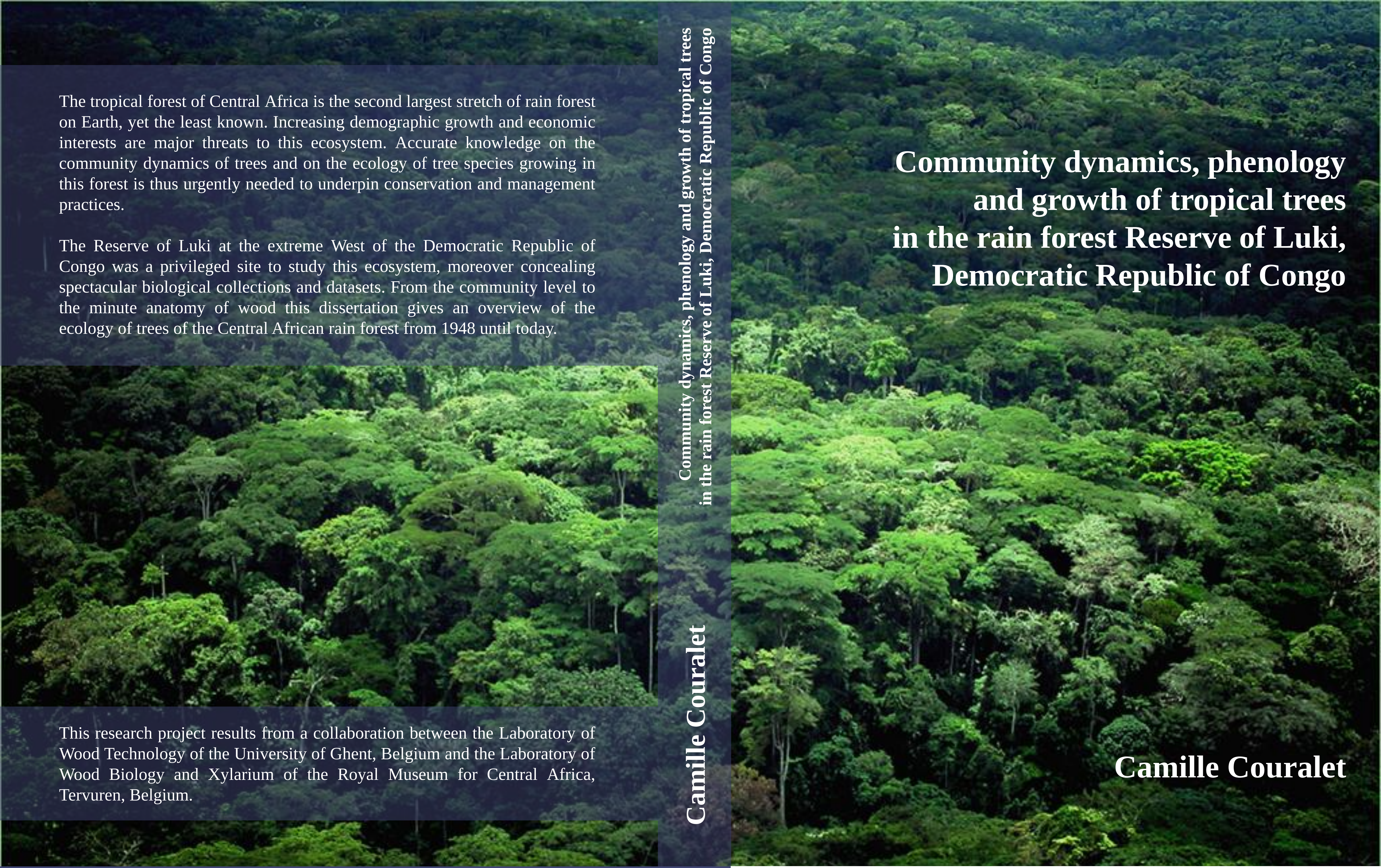

The tropical forest of Central Africa is the second largest stretch of rain forest on Earth, yet the least known. Increasing demographic growth and economic interests are major threats to this ecosystem. Accurate knowledge on the community dynamics of trees and on the ecology of tree species growing in this forest is thus urgently needed to underpin conservation and management practices.

The Reserve of Luki at the extreme West of the Democratic Republic of Congo was a privileged site to study this ecosystem, moreover concealing spectacular biological collections and datasets. From the community level to the minute anatomy of wood this dissertation gives an overview of the ecology of trees of the Central African rain forest from 1948 until today.

This research project results from a collaboration between the Laboratory of Wood Technology of the University of Ghent, Belgium and the Laboratory of Wood Biology and Xylarium of the Royal Museum for Central Africa, Tervuren, Belgium.

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Community dynamics, phenology and growth of tropical trees
in the rain forest Reserve of Luki, Democratic Republic of Congo

Camille Couralet

2010

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UNIVERSITEIT GENT

FACULTEIT BIO-INGENIEURSWETENSCHAPPEN

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Community dynamics, phenology and growth of tropical trees in the rain forest Reserve of Luki, Democratic Republic of Congo

Thesis submitted in fulfillment of the requirements for
the degree of Doctor of Philosophy in
Applied Biological Sciences

by

Camille Couralet

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ABBREVIATIONS

AC	autocorrelation
AMS	accelerator mass spectrometry
asl	above sea level
BP	band-pass
BTC	Belgian development agency
CAN	canopy shade-bearer species
CZ	central zone
DEF	defoliation
dbh	diameter at breast height
DISS	dissemination of fruits
DRC	Democratic Republic of Congo
FAO	Food and Agriculture Organisation of the United Nations
FL	flowering
FR	fruiting
Glk	*Gleichäufigkeitskoeffizient*
HEL	long-lived heliophilous and semi-heliophilous species
IAWA	International Association of Wood Anatomists
IDH	intermediate disturbance hypothesis
INEAC	Institut National pour l'Etude Agronomique du Congo belge
INERA	Institut National pour l’Etude et la Recherche Agronomiques
MAB	Man and Biosphere
MS	mean sensitivity
NESS	normalized expected shared species
NTFPs	non-timber forest products
OUT	area of outgrown wood formed in reaction to pinning
PAR	tangential length of parenchyma formed in reaction to pinning
PIO	pioneer species
RMCA	Royal Museum for Central Africa
RS	rainy season
RWI	ring-width index
SD	standard deviation
TVBP	t-value Baillie-Pilcher
Tw	Tervuren wood
UH	uniformisation par le haut (transformation thinning)
UND	understory species
WWF	World Wild Fund


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MAYUMBE, BAS-CONGO, RDC.
"POSTE DE LUKI"
ENTREE ET SORTIE CONTROLEES

CHAPTER 1

General introduction

OUTLINE OF THE THESIS

Although threatened by increasing demographic growth and economic interests the tropical forest of Central Africa is still the best preserved stretch of rain forest on the planet and yet the least known. The Reserve of Luki West of the Democratic Republic of Congo was a privileged site to study this ecosystem, moreover concealing spectacular datasets about the local climate and the biological resources of the Mayombe forest. An important goal of this study was to exploit the unique documents found in Luki witnessing the work done more than half a century ago in the Reserve. These exceptionally rich datasets were the starting point that led us to explore many ecological aspects of the surrounding forests still nearly unknown in tropical Africa. From the community level to the minute anatomy of wood, this work gives an overview of trees of the Central African rain forest of Luki from 1948 until today. More specifically, this study may contribute to answer ecological questions about the ligneous communities of species-rich tropical forests that remain debated.

CHAPTER 1 is a general introduction to the conducted research.

CHAPTER 2 explores long-term inventory data to characterize the present state of the forest of Luki 58 years after transformation thinning and to assess the influence of perturbations on the ligneous community.

CHAPTER 3 highlights the various phenological patterns of tree species and groups of species in relation with seasonal and inter-annual climate variability based on a 10-year record of defoliation, flowering, fruiting and dissemination of fruits.

CHAPTER 4 reports the dendrochronological study of three abundant understory tree species of Central African forests with investigations on differences in inter- and intra-annual growth patterns and climate/growth relationships. CHAPTER 5 reports a similar study for two major timber species of the same forests.

CHAPTER 6 focuses on the cambial activity underlying the macroscopic phenomenon previously reported for the study species. Rhythms of cambial activity in relation with climate are examined with monthly resolution using the cambial pinning method.

CHAPTER 7 is a general summary of the results presented in this dissertation and a discussion on possible outlooks.

THE CENTRAL AFRICAN RAIN FOREST

With an estimated 200 million ha, the Central African rain forest of the Congo Basin is the second largest continuous block of rain forest after the Amazon (Fig. 1-1) (Ruiz Perez *et al.* 2005, Laporte *et al.* 2007b). An estimated area of 155.5 million ha belongs to the Democratic Republic of Congo (DRC) where it represents seventeen billion metric tons of carbon (Laporte *et al.* 2007a, de Wasseige *et al.* 2009b). This forest also hosts outstanding species diversity and is interrelated with local and global climate (Phillips 1998, Lewis *et al.* 2006, Clark 2007). In the DRC it provides food, shelter, energy and livelihood for about 35 million people (Trefon 2006, de Wasseige *et al.* 2009b) by supplying arable land, timber for local use or trade, firewood, charcoal and NTFPs (Non-Timber Forest Products, such as medicines or food) (BTC 2007). As an example, wood energy represents more than 80 % of total domestic energy consumption in Africa (FAO 2006, de Wasseige *et al.* 2009b). Among other ecosystems rain forests are thus particularly threatened by human influence since they fulfil people's daily vital needs and can be a major source of income.

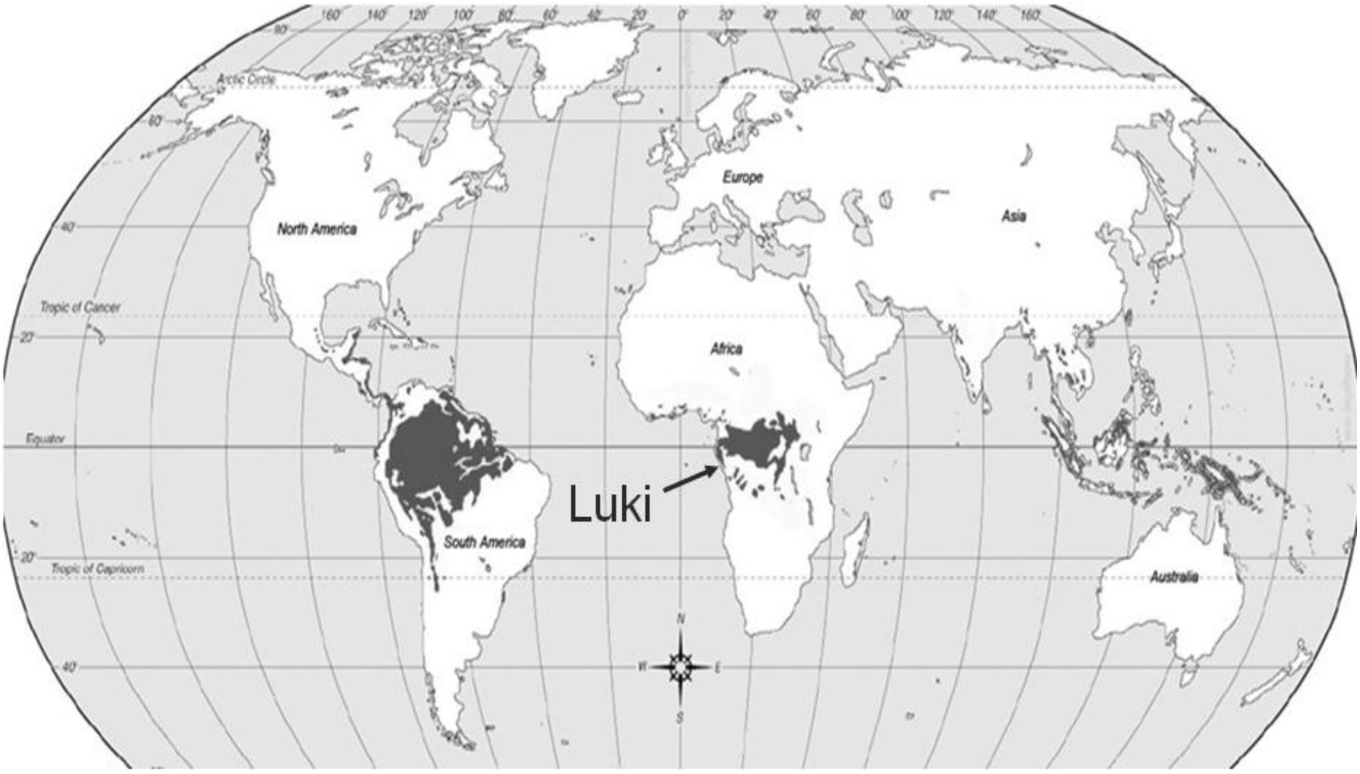

FIGURE 1-1. Distribution of tropical rain forests (in dark grey) on Earth.

Rapid demographic growth in the Congo Basin (2.87 % per year between 2000 and 2005) may lead to the doubling of the population in the next 25-30 years (de Wasseige *et al.* 2009a).

Consequently, deforestation levels that were relatively low until now and mainly associated with slash-and-burn agriculture are likely to increase drastically in the region (FAO 2006). The DRC is moreover gaining political and economic stability, which opens the way to massive investments in the logging sector or for future conversion of forests mainly into oil palm plantations (Trefon 2006, Laporte *et al.* 2007b). This combination of factors and strong synergies between consequent habitat fragmentation and climate change are expected to accentuate ecosystem degradation (Loreau *et al.* 2003). However, compared to other vegetation types tropical forests are poorly understood, mainly because of their structural and biological complexity and the extended time scale due to the longevity of trees. In addition, political instability in tropical Africa has often hindered fieldwork and scientific collaboration, which partly explains the scarcity of long-term and coordinated studies about African forests (Chapman *et al.* 2005, Trouet *et al.* 2006). The ecology of Central African forests remains hardly known and the literature on species diversity, tree growth and phenological rhythms often lacks reference to African data (Parmentier *et al.* 2007). As a consequence, knowledge on the composition and dynamics of African forests and on their relations to disturbances and climate variations remains incomplete (Swaine *et al.* 1990, Hawthorne 1995, Sheil and Burslem 2003, ter Steege 2003, Parmentier *et al.* 2005, Réjou-Méchain *et al.* 2008).

THE RESERVE OF LUKI

General situation

The Reserve of Luki is located at the extreme West of the DRC approximately 120 km from the Atlantic coast, 450 km from the capital, Kinshasa, and 30 km from the port city of Boma (Fig. 1-2). The latitudes 05°30’ and 05°43’ South and the longitudes 13°04’ and 13°17’ East form its limits. It covers about 33000 ha, which is small compared to other protected areas in the DRC (Nsenga 2004). The Reserve moreover lies in a densely populated area with very high demographic growth. Having reached + 292 % in the surrounding villages for the decade 1993-2003, it is an imminent threat to this ecosystem (UNESCO-MAB 1996, Nsenga 2004). However, until very recently industrial logging inside the Reserve has been limited and forests have been relatively well preserved. The Reserve of Luki is consequently a privileged site to study ecological aspects of Central African forests that remain poorly known.

Topography and geology

The Reserve lies in a hilly landscape with an altitude range of 150 to 500 m asl (above sea level). The forest is crossed by a dense network of rivers and streams with seasonal variations in discharge. The sloppy terrain favours heavy erosion and prevents the formation of deep soils, so that the source rock often appears less than 1.5 m under the surface (Monimeau 1990). The Mayombe region was formed on schist and sandstone that have been affected by metamorphism at various levels. As a consequence the soils are very heterogeneous and make pedological and geological mapping difficult in the region. However, the soils in the Reserve of Luki have been described as generally ferrallitic, acid and with poor chemical content (Senechal *et al.* 1989, Monimeau 1990).

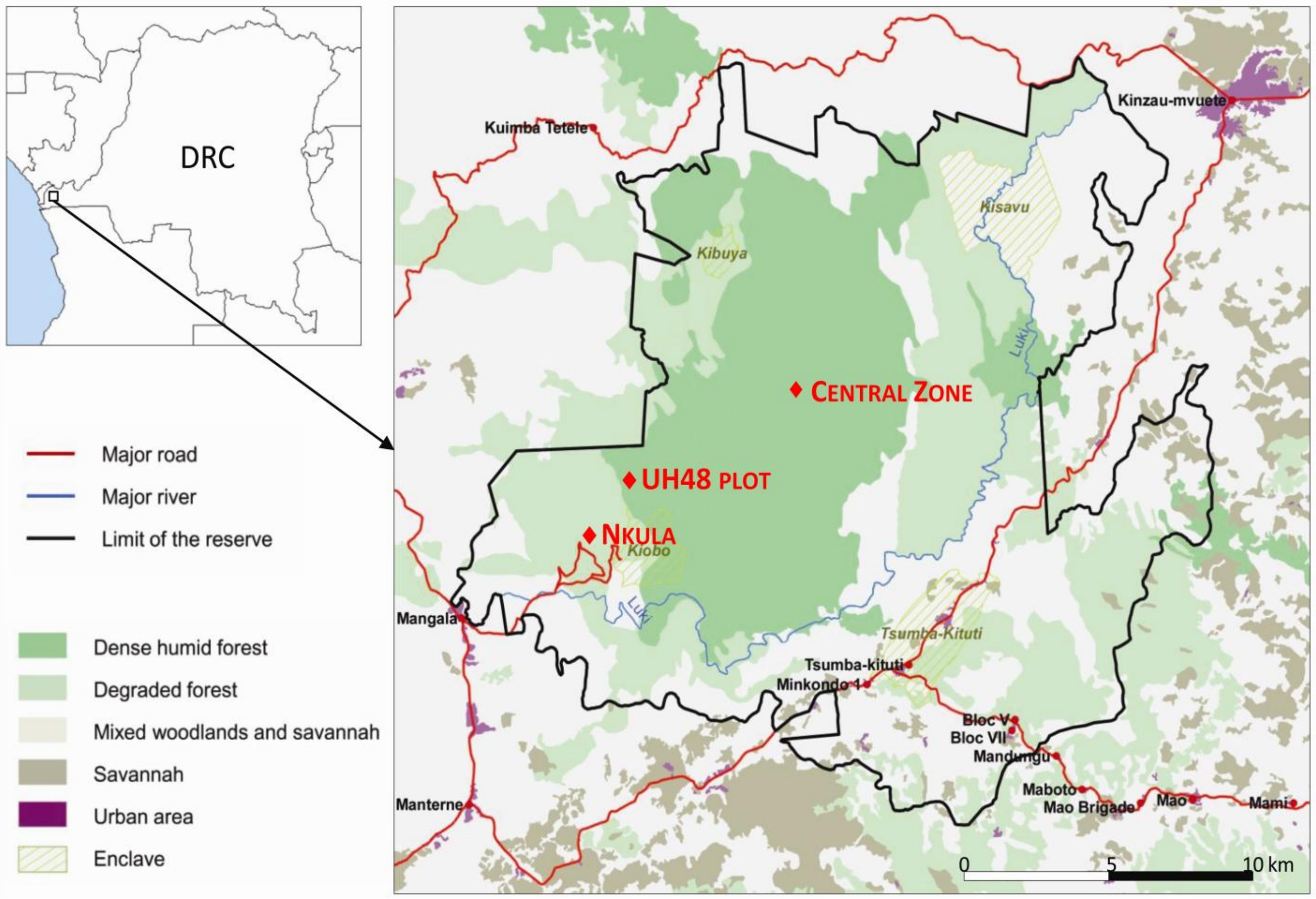

FIGURE 1-2. Map of the Reserve of Luki with the study sites: the UH48 plot, the Central Zone and the Nkula forest stand.

