with progressively finer sand paper. Digital images (1600 dpi) of the tree cores and stem discs were acquired using a high-resolution flatbed scanner (Epson Expression 10000 XL) and analyzed in the WinDENDRO program for tree-ring analysis (version 2009b; Regent Instruments Canada Inc.). All tree-ring boundaries were marked manually on the screen and measured to the nearest 0.001 mm (Fig. 6.1). Very large stem discs were measured to the nearest 0.01 mm using a LINTAB 5 measurement device and TSAP software (Rinntech). Ring-width series were first visually cross dated within trees and then among trees. Afterwards they were checked for dating errors with the computer program COFECHA (Holmes 1983). The annual character of the rings was verified by various means, such as radiocarbon dating (Fig. S6.1), chronology production (Thailand; Vlam et al. 2014b), earlier cambial wounding experiments (Brienen and Zuidema 2003, Baker et al. 2005, Lopez et al. 2012) and dating of trees of known age (*Schizolobium amazonicum*; P. van der Sleen, *unpublished results*).

Release analysis

All calculations and statistical analyses were performed in the R program environment for statistical computing, version 3.0.2 (R Core Team 2013). To identify releases in tree-ring series, first all dbh-increment data was power transformed to reduce heteroscedasticity, because this is often present in tree-ring series (Druckenbrod et al. 2013)2%. For the power transformation we expressed annual raw diameter increment values as a function of diameter (Fig. 6.2a). After power transformation the data was standardized for size dependent differences in growth rates, using a rigid generalized linear model (GAM) fit (Fig. 6.2b). Using the residual diameter growth series (Fig. 6.2c) we calculated ΔG_{10} as follows:

$$\Delta G_{10i} = M_2 - M_1$$

where for the year *i*, ΔG_{10i} is the difference between the mean diameter increment in two consecutive 10 year periods: M_1 and M_2. For example when ΔG_{10} is calculated for the year 1960: M_1 is defined as the mean diameter increment for the years 1951-1960 and M_2 is the mean diameter increment for the period 1961-1970. Because ΔG_{10} is a 10-year running mean, these values cannot be calculated for the first 9 years and the last 10 years in each series. After calculating the ΔG_{10}-values for every year in the dataset, a year of release was defined as:

$$r_i \begin{cases} 0 \text{ if } \Delta G_{10i} < \sigma(\Delta G_{10total}) \\ 1 \text{ if } \Delta G_{10i} > \sigma(\Delta G_{10total}) \end{cases}$$

where r_i is the occurrence of a release in year *i*, σ is the standard deviation and $\Delta G_{10total}$ is the total number of ΔG_{10}-values calculated per species. Only a growth increase lasting for ≥5 consecutive years was considered a sustained release (Brienen and Zuidema 2006a, De Ridder et al. 2013). Therefore, the resulting binary release data series were scanned for windows ≥5 consecutive years in which the ΔG_{10}-values surpassed the release threshold (Fig. 6.2d). The year of release was then marked as the year of the most extreme ΔG_{10}-value across the ≥5 year window in which the release threshold was passed (Druckenbrod et al. 2013). This year was determined as the year of growth release.

For this study we were interested in growth releases associated with canopy gaps. Therefore we restricted our analysis of temporal trends in growth release frequency to the period in which trees had not reached the forest canopy. Based on field observations in the three sites this threshold was set a dbh of 27 cm. Therefore we restricted all analyses to diameter increments when trees were <27 cm dbh. We then used generalized linear mixed models (GLMMs) (Bolker et al. 2009), to test the release absence/presence data on significant temporal trends in release occurrence. This model setup explicitly accounts for differences between species, for example in age and release frequency. Model fitting was done using the lme4 package (Bates et al. 2013) and based on restricted maximum likelihood estimation, specifying a binomial error structure. First we used a GLMM with release occurrence as a dependent variable, year as a fixed factor and each individual tree as a random effects. To analyze site-level trends in release frequency we also analyzed data per country using species and tree as nested random effects. Then a third analysis was performed including data from all three sites, by using country, species and tree as nested random effects. The 'pan-tropical' model was stated as following:

```
model <- glmer( Release ~ Year + ( 1 | Country / Species
/ Tree), family = binomial)
```

Besides canopy dynamics driving decadal variability in release frequency, climate variability may also explain part of the variability. We used the Palmer Drought Severity Index (PDSI) as a proxy for the local climatological conditions. Gridded PDSI-values for the period were obtained from the KNMI Climate Explorer website (Trouet and Van Oldenborgh 2013) for the period: 1913-2005, Bolivia; 1916-2005, Cameroon; 1870-2005, Thailand. The PDSI is a measure for soil moisture availability, in which a value of 0 indicates normal moisture conditions, while negative values indicate dry and positive values indicate wet conditions. From the monthly PDSI values we calculated 10-year mean PDSI values. To determine the effect of climate variability on the occurrence of growth releases we included annual PDSI values as an additional fixed factor in the mixed-effects model:

```
model <- glmer( Release ~ Year + 10yr.PDSI + ( 1 | Country
/ Species / Tree), family = binomial)
```

Table 6.2 Overview of the releases calculated per study species. Ecological guild (ST, shade-tolerant; PST, partial shade-tolerant; LLP, long-lived pioneer). N_{trees} is the total number of trees included in the model. $N_{release}$ is the total number of releases that was found. N_{years} is the total number of years in the analysis. Rate of release is the total number of releases found divided by the total number of years in the analysis.

Country	Species	Guild	N_{trees}	$N_{release}$	N_{years}	Rate of release
Bolivia	*Ampelocera ruizii*	ST	86	23	2215	0.010
	Cariniana ianeirensis	PST	90	64	5057	0.013
	Hura crepitans	PST	73	8	2036	0.004
	Schizolobium amazonicum	LLP	87	0	0	0
	Sweetia fruticosa	LLP	101	62	4837	0.013
Cameroon	*Brachystegia cynometroides*	PST	123	114	10407	0.011
	Brachystegia eurycoma	PST	126	113	9314	0.012
	Daniellia ogea	LLP	104	192	13396	0.014
	Terminalia ivorensis	LLP	61	54	5573	0.010
Thailand	*Afzelia xylocarpa*	LLP	100	60	6701	0.009
	Chukrasia tabularis	PST	102	53	5065	0.010
	Melia azedarach	LLP	71	11	1577	0.007
	Neolitsea obtusifolia	ST	100	58	6296	0.009
	Toona ciliata	LLP	58	46	2371	0.019

[1] Ecological Guilds: Bolivia (Peña-Claros et al. 2008b), Cameroon (Hawthorne 1995), Thailand (Baker et al. 2005) and the definitions are in accordance with (Poorter et al. 2006).

Results

In total we counted 858 release events among the 14 species over the period 1746-2002 (Table 6.2). More than half of the releases (473) were counted in the four Cameroonian species. This relatively high number of releases is partly explained by the comparatively high number of years it took *B. cynometroides*, *B. eurycoma* and *Daniellia* to reach 27 cm dbh. The mean release rates of these species were relatively comparable to the mean release rates of the species from the other two sites. Only one species, the highly-shade intolerant long-lived pioneer *Schizolobium* from Bolivia, did not show a single release. Two other species, the partial shade-tolerant *Hura* from Bolivia and the long-lived pioneer species *Melia* from Thailand showed very little releases and a comparatively low release rate. The low number of releases in these species can mainly be attributed to the high-light preference for establishment of these species, indicated by the high juvenile growth rates (Table 6.1). Juveniles either establish under high-light conditions and maintain high growth rates over the entire juvenile phase (i.e. one single sustained release), or perish when they are shaded by other individuals. The only species with an considerably higher release rate was *Toona* from Thailand. This species showed a release rate that was about two times higher than the overall mean for the three sites.

Table 6.3 GLMM regression coefficients per species. Per species results for two GLMMs are shown, one model that includes only year as a fixed factor and one model that includes both year and 10-year mean PDSI as a fixed factors. Model selection was based on AIC. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

		Without Climate		With climate		
Site	**Species**	**Period**	**Year**	**Period**	**Year**	**PDSI**
Bolivia	*Ampelocera ruizii*	1938-2000		1939-2000		
	Cariniana ianeirensis	1874-2001	-0.012**	1917-2000		
	Hura crepitans	1857-2001	-0.022*	1917-2000	-0.045**	
	Sweetia fruticosa	1800-2001		1917-2000		
Cameroon	*Brachystegia cynometroides*	1865-2002	-0.014***	1920-2000	-0.018***	
	Brachystegia eurycoma	1830-2001	-0.011***	1920-2000	-0.013**	
	Daniellia ogea	1746-2001		1920-2000		
	Terminalia ivorensis	1843-2001	-0.012**	1920-2000		
Thailand	*Afzelia xylocarpa*	1833-2001		1874-2000		
	Chukrasia tabularis	1838-2001		1874-2000		
	Melia azedarach	1902-2001	0.194**	1902-2000	0.215**	
	Neolitsea obtusifolia	1885-2001		1885-2000		
	Toona ciliata	1869-2001		1874-2000	0.015	0.249*

Changes in release frequency over time

The GLMM-analysis per species revealed either no trend in release frequency, or a significant decrease in the number of growth releases over the past 100-200 years (Table 6.3). The only exception was *Melia* from the site in Thailand, which showed a significant increase in the occurrence of growth releases over time (Fig. S6.2). The analysis per country revealed a significant decrease in release frequency for the sites in Bolivia and Cameroon (Fig. 6.4b,c). At the site in Thailand we found no significant trend in occurrence of growth releases over the period 1833-2001 (Fig. 6.4c). Across the three sites also significant trend of decreasing release frequency over the period 1746-2002 emerged (Fig. 6.3; Table 6.4).

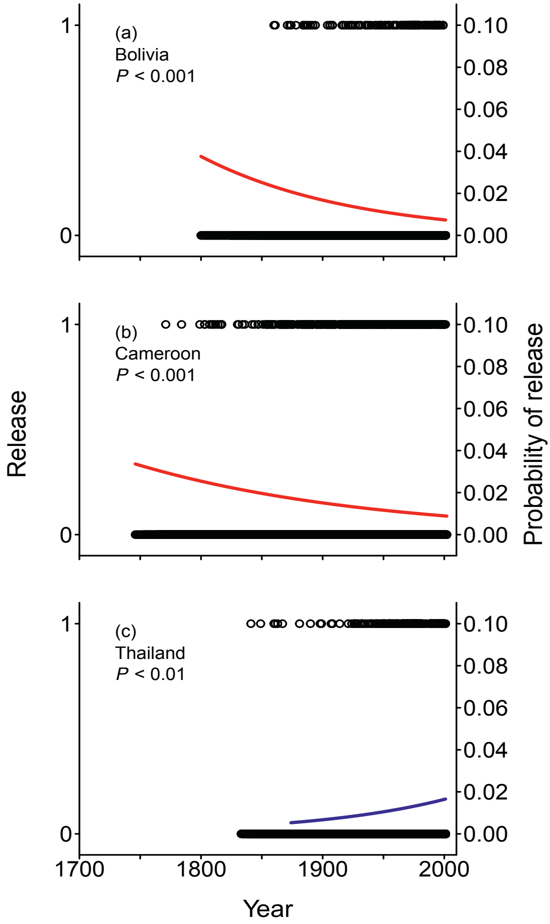


Figure 6.3 Trend in century-long release frequency for the sites in Bolivia (a), Cameroon (b) and Thailand (c). The red curves indicate the GLMM fit. The blue line indicates the GLMM fit including both year and climate as fixed factors. Significance of the fixed effect is indicated by *P*. Note that the trend was displayed on the secondary axis.

Climate as an explaining factor for release frequency

The strongest effect of climate as a driver of release frequency was found for the site in Thailand. We found that release frequency of *Toona* was higher in periods with relatively wetter climatological conditions (Table 6.3; Fig. S6.2). Including mean 10-year PDSI values as an fixed factor in the GLMM for the site in Thailand strongly decreased the AIC value. This new model showed a significant increase in release frequency over the period 1874-2000 and a significant positive effect of higher 10-year mean PDSI values on release frequency (Fig. 6.5). This means that the probability of a growth release increased during periods with wetter climate conditions. We did not find evidence for a significant climate effect on the release frequency of species at the sites in Bolivia and Cameroon. Note that due to the restricted number of years for which PDSI values were available that the period of analysis was reduced to <100 years for the sites in Bolivia and Cameroon. Similarly by, including 10-year mean PDSI values as an fixed factor in the GLMM for analyzing release frequency across the three sites did not decrease the AIC-value of the pan-tropical model.

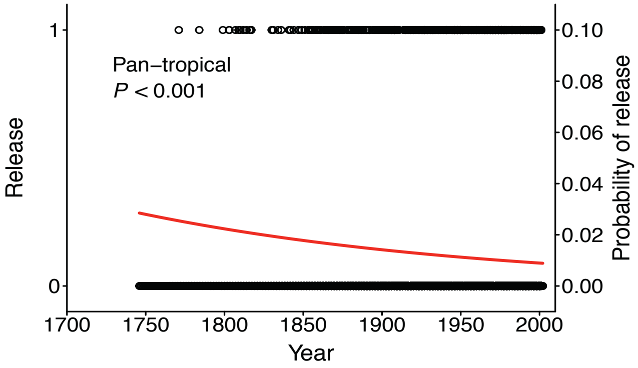


Figure 6.4 Pan-tropical trend in century-long release frequency. The red curve indicates the GLMM fit. Significance of the fixed effect is indicated by *P*. Note that the trend was displayed on the secondary axis.

Discussion

Using tree rings to study tropical forest dynamics

In this study we used growth releases from tree-ring data to analyze trends in forest stand dynamics at centennial timescales. In the 'pan-tropical' GLMM we combined data from the three different sites and we found a significant decrease in release occurrence over the past ~250 years. Analysis of individual sites also revealed indications for significant changes in release frequency of understory trees. In Bolivia and Cameroon we found a significant decrease, whereas in Thailand we found a significant increase in release frequency over time, when controlling for climate. We are aware that growth-release data obtained from tree-ring measurements is a mere proxy for local forest stand dynamics. The tree-ring approach is very different from the conventional way to study tropical forest dynamic in permanent plot studies, in which a full census is made of tree recruitment and mortality rates (e.g., Phillips et al. 2004, Murphy et al. 2013). However, in temperate forests a clear link between known canopy disturbance events and the timing of growth releases in the surviving trees has been established (Druckenbrod et al. 2013). These findings suggests that growth releases are an adequate proxy for the timing of actual canopy disturbance.

Potentially, the difference in the temporal scale of permanent plot studies versus tree-ring studies may lead to different results on temporal trends in forest dynamics. For example relatively short-term climate variability may play a more dominant role in decadal scale observation from permanent plot studies as opposed to the century-long observations from tree-ring data. Also the majority of global change has occurred in the period since 1950 and therefore the most dramatic global change effects on forests may be expected over the past decades. For the analysis in this study we also included the ~150 years prior to this change, potentially explaining some of the differences in findings.

Table 6.4 GLMM regression coefficients per site and the GLMM combining data from the three sites (pan-tropical). Results for two GLMMs are shown, one model that includes only year as a fixed factor and one model that includes both year and 10-year mean PDSI as a fixed factors. Model selection was based on AIC. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

	Without Climate		With climate		
Site	**Period**	**Year**	**Period**	**Year**	**PDSI**
Bolivia	1800-2001	-0.008***	1917-2000	-0.010*	
Cameroon	1746-2002	-0.005***	1920-2000	-0.009***	
Thailand	1833-2001		1874-2000	0.009**	0.153**
Pan-tropical	1746-2002	-0.005***	1874-2000	-0.004**	

To overcome methodological issues leading to erroneous detection of growth releases, treatment of the data prior to analysis was needed. First, we applied very strict standardization procedures using a correction for ontogenetic trends in growth rates (GAM-fit) and any heteroscedasticity in the growth data was reduced by power transformation (Druckenbrod et al. 2013). Both curve-fitting and power transformation are widely applied standardization techniques in tree-ring research (Speer 2010) and this approach proved effective in removing age related growth trends. Any false detection of growth releases due to ontogenetic shifts in diameter growth were therefore unlikely to have occurred in this study. Secondly, 10-yr running mean values were used to calculate growth change over time. This approach has also widely been used in both temperate and tropical dendroecology to study patterns of growth release in trees (Nowacki and Abrams 1997, Baker and Bunyavejchewin 2006b, Brienen and Zuidema 2006a). The growth change method was developed to neutralize both short-term and long-term growth trends associated with climate, while preserving canopy disturbance effects on growth (Nowacki and Abrams 1997). We found, however, that for the site in Thailand still a significant amount of temporal variation in growth releases was due to climatic variation. This climate effect could be captured by including long-term variation in PDSI-values as a fixed effect in the GLMM. We believe that this approach is preferred over stricter standardization of the growth data, because stricter standardization may also remove some of the growth variation related to canopy dynamics. The application of species specific release thresholds based on observed growth change (Druckenbrod et al. 2013), is an elegant alternative to the earlier use of relatively arbitrary release detection thresholds, such as a 25% or 50% increase in growth rate of the trees (e.g., Nowacki and Abrams 1997). We are therefore convinced that the methodology used in this study is as robust as possible for some of the methodological errors that may occur in dendroecological studies.