Climate

The climate in Luki is sub-equatorial humid and corresponds to the *Aw* category of the Köppen climate classification (Peel *et al.* 2007). It is characterized by an annual mean temperature of 24.6°C varying little form year to year and an average precipitation of 1180 mm/yr. A distinct dry period lasts from June to September with less than 50 mm monthly rainfall but the relative air humidity is constantly high, always above 80% (Fig. 1-3). This is explained by a clear reduction of solar radiation during the driest months since the cold Benguela stream in the Gulf of Guinea creates a thick, low-level, non-precipitating cloud layer that is present over the area during the whole dry season (Pendje and Baya ki 1992). Solar irradiance is blocked and the daily mean temperature is lower than in the rainy season (Lubini 1997).

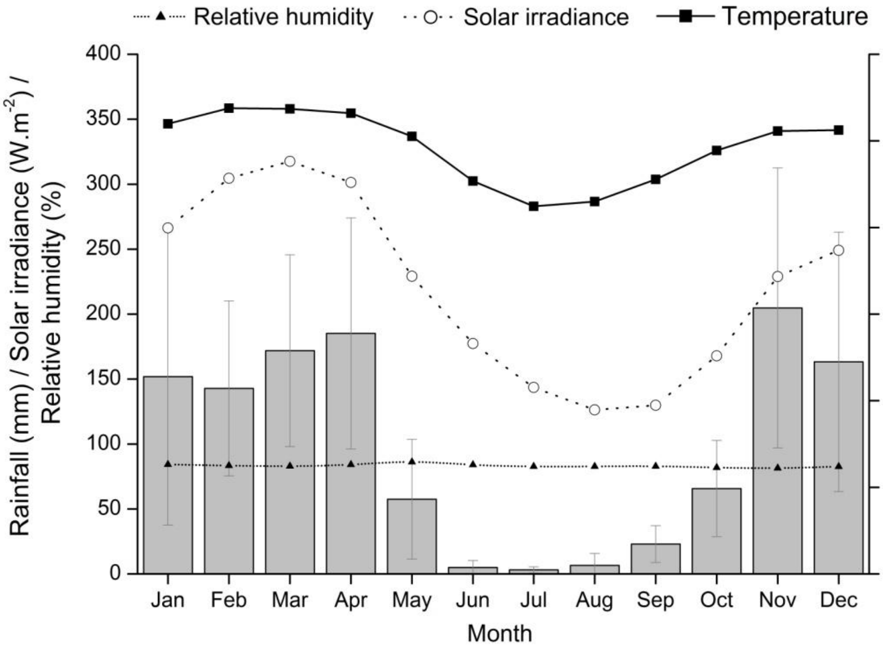

FIGURE 1-3. Climate diagram of the Luki meteorological station, DRC: monthly means of rainfall (grey bars, ± standard deviation), temperature, air humidity (1959-2007) and solar irradiance (1959-1994).

Vegetation

The Reserve of Luki is the southernmost remnant of the Mayombe forest, stretching along the Atlantic Ocean from the central coast of Gabon and renowned for its high floristic diversity and the presence of large timber trees (Monteiro 1962). The forest in the Reserve can be generally classified as tropical semi-evergreen (Whitmore 1998) but occurs in a mosaic landscape, with patches of primary forest and secondary forest alternated with agricultural fields and settlements (White 1983). More specifically, the forest in Luki is a mesophilous semi-deciduous forest of the Guineo-Congolian forest domain (Lebrun and Gilbert 1954, Lubini 1997) and consists of a mixture of deciduous and evergreen species in the upper-stratum, and evergreen species in the understory.

COMMUNITY ECOLOGY IN SPECIES-RICH ECOSYSTEMS

The dynamics of tree species composition in tropical rain forests in relation to disturbances remains a debated ecological preoccupation (Chave *et al.* 2002, Sheil and Burslem 2003, Gourlet-Fleury 2005, Chazdon *et al.* 2010). The arrangement of tree species and individual trees in a forest stand can be explained by spatial (e.g. soil properties or topography) or temporal (e.g. disturbance history or climatic variability) variations in environmental conditions, stochastic processes, the dispersal capacities of species and past and present interferences between all living forms (Harms *et al.* 2001, Chave *et al.* 2002, Nangendo *et al.* 2005). To what degree each factor or process influences species composition and repartition in tropical forests is still debated (Hubbell 2001, Jones 2008) but several general mechanisms have been proposed to explain the high floristic diversity of these ecosystems and its maintenance. In community ecology it is traditionally assumed that species differ in their adaptation to the environment or “niche”, which allow them to coexist in the same habitat (Hutchinson 1957, Chase 2005). However, in species-rich ecosystems such as tropical forests this view has been considered inadequate to explain how such high diversity can exist with a handful of limiting resources such as water, light and nutrients. The unified neutral theory of biodiversity (Hubbell 2001) supposes that differences between members of a community are irrelevant to their maintenance. The species composition would only reflect a constantly changing balance between the stochastic appearance (speciation or immigration) and disappearance of species (extinction). This general theory has also been recently debated (Chave 2004, Hubbell 2006) and a novel approach to understanding community dynamics has emerged, invoking plurality rather than neutrality of responses to disturbances (Newbery and Lingenfelder 2009). While rare species might still be considered neutral the more common species may have more determinate responses to changes in their environment. For the common species this suggests species-specific dynamic responses to environmental variations and tends to refute neutrality (or species equivalence).

GENERAL OBJECTIVE OF THIS STUDY

The aim of this study is to get a better understanding of tree community dynamics in the rain forest Reserve of Luki in the DRC. Specific objectives of this general goal are presented in this dissertation, from the community to the anatomical level. First we examine the ligneous community in a 200 ha plot and describe changes since 1948 in reaction to perturbations. Five abundant species are studied in particular: *Prioria balsamifera*, *Terminalia superba*, *Aidia ochroleuca*, *Corynanthe paniculata* and *Xylopia wilwerthii.* By examining the phenological and growth patterns of these common species in relation with climate variations we wish to find out if they respond similarly to the same environmental conditions or on the contrary if their responses are heterogeneous (or plural).

SPECIFIC AIMS AND STRUCTURE OF THE DISSERTATION

- We first evaluate the present state of the forest in Luki and assess changes in the ligneous community after major perturbations (transformation thinning, timber extraction and local use of forest resources).

- By studying rhythms of leaf and reproductive cycles in relation with climate variations, our goal was to discern if phenological patterns are heterogeneous among species and groups of species.

- Based on the findings about phenological rhythms we analyze radial growth and climate-growth relationships to assess the level of variability among tree species with different life-history traits and occupying different forest strata (understory/canopy).

- Eventually, to understand the macroscopic phenomenon previously highlighted we explore the process of wood formation at smaller time and space scales. In the last part of this work we study the rhythms of cambial activity of the study species in relation with climate at the intra-annual level.

COMPOSITION OF THE LIGNEOUS COMMUNITY AND INFLUENCE OF PERTURBATIONS IN A TROPICAL RAIN FOREST

Existing florae of tropical Africa are a good botanical basis to study the ecology of Central African rain forests (Hutchinson 1927-1936, INEAC 1948-1960, Aubréville 1961), however understanding the arrangement of species in communities and its variations in time are next necessary steps to unravel the functioning of this complex ecosystem. Repeated surveys of the same area are the best means to explore tropical forest dynamics but demand long-term perspectives that can rarely be met (Strayer 1986, Burslem and Whitmore 2003, Taylor *et al.* 2008). In the Reserve of Luki a report from the archives of Belgian colonial services was found, summarising a forest inventory performed in the Reserve in 1948 (Donis and Maudoux 1951). The census preceded the application of a silvicultural treatment in a 200 ha plot of mixed semi-deciduous forest (UH48 plot). Since then, timber extraction and forest use by local populations took place in the stand. This created a unique opportunity to know about the forest in 1948 and to assess the influence of a major perturbation (transformation thinning) and subsequent forest use after 58 years. Following the first inventory design and methodology the same plot was censused in 2006. The composition of the tree community, species diversity, size structure and biomass and carbon content were assessed and compared between 1948 and 2006. An additional census was performed in the central zone of the Reserve in 2007 because this area was assumed to be far less disturbed than the rest of the Reserve and was consequently foreseen as a control site.

STUDY SPECIES

Based on the inventory results we selected five study species from different stratae of the forest for their abundance and their importance for local forest use. *Aidia ochroleuca*, *Corynanthe paniculata* and *Xylopia wilwerthii* are abundant small-statured shade-bearer species. They are the most abundant species of the understory and are preferentially harvested for domestic use because they provide solid tools and high-quality charcoal. Two major canopy species were also selected. *Prioria balsamifera* and *Terminalia superba* are tall timber trees found both sought after for logging. The first one is a slow grower developing in the shade and the latter is a light-demanding species mostly emerging in gaps, but both species are major components of the upper canopy layer. Knowledge on these five species will consequently help to support management plans that can meet human needs while ensuring the viability of natural resources.

PHENOLOGICAL RHYTHMS IN TROPICAL TREES

In temperate climates the cycles of vegetation growth and reproduction associated with seasons is one of the most familiar natural phenomena (Fenner 1998). Important annual changes in temperature are systematically accompanied by corresponding cycles in the vegetation: cambial activation and dormancy, leaf cycles from flushing to shedding and reproductive cycles from bud break to dissemination of seeds. In the tropics however, what triggers and influences phenological processes in vegetation is still unclear (Schöngart *et al.* 2002).

The development of trees involves several rhythmic manifestations that are arguably linked to each other (Fig. 1-4). Cambial activity produces wood, a durable material that can be studied long after it was formed. On the other hand, life-history events such as flowering, fruiting or leaf phenology are usually more difficult to study since they do not leave durable traces and require long-term in vivo observations. In the archives of the Reserve of Luki we found records of a large-scale phenological study realised between 1948 and 1957. During ten years 3750 woody plants were monitored for defoliation, flowering, fruiting and dissemination of fruits on a ten-day basis. This unique dataset gathered and digitalised in Luki offered the opportunity to examine the phenological patterns of a great number of individuals and species. We could moreover explore the relationships of leaf and reproductive phenology with contemporaneous climate records.

TROPICAL DENDROCHRONOLOGY AND CLIMATE-GROWTH RELATIONSHIPS

Knowledge on growth rhythms and their relationships with climate variations is basic yet lacking information for most trees species of tropical Africa (Schöngart *et al.* 2006). Dendrochronology or the study of growth rings is a reliable way to assess the growth rates of trees. It can also be a powerful tool for developing high-resolution proxies for climate reconstructions and predictions (Worbes 2002, Fichtler *et al.* 2004, Couralet *et al.* 2005, Trouet *et al.* 2009). This is especially needed in tropical Africa where instrumental climate records are sparse in time and space and cannot show long-term variability and patterns and their driving factors (Nicholson 2001). In this study we wanted to determine whether the five selected species form annual rings and to investigate the influence of the total annual rainfall and its seasonal distribution on diameter growth. We thus performed a classic dendrochronological study by measuring tree rings on stem discs of several trees per species.

Although annual time-series of growth were synchronised and positive correlations with rainfall were revealed for most trees and species, the diversity of patterns between species and between individuals raised questions on tree growth at a time scale lower than a year. Cambial activity was thus examined to obtain closer insight into the cambium dynamics and to elaborate a more direct association between climate and growth, with a higher time resolution.

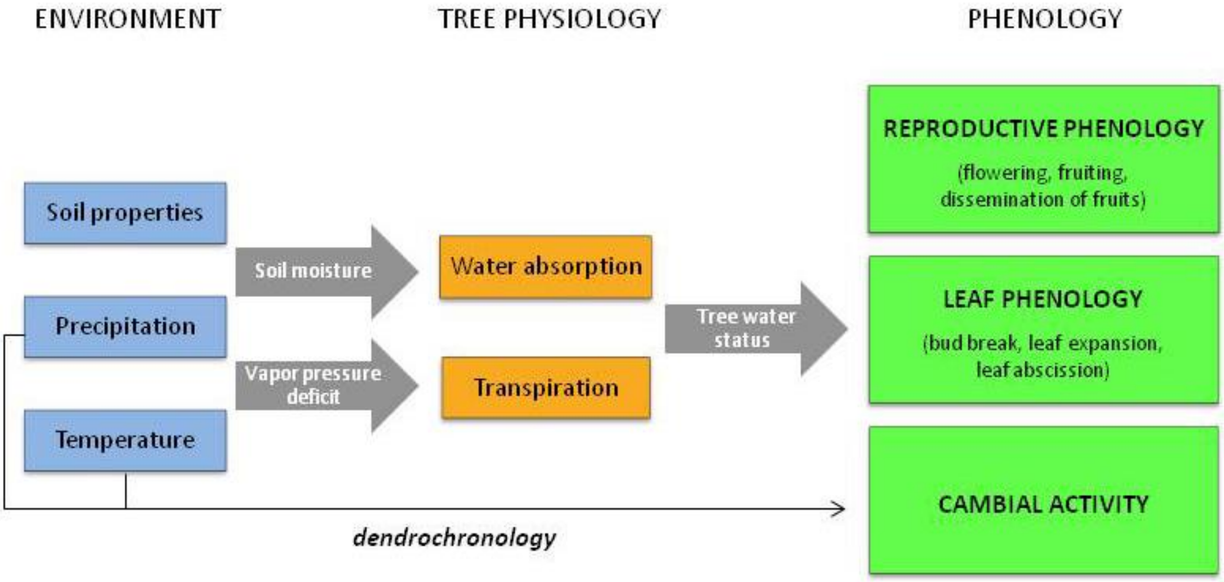

FIGURE 1-4. Causal relations between environmental inputs (left), tree water status and its intrinsic determinants (center) and seasonal development (phenology and cambial activity, right) in tropical forest trees. Based on Borchert (1999).

CAMBIAL ACTIVITY IN TROPICAL TREES

In temperate climates an easy way to approach higher resolution of the annual radial increment of trees is to separate early and late wood in growth rings (e.g. (Buckley *et al.* 2007). Anatomical features varying through growth rings also allow building high resolution profiles, such as wood density (e.g. (Preston 2006) and tracheids or vessels size (e.g. (Sass and Eckstein 1995). However, the need remained to have a precise “timer” of cambial activity during the ongoing growth processes (Seo *et al.* 2007). Various techniques were tested with this objective. For example the periodic extraction of small samples from the cambial zone of trees was developed and improved since the 1980s and is today termed micro-sampling (Deslauriers *et al.* 2003, Mäkinen *et al.* 2003). The “Mariaux window” was one of the earliest ideas to investigate the periodicity of cambial activity in tropical trees growing under a weak seasonality, by cutting window-like wounds in the cambium of trees (Mariaux 1967). Similar cambial wounding but with a needle was implemented by Wolter (1968) and generally applied since then (e.g. Nobuchi *et al.* 1995, Schmitt *et al.* 2000, Dünisch *et al.* 2002, Verheyden *et al.* 2004, Schmitz *et al.* 2008). The technique, nowadays called cambial pinning, is based on the experience that typical features are formed in the cambial zone in response to wounding (Larson 1994). Because of the external impact caused by the needle, the cambium stops forming new cells around the pinning canal and develops specific cells and tissues that can be dated precisely from the time of wounding.

In this study we applied cambial pinnings every month during 17 months on ten trees of each of the five study species, to get additional insight into intra-annual patterns of radial growth and possible relationships with climate variations on a monthly basis.


CAMEL

CHAPTER 2

Long-term community dynamics in response to disturbances in a Central African rain forest

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ABSTRACT

Understanding rain forest dynamics in relation to human disturbances requires long-term studies that are few, even more so in tropical Africa. In this work inventories were repeated with a 58-year span in a stand of the semi-deciduous Mayombe rain forest, west of the Democratic Republic of Congo. The composition and structure of the tree community were characterised and the influence of an extensive transformation thinning applied in 1948 and moderate logging until 2006 was examined. The changes of local species diversity was investigated in particular and compared to predictions under the Intermediate Disturbance Hypothesis (IDH), which state that an intermediate level of disturbances maximises species diversity.

We found that the forest stand had a good resilience capacity 58 years after the transformation thinning, regaining previous size structure and surpassing previous levels of biomass content and species diversity. The major perturbation and the continuous logging seem to have favoured species diversity in this forest, consistent with the patterns predicted under the IDH.

Our results suggest that anthropogenic disturbances maintained at a moderate level by sound management plans involving conservation may thus promote species diversity and good regeneration of the tree communities in tropical rain forests.

Key words: Democratic Republic of Congo, rain forest dynamics, ecosystem resilience, successive forest inventories, silvicultural treatment, Intermediate Disturbance Hypothesis

INTRODUCTION

Species-rich rain forests are highly productive ecosystems that provide multiple goods and services such as timber production, carbon storage and sustained high biodiversity. Forest management and silvicultural treatments aim at maximising these benefits but their long-term effects remain poorly known (Fuhr *et al.* 2001, Horner *et al.* 2009). The long-term consequences of thinning on forest structure, species composition and carbon stocks need to be better understood. Besides, the influence of disturbances on the functioning of the forest is also a debated subject. The Intermediate Disturbance Hypothesis (IDH) predicts maximal species diversity at an intermediate level of disturbance (Connell 1978, Sheil 1999, Bongers *et al.* 2009). The different competitivity of species in different circumstances including topography, absence or presence of pests, light availability, soil fertility and disturbance regime would explain this peaked response of species richness to disturbances. Analyses of tropical forest dynamics in response to disturbances and tests of the IDH are few and the subject remains disputative (Burslem and Whitmore 1999, Sheil and Burslem 2003, ter Steege 2003, Roxburgh *et al.* 2004, Bongers *et al.* 2009). However, in a test of the hypothesis in a Guianan rain forest disturbances were found to be a valid explanation for the maintenance of high species diversity (Molino and Sabatier 2001).

In the humid forests of Central Africa basic knowledge is still lacking on the composition and dynamics of tree communities (Swaine *et al.* 1990, ter Steege 2003, Nangendo *et al.* 2005). Long-term changes in relation to human activities and forest resilience (the speed at which it returns to its equilibrium state after a perturbation) are also not well known (Holling 1973, Webb 2007). The best means to further explore tropical forest dynamics is to study repeated surveys of the same area (Burslem and Whitmore 2003). Ecosystem complexity, the extended time scale due to the longevity of trees and the turbulent history of tropical Africa (Hall and Swaine 1981, Strayer 1986, Burslem and Whitmore 2003, Taylor *et al.* 2008) explain the few number of studies based on long plot history in the region (Swaine *et al.* 1987, Sheil 1995, 2001, Nangendo *et al.* 2005, Taylor *et al.* 2008).

The rain forest Reserve of Luki lies 30 km north of to the port city of Boma at the extreme west of the DRC. Rapid demographic growth in the surrounding villages is a major threat to this ecosystem (Nsenga 2004). According to activity reports from the Reserve and inhabitants of the forest logging and forest use inside the Reserve have been constant but limited until very recently (INEAC 1948-1960b). A report from the archives of Belgian colonial services summarises a forest inventory performed in the Reserve in 1948 (Donis and Maudoux 1951).