There is, however, one methodological error that is hard to quantify and correct for in dendrochronological studies, that is the 'juvenile selection effect' (Landis and Peart 2005). It has been shown that faster growing juveniles of tropical trees have a higher chance of attaining the forest canopy and are therefore more likely to reach old age (Rozendaal et al. 2010a). This implies that in historical tree-ring data the number of fast growing juveniles is likely to be overestimated. Additionally, it has been shown that many seedlings of tropical tree species require one or more growth releases to attain canopy stature (Baker and Bunyavejchewin 2006b, Brienen and Zuidema 2006a). It is therefore possible that fast growing juveniles, showing an above average number of growth releases, are overrepresented in historical tree-ring data. This juvenile selection effect may therefore not only lead to apparent strong decreases in the growth rates of juvenile trees (Baker 2010, Rozendaal et al. 2010a), but also result in an apparent decrease in release frequency over time. It has, however, also been shown that the mortality risk for tropical trees >10 cm dbh is fairly constant (Swaine et al. 1987). In this study all analyses were based on juvenile trees in the size class between 0-27 cm dbh. By including relatively large juvenile trees in the analysis, the effect of preferential survival of fast growing juveniles should therefore have been reduced.

Changing forest dynamics over time

Overall the analysis across the three sites indicated decreased release frequency over the past ~200 years. Such decreasing release frequency in understory trees is consistent with a pattern of decreasing gap formation (Soliz-Gamboa et al. 2012). The results presented here are in contrast with permanent plot studies from the Neotropics, in which evidence was found for decadal scale increases in recruitment and mortality rates of seemingly intact tropical forest stands (Baker et al. 2004, Lewis et al. 2004, Phillips et al. 2004, Laurance et al. 2009). But, our results are in agreement with recent evidence for unaltered or decreasing stand dynamics of Australian tropical rain forests (Murphy et al. 2013). Similar to Murphy et al. (2013) we identify recovery after past disturbance, either natural and anthropogenic, as a potential explanation for the observed trends in forest dynamics. The patterns of decreasing gap formation as observed in Bolivia and Cameroon are consistent with recovery from past large scale disturbance. Initial stages of stand development, such as the *stand initiation stage* and the *stem exclusion stage* are more likely associated with growth releases in the juvenile trees (Oliver 1980, Oliver and Larson 1996). In particular, the stem exclusions stage is characterized by high mortality due to strong competition in the dense stand (Oliver and Larson 1996). Mortality of neighboring trees may lead to growth stimulation of surviving trees as a result of increased resource availability, i.e. water and light (Brokaw 1985). A period of high mortality is therefore likely associated with abundant growth releases in surviving trees (Druckenbrod et al. 2013). The reduction in the occurrence of growth releases in the more recent past may reflect a period reduced gap formation. Juvenile trees that regenerated more recently, probably established during the *understory reinitiation stage*. In this stage random mortality of canopy trees is low and therefore high-light and high-nutrient conditions for juveniles are less likely to occur (Oliver and Larson 1996), leading to reduced occurrence of growth release. Only when the forest reaches the *old-growth stage* gap formation will start to increase when large canopy tree die of old age (Oliver and Larson 1996). The evidence presented here suggests that such a phase has not yet been reached in the forests in Bolivia and Cameroon.

Although we lack detailed historical records of past disturbances on any of the three sites, the disturbance histories of the three sites have previously been reconstructed using tree-ring data (Baker et al. 2005, Middendorp et al. 2013). Based on evidence for regeneration failure of current canopy trees it was estimated that the forest canopy cover at the sites in Cameroon and Thailand has increased over the past 100-150 year. The evidence for decreased release frequency at the site in Bolivia is seemingly in contrast with the evidence for abundant regeneration of shade-intolerant trees CHAPTER 5. However, it is also estimated that the site in Bolivia has been recovering from major disturbance in the more distant past. Based on charcoal and pottery found in the soil it is likely that the site in Bolivia was more densely populated until 300-400 years before present (Paz-Rivera and Putz 2009). Therefore also in Bolivia canopy cover may have gradually increased over the past centuries.

Climate induced growth releases

In the sites in Bolivia and Cameroon we found no indication for climate induced growth releases, whereas in Thailand we found indications for such climate induced releases. Earlier research suggested that climate is a major limiting factor for tree growth at the site in Thailand, driving substantial annual growth variation in trees (Vlam et al. 2014b). Severe drought events (i.e. more negative PDSI-values), were observed to result in strongly reduced growth rates of the trees, with the potential to last for several years (Vlam et al. 2014b). Favorable climatological conditions, either increased precipitation or lower summer temperatures, have been observed to result in sustained growth release of tropical dry forest trees (Brienen et al. 2010b). As mentioned earlier these climate-induced growth releases were not completely removed by the standardization procedures used in this study.

Climate change induced alterations in rainfall patterns and temperature may potentially lead to an increase in the occurrence of extreme drought events in the tropics (Malhi and Wright 2004, Laurance et al. 2009). These extreme droughts may subsequently lead to prolonged growth suppressions in trees or even mortality of canopy trees (Phillips et al. 2009), ultimately resulting in long term changes in the rate of canopy gap formation in tropical forests. However, so far we have found evidence for a moderate 0.1° C decadal increase in temperature since 1950, but no evidence for a significant change in precipitation levels in any of the three sites (KNMI Climate Explorer 2013; (Trouet and Van Oldenborgh 2013). Any dramatic change in canopy dynamics due to climate change is therefore not yet expected.

Natural variability versus global change

Her we reported on century-long decrease in releases frequency in two sites and a significant increase in releases frequency in another site. A similar study by Rozendaal et al. (2011) for a site in northern Bolivia revealed no directional trend in forest dynamics. These results suggest that past disturbance and climate stochasticity are both major drivers of long-term forest stand dynamics and that significant positive and negative trends in release frequency can be expected. This is notably different from a predominantly positive trend that was hypothesized based on increased resource availability due to elevated atmospheric CO_2 levels. Any short-term, i.e. decadal scale, trends in tropical forest dynamics should therefore be interpreted with caution, because short term forest dynamics may be affected by long-term trends in forest stand development and climatic variation.

Acknowledgements

We thank students and fieldwork staff for their valuable contribution to this project. We thank the National Research Council of Thailand the Department of National Parks, Wildlife and Plant Conservation for granting permission to carry out fieldwork in the Huai Kha Khaeng Wildlife Sanctuary. We thank the personnel of the logging companies Transformation REEF Cameroon and La Chonta Ltd. Bolivia for their cooperation. We acknowledge Roberto Quevedo of the Carrera Forestal UAGRM Bolivia, Martin Tchamba of the Forestry department, University of Dschang, Cameroon and Somboon Kiratiprayoon, Thammasat University, for their contribution. Mart Vlam, Peter van der Sleen, Peter Groenendijk and Pieter Zuidema were financially supported by the European Research Council (ERC, grant #242955).

Appendix

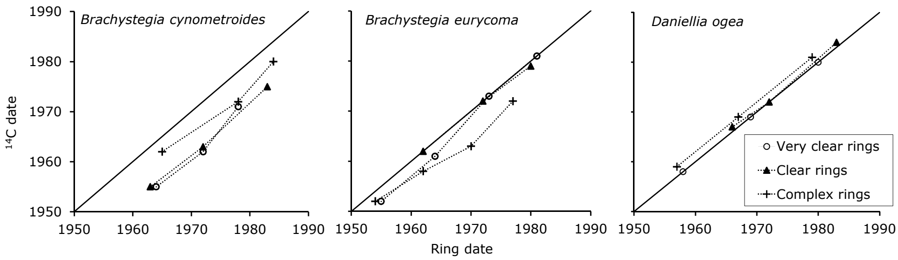


Figure S6.1 14C bomb-peak dating confirms annual ring formation in three species from Cameroon, but also points to dating errors in two species (Groenendijk et al. 2014). We tested whether ring based age estimations matched well (within 1 year margin of error) with 14C based age estimations. We used three different types of samples: tree discs with very clear rings (open circles); increment cores with clear rings (closed triangles) and cores with complex rings (crosses), e.g., with suppressions or strong wedging rings.

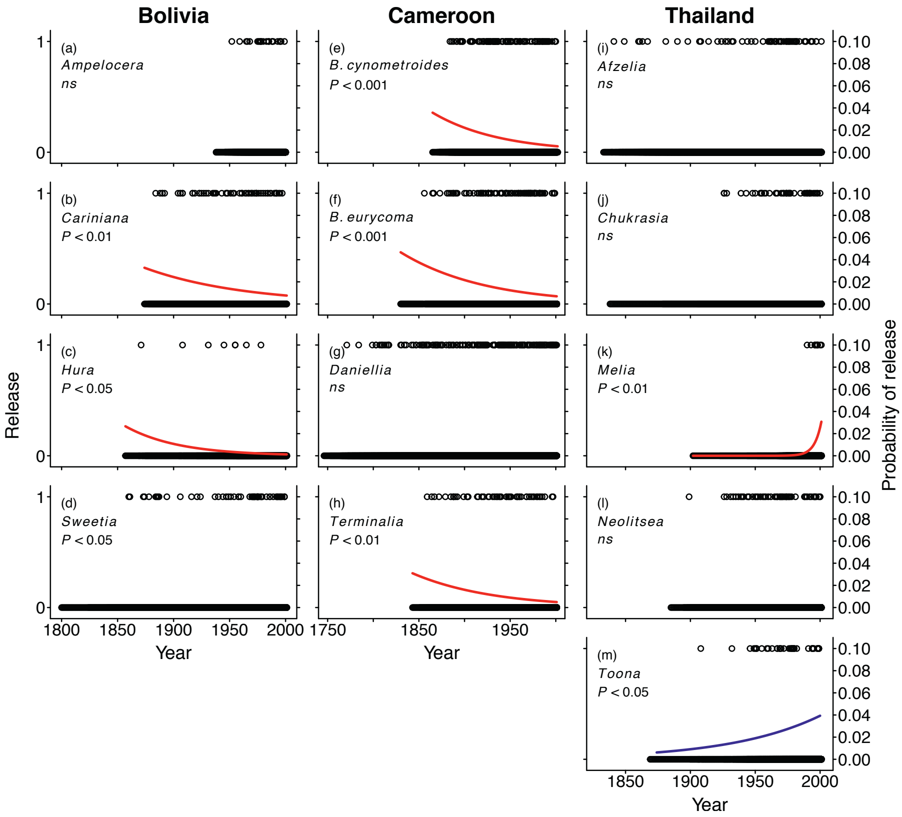
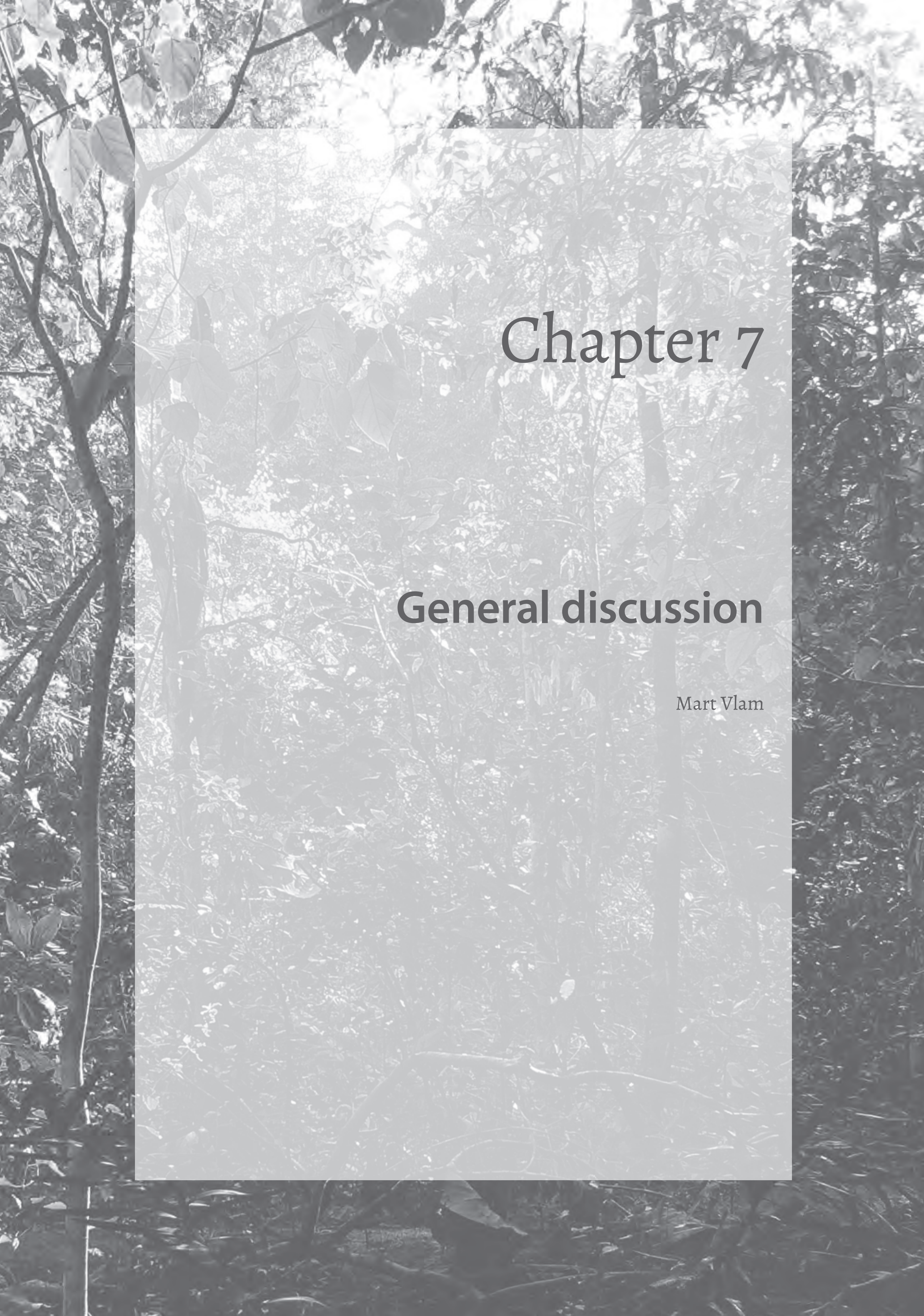


Figure S6.2 GLMM-fit per species. The red curves indicates GLMM fit. The blue line indicates the GLMM fit including both year and climate as fixed factors. Significance of the fixed effect parameters is indicated by *P*. Note that the trend was displayed on the secondary axis.



Chapter 7

General discussion

Mart Vlam

Tropical forest dynamics

From single treefall gap to stand-replacing disturbance

The image of tropical forests as ancient and immovable systems is changing, as it is increasingly being recognized that tropical forests have long been impacted by large-scale and high-intensity natural and human-induced disturbances (Nelson et al. 1994, Whitmore and Burslem 1998, Burslem et al. 2000). Here, I refer to these disturbance as occasional, spatially extensive events that affect at least several hectares of forest, but may be heterogeneous in intensity (Whitmore and Burslem 1998, Splechtna et al. 2005, Baker and Bunyavejchewin 2009). All disturbances in tropical forests are part of a continuous spectrum of events that act at varying scale and intensity. At one end of the spectrum is the mortality of one or a few trees, which is usually referred to as forest gap-phase dynamics (Whitmore 1998). In general, the process of gap-phase dynamics is relatively continuous over time and of small spatial scale, affecting no more than several hundreds of square meters of forest (Oliver and Larson 1996). This process of gap-phase dynamics and associated tree regeneration has been well described for tropical forests (Denslow 1980, Brokaw 1985). At the other end of the spectrum are high-intensity and large-scale disturbances that may impact several hectares to many square kilometers of forest and occur only once in every several decades to hundreds of years (Chambers et al. 2013). Evidence has been accumulating that tropical forests are occasionally subject to these intense canopy disturbances, including wildfires (Baker et al. 2008), multiple-hectare blowdowns (Nelson et al. 1994, Vandermeer et al. 2000, Gleason et al. 2008), and region-wide tree mortality due to extreme droughts (Slik 2004, Nepstad et al. 2007). The various forms of disturbances in tropical forests are further described in Text box 1. These high-intensity or large-scale disturbances may have a lasting effect on tropical forest stand structure and dynamics (Chai and Tanner 2011).