The census preceded the application of a silvicultural treatment in a 200 ha plot of mixed semi-deciduous forest (UH48 plot). Since then timber extraction remained moderate in the stand because of the protected status of the Reserve. This provoked a unique opportunity to examine the long-term changes of local species diversity, basal area distribution and biomass content in a Central African humid forest after a major perturbation (transformation thinning in 1948) and moderate forest use.

The present study is based on two successive inventories of the UH48 plot, in 1948 and 58 years later in 2006. In addition, a census of the central, arguably less disturbed zone of the Reserve performed in 2007 was used for comparison. Using ordination techniques the major structure of the ligneous community in the UH48 plot in 2006 was first explored to characterize the present state of the forest in Luki and examine the repartition of species according to different landscape types (slope, plateau and field). Then the floristic compositions of the communities were described and biodiversity indices were compared. The size distributions of basal area were also analysed for all trees and for groups of species (canopy and understory shade-bearers, and heliophilous species) and biomass and carbon contents were estimated. This investigation allowed assessing the changes in the ligneous community of a tropical rain forest after extensive anthropogenic disturbances and finding out if the maintenance of a moderate level of disturbance favours species diversity, as proposed by the IDH.

MATERIALS AND METHODS

STUDY SITE: THE RESERVE OF LUKI AND THE UH48 PLOT

The Reserve of Luki is the southernmost remnant of the Mayombe forest, a peninsula of the Congo Basin rain forest renowned for its high floristic diversity (Monteiro 1962, Lubini 1997, Nsenga 2004). The main vegetation cover is a tropical semi-evergreen rain forest of the Guineo-Congolian domain (Lebrun and Gilbert 1954, Whitmore 1998) but except in a non easily accessible central zone patches of secondary forests and agricultural fields are frequent.

In 1948 a 200 ha stand of semi-deciduous forest on a sloping terrain was selected in the Reserve to test a silvicultural treatment called “uniformisation par le haut” (UH, transformation thinning) (Donis and Maudoux 1951). The management operation aimed at turning the mixed natural forest into a more uniform (sizes) and homogenous (species) stand, better suited for future commercial exploitation. The biggest trees (above 200 cm of gbh) and all trees of non-timber species were removed by poisoning or debarking to release space, light and nutrient availability. Besides, all trees smaller than 20 cm of girth at breast height (gbh) and all shrubs and lianas were eliminated to clear the understory.

Prior to the transformation thinning approximately 10 % of the UH48 plot were inventoried. Along 21 parallel 10 m-wide transects of various lengths placed every 100 m from South to North, all trees above 20 cm of gbh (~6.4 cm of diameter) were identified to species and measured for gbh (Fig. 2-1). Regeneration (trees below 20 cm of girth below the first branch) was also censused in 10 m x 10 m subplots placed every 100 m along the transects and representing 1 % of the plot. The raw inventory data from 1948 was not available but a detailed report was published (Donis and Maudoux 1951). Methods were explained and the abundance of trees per size class was given for all the recorded species in two distinct topographic zones: the slope and the plateau.

After the inventory and silvicultural treatment, regular maintenance and exploitation were planned during the next decades but did not take place. Being close to the limits of the protected zone and to good roads, the UH48 plot was very prone to be influenced by the surrounding rapid human population growth. However, its integrity was relatively preserved thanks to its status of ancient experimental plot and to globally poor soil quality. Only limited areas on the outside of the stand were cleared to settle agricultural fields on locally flat and fertile ground. One small-scale illegal logging campaign occurred in 1994 in the UH48 plot, but the number and species of withdrawn trees remained concealed.

INVENTORY DESIGN

Transects were laid in the UH48 plot in 2006 following the original work of Donis and Maudoux (1951) and the exact same procedure was used for the inventory of trees to enable direct comparisons. These transects were additionally divided into portions of 10 m x 100 m where 10 m x 10 m regeneration subplots were embedded (Fig. 2-1). In 2007 a similar additional census was performed in the central zone of the Reserve (CZ). This core of rain forest was supposedly less disturbed than the surroundings because of poor accessibility (rocky and steep ridges, long distance from inhabited areas and from roads suitable for vehicles). Consequently, because anthropogenic disturbances were assumed to be very limited in the Central Zone compared to the UH48 plot the Central Zone was foreseen as a control site to interpret the results from the UH48 inventories. Trees above 60 cm of gbh were identified and measured in three 10 m-wide parallel transects totalising 12 ha. All species names recorded in the different inventories were verified in available florae and collections. Name changes were accounted for and errors were corrected using digital databases (Aluka 2007, Metafro 2009) and by examining herbarium specimens. Eventually, 0.1 % of all inventoried trees (38 individuals) could not be identified and were marked as "unknown".

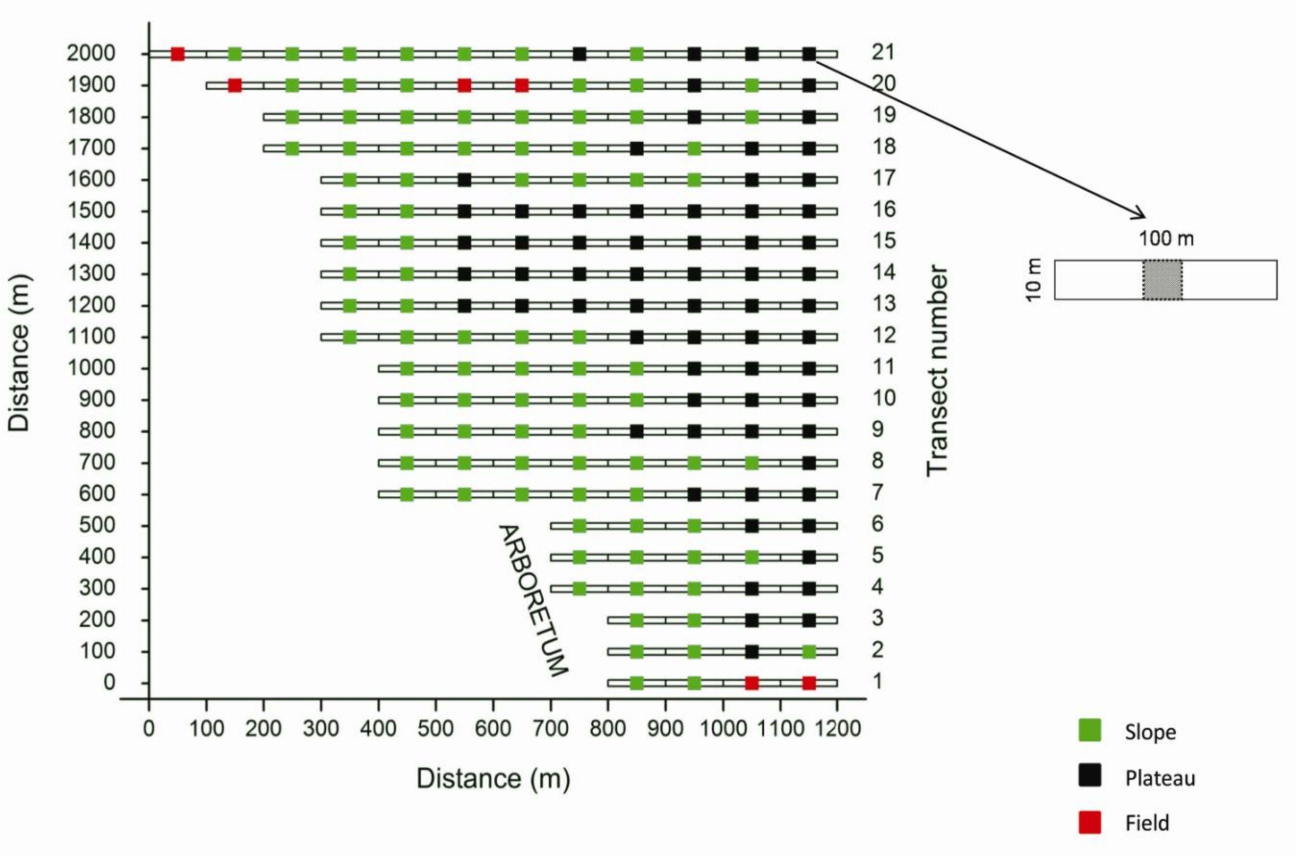

FIGURE 2-1. Inventory design in the UH48 plot based on the systematic design used in 1948 (Donis and Maudoux 1951). All trees above 20 cm of gbh were inventoried in 20 10 m-wide parallel transects distributed every 100 m and representing approximately 10 % of the plot. Transects were divided into 164 10 m x 100 m sections where 10 m x 10 m subplots were embedded for the inventory of regeneration (trees below 20 cm of gbh). Subplots are coloured according to topographic categories specified in 1948 ("Slope" and "Plateau") and the category "Field" added in 2006.

ANALYSES OF THE INVENTORY RESULTS

To represent the species arrangement in the UH48 plot and possibly exhibit some features observed in the field, species were ordinated in a two-dimensional space. The aim was to explore the major structure in the arrangement of species, without a set of environmental variables to use as constraints for the ordination. The only assumption was that the distribution of species depending on environmental variables was unimodal rather than linear.

Based on a matrix containing the abundances of all species for each subplot in the UH48 plot in 2006, species were thus ordinated using a detrended correspondence analysis (DCA) (Hill and Gauch 1980, Ter Braak 1987, Legendre and Legendre 1998) in the R software (RDevelopmentCoreTeam 2009). The subplots were then projected in the ordination space to reveal possible tendencies of species arrangements depending on their topographic class (slope, plateau or field).

Floristic composition was compared qualitatively between the four available inventories: in the UH48 plot in 1948 before (UH48pre) and after (UH48post) the transformation thinning and in 2006 (UH48-2006), and in the Central Zone in 2007 (CZ-2007). Values of basal area (BA, in m^2/ha) calculated per species were also compared.

The grouping of species contains a fair amount of subjectivity and ideally it would be preferable to consider species individually. However, a simplification by groups of species seems necessary to use most of the data gathered from the inventories and get an insight into the general functioning of the forest (Gourlet-Fleury 2005). In this study species were grouped according to their main functional traits and the timing of their dominance in forest succession (Swaine and Whitmore 1988, ter Steege *et al.* 2002, Chazdon *et al.* 2010). The classification proposed by Hawthorne (1995) was chosen as a reference because of the high number of common species between Luki and his study site in Ghana. The maximum potential size of the trees was also considered, indicating in which forest layer (understory or canopy) the species are mostly found. This approach resulted in four functional groups:

- CAN: long-lived shade-tolerant species mostly found in the canopy e.g. *Entandrophragma spp.*, *Prioria balsamifera*, *Hylodendron gabunense*;
- UND: long-lived shade-tolerant species generally small-statured and confined to the understory e.g. *Aidia ochroleuca*, *Corynanthe paniculata*, *Xylopia wilwerthii*;
- HEL: long-lived heliophilous or semi-heliophilous species mostly found in the canopy, corresponding to the “non-pioneer light-demanding” guild of Hawthorne, e.g. *Terminalia superba*, *Pycnanthus angolensis*;
- PIO: short-lived light-demanding species mostly emerging in gaps, e.g. *Musanga cecropioides*, *Myrianthus arboreus.*

Basal area (m^2/ha) of all trees was summed in 20 cm-wide classes of gbh for the four inventories. The resulting distributions were then compared quantitatively. Statistically unbiased indices of species diversity within samples and species similarity between samples were calculated for the UH48 plot and the central zone. To overcome sample size differences, indices were compared using subsampling (or rarefaction) principles with the program BiodivR 1.1 (beta release) (Hardy 2009). Diversity was expressed by (1) the Simpson's index of diversity (D), (2) the expected number of species found in a subsample of size k (S_k), and (3) the "equivalent number of species" corresponding to the former indices. Similarity between two samples was expressed by the generalization of the Morisita-Horn index, the NESS (normalized expected shared species) index (Grassle and Smith 1976). The subsampling size k is a parameter of the NESS index that controls for the weight given to rare species (when k is big) or common species (when k is small).

RESULTS

THE UH48 PLOT IN 2006

Only five true pioneer species (group PIO, short-lived and strict light demanding species) were found among the 260 species inventoried and their basal area represented between 0.3 and 1.4 % of the total basal area in the four inventories (Appendix 1). Consequently, this study will only focus on three main functional groups of the ligneous community: the canopy shade-bearers (CAN), the understory shade-bearers (UND) and the long-lived heliophilous species (HEL).

The DCA of the inventory data from UH48-2006 revealed a homogenous repartition of species of these three main functional groups CAN, UND and HEL (Fig. 2-2A). The projection of the subplots highlighted a grouping in relation to the three topographic classes (Fig. 2-2B). "Field" subplots all appeared on the same part of the plot, in the top left quarter. Subplots on sloping terrain ("slope") were however more grouped on the left and subplots on the plateau, on the right. The areas occupied specifically by each topographic class were displayed on the species plot (Fig. 2-2A). Heliophilous species were almost all found in the "field" area. *Aidia ochroleuca* (1), *Xylopia hypolampra* (9), *Xylopia wilwerthii* (10) and *Cola mahoundensis* (2) came out at the extremes of the cloud formed by the "slope" subplots. Besides, *Terminalia superba* (8) appeared in the middle of the projection plane and *Corynanthe paniculata* (3), *Hylodendron gabunense* (5) and *Prioria balsamifera* (6) at the crossing of the "slope" subplots and the "plateau" subplots zones.

In 1948, 130 different tree species were identified in the UH48 plot before the transformation thinning treatment (UH48pre), of which 68 were still present after the treatment (UH48post). In 2006, 180 species co-existed in the same plot (Appendix 1). Among the most abundant understory species in UH48pre were *Xylopia wilwerthii*, *Aidia ochroleuca*, *Corynanthe paniculata* and *Cola mahoundensis* (Table 1). The first three were all removed by the treatment but in 2006 they were again among the most frequent species in the plot. On the contrary *C. paniculata* trees were not removed by the treatment and remained abundant until 2006. Therefore the composition of the understory in 2006 was similar to 1948 before the treatment. In the canopy layer *Hylodendron gabunense* and *Dialium pachyphyllum* were among the most numerous in UH48pre. They were spared by the treatment and had similar abundance positions from UH48pre (respectively 4th and 8th) to 2006 (6th and 10th). Other frequent species in UH48pre (*Monodora angolensis*, *Garcinia epunctata*, *Diospyros sp.)* were removed by the treatment but did not return to similar levels in 2006, while some species that were initially not frequent became prevalent in 2006 (*Polyalthia suaveolens*, *Staudtia kamerunensis*, *Maranthes glabra*). The floristic composition of the central zone appeared to be very different from the UH48 plot at any date, with no common species with UH48pre and only one common species with UH48post (*Cynometra lujae*) and UH48-2006 (*Dialium corbisieri*).

TABLE 2-1. Lists of the 10 most abundant tree species (gbh > 20 cm and > 60 cm for the central zone) in the UH plot before (UH48pre) and after (UH48post) the transformation thinning and in 2006 (UH48-2006), and in the central zone of the Reserve of Luki in 2007 (CZ-2007).

UH48pre	**UH48post**	**UH48-2006**	**CZ-2007**
Xylopia wilwerthii	*Corynanthe paniculata*	*Xylopia wilwerthii*	*Cola griseiflora*
Aidia ochroleuca	*Hylodendron gabunense*	*Aidia ochroleuca*	*Cynometra lujae*
Corynanthe paniculata	*Dialium pachyphyllum*	*Corynanthe paniculata*	*Julbernardia brieyi*
Hylodendron gabunense	*Xylopia parviflora*	*Cola mahoundensis*	*Julbernardia seretii*
Cola mahoundensis	*Polyalthia suaveolens*	*Polyalthia suaveolens*	*Diospyros laurentii*
Monodora angolensis	*Celtis mildbraedii*	*Hylodendron gabunense*	*Dialium corbisieri*
Garcinia epunctata	*Staudtia kamerunensis*	*Dialium corbisieri*	*Prioria oxyphylla*
Dialium pachyphyllum	*Prioria balsamifera*	*Staudtia kamerunensis*	*Nesogordonia leplaei*
Xylopia parviflora	*Cynometra lujae*	*Maranthes glabra*	*Trichilia gilgiana*
Diospyros sp.	*Nesogordonia leplaei*	*Dialium tessmannii*	*Strombosia pustulata*

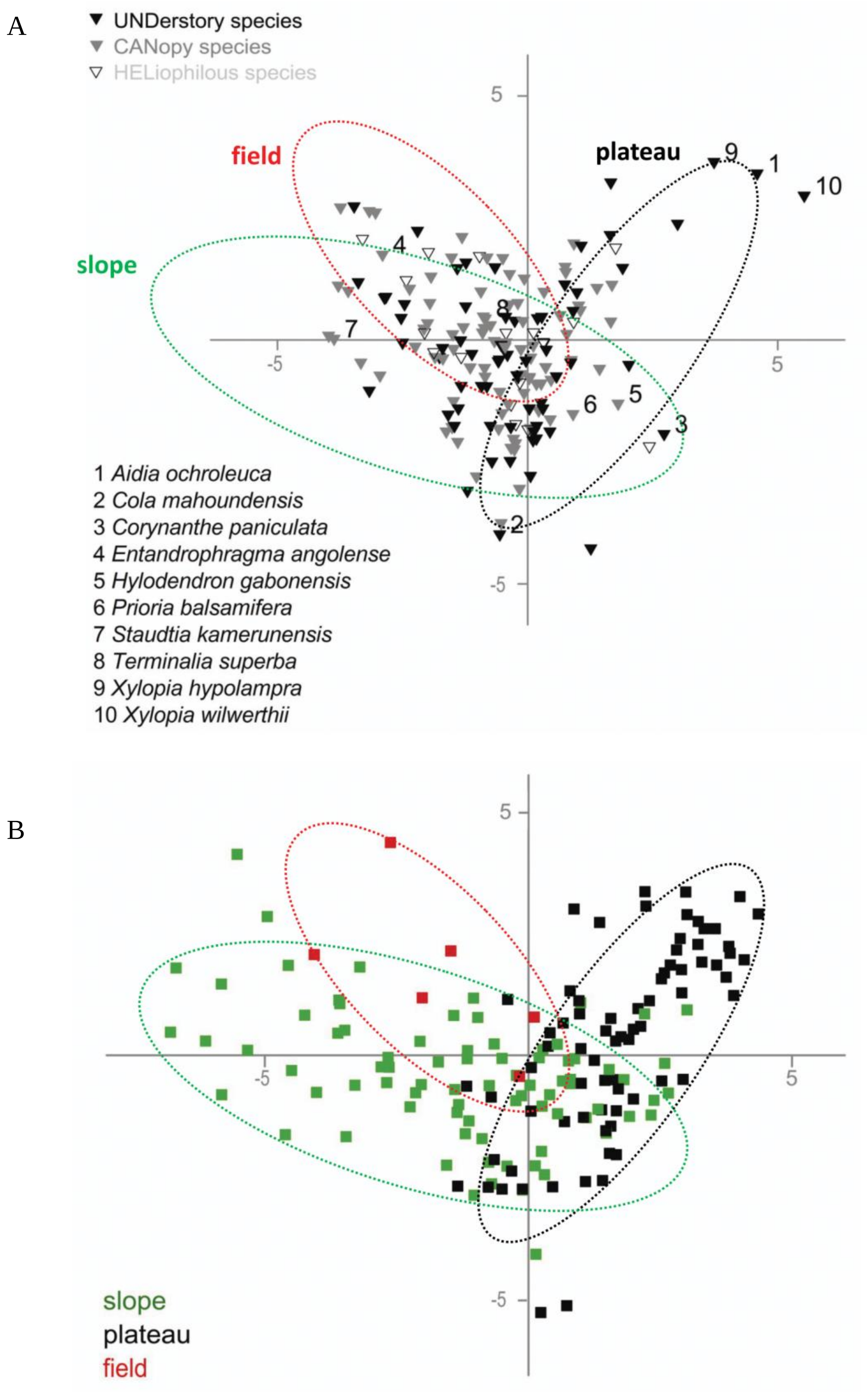

Figure 2-2. (A) Ordination based on a detrended correspondence analysis (DCA) of all tree species identified in the UH48 plot in 2006. Only the ten most abundant species are named. Eigenvalues: axis 1 = 7.2, axis 2 = 6.1, axis 3 = 4.8, axis 4 = 3.9. (B) Projection of the 164 inventory subplots according to their species composition revealing regions of the ordination space corresponding to each topographic class (slope, field, plateau).