Forest disturbance spectrum

For a better interpretation of forest disturbance and its causes, it is useful to introduce a conceptual model of the forest disturbance spectrum (Fig. 7.1). The x-axis is the disturbance intensity gradient describing the proportion of overstory vegetation being removed. Low intensity disturbances mainly result from occasional mortality of a single canopy tree, for example due to old age or disease. An intense disturbance event may result in the removal of all dominant canopy trees, as occurs, for example, after a downburst event (Nelson et al. 1994). The secondary axis (y-axis) defines the scale of the disturbance: from the death of a single tree to a widespread increase in tree mortality resulting from an extreme drought (Slik 2004). It should be noted that disturbances that are considered large scale in tropical forest ecosystems may be considered small scale in temperate forests, where, for example, large crown fires may kill trees over hundreds of square kilometers (Kashian et al. 2005). Other canopy disturbances may be spatially extensive, e.g a drought affecting hundreds of square kilometers of forest, but with a low or heterogenous impact.

Stages of stand development

The recovery process after intense large-scale disturbance is well described and expressed as several stages of stand development which to a certain extent can be anticipated (Oliver 1980, Oliver and Larson 1996). In this thesis I used the developmental stages of forest development as described by Oliver and Larson (1996). Although these stages have mainly been based on studies in temperate forests, the basic concept can also be applied to describe stand development of tropical forests, particularly as tropical forests may be affected by large-scale and/or high-intensity disturbances similarly to temperate forests. In the first stage of stand development after a stand-replacing disturbance, an initial cohort of shade-intolerant tree species establishes. These trees may invade the area for several years during the 'stand initiation stage'. This stage is followed by a period of low recruitment and high mortality: the 'stem exclusion stage'. In this period the initially established cohort grows towards full canopy stature, but the dominant species in the stand may alternate. In the subsequent stage, 'the understory re-initiation stage', new trees may appear in the space under the tall forest canopy. The final stage is the 'old growth stage': it is characterized by irregular death of canopy trees due to old age and is probably also the stage of forest development that has received most attention from tropical forest ecologists (e.g., Denslow 1980, Brokaw 1985).

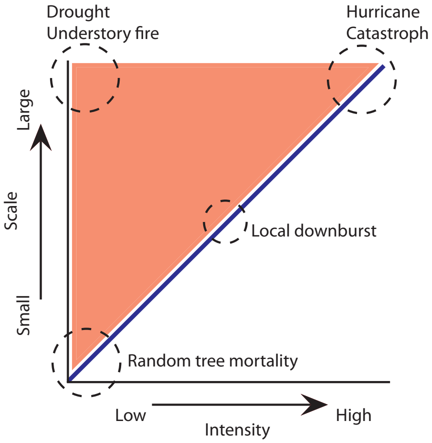


Figure 7.1 Conceptual model of the forest disturbance spectrum (*original idea by Patrick J. Baker*). The x-axis explains the intensity (energy) of the disturbance event. This intensity is based on the amount of overstory vegetation removed: low-intensity disturbances leave some of the pre-disturbance trees alive, whereas high-intensity disturbances kill all the existing trees above the forest floor vegetation (Oliver and Larson 1996). The y-axis refers the area affected by the disturbance: from death of a single canopy tree, affecting several hundred square meters of forest, to region-wide events affecting thousands of square kilometers. The area shaded red represents the most probable combination of intensity and scale. The area under the blue line is assumed to be outside the potential disturbance spectrum.

Text Box 1. Tropical forest disturbance

Wind disturbance

Evidence of trees being uprooted by wind has been found in almost every forested region of the world (Oliver and Larson 1996). (Everham and Brokaw 1996) provides a detailed overview of the knowledge on temperate forest damage and recovery after catastrophic wind. The range of wind damage to forests is enormous (Foster et al. 1998), but windfall usually results in a diffuse pattern of small and large canopy gaps (Oliver and Larson 1996, D'Amato and Orwig 2008). Evidence of damage caused by hurricanes and downbursts has been reported from tropical forests in Australia (Gleason et al. 2008), Asia (Baker et al. 2005), West Africa (Chuyong et al. 2004), the Caribbean (Lodge et al. 1991, Sanford et al. 1991, Vandermeer et al. 2000) and the Amazon (Nelson et al. 1994, Negrón-Juárez et al. 2010).

These wind events are known to alter the structure and functioning of forest ecosystems and may affect hundreds of square kilometers of forest (Foster et al. 1998). Hurricanes may damage the forest canopy, uproot trees, expose mineral soil and increase nitrogen and phosphorus input into the soil (Lodge et al. 1991, Ashton 1993, Gleason et al. 2008). The resulting high nutrient and light levels allow trees to quickly colonize canopy gaps. In the decades after the disturbance, the recovering forest will have a lower total biomass, but higher productivity (Sanford et al. 1991, Chambers et al. 2013). The long-lived pioneer tree species may achieve emergent status and produce wide, spreading and exposed crowns, which in combination with their low wood density, makes the tree more vulnerable to stem breakage (Nelson et al. 1994, Oliver and Larson 1996). Thus, as time since the last disturbance progresses and the trees grow larger, the stand becomes more susceptible to windthrow.

Fire

In tropical forests two types of wildfires may occur. The first are large crown fires. Although more commonly associated with boreal and temperate ecosystems, they may be so catastrophic that entire stands are replaced. The second are understory fires. These fires with smaller flames and lower temperatures are more commonly associated with the humid tropics (Cochrane 2009). Although fire in moist tropical forests is usually of low intensity, it may affect large areas (Pinard et al. 1999, Baker et al. 2008). The smaller flames (i.e. 5-50 cm long) and relatively low temperatures (Wanthongchai et al. 2011) of the understory fires do not usually result in high tree mortality (Baker et al. 2008). In years of extreme drought, such as the 1997-1998 El Niño event, however, wildfires may lead to extensive dieback of tropical forest (Siegert et al. 2001, Cochrane 2009) and kill many tree seedlings and saplings (Van Nieuwstadt and Sheil 2005, Baker et al. 2008). It has been reported that increased mortality of large trees continues for years after a wildfire: for example, when heavy rains and strong winds knock over weakened trees (Barlow et al. 2003, Baker and Bunyavejchewin 2009). Most fires in seasonal tropical forests are anthropogenic in origin, usually started by farmers to clear agricultural fields adjacent to the forest (Johnson and Dearden 2009). Information on natural fire regimes in seasonal evergreen tropical forests is scarce, but it is believed that historically, fires were less frequent (Pinard et al. 1999, Johnson and Dearden 2009). If humans do not start the fires, lightning might, but this happens rarely and does not usually result in large wildfires (Tutin et al. 1996, Saha and Howe 2001).

Drought-induced tree mortality

Prolonged droughts potentially associated with El Niño events have been shown to induce extensive mortality of canopy trees (Van Nieuwstadt and Sheil 2005, Nepstad et al. 2007). (Phillips et al. 2009) showed that large trees and trees with less dense wood (e.g., long-lived pioneers) are more susceptible to drought-related mortality. In this way, droughts may cause the type of widespread, diffuse, disturbances leading to increased recruitment of shade-intolerant tree species (Slik 2004). Newbery et al. (2004) related the establishment of the large African canopy tree *Microberlinia bisulcata* (Fabaceae) in Cameroon to extensive 19th century droughts. The intense El Niño Southern Oscillation events in 1982-1983 and 1997-1998 resulted in extreme drought conditions in Southeast Asia (Baker and Bunyavejchewin 2009) which, together with the associated fires, caused widespread tree mortality in tropical forests throughout Southeast Asia (Siegert et al. 2001, Page et al. 2002).

Anthropogenic forest clearance

The role of historic human disturbance in what we call 'pristine' or 'virgin' tropical forests today is increasingly being recognized (Foster et al. 1999, White and Oates 1999). Patches of *terra preta* (dark earth of anthropogenic origin) have been found throughout the Amazon basin, and soil pits dug in such soil in forests in the Bolivian Amazon have yielded charcoal and pottery fragments (Paz-Rivera and Putz 2009). The precise extent of the past human populations in the Amazon is, however, still debated (Tollefson 2013). There is also evidence that forests in central and West Africa have long been impacted by humans (White and Oates 1999, Paz-Rivera and Putz 2009). Similarly to the situation in the Amazon, apparently ‘pristine’ forests are growing in areas that were once probably densely inhabited. There have been waves of human settlement through central and West Africa, interspersed with periods of population collapse (Malhi et al. 2013). These fluctuations may have been partly climate-driven, but they also resulted from colonial policy that forced people to live close to roads (Malhi et al. 2013). The areas they abandoned were reclaimed by the forest, probably resulting in the establishment of many shade-intolerant tree species. This legacy of former land use may explain the apparent dominance of long-lived pioneer tree species in the canopy of West and central African forests, (e.g., Poorter et al. 1996, Newbery et al. 2013).

Extinction of vertebrate seed dispersers

Several studies have pointed out the effect that the decimation of large vertebrates by hunting has on the regeneration of tropical tree species. (Terborgh et al. 2008) found indications for reduced recruitment rates of animal-dispersed tree species in Peruvian tropical forest. For Congo, it has been shown that elephants are important in the seed dispersal of various tree species (Blake et al. 2009). A recent study conducted ~ 200 km from the study area in Cameroon has shown that as a result of high hunting pressure, the recruitment of animal-dispersed tree species has failed (Effiom et al. 2013).

Internal versus external drivers of change

The role of past disturbances in current stand structure, species composition and dynamics of tropical forests has attracted extra attention in the light of recently reported changes in tropical forest dynamics (Chave et al. 2008, Chambers et al. 2013). Remeasurements of tree diameter in permanent sample plots have revealed significant increases in aboveground biomass of ‘old growth’ tropical forest stands in the Amazon and Africa (Phillips et al. 1998, Baker et al. 2004, Lewis et al. 2009b) , and also increasing tree recruitment and mortality rates (Baker et al. 2004, Lewis et al. 2004, Phillips et al. 2004, Laurance et al. 2009). But other long-term forest monitoring plots have shown no recent changes in tree growth rates, (Clark et al. 2010), or have found contrasting trends of decreasing growth rates (Feeley et al. 2007b) and stem density (Murphy et al. 2013).

These apparently contradictory findings have led to considerable uncertainty regarding the magnitude of global change effects on tropical forests (Wright 2005, Körner 2009). Two main hypotheses have been suggested as an explanation for the observed changes. The first is that tropical forest dynamics are changing as a result of global change – for example, due to growth being stimulated by elevated atmospheric CO_2 levels (Malhi and Phillips 2004, Lewis et al. 2009a). But the other hypothesis posits that long-term processes such as recovery from past disturbance may result in very similar trends in tree growth and forest biomass (Fisher et al. 2008, Chambers et al. 2013) and may accidentally be mistaken for a global change effect.

The difficulty is that both CO_2 fertilization and recovery from past disturbance are characterized by a gradual increase in forest stand biomass (Chazdon 2003, Chave et al. 2008). At present, tropical forest stand dynamics are primarily studied using measurements at the scale of decades from permanent sample plots (e.g., Baker et al. 2004, Clark et al. 2010). However, large-scale natural or anthropogenic disturbances that happened centuries ago may continue to affect tropical forest stand dynamics today(Chai and Tanner 2011). Clearly, there is a great need for better understanding of the disturbance history of tropical forests. The approach used in this thesis to achieve this was forensic forest ecology: the combination of tree-ring analysis and spatial statistics in order to gather all possible clues, such as tree age and life-time growth rates of trees, in order to reconstruct historic tropical forest stand dynamics.

Forensic forest ecology: combining tree-ring data and spatial statistics

Annual rings in tropical trees

Most of the conclusions drawn from the research described in this thesis rely on analysis of tree-ring derived age distributions in combination with a spatial analysis of tree age. Tree-ring derived age estimates of trees have been used to reconstruct the stand history of boreal (Agren and Zackrisson 1990, Kuuluvainen et al. 2002, Fraver et al. 2008) and temperate forests (Lorimer 1980, Rentch et al. 2003, Rubino and McCarthy 2004, Simkin and Baker 2008). In tropical forests, however, tree-ring analysis has not commonly been applied, due to the perception that tropical trees lack annual rings (Lieberman et al. 1985, Whitmore 1998). This perception can be traced back to the idea that tropical forests do not have a seasonal climate. However, many tropical forests do experience an annual dry season, which results in cambial dormancy in trees and the subsequent formation of annual rings (Worbes 1995).

The annual character of the rings of the 14 species used in this thesis was verified by various means. For four Bolivian species, *Ampelocera ruizii, Cariniana ianeirensis, Hura crepitans* and *Sweetia fruticosa*, scars in the wood produced by the 1995 fire in La Chonta were used to prove that the rings were indeed annual (Brienen and Zuidema 2003, Lopez et al. 2012). The annual nature of *Schizolobium amazonicum* rings was determined by counting rings of trees of known age in a plantation forest ~200 km from the study area (P. van der Sleen, *unpublished results*). To verify dating accuracy of *Brachystegia cynometroides, Brachystegia eurycoma* and *Daniellia ogea* from Cameroon, we used the bomb-peak dating method (Worbes and Junk 1989). This revealed that the dating of *Brachystegia eurycoma* and *Daniellia ogea* rings was very accurate, but some uncertainty remained about the ring identification of *Brachystegia cynometroides* (CHAPTER 5). This dating error of around 10% in *B. cynometroides* was presumably caused by the erroneous allocation of false rings, which led to a general underestimation of *Brachystegia cynometroides* ages. The annual nature of *Terminalia ivorensis* rings had been proved earlier by a cambial wounding experiment (Detienne et al. 1998). Similarly, the annual nature of the rings of the five Thai species, *Afzelia xylocarpa, Chukrasia tabularis, Melia azedarach, Neolitsea obtusifolia* and *Toona ciliata* had also been proved earlier by a cambial wounding experiment performed in Huai Kha Khaeng (Baker et al. 2005). More evidence for annual growth periodicity was presented in CHAPTER 2 of this thesis, where it was shown that the tree-ring chronologies of *Afzelia xylocarpa, Chukrasia tabularis, Melia azedarach* and *Toona ciliata* tree-ring chronologies were correlated with seasonal climate data. It goes without saying that before beginning any dendroecological analysis, it must be established that the tree rings to be studied are indeed annual. For convenience, I will from now on refer to all species by their genus names, except for the two *Brachystegia* species.

Rationale for using tree-age distributions

Dendroecology – the use of tree-rings to study ecological processes – has only relatively recently been applied to reconstruct the stand dynamics of tropical forests. Examples of the use of this method include studies in the Neotropics (Rozendaal et al. 2011), West Africa (Worbes et al. 2003) and Southeast Asia (Baker et al. 2005), where the method has been applied to single stands. These studies have shown that dendroecology can give us valuable insights into the stand history of tropical forests. In particular, age distributions of shade-intolerant tree species can be used to reconstruct past disturbances, because the successful recruitment and survival of these species requires canopy openings. Under a scenario of constant recruitment and mortality rates, the age distribution of a tree population has a 'reversed-J' shape (Agren and Zackrisson 1990). Deviations from this situation are usually attributed to intense canopy disturbances. Although shade-tolerant tree species do not require canopy gaps for regeneration (Duncan and Stewart 1991), their age distributions may provide information on local stand dynamics. Local changes may, for example, occur because defaunation is leading to recruitment failure of animal-dispersed tree species (Terborgh et al. 2008, Effiom et al. 2013), or because changes in the fire regime are leading to altered tree mortality rates (Van Nieuwstadt and Sheil 2005, Baker and Bunyavejchewin 2006a, Johnson and Dearden 2009).

As explained in CHAPTER 5, we used a set of hierarchical logistic regression functions (Huisman et al. 1993) to test tree age distributions for irregularities. This test allowed us to make robust statements about the presence of recent regeneration failure. Previous dendroecological studies have mainly relied on a visual inspection of the age distribution (e.g., Baker et al. 2005), but earlier studies in temperate regions have used a similar approach for analyzing age distributions: for example, by comparing the fit of an inverse-J shape distribution with the fit of bimodal Weibull functions (Westphal et al. 2006). The hierarchical logistic regression functions are an attractive alternative to test tree age distributions because they provide a clear set of functions and the analysis can easily be applied in the eHOF package in the R software for statistical analysis (Jansen and Oksanen 2013, R Core Team 2013).