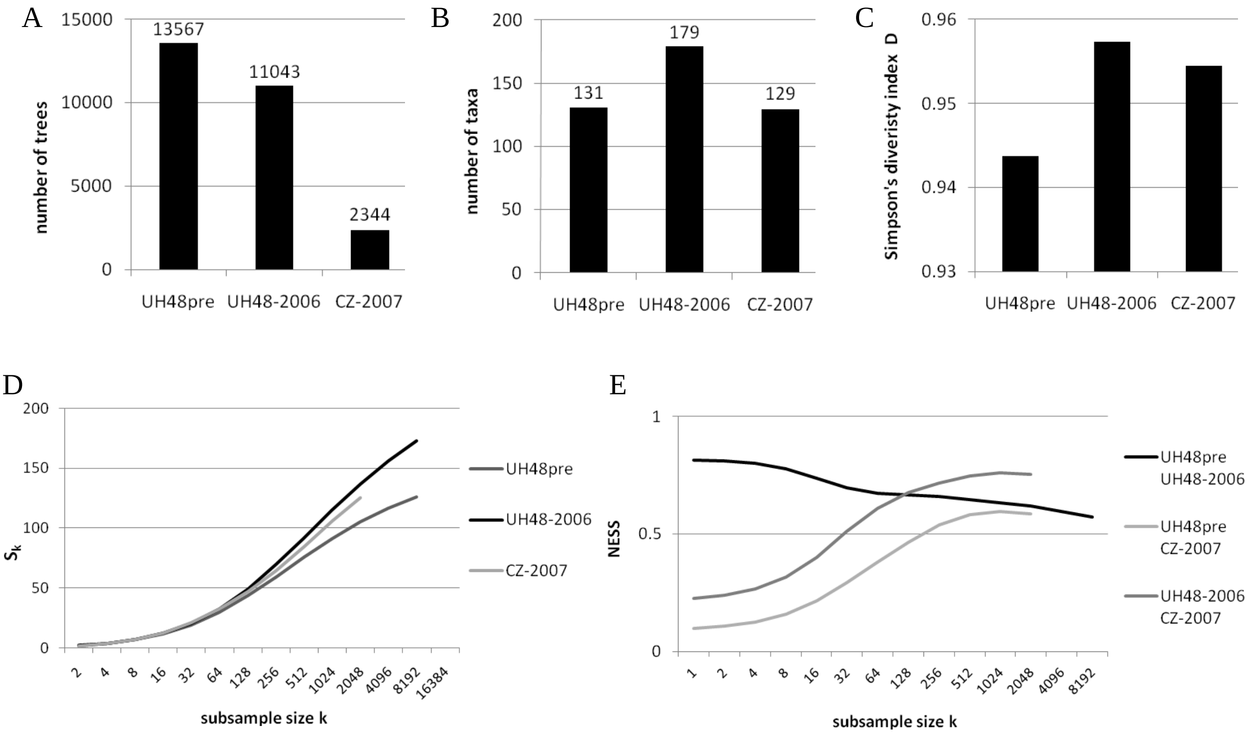

FIGURE 2-3. (A) Sample size, (B) number of taxa and (C) Simpson's diversity index D compared between inventories of the UH48 plot in 1948 before the treatment (UH48 pre) and in 2006 (UH48-2006), and of the central zone of the Reserve of Luki in 2007 (CZ-2007). (D) Comparison of species accumulation curve (S_k) and (E) variation of species similarity using the Morisita-Horn index generalised as NESS, based on rarefaction principles. All inventories were based on the highest inventory diameter limit (gbh > 60 cm) that was used in the central zone.

The total number of trees (gbh > 20 cm) inventoried in the UH48 plot diminished between UH48pre (13,968 trees) and 2006 (11,699 trees) but the number of taxa and the Simpson's diversity index D jointly increased (Fig. 2-3A, B and C). Comparing the species composition of the UH48 plot before the treatment (UH48pre) and in 2006 (UH48-2006) the Morisita-Horn index generalised as NESS was always very high but decreased with increasing subsample size k (Fig. 2-3E). Between the UH48 plot (UH48pre and UH48-2006) and the central zone of the Reserve (CZ-2007) an opposite tendency was observed. NESS was small for k = 1 but increased with subsample size.

Since 1948 the total basal area has increased in the UH48 plot for all functional groups (Fig. 2-4). However, while the gain was very low for the canopy species it was more substantial for the heliophilous species. In the central zone the importance of light-demanding species appeared intermediary between the 1948 and 2006 values in the UH48 plot.

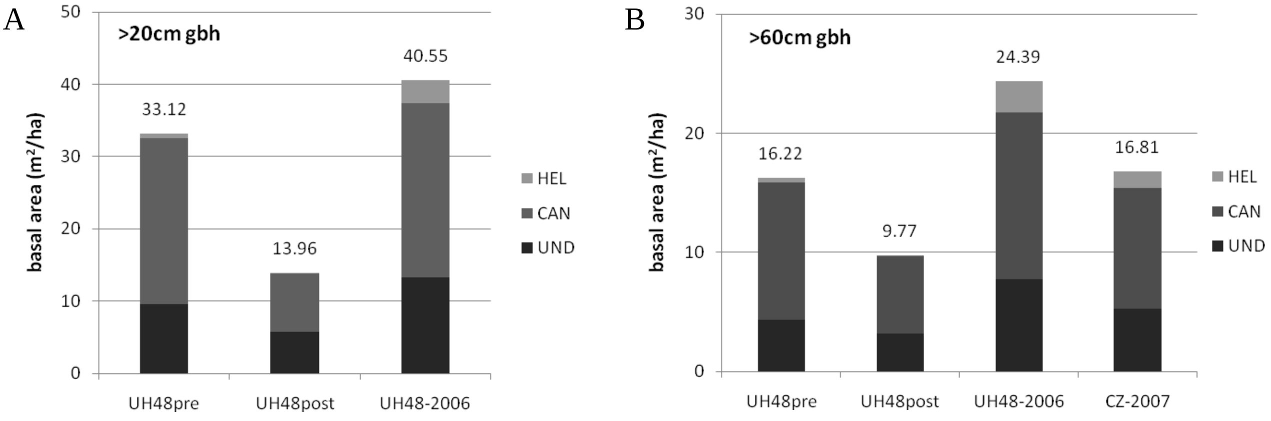

FIGURE 2-4. (A) Basal area of all inventoried trees in the UH48 plot in 1948 before (UH48pre) and after (UH48post) the transformation thinning treatment, and in 2006 (UH48-2006). (B) Comparison with the current state of the central zone of the Reserve (CZ-2007), only for trees above 60 cm of gbh. Species are grouped according to their life history traits: HEL = long-lived heliophilous species, CAN = canopy shade-bearers, UND = understory shade-bearers. Total basal area is indicated on top of the bars.

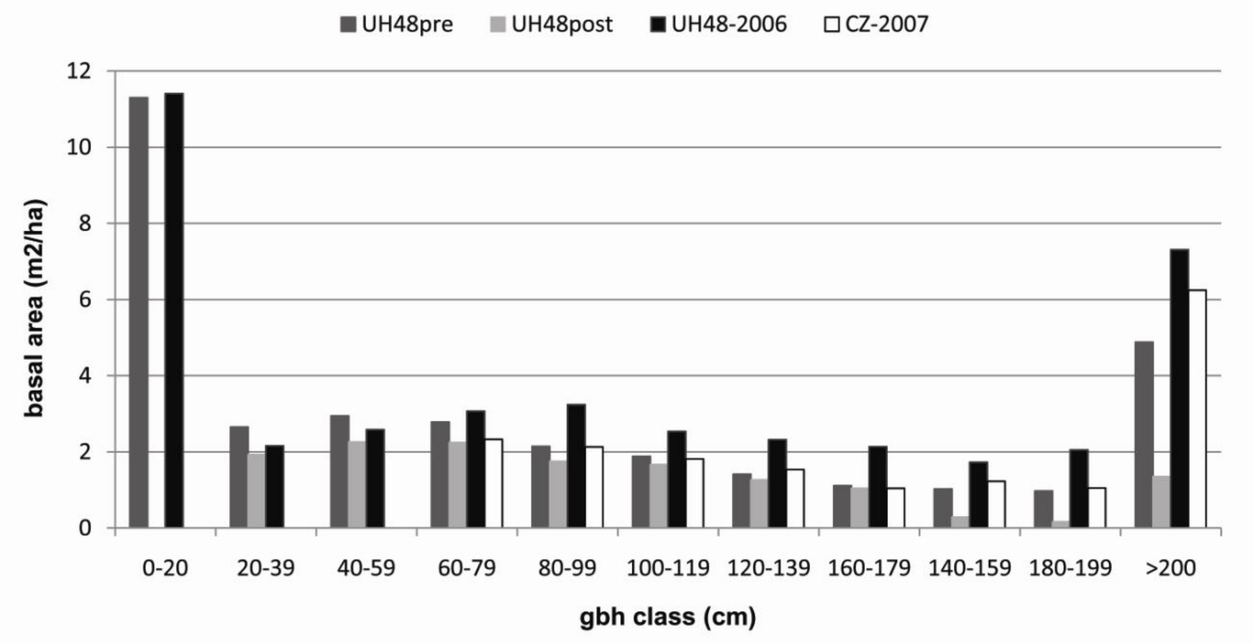

FIGURE 2-5. Size class distribution of basal area for all trees inventoried in the UH48 plot in 1948 before (UH48pre) and after (UH48post) the transformation thinning treatment, in 2006 (UH48-2006) and in 2007 in the central zone (CZ-2007, only > 60 cm gbh) in the Reserve of Luki, DRC.

All basal area distributions had a typical "inverse J-shape" (Fig. 2-5): values were the highest in the smallest size class then decreased more or less steadily towards the bigger sizes, with an accumulation in the highest class (explained by the class having an open superior limit). For trees between 20 and 59 cm of gbh, a lack was visible in 2006 compared to 1948 in the UH48 plot. But for all other size classes the value of basal area was the highest in 2006. In the central zone the basal area was at an intermediary level between UH48pre and UH48-2006, for all size classes.

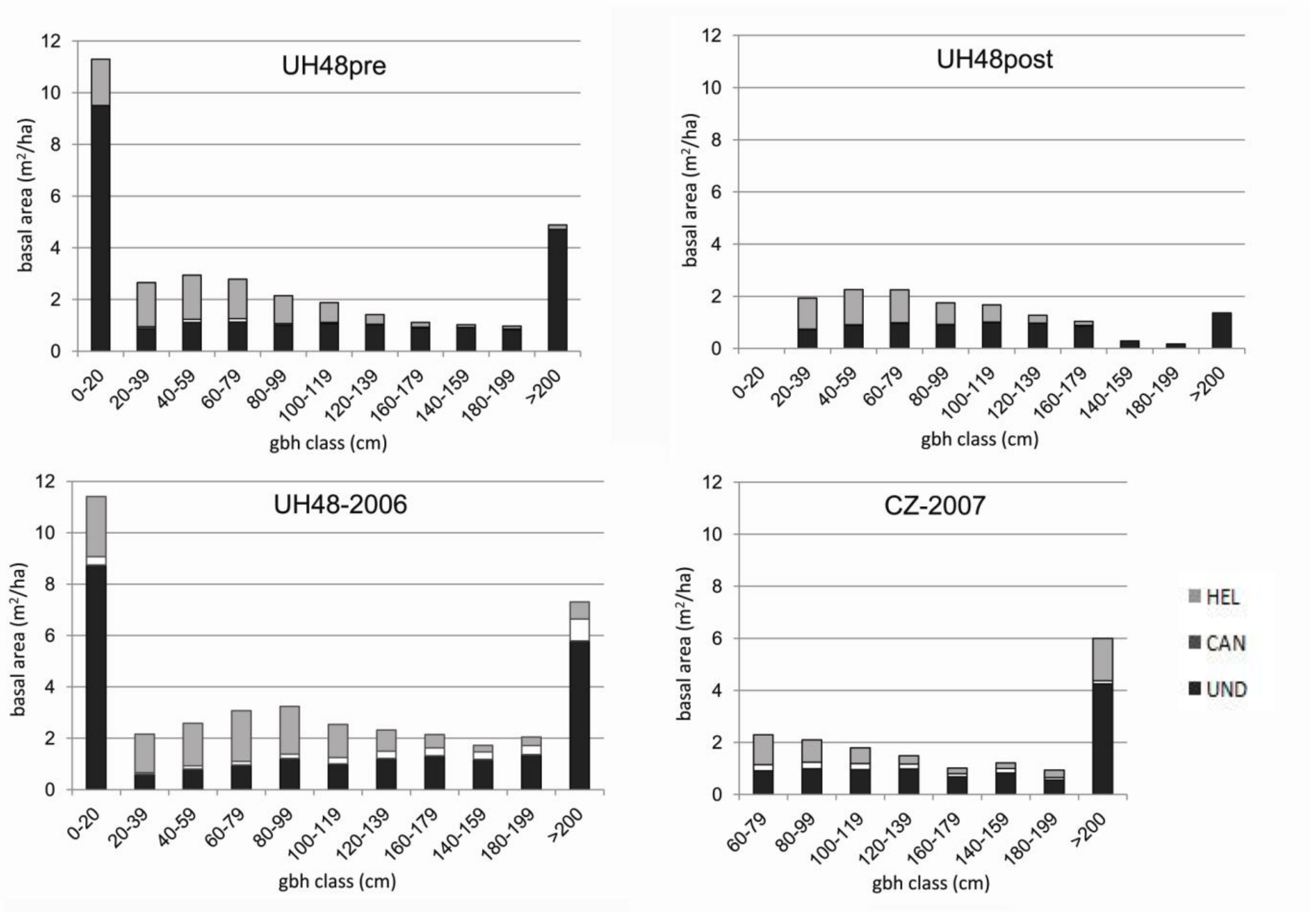

FIGURE 2-6. Size class distributions of all trees inventoried in the UH48 plot in 1948 before (UH48pre) and after the transformation thinning treatment (UH48post) and in 2006 (UH48-2006), and in the central zone of the Reserve of Luki in 2007 (CZ-2007). Species are grouped according to their life history traits: HEL = long-lived heliophilous species, CAN = canopy shade-bearers, UND = understory shade-bearers.

The size distribution of trees of UH48pre showed a “bump” between 20 and 80 cm of gbh (Fig. 2-6). In 2006 a similar shape was observed but seemingly shifted towards bigger gbh values by one or two classes (40-120 cm). In UH48pre trees in the biggest size classes (140 cm of gbh and above) were abundant, at a level similar to the central zone. The treatment in 1948 consisted in harvesting most of these big individuals, therefore they were almost absent in the UH48post basal area distribution. In 2006 however, these big trees were more abundant than 58 years before and also more abundant than in the central zone at the same time.

From UH48pre to UH48-2006 the proportion of light-demanding species increased. In UH48pre they were rare and confined to sizes between 40 and 79 cm gbh, then in UH48post absolutely no heliophilous species remained. In the same plot 58 years later, the proportion was higher and shifted towards bigger size classes (60 cm of gbh and more). In the central zone, heliophilous species were present but mostly in intermediate size classes (60 to 139 cm of gbh).

DISCUSSION AND CONCLUSIONS

The reference flora for Central Africa started being developed in 1948, notably thanks to the inventories used in this study (Hutchinson 1927-1936, INEAC 1948-1960a, Frodin 1964). The botanical identifications reported by Donis (1951) are thus well documented and specimens of unknown or doubtful species were harvested systematically. They were conserved in the herbaria of Luki and of the National Botanic Gardens of Belgium in Meise, which allowed verifications and corrections of species names during the 2006-2007 inventories. Genus and species names that remained ambiguous were not taken into account (they represented less than 1% of the total basal area) and individuals were lumped together at the genus level when the species could not be identified.

The ordination of species and plots in the UH48 plot in 2006 revealed their repartition along two major gradients. The subplots classified as “slope” were grouped on the right side of the graph, suggesting that the horizontal axis may reflect a gradient of disturbance level. The six “field” subplots appeared in the top-left corner of the graph, which may also reflect specific site characteristics. First, agricultural fields in the middle of the forest are similar to big gaps and are synonymous with heavy disturbance, confirming the hypothesis that the horizontal axis may indicate the disturbance level. Second, fields are set very precisely on the most fertile grounds of the forest, suggesting that the vertical axis might indicate soil fertility. The soil preferences of species are however not known and would be needed to confirm this interpretation.

The inverse J-shape of the size-class basal area distributions reflects the good regeneration potential of communities in the UH48 plot in 1948 before the treatment, with abundant regeneration and big trees (“mother” trees). The transformation thinning greatly modified the general structure of the community since all trees of gbh < 20 cm and > 200 cm were removed. These perturbations are different from natural disturbances that would affect trees of all sizes and not specifically a few size classes as shown here in the basal area distributions.

The initial size-structure was however regained in 2006 with both regeneration and big trees being even more abundant than in 1948. The forest stand thus recovered its initial size structure less than 58 years after a major disturbance, indicating a good resilience capacity of the community.

The central zone of the Reserve was supposed to be a reference site for this study. However, the species composition differs considerably from the UH48 plot, both in 1948 and in 2006. Moreover, it appeared to have an important proportion of light-demanding species that require at least some moderate disturbances to establish. The proportion of heliophilous species was more important in the central zone than in the UH48 plot before the transformation thinning, which refuted our assumption. Our results suggest that the central zone must also have been heavily disturbed in the last 58 years.

Looking at individual species, in the different inventories of the UH48 plot most of the understory species were always very abundant. Although they were totally removed from the plot in 1948 they were among the most frequent tree species in 2006. Only two understory species did not withstand the treatment and had very low abundance levels or totally disappeared in 2006 (*Monodora angolensis* and *Garcinia epunctata.).* Understory species globally had a good capacity of recovery after a major disturbance except for a few sensitive species that may have lower dispersal or resprouting capacities. Among shade-bearer canopy species, the large timber trees *Hylodendron gabunense* and *Dialium spp.* were not harvested in 1948 and remained at similar abundance levels until 2006. New canopy species also appeared and became among the most frequent species between 1948 and 2006, such as *Staudtia kamerunensis* or *Polyalthia suaveolens*.

Values of species diversity in Luki were globally low, validating the relatively poor diversity of rain forests in Africa compared to other parts of the world (Parmentier *et al.* 2007). Assuming equivalent quality of species identification, among the four inventories studied here the UH48 plot in 2006 was the most diverse. There was a gain in species diversity in this stand between 1948 and 2006. The index of species similarity was generally low and increased with subsample size, indicating a large difference in composition for the dominant species but a similar floristic background between the two dates. Dominant species were not harvested in 1948 since the treatment aimed at favouring their growth but some dominant trees were withdrawn from the stand between 1948 and 2006 by illegal logging. However, the basal area of the most sought after dominant species such as *Prioria balsamifera* or *Piptadeniastrum africanum* actually increased, indicating high growth capacity after disturbance. Between the UH48 plot in 1948 before the treatment and in 2006, the index of species similarity was generally high but decreased with the subsample size. This means that the same species dominate both forests and that the difference in floristic composition is mostly due to the less abundant species. In fact, looking at the NESS for k = 2048 (rare species weighing much) it appears that the inventories of 2006 in the UH48 plot and in the central zone are more similar than in the UH48 plot between 1948 and 2006. This would suggest that a global change in floristic composition occurred in the UH48 plot during that time. The augmentation of light-demanding species between 1948 and 2006 confirms this pattern that may be due to heavy disturbances in the stand. However, the number and proportions of shade-bearer canopy species also rose during the same period.

According to the IDH if a disturbance event was not so recent that pioneers dominate, the high tree species richness of a forest stand is explained by intense or frequent large-scale disturbance (Connell 1978). Species diversity in the UH48 plot in 2006 is higher than in 1948 and also than in the central zone of the Reserve at the same time. This would mean that the moderate level of disturbance in the UH48 plot, due to logging by local inhabitants, is favourable to tree species diversity. These recurrent moderate disturbances might have helped to progressively reduce the high increase in competition due to the initial drastic cut and may be an important explanation for the promotion of local species diversity. In line with the IDH, larger-scale or more intense disturbances would however lead to decreasing species diversity over time with late-successional tree species becoming increasingly dominant (Burslem and Whitmore 1999, Sheil and Burslem 2003). Additional analyses on the structure and diversity of the other forest components such as lianas, non-woody plants, fauna and micro-fauna would be necessary to draw conclusions on the present characteristics of the ecosystem and on the possible influences of disturbances.

This study revealed that 58 years after an extensive silvicultural treatment the floristic diversity and biomass content of a rain forest community of trees increased. Moderate disturbances such as logging by local inhabitants may favour tree species diversity and biomass production in rain forest communities. However, forest management plans supporting species diversity must still prevent the intensification of perturbations that would arguably lead to the inverse tendency.

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CHAPTER 3

Ten years of tree phenology in a seasonal rain forest of Central Africa

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ABSTRACT

Knowing the phenological behaviour of rain forest tree species would allow better understanding of natural ecosystem processes and the possible influence of environmental changes. The extensive and long-term observations required are difficult to realise but unpublished records have been preserved that can be exploited today.

In this study ten years of phenological data on 3750 woody plants gathered from 1948 to 1957 in the rain forest Reserve of Luki, West of the Democratic Republic of Congo, were analysed. Patterns of defoliation, flowering, fruiting and dissemination of fruits were drawn for species and functional groups of species and their relationship with rainfall was investigated.

Most tree species have annual rhythms of leaf and reproductive phenology. A wide array of phenological patterns was highlighted, from synchronous annual peaks to continuity. Positive association between leaf phenology and rainfall was proved for the group of canopy species and for the canopy and heliophilous study species. For the heliophilous and understory groups and for the understory study species however, positive correlation with rainfall was found for reproductive phenology (flowering and fruiting). Direct or indirect associations with intra-annual and supra-annual climate variations suggest that changes in environmental conditions may affect phenological patterns of tropical trees thus species interactions and ecosystem dynamics in general.

Key words: Central African rain forest; tropical tree phenology; climate-phenology relationship; ancient datasets.

INTRODUCTION

Phenology (from the Greek *phainein*, to show or appear) is the study of recurring life-cycle events including leaf fall, flowering, fruiting and seed dissemination (Fenner 1998, Berlin *et al.* 2000, Morisette *et al.* 2009). It has mostly been studied in the temperate zone where phenological patterns comply with regular climate seasonality (Newstrom *et al.* 1994, Menzel *et al.* 2005). In winter low temperatures limit cambial activity and cause dormancy in most plants, then the reproductive and leaf cycle resume in spring when temperatures and photoperiod rise again. In the humid tropics phenological events can also be initiated and driven by environmental factors such as temperature, precipitation and day length (Menzel *et al.* 2005, Sundarapandian *et al.* 2005, Brearley *et al.* 2007). Nevertheless, even during the dry season humidity and temperature are rarely low enough to be strict limiting factors. This allows for high plasticity and induces a high diversity of phenological patterns (Frankie *et al.* 1974, Newstrom *et al.* 1994, Borchert 1999). Consequently, in a tropical rainforest it is common to observe very different phenological stages simultaneously on different tree species but also on trees of the same species (Capon 1947, Whitmore 1998). In the same forest stand and within the same species a tree can start flowering while another is releasing fruits close by, or one can be completely leafless while new leaves are flushing on a neighbour.

Phenological events are controlled by a combination of abiotic and biotic factors that determine the occurrence or inhibition of physiological events (Daubenmire 1972, Ims 1990, van Schaik *et al.* 1993, Borchert 1999). In temperate climates they are mostly driven by changes in temperature or photoperiod, which explains the global synchronicity among trees (Rutishauser *et al.* 2007). In the tropics tree phenology can also be associated to variations of climate or day length but endogenous factors seem to be more important than in temperate trees (Reich and Borchert 1984, Tutin and Fernandez 1993, Borchert *et al.* 2005). Depending on the species and site, endogenous and seasonal environmental factors contribute in varying proportions to the tree water status which is the primary driver of phenology in tropical trees (Borchert 1999, Singh and Kushwaha 2005). A diverse array of phenological strategies are consequently found in tropical forests (Bawa *et al.* 2003, Singh and Kushwaha 2006, Stevenson *et al.* 2008) with possible intra-specific plasticity (Bullock and Solis-Magallanes 1990, Borchert *et al.* 2004).

Phenological patterns and their changes in relation to climate have been documented at the community level for several tropical ecosystems including rain forests (Lowman 1992, van Schaik *et al.* 1993, Chidumayo 1994, Chapman *et al.* 2005, Wright and Calderón 2006).

Experimental evidence is however lacking at the species level because extensive field studies imply methodological demands that are rarely fulfilled (Stiles 1975, Wright and Cornejo 1990, Stevenson *et al.* 2008). Time-wise, the lifespan of a tree commonly extends far beyond the one of a researcher and projects running more than a few years are scarce. In addition, for practical matters such as location and manpower few field stations exist that would allow the fine-scale monitoring of enough trees. As a consequence long-term and extensive phenological studies in the humid tropics are rare (Newstrom *et al.* 1994, Newbery *et al.* 2006, Wright and Calderón 2006, Stevenson *et al.* 2008). In Central Africa, two studies have been reported in Uganda (Chapman *et al.* 1999, Chapman *et al.* 2005).

Better knowledge of the phenological rhythms of tropical trees would help to improve forest management plans. It would also be useful for dendrochronological studies, since tree ring formation has been found to associate with clear phenological rhythms in several tropical and sub-tropical species (Amobi 1973, Heinrich and Banks 2006). The lack of phenological information also limits the understanding of the ecology and evolution of tropical plant species and communities (Newstrom *et al.* 1994). The timing of life-cycle events such as flowering or seed production has direct influence on population dynamics. Phenological rhythms play an important role in the interference between trees e.g. for the access to resources and for pollination, or in mechanisms of plant speciation. Moreover, not only plants but also animals depending on plant resources can be affected by variations in phenological patterns. Knowing the relationships between phenology and climate would also allow inferring the evolution of ecosystems under the foreseen modifications of climate, which is expected to be globally warmer and drier in tropical Africa (Malhi and Wright 2004, Boisvenue and Running 2006, Boko 2007, Bonan 2008, Koenig 2008).

The existence of long-term phenological observations sometimes recorded decades ago and the recent renewal of scientific research in the Democratic Republic of Congo (DRC) give a chance to fill the knowledge gap on the phenology of tropical trees. In the 1940s and 1950s extensive studies were set on forests of the Congo Basin, including a large phenological survey launched in 1948 in the reserve of Luki, at the extreme West of the DRC. During ten years, 3750 individuals of various woody species were monitored on a ten-day basis for defoliation, flowering, fruiting and dissemination of fruits. Tree species were pooled in three groups (CAN = canopy shade-bearers, UND = understory shade-bearers, HEL = long-lived heliophilous species, see Chapter 2) according to their main functional traits and the timing of dominance in forest succession (Swaine and Whitmore 1988, ter Steege *et al.* 2002, Chazdon *et al.* 2010). The ten-year record of phenological observations was analysed to address the following questions about the leaf and reproductive cycles of tropical tree species. Are there regular rhythms in the phenology of trees in a tropical rain forest? Are phenological patterns shared among species and groups of species or are there large inter- and intra-specific variations in phenological rhythms? Are intra-annual or year-to-year variations associated to changes in climate?

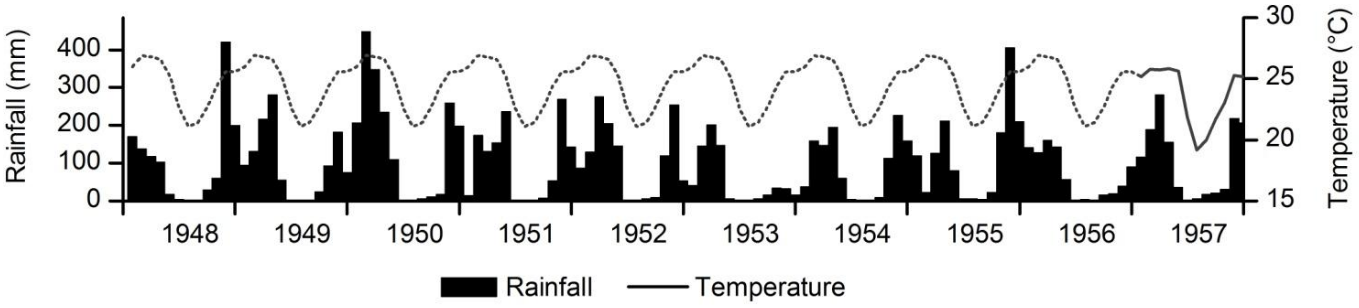


FIGURE 3-1. Records of rainfall (mm) during the ten years of monitoring and of temperature (°C) for the year 1957 from the meteorological station of Luki, DRC (5°28'-5°42' N, 13°4'-13°18' E). For the rest of the period, average of temperature values from 1957 to 2006.

MATERIALS AND METHODS

STUDY SITE

The Luki forest Reserve is located in the south-western DRC 30 km north from the port city of Boma. It is the southernmost remnant of the highly diverse Mayombe forest (Monteiro 1962). Average annual temperature and rainfall estimates are 24.6 °C and 1180 mm, respectively. During the period of monitoring, annual rainfall was remarkably low between 1951 and 1954 (Fig. 3-1). Rainfall is seasonal in the region. A major dry period with less than 50 mm of monthly precipitation occurs from June to September and a minor one around February (Couralet *et al.* 2010). However the hilly landscape and the vicinity of the Atlantic Ocean cause frequent mists and dense cloud cover that maintain relative air humidity always above 80 % (Senechal *et al.* 1989, Pendje and Baya ki 1992, Lubini 1997, Couralet *et al.* 2010). Despite relatively low rainfall the vegetation of Luki is thus a tropical semi-evergreen rain forest of the Guineo-Congolian forest domain (Lebrun and Gilbert 1954, Lubini 1997, Whitmore 1998).

MONITORING AND DATA ANALYSIS

In the forest Reserve of Luki 3750 ligneous individuals were monitored every ten days from January 1948 to December 1957 for defoliation (defined as leaf shedding, not as complete leaflessness), flowering, fruiting and dissemination of fruits (Appendix 1). Data was handwritten on notebooks that were conserved in the herbarium of Luki and were digitalised in Excel files from 2006 to 2008 on the spot. Species were referred to by vernacular names (Kiyombe language) and the corresponding scientific names were found thanks to the field botanist M. Ngoma and African florae (Hutchinson 1927-1936, INEAC 1948-1960, Aubréville 1961). Among all individuals 15 were lianas and 93 remained in the category "unknown", either because they were unidentified at the time of monitoring or because their vernacular name could not be associated to a present scientific name. Eventually, phenological data on 3642 trees of 158 species were used for this study. The dataset was analysed for individuals lumped into species and in groups of species formed according to functional traits (see Chapter 2). In each group, representative species with high number of observations were selected for this study (Appendix 1):

- group CAN (canopy) including *Prioria balsamifera* (Fabaceae/Caesalpinioideae): species mostly confined to the canopy, shade-tolerant and slow-growing;
- group HEL (heliophilous) including *Terminalia superba* (Combretaceae): species emerging in gaps, light-demanding and fast-growing;
- group UND (understory) including *Xylopia wilwerthii* (Annonaceae), *Corynanthe paniculata* and *Aidia ochroleuca* (both Rubiaceae): species mostly confined to the understory, small-statured and slow-growing.

The proportion of trees for which a phenological event was observed was calculated for every ten-day period and time-series were plotted over the ten years of monitoring. In addition, to highlight seasonal tendencies the proportions of trees were averaged for the whole period into monthly values represented on annual bar-graphs. Methodological details, e.g. on how the phenological stages were determined or how the observations of the crowns were made, were not available.

The phenological data was also compared with contemporaneous climate variations. Rainfall records were available from the Luki meteorological station for the whole monitoring period but air temperature was available only for the last year (1957). Both climate variables are moreover significantly correlated (r = 0.64, P < 0.01, 1957-2006). The relationships between phenology and climate were thus analysed using rainfall data only. First, to study the impact of rainfall variations on the onset of phenological events, “wet”, “dry” and “normal” years were selected. If the annual sum of precipitation was above *average + 1 SD* (standard deviation) the year was qualified “wet”, if it was below *average - 1 SD* the year was qualified “dry” and if it was between these two values the year was considered “normal”. We then examined the average starting time of each phenological event in the three types of years to see if variations in rainfall levels would associate with variations in the onset of phenological events. Furthermore, for the five study species and the three groups of species Pearson correlations were calculated between the maximum amounts of trees showing defoliation, flowering, fruiting or dissemination of fruits and the annual sum of precipitation during the same period (1948-1957).

RESULTS

GENERAL TENDENCIES IN PHENOLOGICAL ACTIVITIES DURING THE TEN YEARS OF MONITORING

The time-series of phenological events revealed annual periodicity in defoliation, flowering, fruiting and dissemination of fruits for all study species and groups of species, although most clearly for *Prioria balsamifera*, *Terminalia superba*, *Xylopia wilwerthii* and the group of heliophilous species (Fig. 3-2 and 3-4). Besides, a general decrease in the proportion of trees showing a phenological event was observed for all groups from 1951, reaching a minimum in 1954 then re-gaining previous levels in 1957. Notably, for *T. superba* there was no progressive decrease but only in 1954 levels were very low for all phenological events (more than half the average of the other years). A delay of up to five months in the timing of all phenological processes was moreover associated to this drop for all species, e.g. for *P. balsamifera* the maximum proportion of trees flowering during a reproductive cycle was 53% in December 1948 but 10 % in February 1954. Previous values and timing were regained in the following one or two years for all species.

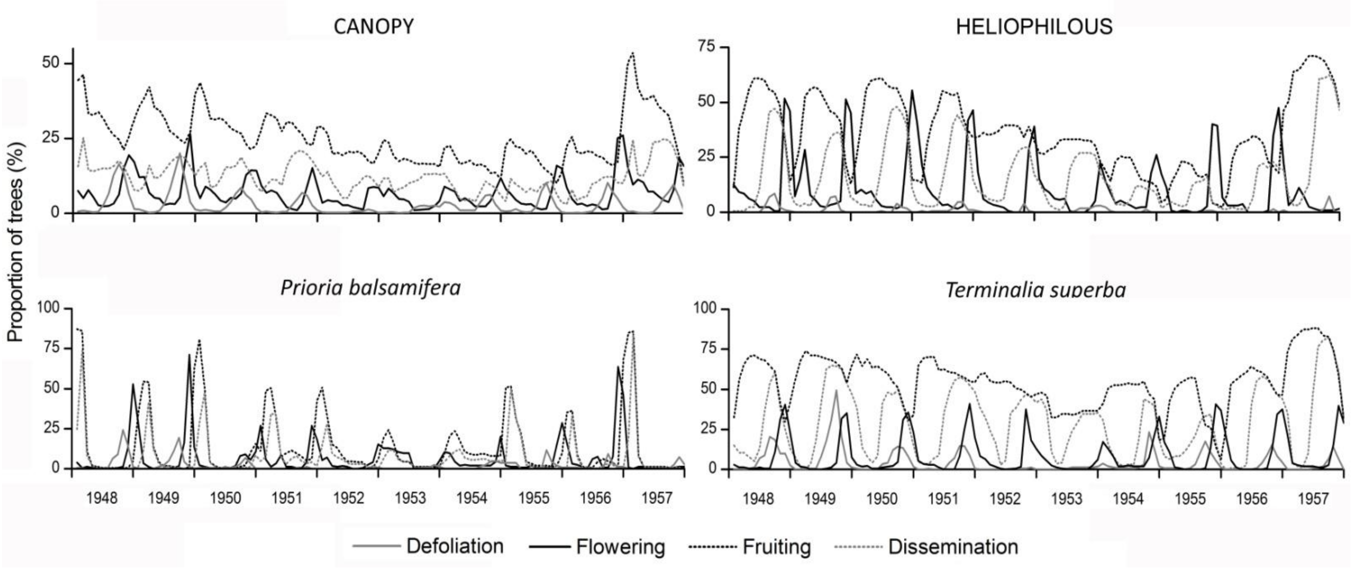


FIGURE 3-2. Monthly time series of reproductive and leaf phenology for the canopy group including *Prioria balsamifera* and the heliophilous group including *Terminalia superba* from 1948 to 1957 in the Reserve of Luki, DRC.

LEAF PHENOLOGY

In the three functional groups leaf shedding started at the end of the dry period (August-September) and was maximal at the transition between the dry and rainy seasons (Fig. 3-2 to 3-5). The highest proportions of simultaneously leaf-shedding trees were found for the canopy group and the lowest for understory species. Shade-tolerant canopy species had the clearest pattern of defoliation with up to 20 % of trees simultaneously shedding leaves, with a maximum in August-September. For *P. balsamifera* defoliation was maximal every year in August. Defoliation also occurred every year around September in the group of heliophilous species but only for a very limited amount of trees (less than 5 % of the monitored trees). *T. superba* however had the highest amounts of trees shedding leaves simultaneously (49 %), in September 1949 (Fig. 3-2). For understory trees only a small proportion of trees shed leaves (less than 2 %), also during the transition between dry and rainy seasons. The maximum of 3 % was reached in October 1948 for *C. paniculata*, while defoliation was never observed during the monitoring period for *A. ochroleuca* (Fig. 3-4 and 3-5).