Rationale for using spatial statistics

To date, most dendroecological studies have focused solely on the age distribution of a population of trees or of a forest stand (e.g., Agren and Zackrisson 1990). However, information on tree age in combination with the location of a tree can yield valuable additional information on the spatial distribution of tree age in the stand (Rozas 2003, Dimov et al. 2005). The availability of accurate hand-held GPS devices has made this technique easily accessible to any researcher interested in applying it. As described in CHAPTER 4, we used a GPS device (Garmin GPSMAP 60C Sx) for mapping the location of each sample tree. We estimated that the average mapping accuracy under the tall >40 m high forest canopy was around 4 m, which is an acceptable accuracy when sampling large (>5 cm dbh) trees in a multi-hectare plot.

The rationale for using spatial statistics in forest disturbance reconstruction studies is that after a canopy disturbance, the seedlings of shade-intolerant tree species tend to establish in even-aged patches (Oliver and Larson 1996). Juveniles of long-lived pioneer species are especially shade-intolerant and need large canopy gaps that create adequate light levels (Denslow 1980, Brokaw 1985). As a result, the spatial signature of past disturbance can be maintained for centuries in the spatial distribution of tree ages, as demonstrated in CHAPTERS 3,4,5. When major canopy disturbances have occurred in the past, the tree-age distribution over substantial areas will be non-random, because trees of a similar age co-occur in former gaps (Duncan and Stewart 1991). However, such even-aged groups of trees may be obscured in the age distribution if two or more overlapping groups occur in the same area. In CHAPTER 3, for example, we reported on three spatially distinct age cohorts: two younger cohorts and one older cohort. These three spatially discrete cohorts would not have been discernible in the unimodal age distribution. Therefore the spatial analysis added valuable additional information about the historic regeneration pattern of this species.

Measures of spatial autocorrelation

Other researchers have used spatial statistics to establish the patch size of similarly aged trees in boreal (Jordan et al. 2008) and temperate forests (Rozas 2003, Dimov et al. 2005). Several different methods have been used. In this thesis, a variety of methods was applied (CHAPTERS 3,4,5). (Legendre and Fortin 1989) stated that any quantitative analysis of spatially structured phenomena should start by simply mapping the variable. I did this by converting GPS coordinates of the sample locations to the UTM format (Universal Transverse Mercator coordinate system). These points could then be plotted on a simple xy-plot and any attribute (for example, tree age) was then used to adjust the size of the dots (see CHAPTER 4). The resulting map often reveals strong spatial dependencies that are later confirmed by spatial statistical analysis.

Text box 2. Spatial statistics

Ripley's K function

Ripley's *K* function (Ripley 1977), its linearized form (the *L*-function; (Besag 1977) and related techniques such as the O-ring statistic (Splechtna et al. 2005) are used to analyze spatial patterns in tree distribution.

Moran's I coefficient

Moran's *I* coefficient (Moran 1950) is based on a pairwise comparison of the values over fixed distance classes. For trees in a forest these values may include, for example, biomass, height, volume, or – as in our case – tree age. Using Moran's *I* coefficient, the spatial autocorrelation in – for example – tree age can be modeled and plotted in a graph called a correlogram, see CHAPTER 4 and also (e.g., Duncan and Stewart 1991, Rozas 2003). This spatial autocorrelation analysis should not be performed with fewer than 30 sample points, because otherwise the number of pairs in each distance class will become too small to produce robust results (Fortin et al. 1989). The size of the distance (*d*) for the comparison of values is arbitrary, but should not be smaller than the precision of the measurements.

Mark correlation function

Alternatively, the mark correlation function, introduced by (Stoyan 1984), is used in forest ecology to analyze the spatial correlation of tree attribute 'marks' in an observed point pattern given by the discrete locations of the trees (Illian et al. 2008). The mark correlation function removes the signal of spatial aggregation and shows directly the mutual inhibition or stimulation of tree 'marks', e.g., biomass or age (Law et al. 2009).

Mapping: simple interpolation, semivariogram and kriging

There are various interpolation methods (linear and otherwise) for producing simple maps of the spatial distribution of a variable, including inverse distance weighted interpolation (IDW). As explained in CHAPTER 3, we used IDW to create topographic maps of the study area based on GPS-derived altitude measurements. To create interpolated maps of tree age, we used the geostatistical technique of kriging, which also takes into account the spatial autocorrelation structure function: the semi-variogram. The semi-variogram, or variogram, is related to previously described spatial correlograms (Legendre and Fortin 1989). Kriging allows for various sampling designs, but random or systematic cluster designs are preferably used, because they yield more information about the spatial structure than a systematic design (Fortin et al. 1989).

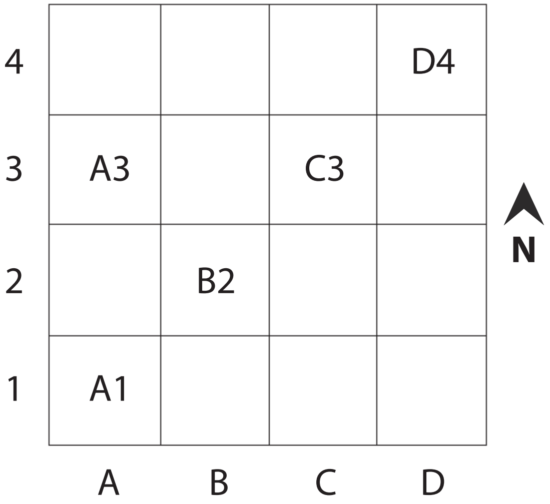


Figure 7.2 Raster with 300 x 300 m grid cells, 144 ha in total, as used for sampling the trees. A1, A2, B2, C3 and D4 are examples of the codes used to identify raster cells. We used this raster design to gather samples in clusters (see also: Fig. 7.3) and to represent the larger area. To achieve an adequate sample size (i.e. ~100 trees per species) additional raster cells were added later (Bolivia and Thailand).

The clustered sampling design we used worked well for locally abundant species such as *Ampelocera* at the site in Bolivia, *B. eurycoma* at the site in Cameroon, and *Neolitsea* at the site in Thailand. These trees were all sampled in a 50 m radius around a randomly assigned sampling point within the 300 x 300 m raster (Figs. 7.2, 7.3). If all individuals of a species were sampled following this clustered sampling design, classical cluster analysis techniques such as Ripley's *K* function (Ripley 1977) could not be applied. Due to the way in which *K* is calculated, spurious ~100 m clusters are revealed by the model and may lead to the erroneous conclusion that trees of this species are spatially clustered. On the other hand, the Ripley *K* function is very suitable if all individuals of a species in an area have been sampled. So, in CHAPTER 3, to assess whether the aggregation of individual *Melia* trees deviated from a random distribution, we used the Ripley K function because we had sampled all the *Melia* trees (>5 cm dbh) in the 316 ha study plot.

Measures of spatial autocorrelation can also be used to determine whether the values of neighboring points are more (aggregation), or less (segregation) similar to each other than expected from a random distribution (Fortin et al. 1989). In CHAPTER 4 we used the Moran's *I* function with distance classes of 100 m to assess the spatial structure in age of *Afzelia* trees. We used 100 m steps to obtain at least 15 tree pairs per distance class, because if smaller distances and subsequently smaller sample sizes are used, the assumption of normality may be violated (Upton and Fingleton 1985). This limited our analysis to assessing age structure at a coarse spatial scale, i.e. those regeneration events caused by large-scale and/or high-intensity disturbances. In CHAPTER 3 we also used the mark correlation function to describe the spatial relation of tree age. The mark correlation function is related to the semivariogram and the Moran's I coefficient. However, we found that this function is not suitable for studying spatial dependence in tree attributes if the data have been collected in a clustered sampling design.

We used geostatistics, i.e. kriging, to create interpolated maps of tree age. In general, kriging is not adversely affected by a clustered sampling design (Webster and Oliver 2001). The raster structure ensured that the random clusters were well dispersed and no underrepresentation of other areas occurred (Webster and Oliver 2001). Using a clustered sampling design enabled us to test the spatial dependence of tree attributes at various spatial scales (Fortin et al. 1989). When, as in our case, there is no prior knowledge of the spatial structure of the variable being tested, a design that uses several different sampling steps is always recommended (Fortin et al. 1989). Others have also used kriging to produce detailed maps of the spatial distribution of tree ages in temperate forests (e.g., Rozas 2003). The maps in CHAPTERS 3 and 5 of this thesis were all produced using the semivariogram and kriging. We found limited evidence for spatial structures in tree age, but the study design did not seem to be a confounding factor. The lack of spatial dependencies probably originated from the regeneration strategies of the species, i.e. establishment after widespread but diffuse disturbance (CHAPTER 5). But also the coarse spatial scale at which tree age data was collected may have resulted in the limited evidence for spatial aggregation.

There is some discussion on whether geostatistics should be used to interpolate attributes of individual trees (Law et al. 2009). For interpolation, a continuous spatial distribution of the variable is assumed, whereas the spatial distribution of trees in a forest is a point pattern of discrete points in space. However, the spatial distribution of tree attributes such as biomass, height, crown volume or tree age can be considered to be continuous (Chen et al. 2004). These tree attributes are an expression of spatially continuous factors such as soil characteristics, water availability, topography, and disturbance history (Dimov et al. 2005). In this way, trees can be seen as spatially fixed 'data loggers'; I would argue that this justifies our use of kriging techniques.

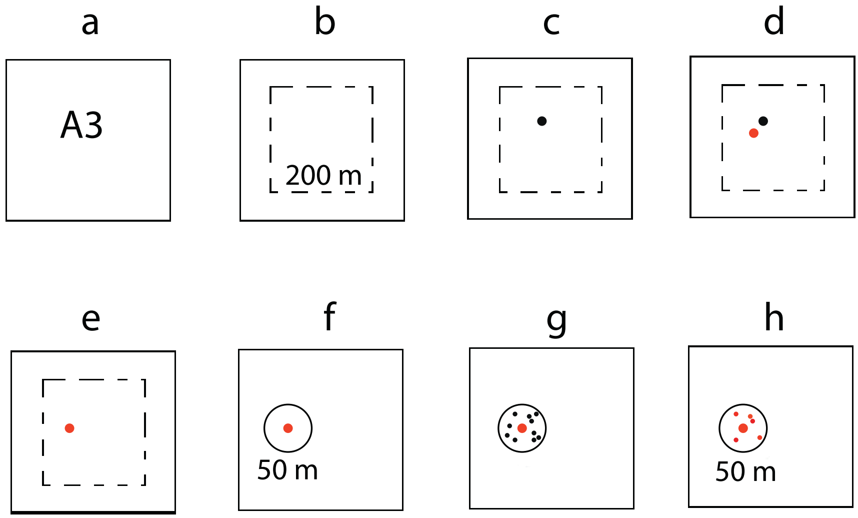


Figure 7.3 Schematic representation of the sampling design. Step (a): one individual raster point is selected randomly. (b) The area within 50 m of the raster border is disregarded (c) A random point is allocated to the 200x200 m area, e.g., in raster cell 'A3' (Fig. 7.2) . (d) In the field we look for the nearest tree of one of the target species, the 'initial tree' indicated by the red dot. (e) The previously selected point is no longer used and the initial tree is marked in the GPS, e.g., 'A3IT'. (f) An imaginary circle with a radius of 50 m is drawn around the initial tree: the ~8000 m2 'sample plot'. (g) All target trees are identified within 50 m from the initial tree. (h) A random subset of these target trees and the initial tree is sampled.

Coarse spatial scales versus pooling species

In all the chapters of this thesis the scale at which the research was conducted was rather coarse: we never sampled more than one tree per ~1.5 ha, and the scale at which the 'rarest' species, e.g., *Melia* or *Terminalia* could be sampled was only <1 tree per 4 ha. Finding evidence for clustered regeneration at fine spatial scales, i.e. at the level of single treefall gaps, would require a sampling scheme with a much higher resolution (Dimov et al. 2005). One way of doing this would be, for example, to pool tree-ring data of different co-occurring shade-intolerant tree species (Rogers 1999), as has been done for species-poor boreal and temperate forests (e.g., *Pinus ponderosa* and *Pseudotsuga menziesii* dominated forests in Canada (Jordan et al. 2008)). However, there are disadvantages of combining data from different species. Species belonging to the same ecological guild may differ widely in various traits, such as maximum growth rates, minimum required gap size and maximum life span. As a result, patterns may arise that are induced by species traits rather than by stand processes. To take an example from this thesis: combining age data collected from long-lived *Afzelia* trees with age data on shorter-lived *Melia* trees at the site in Thailand proved not to be useful. Although both species are classified as long-lived pioneers, their seedlings probably have different requirements for successful establishment. Juveniles of *Melia* have much faster high mean growth rates (with mean diameter growth of 19.5 mm yr^{-1}) compared to *Afzelia* juveniles (mean diameter growth of 6.6 mm yr^{-1}). Also, the maximum observed ages are very different: 121 years for *Melia* versus 281 years for *Afzelia*. These large differences in species traits may result in spurious inferences about the spatial distribution of tree age when species are pooled. The high species diversity of tropical forests and the relative scarcity of ring-producing species make it unlikely that pooling species will allow stand dynamics to be analyzed at the scale of meters, as has been done in temperate forests (e.g., Sánchez Meador et al. 2009).

Finally, analyses in this thesis show that a combination of tree age distributions and spatial statistics can improve understanding of long-term tropical forest dynamics. The sampling design used, in which clustered sampling was applied for common tree species and a more opportunistic sampling design for rare species, proved practical in the field. The resulting data was of sufficient quality to allow the application of spatial analysis techniques such as the Moran's *I* coefficient, mark correlation and kriging. Ripley's *K* function could not be used for tree species that were sampled following the clustered sampling design, because this design would automatically generate such spatial clusters. Future studies using a similar combination of dendroecology and spatial statistics could contribute to our understanding of the prevalence of large-scale disturbances in tropical forests. A promising new approach would be to combine age data (CHAPTERS 3,4,5), with data on growth releases (CHAPTER 6) in a spatial analysis. Growth releases and establishment of shade-intolerant species both reflect canopy disturbance events and are therefore expected to be correlated in space and time. Unfortunately, such an analysis was beyond the scope of this thesis.

Limitations of tree-ring research

The use of static age distributions

There are limitations to the use of tree-rings for the reconstruction of forest stand dynamics. They are related to: (1) how trees are usually sampled in dendroecological studies, i.e. only living trees (2) the challenge of upscaling observations on individual trees (or tree populations) to entire forest stands and (3) the limited number of tropical tree species that produce tree rings.

Nearly all dendroecological studies in the tropics, and many – but not all – studies in the temperate regions (e.g., Fraver et al. 2008), use wood samples only from living or recently felled trees. This may bias the sample set, because living trees tend to form a non-random subset of the total tree population in any given area (Johnson et al. 1994, Rozendaal et al. 2010a). With respect to this non-random subset, (Brienen et al. 2012) noted that the 'slow-grower survivorship bias' would lead to spurious interpretations of temporal growth trends. This slow-grower survivorship bias is caused by differences in the longevity of fast- and slow-growing trees; fast-growing trees generally live for shorter than slow-growing trees and are therefore underrepresented in historic tree growth data (Brienen et al. 2012). For my research I was not principally interested in growth rates of trees for the reconstruction of stand dynamics. Note, however, that in CHAPTER 4 we did compare growth rates. But the slow-grower survivorship bias stresses the fact that our sample set represents a snapshot of the population: it does not include trees that during the reconstruction period were recruited and died (Johnson et al. 1994). This problem could partly be addressed by including dead trees in the sampling design. For example, (Fraver et al. 2008) included all living and dead trees (i.e. standing dead trees; snags) ≥ 5 cm dbh for stand reconstruction in a boreal old-growth forest. However, the fast decomposition rates in tropical forests will limit the use of dead trees for dendroecological studies. The use of dead trees is further complicated by the lack of high quality species-specific chronologies, which are crucial for accurately dating time of death, and thereby time of recruitment, of already dead trees. Not including dead trees in the sampling design means that in the age distribution the older cohorts usually not only show up with fewer trees than were originally present, but also have a higher proportion of slow-growing individuals.