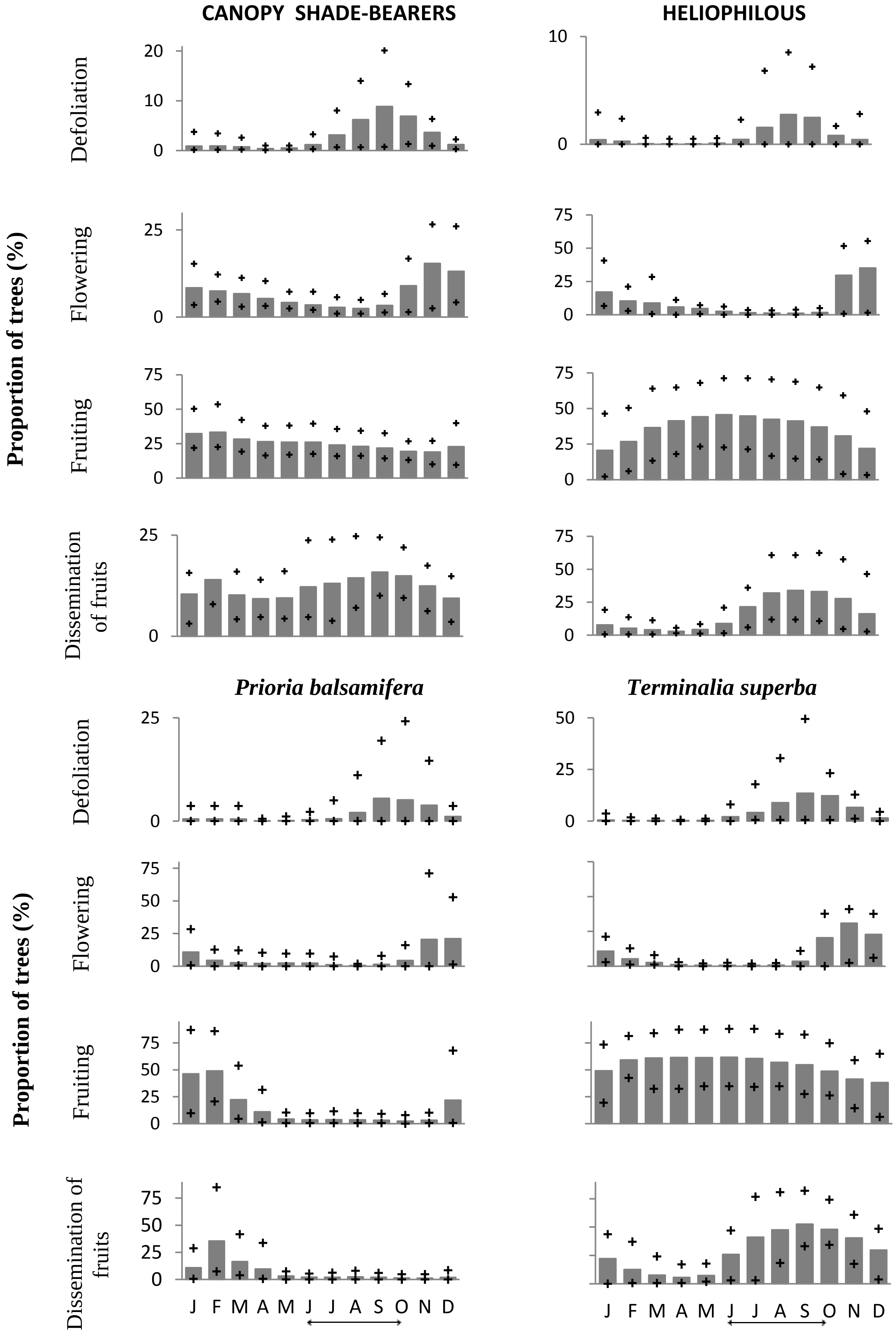


FIGURE 3-3. Phenological seasonality for the functional groups of canopy shade-bearers and long-lived heliophilous species and representative species *P. balsamifera* and *T. superba*, respectively. Bars represent average proportions and crosses indicate maximum and minimum values for the period 1948 -1957 in the reserve of Luki, DRC. Black arrows indicate the dry season.

REPRODUCTIVE PHENOLOGY (FLOWERING, FRUITING AND DISSEMINATION OF FRUITS)

Overall, the different reproductive stages were observed in all periods of the year (Fig. 3-2 to 3-5). The heliophilous group had the clearest periodicity of reproductive stages (Fig. 3-2). Sharp flowering peaks were observed just after defoliation, in a short period around November thus at the beginning of the rainy season. Flowering was maximal around November for *T. superba* and was observed on up to 40 % of the trees during the years of monitoring, except in 1954 where this maximum was much lower. A second peak of flowering was sometimes observed at the end of the rainy season (March-April) for the light-demanding species, most clearly in 1948 and 1957. Fruiting and dissemination of fruits followed flowering with a lag of approximately five and ten months, respectively. Both events were also spread in time. Fruits were for example observed on 45 % of *T. superba* trees or more all year long (Fig. 3-2). For canopy and understory species the flowering was also maximal in September-October but the amount of concerned trees was much smaller and peaks were less sharp than in the heliophilous group (Fig. 3-2 and 3-4). Moreover, maximum production and dissemination of fruits occurred early after flowering peaks (one or two months), unlike for light-demanding species. *P. balsamifera* also had clear reproductive patterns (Fig. 3-2 and 3-3). Flowering started in August and reached a maximum around December. Fruits were then mostly formed in February and rapidly disseminated afterwards. Among the three small-statured shade-tolerant species, *X. wilwerthii* stood out with very clear seasonality of reproductive processes contrary to the spread patterns of *C. paniculata* and *A. ochroleuca* (Fig. 3-5). *X. wilwerthii* flowered approximately one month before the other species and showed the highest proportions of trees flowering at the same time (45 % on average in October). Flowering was observed all year long on *C. paniculata* and *A. ochroleuca* trees with maxima in March and November, respectively.

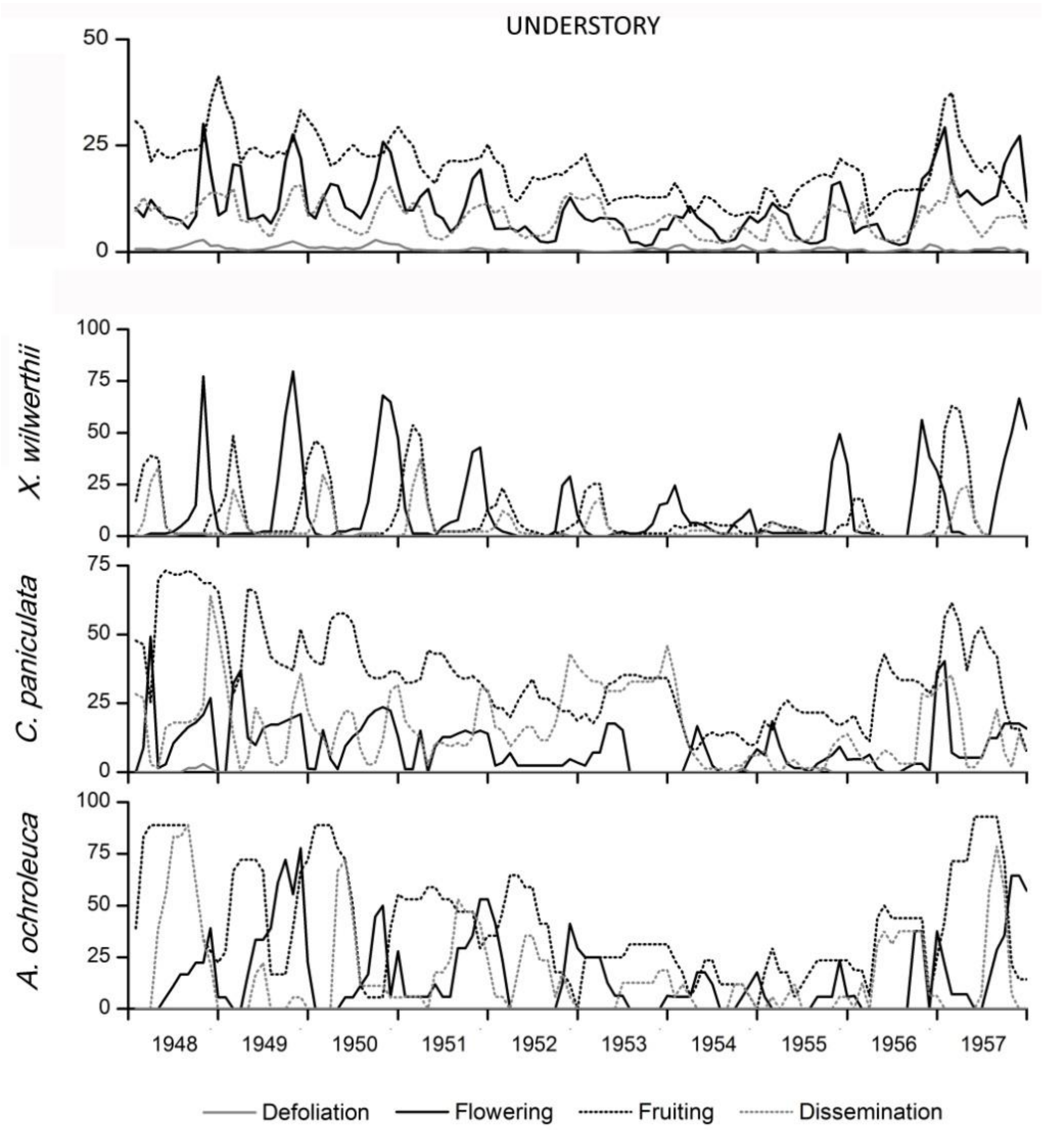


FIGURE 3-4. Monthly time series of reproductive and leaf phenology for the understory group and representative tree species from 1948 to 1957 in the Reserve of Luki, DRC.

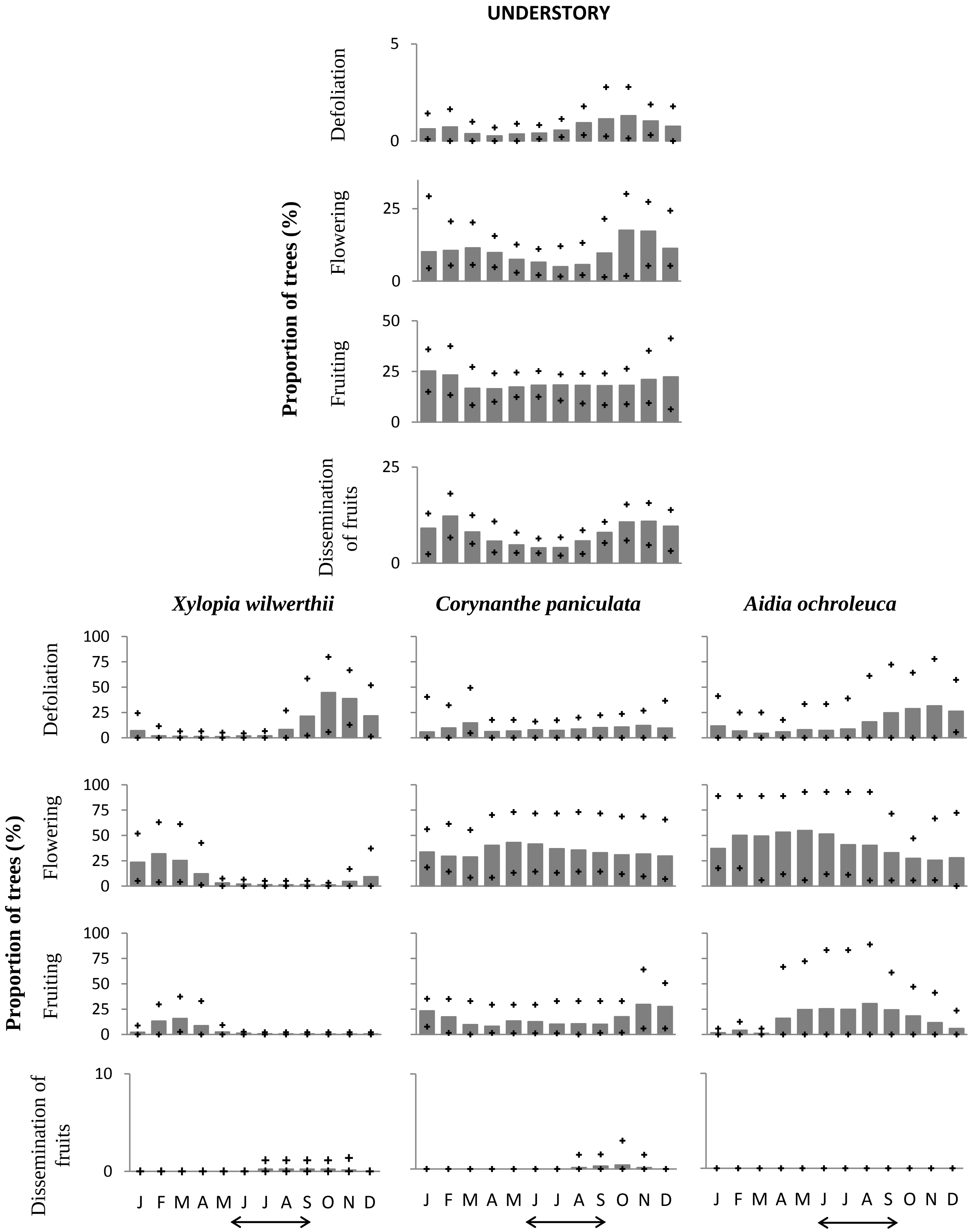


FIGURE 3-5. Phenological seasonality for the functional group of understory species and three representative species. Bars represent average proportions and crosses mark maximum and minimum values for the period 1948-1957 in the Reserve of Luki, DRC. Black arrows indicate the dry season.

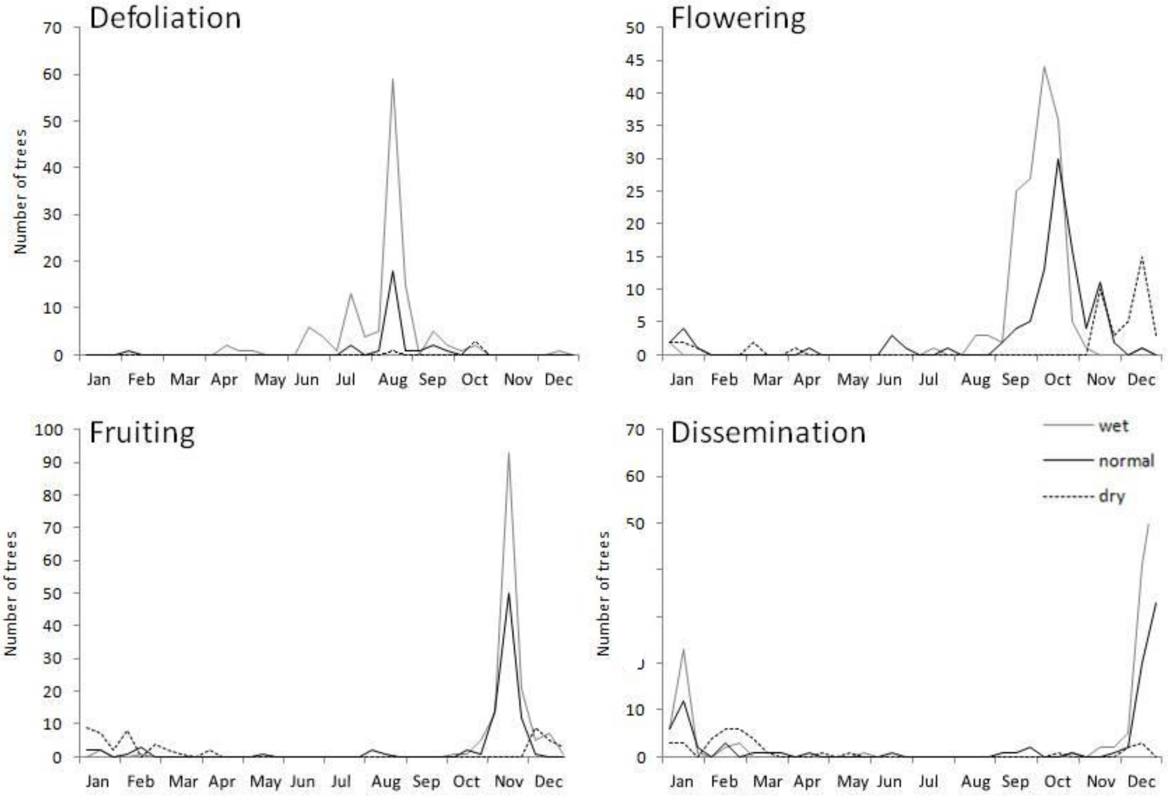
PHENOLOGICAL EVENTS IN RELATION TO RAINFALL

Flowering generally started at the beginning of the rainy season for *P. balsamifera*, *T. superba* and *X. wilwerthii* (Fig. 3-6). For *C. paniculata* and *A. ochroleuca* flowering was spread through the year. Two flowering peaks were observed for these understory species, the first at the beginning of the rainy season (September-October) and the second at the re-start of rains after the minor dry season (March). However, for the five study species the onset of the reproductive cycles varied depending on the annual sum of rainfall. In wet years flowering, fruiting and fruit dissemination occurred slightly earlier than in normal years but most clearly, in drier years the reproductive cycles were shifted towards later in the year. This was especially visible for the tall species *P. balsamifera* and *T. superba*. Concerning defoliation data was not sufficient and no clear shift appeared depending on rainfall levels, but for *P. balsamifera* leaf shedding was noticeably the clearest during wet years.

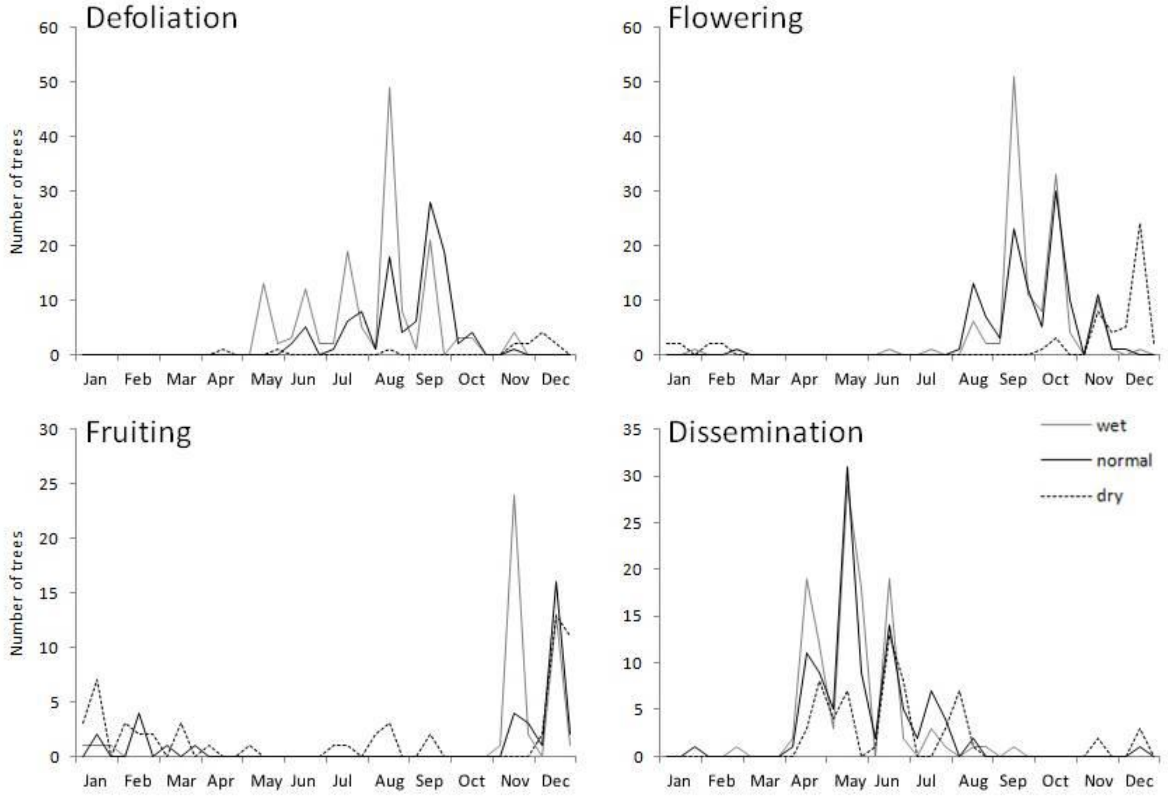
For the canopy species including *P. balsamifera* high positive correlations were found between the maximum amount of trees shedding leaves and total annual rainfall (Table 3-1). For *T. superba* a similar positive association was found between defoliation and rainfall, furthermore flowering was also positively correlated with rainfall. Likewise, significant positive correlations between flowering and rainfall were found for the groups of heliophilous and understory species and for *X. wilwerthii.* A positive association of reproductive cycles with rainfall was also highlighted for the other two understory species *C. paniculata* and *A. ochroleuca,* concerning fruiting.

TABLE 3-1. Pearson's correlation between the maximum number of trees for which defoliation (DEF), flowering (FL), fruiting (FR) or dissemination of fruits (DISS) was observed each year and the annual sum of rainfall. ns = non significant correlations ($P < 0.05$).

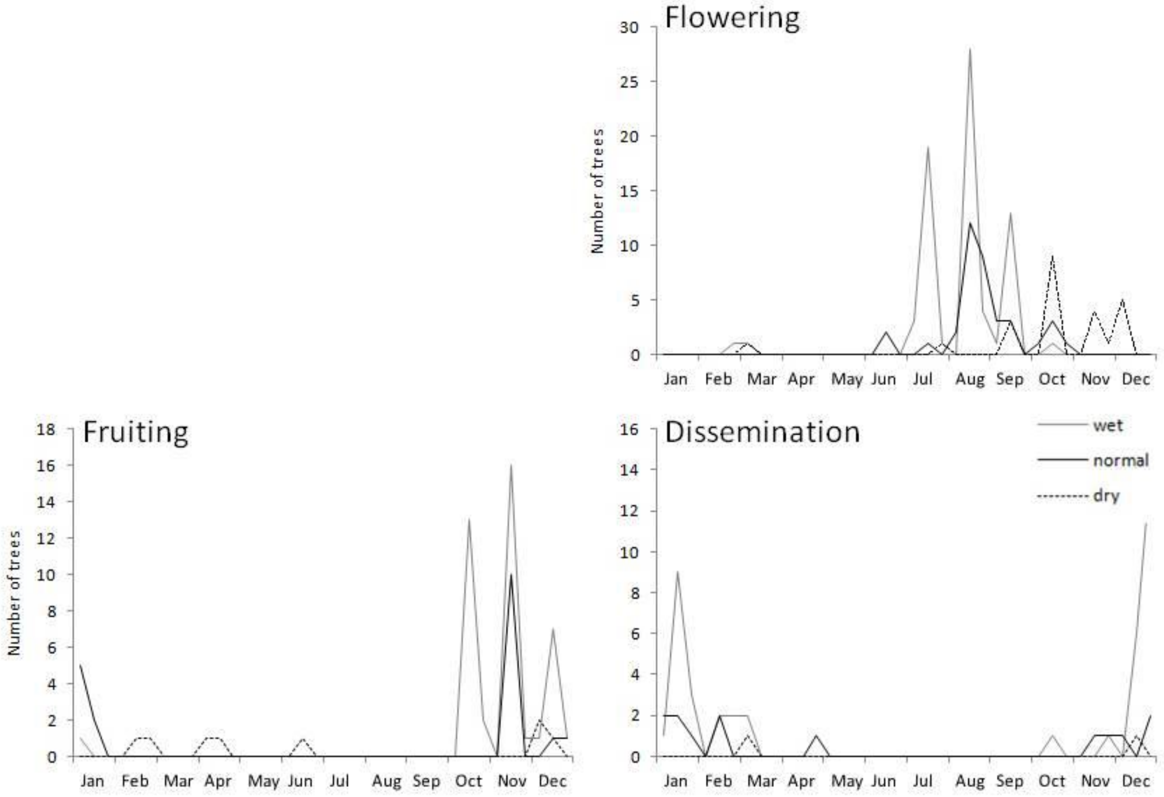
	DEF	FL	FR	DISS
Prioria balsamifera	**0.73**	ns	ns	ns
Terminalia superba	**0.78**	**0.68**	ns	ns
Xylopia wilwerthii	ns	**0.73**	ns	ns
Corynanthe paniculata	ns	ns	**0.78**	ns
Aidia ochroleuca	-	ns	**0.67**	ns
CANOPY	**0.85**	ns	ns	ns
HELIOPHILOUS	ns	**0.67**	ns	ns
UNDERSTORY	ns	**0.68**	ns	ns



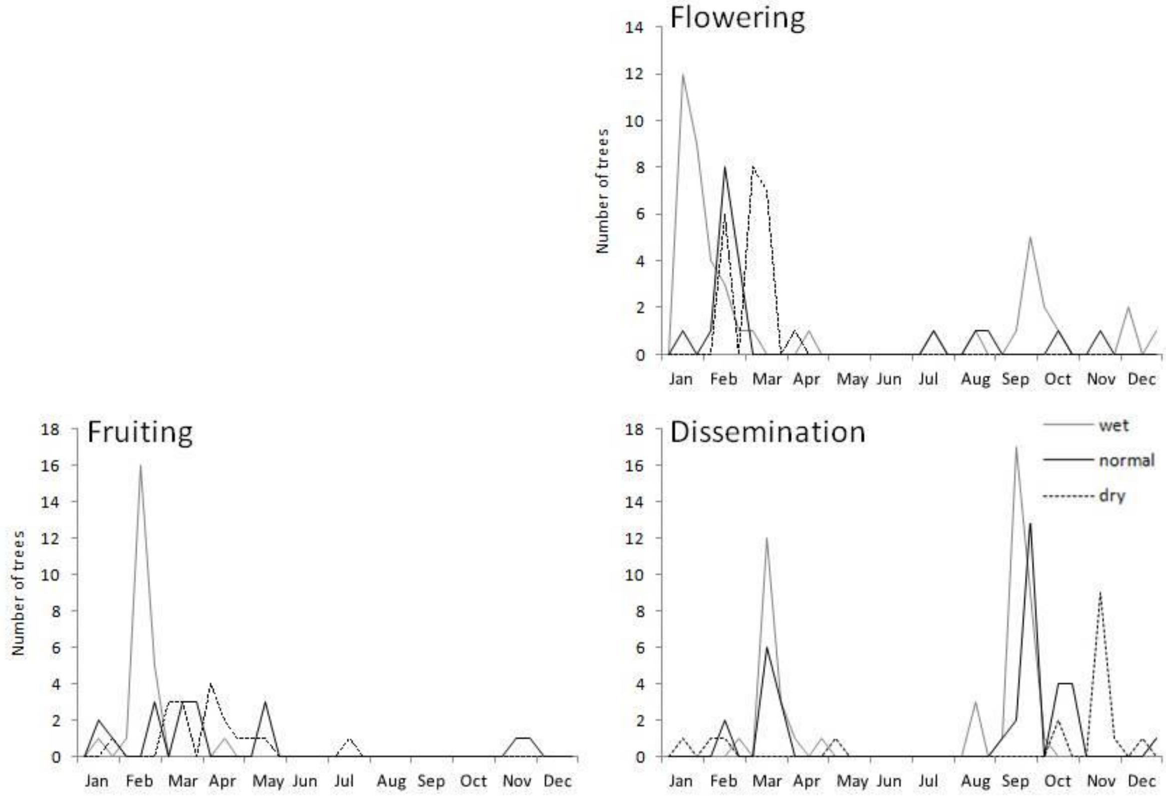
Prioria balsamifera



Terminalia superba



Xylopia wilwerthii



Corynanthe paniculata

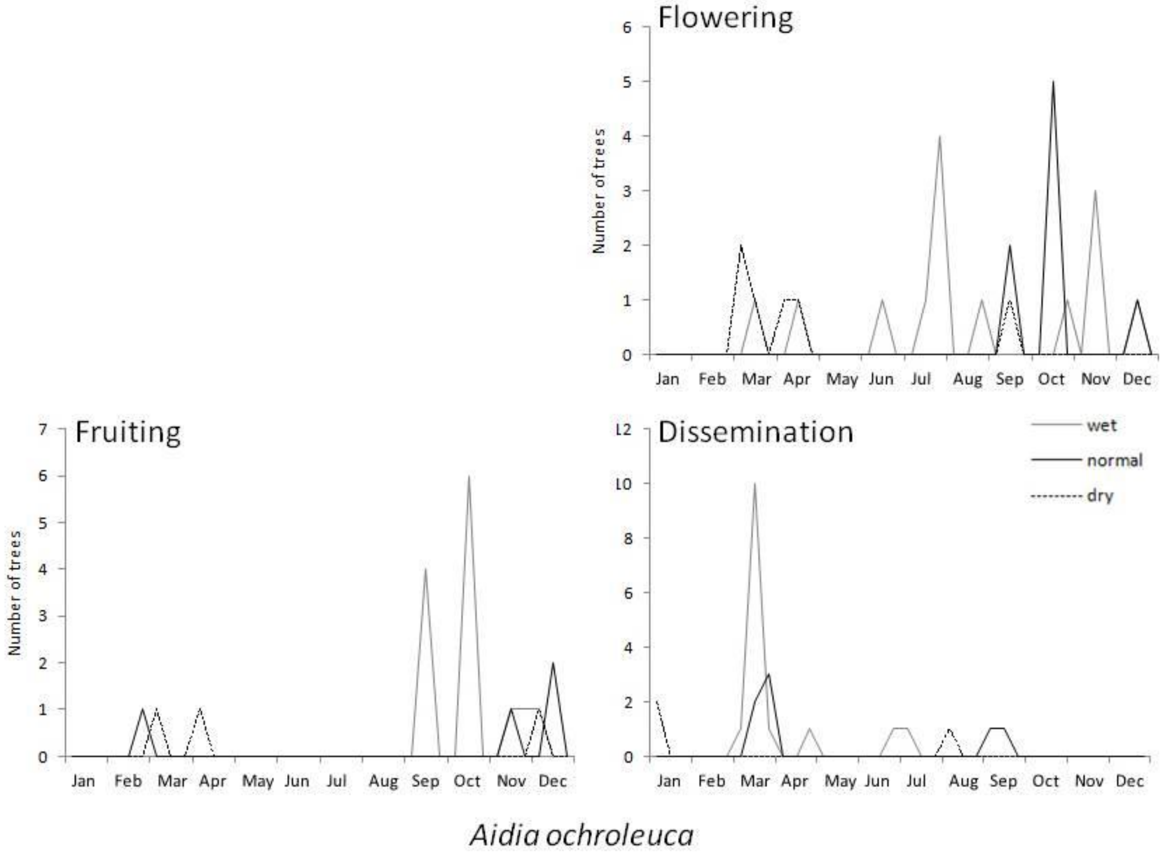


FIGURE 3-6. Onset of defoliation, flowering, fruiting and dissemination of fruits in wet, normal and dry years for the five study species between 1948 and 1957 in the Reserve of Luki, DRC.

DISCUSSION AND CONCLUSIONS

The ten-year long phenological monitoring of trees in Luki (1948-1957) revealed annual rhythms of leaf and reproductive cycles for species and groups of species. The frequencies of observations within species were however always low. For example the maximum proportion of trees of the same species flowering simultaneously was 55 % but the average of maxima was only 17 %. Trees of the same species were thus usually at different phenological stages at the same time, confirming the important intra-specific variability of phenological patterns commonly observed in tropical rain forests (Capon 1947, Frankie *et al.* 1974, Newstrom *et al.* 1994, Whitmore 1998, Borchert 1999).

TABLE 3-2. Synthesis of the seasonality of phenological events for *Prioria balsamifera* (P), *Terminalia superba* (T), *Xylopia wilwerthii* (X), *Corynanthe paniculata* (C) and *Aidia ochroleuca* (A) and for the functional groups of canopy (CAN), heliophilous (HEL) and understory (UND) species. Symbols indicate the month where defoliation (🍂), flowering (❀), fruiting (🍎) and dissemination of fruits (✱) was observed in the maximum proportion of trees and dashes indicate that the event was observed on at least 20 % of the trees (averages from 1948 to 1957 in the Reserve of Luki, DRC). The rainy season is displayed in grey.

		J	F	M	A	M	J	J	A	S	O	N	D
Defoliation	P									🍂			
	T									🍂			
	X										🍂		
	C										🍂		
	A				*no defoliation observed*								
	CAN										🍂		
	HEL										🍂		
	UND										🍂		
Flowering	P											-	❀
	T										-	❀	-
	X									-	❀	-	-
	C			❀									
	A								-	-	-	❀	-
	CAN									-	❀	-	-
	HEL			❀									
	UND										❀	-	
Fruiting	P	-	🍎	-									
	T	-	-	-	-	-	🍎	-	-	-	-	-	-
	X	-	🍎	-									
	C	-	-	-	-	🍎	-	-	-	-	-	-	-
	A					🍎							
	CAN	-	🍎	-									
	HEL	-	-	-	-	🍎	-	-	-	-	-	-	-
	UND	🍎	-	-	-	-	-	-	-	-	-	-	-
Dissemination of fruits	P		✱										
	T						-	-	-	✱	-	-	-
	X			✱									
	C	-	-								-	✱	-
	A					-	-	-	✱	-	-		
	CAN			✱									
	HEL	-	-								-	✱	-
	UND		✱										
Season		▨	▨	▨	▨	▨	*Dry season*				▨	▨	▨

LEAF PHENOLOGY

A. ochroleuca was the only strict evergreen species in this study, with no leaf shedding observed during ten consecutive years. For all other species and groups of species common periods of defoliation with annual frequencies were observed, reaching maxima in September-October thus at the transition between the dry and rainy seasons (Table 3-2). Leaf fall was however very limited and spread through the year for understory species, thus we did not find any significant relationship with monthly rainfall data. Species remaining evergreen through the dry season are supposed to have access to groundwater (Borchert 1994, Williams *et al.* 1997). Moreover, variations in air and soil humidity may be less strong for understory species growing under a dense vegetation cover, than for taller trees directly exposed to climate variations. Thus, *P. balsamifera* and *T. superba* had clear defoliation patterns and leaf shedding appeared to associate positively with total annual rainfall. Moreover leaves are most likely shed during wet years. The timing of leaf fall is often linked with some change in environmental conditions such as water availability, temperature or photoperiod (Fenner 1998). In tropical trees growing under seasonal climate leaf fall is known to coincide with the attainment of seasonal minima in leaf water potential (e.g. (Opler *et al.* 1980, Bullock and Solis-Magallanes 1990, Heinrich and Banks 2006), which is probably the case in September-October in Luki after several months with no rain. Besides, the increased leaf fall during especially wet years reveals an unusual phenological pattern. Rainfall induced leaf abscission was previously observed but remains rare (Elliott *et al.* 2006, Mehltreter and Garcia-Franco 2009).

Globally, the amounts of trees simultaneously shedding leaves were always low, reaching a maximum of only 50 % for *T. superba*, yet designated as a typical deciduous tree. The constantly high levels of air humidity in Luki (Lubini 1997, Couralet *et al.* 2010) may explain that trees generally suffer little water deficit. Leaf fall may thus be partial for most trees, even for species that are usually strictly deciduous but have intermediary habits in such climate conditions. This capacity to modify the occurrence and timing of leaf abscission depending on the environment highlights the phenological plasticity of tropical trees, which was already showed for temperate trees growing in tropical climates (Borchert *et al.* 2005) or for tropical species with large distribution ranges (Borchert *et al.* 2004).

REPRODUCTIVE PHENOLOGY

Annual synchronicity of reproductive phenology was observed among tree species and groups of species in Luki between 1948 and 1957. Levels of reproductive events (flowering, fruiting and dissemination of fruits) were globally high in 1948 and 1949 but steadily decreased between 1950 and 1955. Frequencies were especially low in 1954 for all species, which may be explained by the very low rainfall in 1953 and 1954 caused by an El Niño event. Annual sums of precipitations were slightly above average in 1948 and 1949 (1268 and 1260 mm respectively, compared to 1180 mm on average for the period 1948-2006) and extremely high in 1950 (1845 mm). The reproductive processes observed during those years may thus have been above their usual levels. On the other hand, the annual sum of precipitation was only 654 mm in 1953, which was the driest year of the period 1948-2006. Until 1955 the sum of rainy season precipitations remained below average, with monthly rainfall never above 300 mm. Trees may thus have suffered water deficit, resulting in weakened and/or delayed reproductive activity. The tendency was most marked for light-demanding species usually growing in open spaces and consequently more prone to experience temporary droughts. Moreover, mast fruiting years were observed for all species and groups of species in 1956-57 thus when rainfall levels regained high levels after a four-year drier period. Positive correlations between the frequencies of reproductive events and rainfall also support the view that the reproductive activity of tropical rain forest trees is globally associated to rainfall levels, through changes in tree water status (Augspurger 1981, Borchert 1998, Singh and Kushwaha 2005).

In most species and groups of species flowering occurred immediately after defoliation at the beginning of the rainy season but later for *C. paniculata* and the heliophilous group, in March. These two tendencies were also found in the group of understory trees, with flowers mostly formed in the early rainy season but a second peak being commonly observed at the end of the season. The first flowering peak may be caused by the influence of the first rains after the dry season on bud break. In Luki the dry season is cloudy and solar irradiance gets higher during the rainy season. It is maximal in March (Couralet *et al.* 2010) and could explain the second peak of flowering. These two flowering patterns correspond to two tendencies previously reported in tropical forests. In seasonal tropical climates flowering is often triggered by the first rains of the rainy season thus concentrated in the transition from the late dry to the early wet season (Murali and Sukumar 1994) but flower production may also coincide with peaks of irradiance (Wright and van Schaik 1994).

Subsequent fruit formation mostly occurred during the second half of the rainy season in Luki, as observed in other studies (Selwyn and Parthasarathy 2007). Fruiting was however observed all year long for the heliophilous and understory groups and more specifically for *T. superba* and *C. paniculata*. The double-winged samaras of *T. superba* and the winged seeds contained in the *C. paniculata* capsular fruits seem to remain on the tree crowns for a while and to be wind-dispersed progressively. Moreover, the maximum dissemination of fruits was observed before the end of the rainy season for most species but at the beginning of the following one for *T. superba* and *C. paniculata*. Our results support the hypothesis that adequate development time from flowering to fruit dissemination has been favored so that seeds are released in rainy periods when germination is most likely to be induced and seedlings start growing with low probability of drought (Garwood 1983, Stevenson *et al.* 2008). Although other abiotic factors must be involved these results confirm the direct or indirect role of rainfall on physiological processes promoting bud break and subsequent flowering in tropical trees (Augspurger 1981, Fenner 1998).