In their study (Johnson et al. 1994) showed the hazards of inferring stand dynamics from static age distributions. After intense canopy disturbance, the initial cohort of shade-intolerant tree species establishes in the so-called 'stand initiation stage: a period characterized by high recruitment and low mortality rates (Oliver and Larson 1996). After this, a period of low recruitment and high mortality follows: the 'stem exclusion stage'. In this period, the initially established cohort is growing towards full canopy stature. If ages are reconstructed based on the current living trees, i.e. the situation at a given moment in time, it may seem as if a period of recruitment failure occurred after the current canopy trees established (see: Fig. 7.4). We found some indications for this phenomenon in the tree age distributions from our study sites. For example, some recent recruits of long-lived pioneers such as *Toona* and *Terminalia* may have arrived due to this effect (CHAPTER 5). These recent recruits of shade-intolerant tree species do not necessarily indicate a new period of enhanced regeneration, because these trees are highly unlikely to attain canopy stature. On the other hand, as described in CHAPTER 5, populations of many of the tree species showing recent recruitment failure have had no recruits in recent decades, e.g., *B. cynometroides*. I would therefore argue that using static age distributions has not had major consequences for the findings on regeneration dynamics of the species described in this thesis.

Scaling up from individual trees to entire forest stands

In this thesis research I set out to reconstruct a few centuries of the disturbance history of large (several hundred hectares) tropical forest stands. But it turned out that accurate age estimates and growth rates could be obtained from only four or five selected species per stand. For example, in Thailand we analyzed five species out of the approximately 300 species that occur naturally in the area

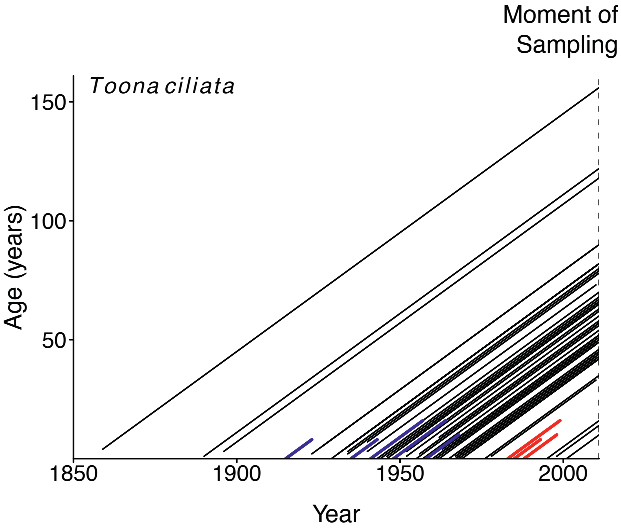


Figure 7.4 A lexis diagram showing the total lifespan of trees (colored lines) or lifespan until the time of sampling for living trees (black lines); based on (Johnson et al. 1994). Black lines represent *Toona ciliata* trees that are actually present in the dataset (individuals missing <10 rings to the pith). The colored lines represent hypothetical individuals that did not survive till the year of sampling; blue lines represent individuals that did not survive in a period in which other trees attained the canopy, red lines represent individuals that established in a period in which no trees are estimated to attain canopy stature.

(Bunyavejchewin et al. 2009). Ideally, each individual tree of each species in a stand, whether dead or alive, would have been sampled and dated. To my knowledge, only the study by (Worbes et al. 2003) has age-dated nearly all the living trees in a broad-leaved tropical lowland forest. In that study, tree-ring samples were taken from trees with a dbh >10 cm in a 1 ha plot in a semi-deciduous natural forest stand in Cameroon. This was only possible because the stand was dominated by the ring-forming long-lived pioneer *Triplochiton scleroxylon*. However, most tropical forests have a much higher tree species diversity and usually only a subset of those species forms annual rings (Baker et al. 2005). Also, some of the species with the most readily identifiable rings may occur infrequently in the study area, e.g., *Toona* in at the study site in Thailand and *Terminalia* at the site in Cameroon. This will necessarily require findings on individual trees to be extrapolated to the stand level. Of course, this raises questions on how representative those target species are for the entire forest stand. I would argue that many species in the present study can be regarded as ‘disturbance indicator species’, i.e. long-lived pioneer or partial-shade-tolerant species whose regeneration is favored by large canopy openings, e.g., *Afzelia* (CHAPTER 4). Their age distributions should therefore provide clues on the occurrence of past canopy disturbance.

The 14 species studied in this thesis are clearly nevertheless a non-random subset of the respective local tree species communities. Their selection was mainly based on the presence of visually detectable rings and relatively high local abundance. But, although we focused on relatively common species, some of the most common tree genera, e.g., the *Dipterocarpaceae* in Thailand, were not included in the study because they lack growth rings. This puts a limitation on the generalizations that can be made on the dynamics of the forest stand as a whole. Therefore any method that enables the reconstruction of annual diameter increment values for 'ringless' species is a very welcome addition to dendroecology.

Species lacking visually detectable rings

The recent attention paid to tropical tree-ring research has greatly improved understanding of the occurrence of visually detectable annual rings in tropical tree species. We know that reliable annual rings can be found in tree species throughout the tropics and that they occur under various climatological conditions (Zuidema et al. 2012). On the other hand, it has now been firmly established that tree species from large families such as the Dipterocarpaceae generally lack visually detectable rings (Poussart et al. 2004, Baker et al. 2005, Ohashi et al. 2009).

Novel methods for measuring and counting rings in species that lack visually detectable rings are currently being developed, such as the use of stable isotopes (Loader et al. 2011, Schollaen et al. 2013). The intra-annual variation in the isotopic carbon composition, $\delta^{13}C$ values, of the wood can be used to study cyclicity in growth (Poussart et al. 2004, Verheyden et al. 2004, Ohashi et al. 2009). The cyclicity in $\delta^{13}C$ values in the wood is associated with the water availability for the trees and is therefore related to the seasonality in rainfall (McCarroll and Loader 2004). Intra-annual variations in stable oxygen isotope ratios ($\delta^{18}O$) values in the wood have also been used to study the relation with rainfall patterns over the year (Poussart et al. 2004, Verheyden et al. 2004, Schollaen et al. 2013).

Growth-ring reconstructions based on stable isotope analysis on tree species that lack visually detectably rings could potentially provide valuable contributions to dendrochronology and dendroecology. This approach allows for a wider and more representative analysis of historic tree growth. But although the costs of isotope analysis have fallen considerably over recent decades, they are still higher than those of traditional methods of tree-ring analysis, and this is still hampering large-scale applicability. Costs need to drop much more before the approach becomes an attractive option. Reproducing a pan-tropical study like this one would require approximately 300,000 rings to be reconstructed on the basis of stable isotope ratios. This would mean that hundreds to thousands of wood samples per tree would need to be analyzed (e.g., 50 samples per cm; Ohashi et al. 2009) at a cost of 3-4 euros ($\delta^{13}C$) or 7-8 euros ($\delta^{18}O$) per sample. Thus the total cost of isotope analysis will quickly escalate to millions of euros. And as well as the prohibitive costs, there would be problems of logistics and laboratory capacity to overcome before such huge numbers of isotope samples could be processed. It is therefore hard to say whether the stable isotope reconstructions for 'ringless' species will remain a niche discipline or will ever become a widely applied approach.

Although there are clear limitations to the application of tree-ring analysis in the tropics, the method is probably here to stay and may yet expand when new analysis techniques, such as those described above, become more widely available. Tree-ring analysis can provide the much needed centennial scale perspectives on tropical forest dynamics and global change effects on tropical tree growth. Some of the limitations of tree-ring research, such as the scaling issue and the restricted number of species with visually detectable rings, require a combination of tree-ring analysis with more short-term data from repeated measurements in permanent sample plots (Zuidema et al. 2013). Such a combined approach may provide the much needed understanding of the mechanisms driving long-term stand dynamics in tropical forests.

Long-term variation in tree regeneration dynamics

A legacy of past disturbance

This study is one of the first aiming to reconstruct tropical forest stand dynamics at the timescale of a centuries. The study is intermediate in spatial and temporal scale between the permanent sample plot studies which describe forest dynamics at a maximum decadal scale and over a <50 ha area (e.g., Lewis et al. 2004, Phillips et al. 2004) and the reconstructions of tropical forest cover at millennial timescales (e.g., Daïnou et al. 2010, Lebamba et al. 2012). Based on our reconstruction we reported on evidence for strong recent recruitment failure in all species from Cameroon and Thailand (CHAPTER 5). In Bolivia we found mostly continuous recruitment rates and a strong recruitment peak in the late 1990s for one shade-intolerant species. These were all indications for the occurrence of severe canopy disturbances (CHAPTER 5). Such historic large-scale and/or high-intensity disturbances are likely to produce long-term legacies in both the physical (e.g., tree age/size distribution) and biological (e.g., species composition) structure that influence forest ecosystem processes for decades or centuries (Foster et al. 1998). In this section I will discuss four drivers of severe disturbance in tropical forests: wind, fire, drought and human presence (see also text box 1). From our analysis it became clear that the forests at all three sites probably bear the legacy of one or more of these disturbance factors.

Evidence for past disturbance in the three sites

In CHAPTER 5 the tree population age distributions of the three forest sites were discussed and some of the most likely disturbance drivers were presented. In La Chonta Bolivia some of the recruitment opportunities were probably fire-related. In TRC Cameroon, past human land clearance or extreme droughts may have resulted in canopy openings, and in HKK Thailand fire and wind were identified as major disturbance drivers.

It is likely that 300-400 years ago La Chonta was much more densely populated (Paz-Rivera and Putz 2009). However, the sudden decline in population density and the concurrent abandonment of agricultural plots >300 years ago outdated by far the age of the oldest tree that was sampled in Bolivia. It is therefore unlikely that ancient anthropogenic disturbance played a direct role in the regeneration of any of our study species. The oldest tree that we encountered in our sample set from La Chonta Bolivia was a 220-year-old specimen of *Sweetia*. Trees of all other species were younger than 170 years. This suggests that the long-lived pioneer and partial-shade-tolerant trees that we studied had not established in the initial period after people had abandoned their cleared areas. However, according to local informants, some of the largest trees in the forest, such as the >2 m diameter *Ficus sp.* trees, may have established during this period of large-scale forest recovery. On the other hand, we do know that past intense disturbances may have a long-lasting (>150 year) effect on tree species composition (Chai and Tanner 2011). The dominance of long-lived pioneer and partial-shade-tolerant tree species may therefore be a legacy of this past disturbance – a disturbance that is prolonged by more recent disturbances resulting from, for example, drought and fire.

Recent (>50 years) recruitment failure of long-lived pioneer and partial-shade-tolerant tree species at the site in Cameroon provides strong evidence for canopy disturbance that occurred some 100-150 years ago. In CHAPTER 5 we suggested that the most likely cause of large forest clearings and subsequent regrowth of the forest was fluctuations in the density of the human population. Natural disturbances (for example, those caused by fire or wind) were less likely. Windthrow has been reported to flatten areas of up to 1 ha in the nearby Korup National Park, but the origin of these winds remained unknown, because hurricanes do not seem to occur in the area (Chuyong et al. 2004). However, new evidence for large-scale wind disturbance in Cameroonian forests has recently emerged. It has been reported that ~3000 ha of forest in southwest Cameroon was flattened by a violent windstorm in July 2010 (*R. Feteke, personal comment*). This observation sheds new light on the potential causes for large-scale disturbances in West African forests; maybe the effect of severe wind disturbances has been underestimated for this region.

At the study site in Thailand, the most likely causes for disturbance are wind and fire; these events are relatively well documented (Baker et al. 2008). There is very little information available on past human activities in this area. It has been suggested that at the location of the current ranger station 'Kapook Kapiang' ~3 km from the study area there used to be a small village prior to the establishment of the Sanctuary. Such villages were relocated outside the park in the late 1980s (Johnson and Dearden 2009). In their paper (Baker et al. 2005) suggested that in the late 1500s and 1700s Thai and Burmese armies mainly passed to the north and to the south of the area and are therefore unlikely to have caused a severe forest disturbance. Defaunation due to overhunting probably played a role in HKK in the decades prior to the installation of the Sanctuary, but with the establishment of the Sanctuary infrastructure, wildlife is now better protected. Today, HKK supports populations of large endangered mammals, including the Asian elephant (*Elephas maximus*), gaur (*Bos gaurus*) and white-handed gibbon (*Hylobates lar*). It is therefore unlikely that defaunation, i.e. a lack of vertebrate seed dispersers (cf. Terborgh et al. 2008), is responsible for the recent recruitment failure at the site in Thailand.

High-quality records of forest disturbance

Studies on disturbance history in temperate regions are often able to use high-quality historical records on past natural or anthropogenic disturbances (e.g., Rozas 2003, Druckenbrod et al. 2013). In tropical forest research, however, records of past disturbances or climate tend to be incomplete or absent. This limits the potential to reconstruct tropical disturbance regimes. But there are several methods that can be used to determine the exact drivers of past disturbance in tropical forests, such as (1) tree-ring-derived drought reconstructions, (2) dating fire scars in the wood, and (3) the use of archeological specimens.

Climatic extremes in the tropics have been reconstructed from long-term tree-ring chronologies (e.g., Buckley et al. 2007, Cook et al. 2010). Buckley et al. (2010) used a >750-year reconstruction of drought severity based on *Fokienia hodginsii* tree-ring data and related periods of prolonged drought to the demise of Angkor, the capitol of the Khmer Empire in Cambodia. This drought atlas may also be used to estimate periods of increased tree mortality and associated regeneration pulses of shade-intolerant tree species. In CHAPTER 4 a relation was demonstrated between *Afzelia* regeneration rates and wetter climate conditions. These climate conditions were inferred from Cook et al. (2010) Monsoon Asia Drought Atlas.

Past occurrences of forest fires have been reconstructed by dating fire scars in temperate forest trees (e.g., Jordan et al. 2008). Such techniques may also be applicable in high quality annual- ring-producing tropical tree species such as *Cedrela odorata* for the Neotropics, *Entandrophragma* species in Africa or *Toona ciliata* and *Tectona grandis* in Southeast Asia. For accurate dating of fire scars, whole-stem sections are required instead of increment cores. However, in protected areas it is often not possible to collect whole-stem sections . In Thailand, the total ban on logging and the strict protection of the HKK world heritage area meant that our sampling was restricted to increment cores. We were therefore not able to assess the presence of datable fire scars in the samples collected in Thailand. In Bolivia we were able to collect some stem sections and it was noted that fire scars occurred in the wood of *Cariniana* and that the dating of these scars was consistent with a known fire event in 1995. (Lopez et al. 2012) used the number of tree rings formed between the fire in 1995 and the time of collection of stem sections in 2002 to determine the annual periodicity of tree-ring formation in seven tree species from La Chonta. To my knowledge, no attempt has been made to create a long-term record of fire occurrence in the area using fire scars.

In theory, such a fire chronology could be related to historic recruitment waves in other tree-ring-forming species.

Anthropogenic disturbances can be reconstructed by analyzing soil pits for charcoal fragments or human artifacts such as pottery (White and Oates 1999, Paz-Rivera and Putz 2009). In some cases, radiocarbon dating can then be used to date the fragments and estimate the time since abandonment of the area. It is believed that archeological material is hidden beneath much of the African rainforest (White and Oates 1999), and in South America too there are many indications of past human presence (Tollefson 2013). Age dating of long-lived pioneer species in combination with dating of the archeological material can shed important new light on the magnitude of past human disturbance on the present-day structure and tree species compositions of 'old growth' forests.

The evidence for large-scale and/or high-intensity disturbances in tropical forests has now been corroborated by short-term and direct observations (Vandermeer et al. 2000, Phillips et al. 2009). Using forensic forest ecology, it has been possible to verify the past frequency of such events over a period of centuries. Combining data on tree regeneration dynamics with high resolution disturbance records will further increase our understanding of the role of these disturbances in the ecology of tropical forests.

Implications for tropical forest conservation and timber management

The results presented in this thesis confirm that tropical forests are far from stable pristine systems. They may be struck by violent natural disturbances such as hurricanes and blowdowns (Nelson et al. 1994), extensive droughts and widespread forest fires (Slik 2004), or contain a legacy of intensive land use by humans (White and Oates 1999, Paz-Rivera and Putz 2009). Many (if not all) tropical forests contain a legacy of past disturbance and this will affect their present-day stand structure and species composition. Species may come and go in wave-like regeneration patterns. Stochastic processes of severe disturbance, possibly in combination with climate anomalies (CHAPTER 4), may determine the species composition in a certain forest area for the coming centuries. Large-scale and /or high-intensity disturbances are part of the natural system of forest regeneration and may contribute to maintaining tree species diversity in tropical forests. As long as disturbance intervals exceed the average generation time of trees, they do not directly threaten tree populations. However, in forests where events of high intensity disturbance such as wildfires occur very frequently, they may become a threat to tree species diversity (cf. Johnson and Dearden 2009). But as long as disturbances only occasionally cause widespread canopy loss, the populations of many long-lived pioneer and partial-shade-tolerant tree species will be able to regenerate naturally.

This ability to regenerate naturally may also have important implications for forest management. The large long-lived pioneer trees are among the most commercially important tropical timber species, e.g., *Swietenia macrophylla* in the Amazon (Grogan et al. 2008) and *Entandrophragma* species in Africa (Hall et al. 2003). For successful regeneration, these species probably rely on large canopy openings created by large-scale and/or high-intensity disturbances (Gullison et al. 2003). Rare severe disturbances may therefore be crucial for maintaining tree species populations (Nelson et al. 1994) and tropical timber stocks. Current logging practices, especially reduced-impact logging, in which many small gaps are created, may be insufficient to create regeneration niches for many long-lived pioneer species (Schwartz et al. 2012). The advances in knowledge on the regeneration association of these species with severe canopy disturbances may therefore contribute to better management of tropical forest timber reserves.

Long-term changes in forest stand dynamics

Decreasing release frequency

It is clear that tropical forests are dynamic systems, but are tropical forest dynamics changing as a result of global change? Growth stimulation as a result of the CO_2 fertilization effect has been related to increased stem turnover (Phillips et al. 2004). Repeated measurements from permanent sample plots have revealed significant increases in aboveground biomass of tropical forest stands (Phillips et al. 1998, Baker et al. 2004, Lewis et al. 2009b) and increased recruitment and mortality rates (Baker et al. 2004, Lewis et al. 2004, Phillips et al. 2004, Laurance et al. 2009) at the timescale of decades. However, other permanent sample plots have shown that tree growth rates are not changing (Clark et al. 2010), or that they are slowing down (Feeley et al. 2007b) and that stem density is decreasing (Murphy et al. 2013).

In CHAPTER 6 the century-long changes in forest dynamics were analyzed, using tree-ring data. Growth releases in diameter increment series of individual trees were used as a proxy for the occurrence of canopy gaps. This analysis revealed a significant decrease in release frequency over time across the three sites. The decrease in releases suggests that gap formation in the forest canopy has also decreased over time. This trend is opposite to the dominant observation from permanent sample plots, which is that globally, tropical forest dynamics are increasing (Phillips et al. 2004).

Why do most findings from permanent sample plots show increased dynamics, whereas we found decreased or unaltered dynamics? First of all this could be due to the very different approaches used to study trends in forest dynamics in permanent plots versus tree-ring studies. In permanent plots, actual census data on tree recruitment and mortality is used (e.g., Phillips et al. 2004, Murphy et al. 2013), whereas we used a proxy for canopy dynamics. Secondly, we analyzed trends over 100-200 years, whereas in a typical permanent plot study rarely more than 30 years of data is available. Because our approach uses a proxy for canopy dynamics it would be interesting to do a quantitative test on the quality of the method used. One way this could be done is by modeling individual tree-ring series for a forest in which artificial or natural thinning of the stand occurs. In this way, growth releases could be forced into the data in various schemes. The occurrence of growth release and the subsequent trend over time could then be related to the known thinning scheme. Similar analysis could also be applied to real tree-ring data from a managed forest or forest plantation with a known thinning scheme. In our analysis of growth release we used some of the methodological insights gained by the study by Druckenbrod et al. (2013) in which known disturbance events were used to calibrate the detection rate of growth releases. Further investigation of the relation between known canopy gap formation in tropical forests and the subsequent growth response, such as after selective logging (e.g., Sleen et al. 2013), can be used to validate this link.

Alternatively, the differences in forest dynamics may be due to the stand history of the forests. A pattern of decreased stand dynamics is consistent with a process of forest recovery after past large-scale disturbance (Sheil et al. 2000). Based on our analysis in CHAPTER 5 we concluded that the forests in Cameroon and Thailand probably experienced an period of increased canopy disturbance around 100-150 years ago. This means that these forests are still recovering from the disturbance. The developmental stages associated with recovery after past disturbance (Oliver and Larson 1996) may explain some of the patterns found. In particular, the early stages in stand development, such as the stem exclusion stage, may have above-average tree mortality rates and therefore more growth releases can be expected further back in time. Forest recovery may therefore satisfactorily explain the decreasing stand dynamics of the site in Cameroon and the lack of any significant trend in Thailand. The forest in Bolivia may also still be recovering from sudden abandonment 300-400 years ago (Paz-Rivera and Putz 2009). However, based on the information on the disturbance history at the site in Bolivia, we would have expected stand dynamics to increase, not decrease. The high regeneration rates of shade-intolerant tree species and the occurrence of a widespread fire in 1995 suggest that the forest has been disturbed relatively recently.

In general, the evidence for a decrease in forest stand dynamics was strong in both Bolivia and Cameroon. This pattern is best explained by a local process of stand development following past severe disturbance, rather than by processes mediated by global change. It is now time to extend this approach to other forests, both temperate and tropical, for example using a tree-ring approach, to further assess the evidence for century-long changes in forest stand dynamics.

Recovery from past disturbance: implications for observed patterns in tropical tree growth and forest biomass

Stand history and growth trends over time

In traditional views on tropical forest dynamics an equilibrium state is often assumed, in which canopy trees are replaced in a process of gap-phase dynamics (Whitmore 1998). Any forest stand deviating from such a long-term equilibrium state is regarded as an anomaly. However, tropical forest stands that are not in such an equilibrium state, in particular after a stand-replacing disturbance, are well known to show temporal trends in biomass and species composition (Sheil et al. 2000, Chazdon 2003). When, using forensic forest ecology, I generated a century-long perspective on the stand history of three tropical forest sites, I found strong indications for past disturbances in all three study sites. These results are consistent with short-term, direct observation of, for example, disturbance induced by wind (Burslem et al. 2000, Negrón-Juárez et al. 2010) or drought (Van Nieuwstadt and Sheil 2005, Phillips et al. 2009). These findings suggest that forests throughout the tropics are likely to contain a legacy of past severe natural or anthropogenic disturbance. This knowledge may have important implications for the interpretation of observed trends in tropical forest biomass and tree growth.

The 'unimodal age distribution effect'

Past severe canopy disturbances may lead to synchronized establishment of long-lived pioneer tree species, which can be observed in unimodal or generally irregular age distributions (see CHAPTERS 4,5). This synchronized recruitment has been well documented for boreal and temperate forests (Agren and Zackrisson 1990), but it may also occur in tropical forests (CHAPTERS 4,5). Such irregular recruitment may have important consequences for the interpretation of observed growth trends in tropical trees, particularly with respect to hypothesized growth trends resulting from global change drivers (Malhi and Phillips 2004).

'Size class isolation' is a method that has recently become popular for analyzing temporal trends in tree growth (Rozendaal et al. 2010a, Zuidema et al. 2011). It was designed to correct for developmental stage related changes in tree growth rates when analyzing long-term trends in tree growth (Text box 3). Using such a method is highly recommended when studying growth rates of tree species with strong size-related differences in mean growth rates, a typical characteristic of trees under fierce competition in dense tropical forests. However, the following example will show that a unimodal age distribution may lead to apparently negative trends in tree growth over time.

The tree-ring data used here to illustrate the case was taken from the long-lived pioneer *Hura crepitans*, because the original age distribution most clearly resembled an inverse J-shape distribution (Fig. 7.6a). This inverse J-shape distribution indicated that in the last 100 years or so, this species has recruited at an approximately constant rate. Using the size class isolation method I calculated growth rates over time (period 1900-2010) for 66 individuals in the fixed diameter category of 20-25 cm dbh. The linear model fit indicated no significant growth trend over time (Fig. 7.6b).

Text box 3. Size class isolation

The size class isolation method specifically aims to analyze tree growth rates over time for trees in the same ontogenetic stage. For example only growth rates (i.e. ring widths) of trees in the size class 5-10 cm dbh are compared. Because tree-ring samples are collected from trees representing all sizes, the mean year for which an extant large tree had a diameter of 5-10 cm will be further in the past than that of an extant small tree (Fig. 7.5).

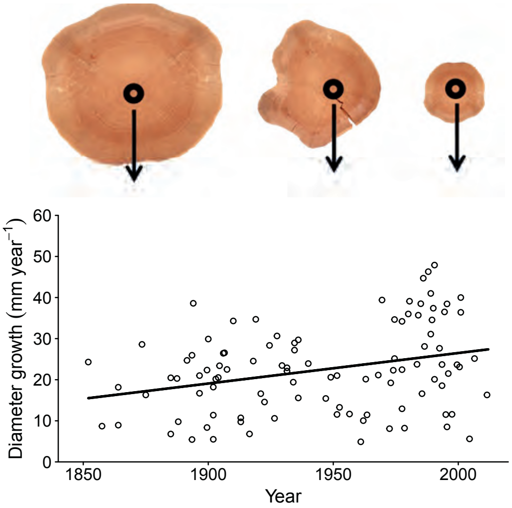


Figure 7.5 Illustration of the size class isolation method. Note that each dot in this graph represents the growth rate of an individual tree in the respective size class. The illustration shows that the diameter growth rates obtained from extant large trees is further in the past than the growth rates of extant small trees (*original illustration by Peter Groenendijk*).

Next, I investigated the hypothetical case that all these trees had not established at a continuous rate, but in pulses, as if following a massive stand-replacing disturbance. In CHAPTER 5 it was shown that such recruitment pulses of shade-intolerant trees may actually occur. In the hypothetical example, I used the same growth data, but the year of establishment was set at a single year: 1950 (Fig. 7.6c). The new linear model fit to the data now indicates a significant negative growth trend over time (Fig. 7.6d). In this new situation, using exactly the same growth data, it seems that high growth rates occurred in the more distant past and low growth rates occurred more recently (Fig. 7.7b). And when growth is expressed as basal area increment instead of diameter growth, similar growth trends over time appear.

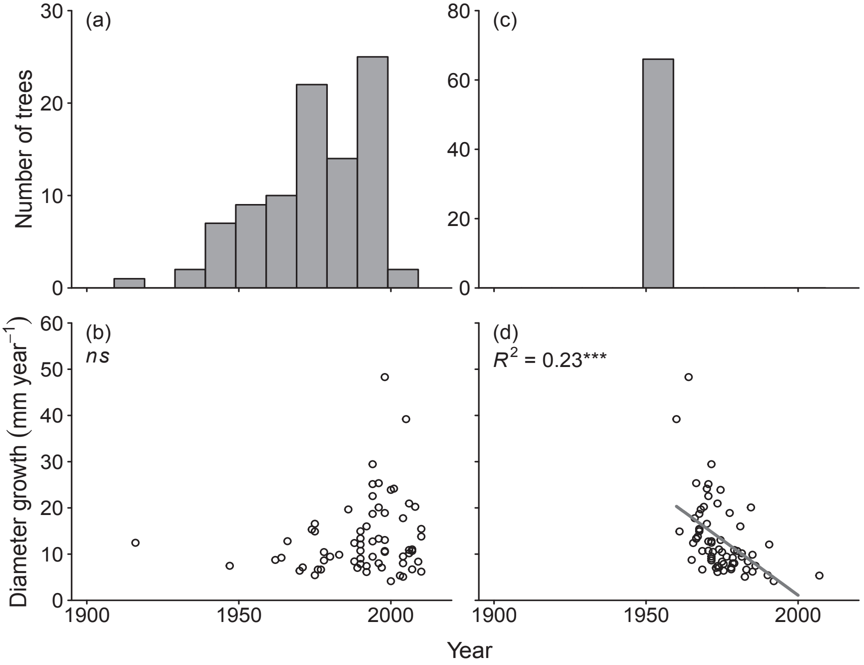


Figure 7.6 Illustration of the unimodal age distribution effect. The panels on the left show the original data for *Hura crepitans* from Bolivia (age histogram n = 93). The two panels on the right use the same growth data, but now modified and assuming that all trees recruited in the year 1950. Note that each dot in the two graphs on the right represents one individual tree (n = 66). Adjusted R-squared of linear model fit is indicated. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; *ns*, not significant.

The significant trend in the hypothetical example can largely be attributed to persistent growth differences among individuals (Fig. 7.7a). Such persistent differences suggest varying canopy positions or possibly genetic differences among individuals that have a lasting effect on growth (Brienen et al. 2006, Brienen et al. 2010b). As a result of these persistent growth differences, the ranking in growth rates is maintained over time, as illustrated by the fan shape of the graph (Fig. 7.7a). For example, the fastest growing *Hura* individuals reach 20 cm diameter in only 10 years, whereas slow growers take 50 years to reach that diameter. These persistent growth differences are strong in *Hura*, but they are certainly not unique to this species (Brienen and Zuidema 2006a). Because inter-tree differences in growth rates are very persistent, the trees that achieve a certain diameter first, so further back in time, are also likely to show high mean growth rates in the size class for which their growth rates were recorded. Slow growers will require more time to reach a certain diameter and are more likely to have low growth rates in the size class for which their growth rates were recorded (Fig. 7.7).

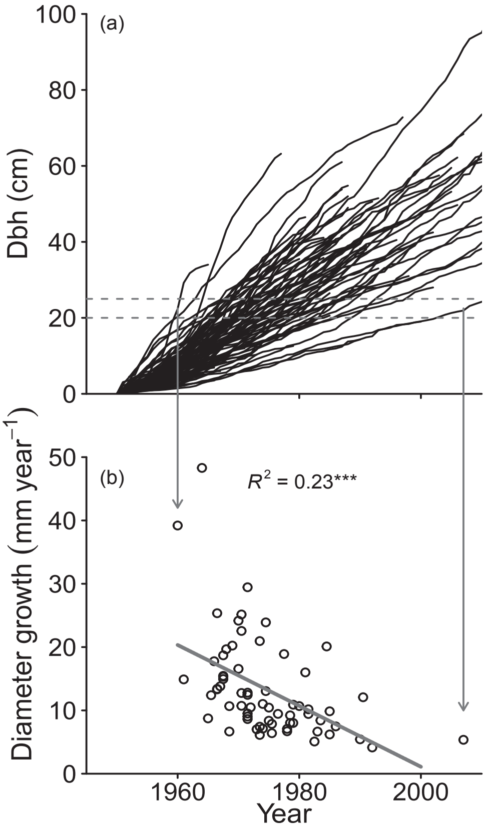


Figure 7.7 Individual growth trajectories (a) and diameter growth rates in the 20-25 cm diameter class (b) for *Hura crepitans* under the hypothetical assumption that all trees established in the year 1950. The fan shape of the graph results from the strong persistent growth differences among individuals. The arrows indicate two individuals at the extremities of the spectrum: the second fastest grower (left; ~40 mm year^{-1}) and a slow grower (right; ~5 mm year^{-1}). Adjusted R-squared of the linear model fit is indicated. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; *ns*, not significant.

In conclusion, a unimodal age distribution combined with strong persistent growth differences and fixed diameter classes for which mean growth rates have been calculated may result in apparently negative growth trends over time. This unimodal age distribution effect is notably different from previously identified sampling biases in tree-ring analysis, such as the 'slow-grower survivorship' and 'big-tree selection' bias (Brienen et al. 2012). Both of these biases result in perceived historic increases in tree growth, whereas the unimodal age distribution effect results in an apparent growth decrease. Furthermore, in effect the unimodal age distribution effect is not a sampling bias, because it is inherent to the local population structure of the species. Therefore, it cannot be overcome by using a different sampling scheme, but should be taken into account in the data analysis. The most straightforward solution would be to restrict growth trend analysis to species showing relatively continuous recruitment rates.

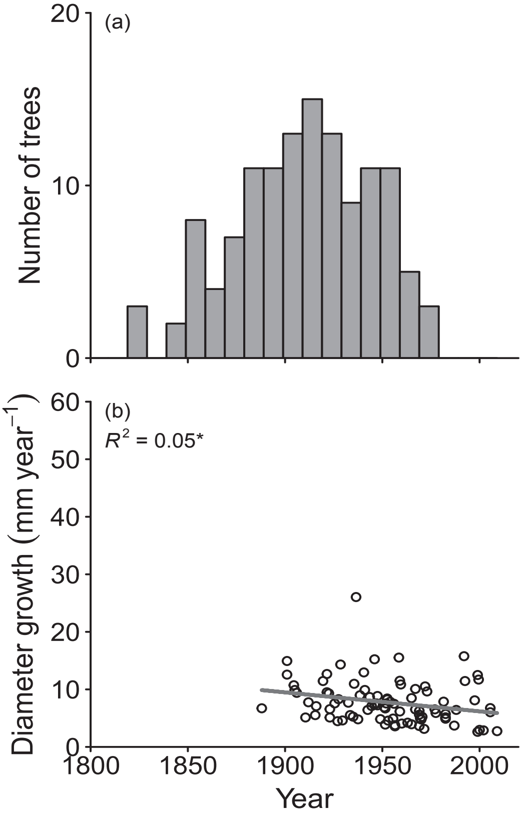


Figure 7.8 Year of establishment distribution of *Brachystegia eurycoma* from Cameroon (a) and diameter growth rates in the 20-25 cm dbh class. Adjusted R-squared of the linear model fit is indicated. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; *ns*, not significant.

The findings above highlight the importance of including knowledge on the disturbance history of a forest in the interpretation of observed growth trends. They also show that forests recovering from past disturbance cannot easily be used for analyzing long-term trends in tree growth if one is interested in addressing questions about the effects of global change on tropical tree growth. Many of the species that we sampled were long-lived pioneers and many of them showed unimodal age distributions, especially those in Cameroon and Thailand (Fig. 7.8a). It is likely that negative growth trends or an absence of positive growth trends in our tree ring data may result from the unimodal age distribution effect (Fig. 7.8b).

Temporal trends in forest biomass and tropical tree growth

Based on the evidence presented in CHAPTERS 3,4 and 5, it was estimated that the forest stands at the sites in Cameroon and Thailand are probably recovering after a severe disturbance that occurred some 100-150 years ago. All three forests are also impacted by additional disturbance factors such as a strong reduction in the number of vertebrate seed dispersers at the site in Cameroon (Effiom et al. 2013) and potentially increased fire frequency in Bolivia and Thailand (Gould et al. 2002, Johnson and Dearden 2009). As a consequence, each forest is expected to show trends in tree growth and biomass, irrespective of global change drivers or climate. These trends may show up in decadal scale measurements from permanent plots, or in decadal to century scale tree-ring data.

Forest stands recovering after a past disturbance, such as presumably those in Cameroon and Thailand, are expected to show gradual increases in aboveground biomass (Chazdon 2003, Baker et al. 2004). As large trees grow ever larger they accumulate more biomass, compensating well for the mortality of subordinate trees (Stephenson et al. 2014). This increase in biomass is probably accompanied by a decrease in diameter growth rates of the trees (see Fig. 7.9). There are two reasons for this decrease. Firstly, long-lived pioneer species that have established initially after a severe disturbance are dominating the forest canopy. As the trees grow larger, assimilates have to be divided over a larger total stem circumference, leading to declining diameter growth rates (Fig. 7.9a,d). But they may also reach the end of their lifespan, entering a phase in which the total leaf area can no longer support the tree's respiratory needs, and the tree will ultimately die of starvation (Oliver and Larson 1996). This can, for example, be observed as the ontogenetic decrease in growth rates of some of the

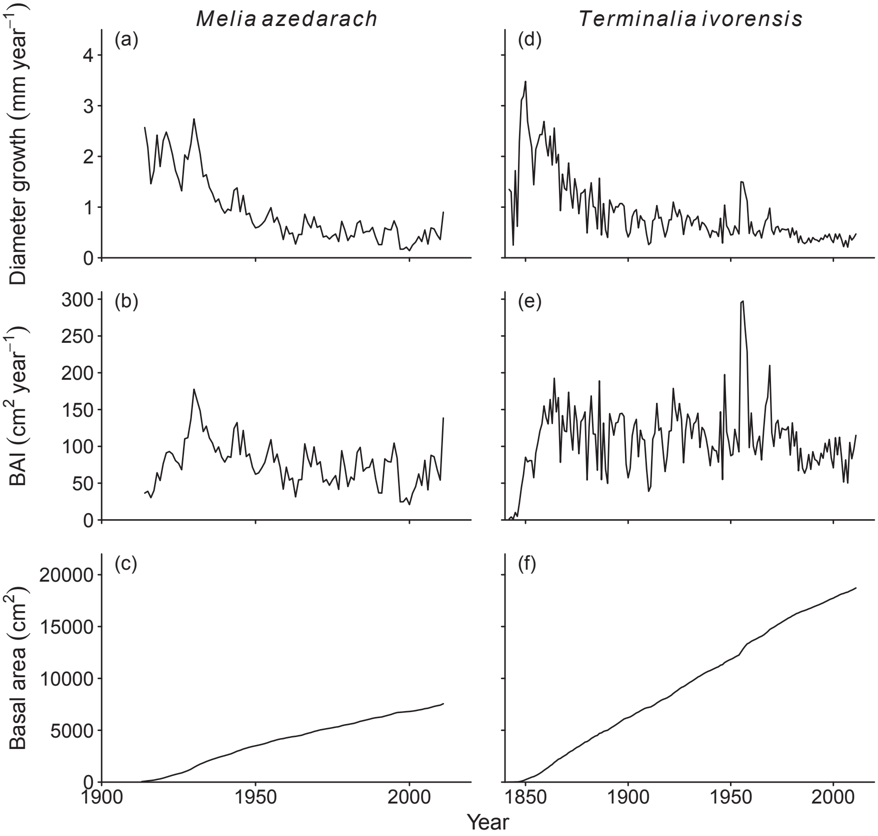


Figure 7.9 Relation between calendar year and diameter growth (top panels), basal area increment (BAI; middle panels) and total basal area (bottom panels) of the long-lived pioneer tree species *Melia azedarach* from Thailand (left) and *Terminalia ivorensis* from Cameroon (right). Tree basal area was shown because it is a good proxy for tree biomass (Baker et al. 2004).

older individuals of long-lived pioneer species (Fig. 7.9a,b). This picture changes when growth is expressed as basal area increment, which is a better proxy for biomass gain of the tree (Baker et al. 2004). Although diameter growth of the tree is declining, biomass (or basal area) gain may be relatively stable (Fig. 7.9 b,e), or even increase with tree size (Stephenson et al. 2014). Secondly, structural changes of the forest stand as a whole that are associated with increasing canopy closure and maximum total foliage lead to reduced productivity (Smith and Long 2001). The forest canopy gradually becomes denser and the understory becomes darker. Understory trees and subordinate trees in general will suffer because of the increased competition for light, and their diameter growth rates will decrease. Canopy trees also experience increasing interference from crowns of neighboring trees, which leads to reduced productivity (Smith and Long 2001). Thus, to sum up, there are several potential mechanisms associated with forest stand development that may lead to apparent changes in individual tree growth or forest biomass over time.

Various drivers of growth change

Recovery from past disturbance may lead to apparent trends in tree growth over time. It will therefore be difficult to investigate the relation between global change and long-term trends in tropical tree growth, especially because correcting for the effect of long-term changes in local stand dynamics of tropical forests on growth and biomass trends will be highly complex. The decadal to century scale at which these changes in dynamics occur, their potentially large spatial extent and the limited information we have on their prevalence, makes it difficult to rule them out. Simply using larger permanent sample plots, e.g., >10 hectare (Chambers et al. 2013), is unlikely to be sufficient if large tracts of tropical forest are impacted by past natural or anthropogenic disturbance. Thus, historic severe disturbances may generate increasing trends in forest biomass that cannot easily be distinguished from those generated by external growth stimulation such as those due to a CO_2 fertilization effect. On the other hand, a unimodal age distribution, which also reflects past severe canopy disturbance, may lead to apparently decreasing growth trends over time. The evidence for changes in stand dynamics in all three sites suggests that tropical forest dynamics are impacted by disturbance–recovery cycles at a century scale. These long-term disturbance–recovery cycles are likely to affect our present-day observations in all aspects, whether these observations are based on tree-ring measurements or repeated measurements from permanent sample plots. Analysis of growth trends using data from trees in forests with completely known disturbance histories, such as the temperate forest plots used by (McMahon et al. 2010), is unlikely to be widely applicable in the tropics. This implies that we should be aware that the stand history may have influenced the observed trends in forest biomass and tree growth.

Tropical forests are more dynamic than we thought

If there is one clear message from this thesis, it is that tropical forests are dynamic systems. Forest dynamics are generated not only by small-scale disturbances due to gap formation resulting from the death of a single tree, but also by disturbances at much larger scales. These large-scale processes may lead to long-term changes in species dominance and affect forest stand structure at a large spatial scale. This realization has important consequences not only for how we look at tropical forests, but also for how we study their dynamics. There is a need to reconsider the way in which we assess the evidence for global change effects on tropical forest dynamics. As stated earlier in this chapter, to date, studies on long-term tropical forest change have implicitly assumed an equilibrium state with respect to long-term stand development of tropical forests. But in the absence of such a long-term equilibrium state, it can be expected that there will be temporal trends as a result of disturbance recovery cycles.

The effect of past disturbance on long-term trends in tropical forest composition, structure and dynamics has long been realized. For example, (Laurance et al. 2004) assessed long-term changes in tree-community composition using 18 1-ha plots across the Amazon. Within this network they found evidence for community changes from shade-tolerant to very shade-intolerant tree species. It was explicitly stated that none of these plots exhibited evidence of current or past disturbance from logging, fires, hunting or major windstorms that could account for the compositional change. Similarly, (Baker et al. 2004) found significant increases in aboveground biomass of 1.22 Mg ha^{-1} yr^{-1} across 59 forest monitoring plots (mean size 1 ha) in Amazonia. They too acknowledge the potential role of natural disturbances in explaining some of the variability between plots: for example, they showed that a flooding event resulted in the strongest biomass decrease in the plots. However, they too argue against stand development following past disturbance having a strong influence on the observed patterns. For example, they state that the canopy of all plots was dominated by non-pioneer species and none of the plots was ‘obviously strongly successional’. At first glance, similar statements could have been made about the successional status of the forests in the three study sites that I presented in this thesis. None of these forests appear to be ‘obviously strongly successional’, i.e., having, for example, a high species diversity and numerous large canopy and emergent trees (Chuyong et al. 2004, Bunyavejchewin et al. 2009). Yet, a reconstruction of the stand history at a timescale of centuries did yield indications of past severe disturbance in all three sites.

The findings presented in this thesis suggest that forests may have a history of past disturbance, which will be revealed only by using a forensic forest ecology approach. The potentially large variation in disturbance histories of tropical forests, and also the variable outcome of stand development – for example, with respect to tree species diversity – may explain some of the very mixed results on long-term growth trends and forest biomass that have been reported in the literature (e.g., Feeley et al. 2007b, Lewis et al. 2009b).

There is a need to reconsider the way in which we assess the evidence for the effects of global change on tropical forests. Future research directions include using long-term data and applying a forensic forest ecology approach to more forests around the world. But, in addition, a better understanding is needed of the mechanisms of observed changes tropical forest dynamics. Reconstructing the timing and spatial extent of past disturbances could certainly contribute to elucidating observed patterns. In this study I have shown that in addition to potentially global change, the key drivers of tropical forest dynamics are long-term stand development following past disturbance and natural climate variability.

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Summary

Tropical forests cover only 7% of the land area on earth, but they harbor an estimated half of all the species in the world and play a crucial role in the global carbon cycle by storing 25% of all carbon in terrestrial ecosystems. Historically, tropical forests have been considered as relatively stable and undisturbed systems mainly driven by small scale gap dynamics. However, this perception of tropical forests as immutable systems has gradually changed over the past decades, recognizing the fact that tropical forests have long been impacted by large scale natural and human-induced disturbances.

The role of large scale disturbances in long-term stand development of tropical forests has recently gained renewed attention as remarkable increases in tree growth rates and tree turnover rates were reported, possibly related to changing site conditions associated with global change. In contrast with this, opposite patterns of decelerating growth rates of tropical trees and decreasing stem density of tropical were also reported. These conflicting findings have led to concern about the way in which forest dynamics are commonly analyzed by remeasuring tree diameter in permanent sample plots for a maximum of three decades. This approach largely neglects the century-long life span of most tropical forest canopy trees and the long-term legacy of possible large scale natural or anthropogenic disturbances that occurred long before the installation of these plots. Hence, there is a need for the analysis of tropical forest stand dynamics that does justice to the long lifespan of trees and the low frequency at which large-scale canopy disturbances occur. Tree-ring analysis provides a possibility to study tropical tree growth and forest dynamics at a century-long time scale.

In this thesis I combine the study of tree rings with spatial statistical analyses, which I refer to as 'forensic forest ecology'. I used forensic forest ecology to gather all possible clues, such as tree age and life-time growth rates of trees, to reconstruct historical tropical forest stand dynamics. All the data was collected within the framework of the TROFOCLIM project and was collected from sites in three countries: Bolivia, Cameroon and Thailand.

My thesis has four objectives. (1) To determine the relation between ring width and annual temperature and rainfall variability, to assess the potential effect of climate change on tropical tree growth. (2) To develop methods that combine tree-ring data and spatial analyses for assessing the evidence of past large scale canopy disturbances in tropical forests. (3) To reconstruct the disturbance history of tropical forest stands by applying a forensic forest ecology approach. (4) To assess the evidence for long-term alterations in tropical forest dynamics.

In CHAPTER 2 we used standardized tree-ring series to assess the climate response of four tree species from the Huai Kha Khaeng Wildlife Sanctuary (HKK), in Thailand. In all four tree species growth was significantly negatively correlated with annual maximum temperatures and positively correlated with dry season precipitation levels. The analysis showed that annual variability in tropical trees growth is (partly) driven by a combination of both temperature and precipitation. The negative correlation between temperature and tree growth could potentially lead to decreasing growth rates of tropical trees as a result of global warming.

A novel approach for reconstructing the disturbance history of tropical forests is presented in CHAPTER 3: the combination of tree-ring analysis and spatial statistics. We used tree-ring derived age estimates and tree locations across a 316-ha plot for 70 individuals of the shade-intolerant pioneer species *Melia*. Although the age distribution suggested that regeneration had been continuous over the past 60 years, spatial analysis suggested discrete regeneration patches indicative for canopy disturbances that occurred around 1960 and 1990. We estimated that either fire or wind was the most likely cause for these canopy openings. This study showed that forensic forest ecology can readily be applied to reconstruct the disturbance history of tropical forest stands.

In CHAPTER 4 the forensic forest ecology approach is used to address the question why tropical tree species often have population structures that exhibit strong recruitment failure. We reconstructed >200 years of estimated establishment rates in a sparsely regenerating population of *Afzelia* in HKK, Thailand. The age distribution of the trees revealed two distinct recruitment peaks (1850 and 1950) which likely resulted from past canopy disturbance. Three lines of evidence supported this interpretation: (1) aggregation of similarly aged trees at large (~500 m) spatial scales; (2) high juvenile growth rates; (3) a significant positive relation between tree age and forest canopy height. Our results indicate that forest patches with occurrence of large *Afzelia* trees have undergone high-severity canopy disturbance, possibly windstorms or fire, prior to establishment.

In CHAPTER 5 we reconstructed tropical forest dynamics at century-long timescales for sites in Bolivia, Cameroon and Thailand. We analyzed population age distributions and spatial distributions of tree ages of 4-5 species on each site and assessed the evidence of large-scale canopy disturbance. We found evidence for irregular regeneration rates of shade-intolerant species in all three sites and evidence for spatial clustering of tree age in two sites. In Cameroon and Thailand we found evidence for strong recent recruitment failure, indicative for stand development following a large-scale disturbance 100-150 years ago. In Bolivia we found evidence for a marked regeneration pulse of a long-lived pioneer species and near constant regeneration rates of the other four species. The findings from all three sites emphasize the role of large scale cycles of canopy disturbance and recovery in driving long-term dynamics of tropical forests.

In CHAPTER 6 we assessed whether stand dynamics of the three forest sites would reveal significant trends over time. We used the occurrence of growth releases in tree-ring series as a proxy for historical canopy gap formation. A growth release is generally defined as an increase in the growth rate of a tree that is sustained for several years and likely reflects an increase in resource availability, e.g., light. We found that species specific trends in release frequency over the past two centuries were predominantly negative. However, after accounting for long-term climate variability, a significant long-term positive trend in release frequency for the site in Thailand emerged. In general the pattern across the three sites indicated decreasing release frequency over time, which is consistent with a trend of decreasing gap formation and increasing canopy density. Our findings suggest that occasional large-scale disturbances, both natural and anthropogenic, and natural climate variability are key drivers of long-term trends in tropical forest dynamics. These drivers may obscure changes in tropical forest dynamics (gap formation) on shorter time scales that are caused by global change.

If one image becomes clear from this thesis it is that tropical forests are highly dynamic systems at different space and time scales. Forest dynamics are generated not only by small-scale disturbances due to gap formation resulting from the death of a single tree, but also by disturbances at much larger scales. These large-scale processes may lead to long-term changes in forest stand structure. This recognition has important consequences for the way we look at tropical forests, but also for the way in which we study their dynamics. There is a need to reconsider the way in which we assess the evidence for global change effects on tropical forests. Future directions include using more long-term data and applying a forensic forest ecology approach to more forests around the world. Furthermore, a better understanding of the mechanisms of observed changes tropical forest dynamics is needed. This study already showed that long-term stand development, natural climate variability and potentially global change are key drivers of tropical forest dynamics. Especially the potentially large variation in disturbance histories of tropical forests may explain some of the very mixed results on long term growth trends and forest biomass that have been reported.

Forensische bosecologie

Speuren naar de geschiedenis van tropische bossen

Mart Vlam

Samenvatting

Hoewel tropische bossen slechts 7% van het landoppervlak op aarde bedekken, herbergen ze toch ongeveer de helft van alle soorten op aarde. Daarnaast spelen tropische bossen een cruciale rol in de wereldwijde koolstofcyclus door 25% van alle koolstof in terrestrische ecosystemen op te slaan. Historisch werden tropische bossen gezien als relatief stabiele en onverstoorde systemen, voornamelijk gedreven door dynamiek op het niveau van de sterfte van een enkele boom. Deze opvatting van tropische bossen als onveranderlijke systemen is echter langzaam aan het veranderen. Tegenwoordig weten we dat tropische bossen altijd al werden beïnvloed door grootschalige natuurlijke en menselijke verstoringen.

De rol van zulke grootschalige verstoringen in de ontwikkeling van tropische bossen heeft recent hernieuwde aandacht gekregen doordat opmerkelijke toenames in boomgroei en omloopsnelheid van bomen zijn gerapporteerd. Deze toenames houden mogelijk verband met veranderende omgevingscondities door ‘global change’. Aan de andere kant zijn ook tegenovergestelde patronen waargenomen van afgenomen groei van tropische bomen en een afgenomen boomdichtheid van tropische bossen. Deze tegenstrijdige bevindingen hebben tot twijfel geleid over de manier waarop de dynamiek van bossen meestal wordt gemeten. Gewoonlijk gebeurt dit namelijk door het herhaaldelijk meten van boomdiameters in permanente proefvlakken voor een maximum periode van ongeveer 30 jaar. Deze aanpak negeert ten eerste grotendeels de eeuwenlange levensduur van de meeste tropische bomen. Ten tweede wordt geen rekening gehouden met de nalatenschap van grootschalige natuurlijke of menselijke verstoringen die plaatsvonden lang voor de aanleg van het proefvlak. Het is daarom noodzakelijk om de dynamiek van tropische bossen te analyseren op een manier die recht doet aan de lange levensduur van bomen en de lage frequentie waarmee grootschalige verstoringen van het kronendak voorkomen. Jaarringanalyse biedt deze mogelijkheid. Door gebruik te maken van jaarringanalyse kunnen we de groei van tropische bomen en de dynamiek van tropische bossen bestuderen op een tijdschaal van eeuwen.

In dit proefschrift combineer ik het gebruik van jaarringen met ruimtelijke statistiek en refereer daarnaar als ‘forensic forest ecology’ (forensische bosecologie). Ik gebruik alle mogelijke aanwijzingen, zoals boomleeftijden en levenslange groeisnelheden van bomen, om de historische opstandsdynamiek van tropische bossen te reconstrueren. Alle data is verzameld binnen het raamwerk van het TROFOCLIM project en is afkomstig uit gebieden in drie landen op drie verschillende continenten: Bolivia, Kameroen en Thailand.

Mijn proefschrift heeft vier doelstellingen. (1) De relatie vaststellen tussen ringdikte en de jaarlijkse variatie in regenval en temperatuur. Zo kan het mogelijke effect van klimaatverandering op de groei van tropische bomen worden verkend. (2) Het ontwikkelen van een methode waarin jaarringgegevens en ruimtelijke statistiek worden gecombineerd om de aanwijzingen voor historische grootschalige verstoringen in tropische bossen te bestuderen. (3) De verstoringsgeschiedenis van tropische bossen reconstrueren door middel van 'forensic forest ecology'. (4) Vaststellen of er aanwijzingen zijn dat de lange termijn dynamiek van tropische bossen is veranderd over de afgelopen twee eeuwen.

In hoofdstuk 2 gebruiken we gestandaardiseerde jaarringseries om te onderzoeken wat de klimaatafhankelijkheid is van vier boomsoorten in de Huai Kha Khaeng (HKK) Wildlife Sanctuary in Thailand. We hebben gevonden dat voor elk van de vier soorten de groei significant negatief gecorreleerd is met de jaarlijkse maximumtemperatuur en positief met regenval in het droge seizoen. De analyse toont aan dat jaarlijkse variatie in de groei van tropische bomen deels wordt gedreven door een combinatie van temperatuur en neerslag. De negatieve relatie tussen temperatuur en boomgroei kan potentieel leiden tot afgenomen groei van tropische bomen als gevolg van de opwarming van de aarde.

Een nieuwe aanpak voor het reconstrueren van de verstoringsgeschiedenis van tropische bossen laten we zien in hoofdstuk 3. Hier presenteren we de combinatie van jaarringanalyse en ruimtelijke statistiek. We gebruiken daarvoor leeftijden op basis van jaarringen en locaties van de bomen in een gebied van 316 hectare groot. Deze analyse is toegepast op 70 individuen van de schaduwintolerante pionierboom *Melia azedarach*. Hoewel de leeftijdsverdeling van deze soort suggereerde dat de regeneratie continu was over de afgelopen 60 jaar, laat de ruimtelijke analyse zien dat leeftijdsclusters van bomen voorkomen, waarschijnlijk als gevolg van verstoringen die plaatsvonden rond de jaren 1960 en 1990. We vermoeden dat stormen of bosbranden deze verstoringen hebben veroorzaakt. Dit hoofdstuk toont aan dat een 'forensic forest ecology' aanpak kan bijdragen aan het inzichtelijk maken van de verstoringsgeschiedenis van een tropisch bos.

In hoofdstuk 4 wordt de 'forensic forest ecology' aanpak opnieuw toegepast en richten we ons op de vraag waarom tropische bomen vaak een populatiestructuur hebben die wordt gekenmerkt door een afwezigheid van verjonging. We reconstrueerden meer dan 200 jaar van vestigingssnelheden van een spaarzaam regenererende populatie van *Afzelia xylocarpa* bomen in HKK, Thailand. De leeftijdsverdeling van de bomen onthult twee verjongingspieken (rond 1850 en 1950) die waarschijnlijk kunnen worden toegeschreven aan een verstoring van het kronendak in het verleden. Drie aanwijzingen ondersteunen deze interpretatie: (1) een clustering van bomen met dezelfde leeftijd op een grote (~500 m) ruimtelijke schaal; (2) hoge juveniele groeisnelheden van de bomen; (3) een significant positieve relatie tussen boomleeftijd en de hoogte van het kronendak. Onze resultaten duiden erop dat delen van het bos waar grote *Afzelia xylocarpa* bomen staan, vroeger heftige verstoringen van het kronendak hebben ondergaan die waarschijnlijk het gevolg waren van stormen of bosbranden.

In hoofdstuk 5 reconstrueren we de bosdynamiek van de afgelopen eeuwen voor de drie gebieden in Bolivia, Kameroen en Thailand. Hier analyseren we leeftijdsverdelingen en ruimtelijke patronen in de leeftijden van 4 tot 5 soorten per gebied en we evalueren de aanwijzingen voor grootschalige verstoringen van het kronendak. We vonden aanwijzingen voor onregelmatige regeneratiesnelheden van schaduwintolerante soorten in elk van de drie gebieden en daarnaast aanwijzingen voor ruimtelijke clustering van boomleeftijden in twee gebieden. In Kameroen en Thailand vonden we aanwijzingen voor een recente beperking van de verjonging. Dit is indicatief voor opstandsontwikkeling volgend op een grootschalige verstoring van 100-150 jaar geleden, omdat juveniele schaduwintolerante bomen veel licht nodig hebben om te overleven. In Bolivia vonden we aanwijzingen voor een duidelijke regeneratiepiek van een pionierboom en daarnaast relatief continue regeneratiesnelheden van de andere vier soorten. Deze bevindingen in de drie gebieden bevestigen het beeld dat cycli van herstel na grootschalige verstoringen een drijvende kracht zijn achter de langetermijndynamiek van tropische bossen.

In hoofdstuk 6 onderzoeken we of de opstandsynamiek van de drie bosgebieden significant is veranderd over de tijd. We gebruiken hiervoor het optreden van 'groeispurten' in jaarringseries als een indicator voor historische openingen in het kronendak. Een groeispurt wordt gedefinieerd als een toename in de groeisnelheid van een boom, die standhoudt voor een aantal jaar en daarom waarschijnlijk een toename in de beschikbaarheid van licht weerspiegelt. We stellen vast dat de frequentie van groeispurts over de afgelopen twee eeuwen is afgenomen. Nadat gecorrigeerd is voor langetermijnvariatie in klimaat, vonden we echter een significante toename van de frequentie van groeispurten voor het onderzoeksgebied in Thailand. Over het algemeen was het patroon over de drie gebieden indicatief voor een afname van de hoeveelheid openingen en daarom een toename in de dichtheid van het kronendak. Onze bevindingen suggereren dat zowel sporadische grootschalige verstoringen als natuurlijke klimaatvariatie belangrijke mechanismen zijn die de dynamiek van tropische bossen aansturen. Deze factoren camoufleren mogelijk veranderingen in de dynamiek van tropische bossen die worden veroorzaakt door klimaatverandering.

Als één beeld duidelijk wordt uit dit proefschrift, dan is het dat tropische bossen dynamische systemen zijn. De dynamiek van tropische bossen wordt niet alleen gestuurd door kleine verstoringen die worden veroorzaakt door de sterfte van een enkele boom, maar ook door verstoringen op een veel grotere ruimtelijke schaal. Deze grootschalige processen leiden tot langetermijnveranderingen in de opstandsstructuur van bossen. De erkenning hiervan heeft niet alleen belangrijke implicaties voor de manier waarop we naar tropische bossen kijken, maar ook voor de manier waarop we de dynamiek van bossen bestuderen. Het is dan ook noodzakelijk om de manier waarop we het effect van klimaatverandering op tropische bossen analyseren te herzien. Toekomstige onderzoeksrichtingen zouden meer langetermijngegevens moeten gebruiken. Daarnaast is het raadzaam om de ‘forensic forest ecology’ aanpak toe te passen op meer bossystemen. Ook is een beter begrip van de mechanismen van waargenomen veranderingen in de dynamiek van tropische bossen hard nodig. Dit proefschrift laat zien dat verstoringen, natuurlijke klimaatvariatie en mogelijk ‘global change’ belangrijke mechanismen in de dynamiek van tropische bossen zijn. In het bijzonder kan de grote variatie in verstoringsgeschiedenis een belangrijke verklaring zijn voor de tegenstrijdige patronen van biomassaontwikkeling van tropische bossen die zijn waargenomen over de afgelopen decennia.

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A PhD project that includes several fieldtrips to Thailand and other tropical countries sounds like great fun. That is exactly what it was! But right now I am also happy that my thesis is complete and I can start looking forward to new adventures. Here I would like to thank the many people that made this project a success.

In the first place I would like to acknowledge my co-promoters Pieter Zuidema and Patrick Baker and promoter Frits Mohren. Pieter, I want to thank you for granting me the opportunity to be part of this adventure. After graduating from my Master in Utrecht I initially had different career plans, but I never regretted that you convinced me to continue for four more years in science. It is incredible how much time you devoted to supervising me and all your other PhD-candidates. Thank you for your guidance and advice, in particular when writing my project proposal, planning fieldwork activities, preparing conference presentations and completing manuscripts. Patrick, thank you for your critical and thorough advice on the interpretation of the results. Your outstanding knowledge on forest ecology was a major inspiration when writing this thesis. Thank you for letting me use your lab facilities in Melbourne. You showed me for the first time some tree ring specimens collected in the Huai Kha Khaeng Wildlife Sanctuary. Dear Frits, thank you for your time and for your ideas on the chapters in this thesis.

The route to doing this PhD started with my master thesis on tropical tree rings. I went to Riberalta, northern Bolvia and assisted two of Pieter's PhD-candidates. Claudia Soliz Gamboa and Danaë Rozendaal, I would like to thank you very much for your thorough introduction into tropical tree-ring analysis. And this is also the place where I have to admit that you were right Claudia. Although I was denying it strongly in the beginning, a future career in tree-ring analysis was indeed lying ahead of me.

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Mart Vlam,
March 31 2014

Short biography

Mart Vlam was born on February 23 1984 in Apel-doorn, The Netherlands. He attended primary education at De Parkenschool in Apeldoorn. At the age of twelve he moved to secondary school at the Gymnasium Apeldoorn and completed his prescience education at the Koninklijke Scholengemeenschap Apeldoorn. He then moved to Utrecht University to attain a Bachelor degree with a major in Biology and a minor in Economy. During his time as student Mart moved to the city centre of Utrecht and he became an active member of students' sport association 'Studenten Badminton Helios'. He was the chairman of the association in the season 2006-2007.

After attaining his Bachelor diploma, Mart specialized in ecology and natural resources management and enrolled for a Master's degree in Environmental Biology. During this Master he was introduced to tropical tree-ring research. He did a Master thesis under supervision of Dr. Pieter A. Zuidema and then PhD-candidate Claudia Soliz Gamboa. Claudia was the first person to teach Mart all the basics of tropical tree-ring analysis during a three-month stay at Universidad Autónoma del Beni in Riberalta, northern Bolivia. After finishing his thesis Mart performed a six month internship at the Minisitry of Agriculture Food Quality and Nature in The Hague. By successfully completing this internship Mart earned a Master's degree in Environmental Biology in August 2009.

Once graduated Mart decided to continue in science and worked as a PhD-candidate within the framework of the TROFOCLIM project. This project resulted from an ERC grant awarded to Dr. Pieter Zuidema. The TROFOCLIM project was aimed at better understanding long-term effects of global change on tropical tree growth. Mart started his PhD at the Ecology and Biodiversity Group at Utrecht University in February 2010. In January 2011 he moved to the Forest Ecology and Forest Management Group at Wageningen University together with Dr. Pieter Zuidema and the other project members. Mart is living together with his partner Sietske Tacoma.

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Vlam, M., Baker, P.J., Bunyavejchewin, S. & Zuidema, P.A. (2014). Temperature and rainfall strongly drive temporal growth variation in Asian tropical forest trees. Oecologia, 174, 1449-1461.

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PhD Education Certificate

PE&RC Training and Education Statement

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

Review of literature (6 ECTS)

- Accelerated tropical forest dynamics (2010-2011)

Writing of project proposal (4.5 ECTS)

- Accelerated tropical forest dynamics (2010)

Post-graduate courses (6.7 ECTS)

- Introduction to R; PE&RC, WUR (2010)
- Introduction to Bayesian statistics; PE&RC, WUR (2010)
- Tree-ring analysis using WinDendro; Monash University, Australia (2010)

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

- Journal of negative results: light-growth relations tropical trees (2011)
- Proceedings of the Royal Society B: relating tropical tree growth to climate (2011/2012)
- Book chapter: liana anatomy (2012)
- Annals of forest Science: spatial point patterns in natural forests (2013)
- Biotropica: tropical forest ecology (2013)

Competence strengthening / skills courses (1.6 ECTS)

- Competence assessment; WGS, WUR (2013)
- Career assessment; VLAG, WUR (2013)
- Communication with the media and the general public; EPS, WUR (2013)

PE&RC Annual meetings, seminars and the PE&RC weekend (2.4 ECTS)

- PE&RC First year weekend (2010)
- PE&RC Day (2011)
- PE&RC Day (2012)
- PE&RC Last year weekend (2013)

Discussion groups / local seminars / other scientific meetings (7.5 ECTS)

- Local seminars on tropical ecology, tree-rings etc. (2010- 2013)
- Symposium tropical ecology ; oral presentation; UvA (2011)
- PE&RC Discussion group ecological theory and application (2011-2013)
- FEM Journal club (2011-2013)
- R Users group; organizer (2012-2013)

International symposia, workshops and conferences (8.5 ECTS)

- Association for Tropical Biology and Conservation; oral presentation; Bonito-MS, Brazil (2012)
- Society for Tropical Ecology; oral presentation; Frankfurt, Germany (2012)
- INTECOL; oral presentation; London, England (2013)
- NAEM; Lunteren (2013)
- NAEM; oral presentation; Lunteren (2014)

Lecturing / supervision of practicals /tutorials (3 ECTS)

- Introductie in de Biologie UU (Tutor) (2010)
- Strategic Planning (2012)
- Ecologie I (2012 / 2013)
- Lecture TRENDS (2012 /2013)

Supervision of MSc Students

- Spatial pattern analysis
- Climate – growth analysis
- Stable carbon isotopes in wood
- Tropical tree-ring analysis

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