While regular annual periodicity was found for maximal frequencies of flowering and fruiting, patterns varied widely among species as commonly seen in tropical forests (Lowman 1992, Newstrom *et al.* 1994). *X. wilwerthii* and *P. balsamifera* had clear flowering and fruiting peaks, but *T. superba* and the heliophilous group showed sharp flowering peaks followed by fruiting spread over several months. Last, for *C. paniculata*, *A. ochroleuca* and the understory and canopy groups, reproductive patterns appeared erratic.

While interpreting the patterns in groups would be hazardous because of the possible flattening effect of averaging, for species each pattern may be a response to a different set of selective pressures. Strong peaks of flowering and fruiting are common for deciduous species and for species that are pollinated and dispersed by animals (Borchert 1999, Stevenson *et al.* 2008) and suggest disadvantages to out-of-season individuals. Moreover, fruiting peaks at the community level may be favored because they avoid the pressure of seed predators through satiation effect (van Schaik *et al.* 1993). On the other hand, irregular patterns may be due to inconsistent selective pressures such as year-to-year variations in environmental conditions or changes in pollinator or predator abundances (Fenner 1998).

PHENOLOGY AND WOOD GROWTH

The relationships between leaf or reproductive phenology and radial wood growth are not clear for tropical trees (Wright and Cornejo 1990, Fenner 1998, Schöngart *et al.* 2002, Heinrich and Banks 2006). Based on results from a previous study (Couralet *et al.* 2010), it appears that the flowering months for *A. ochroleuca* (November, beginning of the rainy season) and *C. paniculata* (March, middle of the rainy season) are also the months where the correlation between rainfall and tree-ring width is maximum. Although these results are based on statistical associations and do not prove causation, these months may be or have been particularly important for the physiology of *C. paniculata* and *A. ochroleuca*. Both species belong to the Rubiaceae family thus are taxonomically related (Petit 1962, Stoffelen *et al.* 1996). Phylogenetic inertia or shared adaptive responses may explain this common timing of flowering and radial wood growth (Stevenson *et al.* 2008). On the contrary no association was found between phenological patterns, growth data and climate for *X. wilwerthii*. As already seen for some brevi-deciduous and evergreen trees, for this understory species phenology and cambium growth seem to be uncoupled from climatic seasonality at sites with low water deficit avoiding seasonal drought stress like in Luki (Borchert 1999). For the canopy shade-bearer *P. balsamifera* and the light-demanding *T. superba* however, we showed that the extent and timing of reproductive events are related to climate variations. For tall tropical tree species the frequencies of trees flowering and fruiting are positively correlated with rainfall and the onset of reproductive cycles is associated to rainfall levels.

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CHAPTER 4

Species-specific growth responses to climate variations in understory trees of a Central African rain forest

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ABSTRACT

Basic knowledge of the relationships between tree growth and environmental variables is crucial for understanding forest dynamics and predicting vegetation responses to climate variations. Trees growing in tropical areas with a clear seasonality in rainfall often form annual growth rings. In the understory, however, tree growth is supposed to be mainly affected by interferences for access to light and other resources. In the semi-deciduous Mayombe forest of the Democratic Republic of Congo, the evergreen species *Aidia ochroleuca*, *Corynanthe paniculata* and *Xylopia wilwerthii* dominate the understory. We studied their wood to determine whether they form annual growth rings in response to changing climate conditions.

Distinct growth rings were proved to be annual and triggered by a common external factor for the three species. Species-specific site chronologies were thus constructed from the crossdated individual growth-ring series. Correlation analysis with climatic variables revealed that annual radial stem growth is positively related to precipitation during the rainy season but at different months. The growth was found to associate with precipitation during the early rainy season for *Aidia* but at the end of the rainy season for *Corynanthe* and *Xylopia*.

Our results suggest that a dendrochronological approach allows the understanding of climate-growth relationships in tropical forests, not only for canopy trees but also for evergreen understory species and thus arguably for the whole tree community. Global climate change influences climatic seasonality in tropical forest areas, which is likely to result in differential responses across species with a possible effect on forest composition over time.

Key words: African rainforest; *Aidia ochroleuca*; climate-growth relationships; *Corynanthe paniculata*; tropical dendrochronology; understory trees; *Xylopia wilwerthii*.

INTRODUCTION

Tropical forests are under combined pressure of global macro-climate changes and deforestation that rapidly modify local climatic conditions (Bonan 2008). In Africa, the average temperature is expected to rise by 3 to 4°C during the 21st century, which is 1.5 times more rapid than the foreseen global temperature change (Boko 2007). Future climate scenarios also predict a 5 to 15 percent decrease in precipitation during the rainy season and a decline of 3 to 4 percent in annual rainfall per decade in the African tropics (Malhi and Wright 2004, Boisvenue and Running 2006). In addition, direct human pressure is likely to increase the vulnerability of forests to these warmer and drier conditions (Koenig 2008). Recent modeling studies showed that deforestation enforces the effects of warming and drought events (Malhi *et al.* 2008). It is however unknown how different forest types will develop under these constraints, since long-term records on responses of tropical tree species to changes in environmental factors are lacking (Clark 2004, Phillips *et al.* 2009). Depending on climate region, forest type or canopy position, tree species can differ in their tolerance to drought and shade (Condit *et al.* 1995, Sterck *et al.* 2006, Engelbrecht *et al.* 2007). The high diversity of species and their variable ecological preferences potentially allow a high diversity of reactions within the tree communities. Yet, testing this hypothesis has so far proved difficult, due to the limited research on species-specific responses to environmental factors in different tropical forest types. Field studies using permanent plots in the tropics provide growth data of at most a few decades and rarely with an annual resolution (Clark *et al.* 2003).

Dendrochronology can provide long-term records of tree growth with annual resolution, but is most successful where climate shows strong and regular seasonality triggering annual ring formation (Jacoby 1989, Schweingruber 1996). Rainforest trees have long been thought not to form annual rings because of weak seasonality and low variability in temperature and day length in the tropics (Whitmore 1998). This persistent assumption caused many dendrochronologists to focus their efforts on temperate trees rather than tropical trees. Such preference is also explained by the extensively complex wood anatomy in tropical trees (Détienne 1989). Nevertheless, across the various tropical biomes and for most trees, alternating environmental conditions induce periods of reduced or suspended cambial activity leading to the formation of identifiable growth layers (Détienne 1989, Mariaux 1995, Worbes 2002). In lowland tropical rainforests, regular growth periodicity allowed the construction of species-specific tree-ring chronologies for several species (Devall *et al.* 1995, Mariaux 1995, Détienne *et al.* 1998, Schöngart *et al.* 2002, Worbes *et al.* 2003, Brienen and Zuidema 2005, Brookhouse 2006, Pumijumnong and Wanyaphet 2006, Schöngart *et al.* 2006, Buckley *et al.* 2007, Lisi 2008, Brienen *et al.* 2009). Such long-term growth series can be cross-compared with climate records to unravel the species-specific sensitivity to past climatic conditions. This is a prerequisite to evaluate the response of vegetation formations to future environmental changes (Condit *et al.* 1995, Pumijumnong and Park 1999, Chidumayo 2005, Trouet *et al.* 2006).

From this perspective, the floristic and structural complexity of tropical rainforests encourages to consider the large range of species they harbor. Much knowledge has been generated on upper-canopy trees that are, at the adult stage, not light-limited and strongly exposed to water stress. On the other hand, the growth of lower-canopy or understory species spending their lifetime under other trees is assumed to be more limited by local site factors such as light than by water (Phipps 1982). Moreover, small-stature trees with ambiguous seasonal variability in leaf fall preferentially use deeper sources of soil water than larger or deciduous trees (Meinzer *et al.* 1999). Ring-width series of understory trees are thus supposed to show a much more variable ontogenetic growth trend, less directly related to external environmental factors and to water stress in particular. Studies of radial growth responses to climate in understory trees of temperate forests support this hypothesis (Liu 1993, Orwig 1997, Rasmussen 2007, Martín-Benito *et al.* 2008). Nevertheless, growth response to climate is hardly documented for evergreen tree species. While in deciduous trees leaf shedding is an obvious sign of cambial dormancy and suggests a clear link between environmental factors and phenology, for evergreen trees this relation is thought to be erratic (Jacoby 1989, Worbes 1999).

We conducted a study on three common, evergreen understory tree species from the Mayombe forest, a tropical semi-evergreen rainforest west of the Democratic Republic of Congo (DRC). Climate changes are expected to affect the region significantly in the 21st century but studies of the influence of climate variations on tree growth in African forests are scarce (Détienne *et al.* 1998, Worbes *et al.* 2003, Couralet *et al.* 2005, Schöngart *et al.* 2006, Sass-Klaassen *et al.* 2008) and to our knowledge still lacking for lower-canopy tree species. We aimed to assess whether dendrochronology is applicable to these understory tree species and if so, whether and how their radial growth dynamics is related to year-to-year and intra-annual changes in climate (temperature, precipitation and solar radiation).

In this study, after demonstrating the annual nature of tree rings in the three understory species investigated (Methods section), we address the following questions: (1) Do trees within and across species synchronize stem growth in response to the same environmental factors? (2) How do trees of different species respond in radial stem growth to year-to-year and within-year variations in climate? We expect to reveal diversity in growth patterns across different understory tree species and given the seasonality in rainfall, we predict positive growth responses to precipitation.

MATERIALS AND METHODS

STUDY SITE

The Reserve of Luki is located in the south-western Democratic Republic of Congo (DRC) (5°28’-5°42’ N, 13°4’-13°18’ E), 30 km north from the port city of Boma (Fig. 4-1). It is the southernmost remnant of the Mayombe forest, stretching along the Atlantic Ocean from the central coast of Gabon and renowned for its high floristic diversity and the presence of large timber trees (Monteiro 1962). The protected forest area covers 32.700 ha of hilly landscape (altitude between 150 and 500 m) on heterogeneous soils, generally ferrallitic and with poor chemical content (Monimeau 1990).

Climate records (1959-2006) were available from the Luki meteorological station for precipitation, air temperature, relative humidity and solar irradiance (Fig. 4-1). The climate is characterized by a mean annual temperature of 24.6°C with limited year-to-year variation and a mean annual rainfall of 1180 mm/yr. A distinct dry period lasts from June to September. Such low annual rainfall and 3 to 4 months with less than 50 mm monthly precipitation generally do not favour the presence of a dense humid forest. However, the strong oceanic influence, the landscape of the region and the self-regulating effect of the vegetation create favourable conditions for the establishment of dense humid forest (Senechal *et al.* 1989, Pendje and Baya ki 1992, Lubini 1997). Mists are present all year long and during the driest months a thick, low-level but non-precipitating cloud layer blocks solar irradiance and causes temperature to drop. The rainfall shortage is thus partially compensated and the relative air humidity remains constantly high, always above 80%. Consequently, despite a clear seasonal rainfall pattern plants may not suffer extreme water stress during the dry season.

The forest of Luki can be generally classified as a tropical semi-evergreen rainforest of the Guineo-Congolean forest domain (Lebrun and Gilbert 1954, Lubini 1997, Whitmore 1998) but occurs in a mosaic landscape with patches of agricultural fields and settlements. It consists of a mixture of deciduous and evergreen tree species in the upper-stratum and mostly evergreen species in the understory.

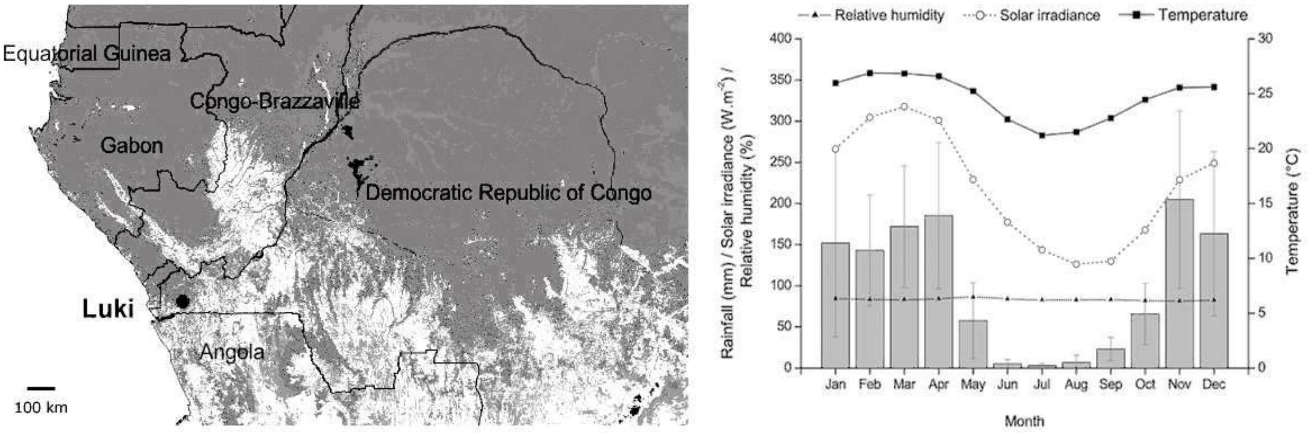

FIGURE 4-1. (A) Location of the study site with simplified vegetation cover of the area from Global Land Cover 2000 (Mayaux 2004): darker zones are a mosaic of evergreen, deciduous and mixed forests with a minimum of 15 percent tree cover. (B) Climate diagram of the Luki meteorological station, DRC: monthly means of rainfall (± standard deviation), temperature, air humidity (1959-2006) and solar irradiance (1959-1994).

STUDY SPECIES

Aidia ochroleuca (K. Schum.) Bullock ex E.M.A.Petit, *Corynanthe paniculata* Welw. (both Rubiaceae) and *Xylopia wilwerthii* Wild. & T.Durand var. cuneata De Wild. (Annonaceae) are abundant and commonly co-occurring species in the Guineo-Congolean rainforests, from Gabon to the eastern DRC (Petit 1962, Schmitz 1988, Senechal *et al.* 1989, Lubini 1997). In the secondary forest of Luki they can contribute to more than 60% of the total basal area (Donis and Maudoux 1951). These evergreen, medium-sized trees of up to 20 m in height and 60 cm in dbh are confined to the lower-canopy level and understory (Aubréville 1961, Petit 1961, Lubini 1997, Lebrun and Stork 2003). *C. paniculata* and *X. wilwerthii* have a straight trunk whereas *A. ochroleuca* is often ramified from the base. All three species are characterized by a very hard and fine-textured wood used by local communities to produce solid tools and high-quality charcoal (Fouarge and Gérard 1964).

SAMPLING AND SAMPLE PREPARATION

Stem discs of five trees per species were collected in 2005. We selected representative trees of each species, with crowns under the closed upper canopy layer and diameters within the predominantly observed range (15 to 40 cm). Trees were cut between 0.5 and 1 m above ground level such that a maximum number of growth rings are visible. The 4-6 cm thick sections were deep-frozen for 2 weeks to prevent insect or fungal attacks and subsequently air-dried. Their cross-sectional surface was planed and sanded up to a grid size of 1200.

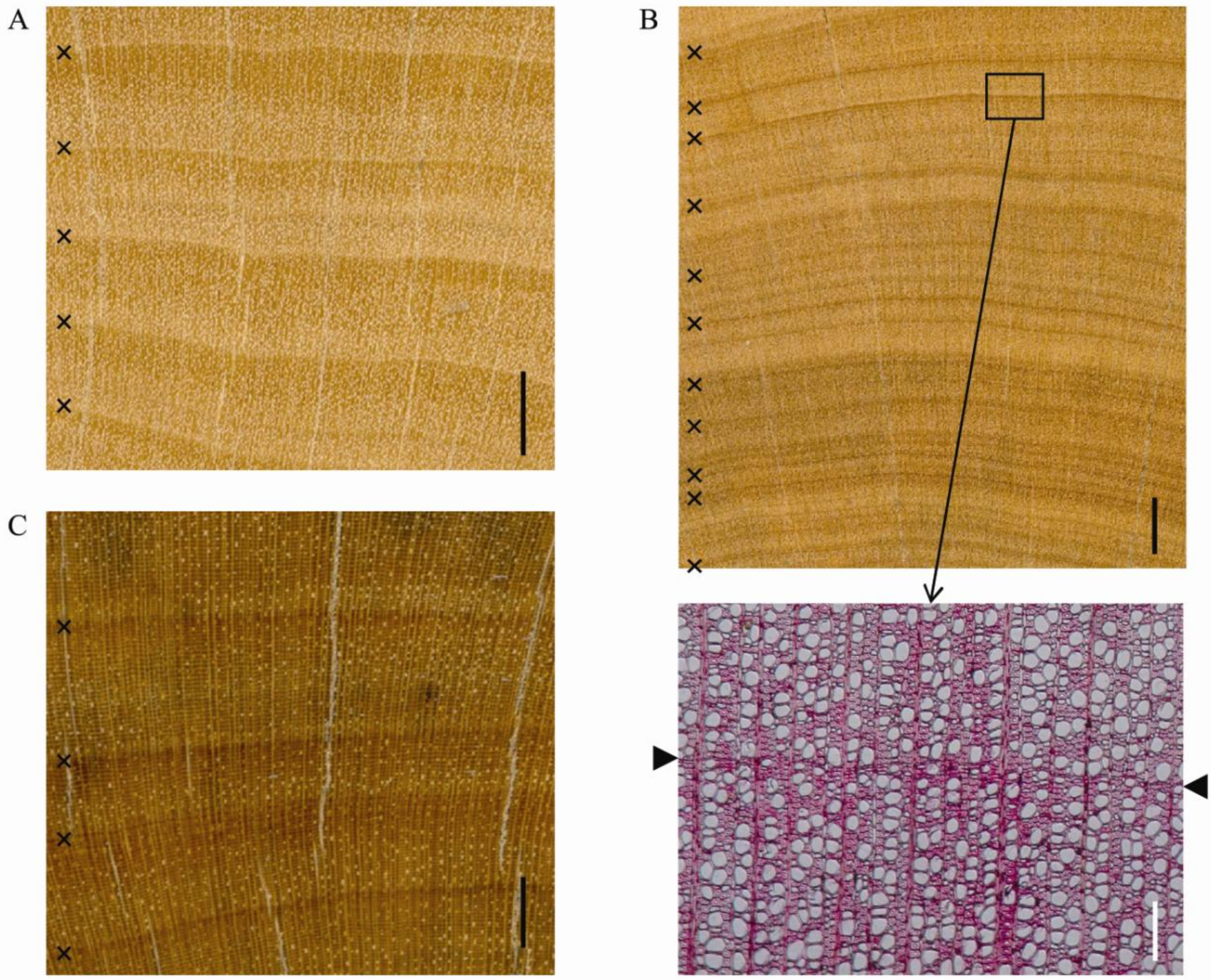

FIGURE 4-2. Tree-ring structure and growth ring boundaries of three understory species of the Luki forest Reserve, DRC. (A) *Aidia ochroleuca*, (B) *Corynanthe paniculata* and (C) *Xylopia wilwerthii*. Black crosses indicate ring boundaries. Radial growth direction is from bottom to top. Black scale bars = 1 cm, white scale bar = 1 mm.

DETECTION OF CONCENTRIC GROWTH LAYERS IN THE WOOD

Growth-ring structure was analysed and characterised macroscopically and microscopically following the IAWA (International Association of Wood Anatomists) hardwood feature list (Wheeler 1989). Ring boundaries of tropical tree species are characterized by a variety of features such as marginal parenchyma bands, alternation of fibre and parenchyma tissues, variation in the vessel size and distribution, variation in the fibre wall thickness, or a combination of all these features (Détienne 1989, Worbes 1995). The wood of the three species is diffuse-porous with different rhythmic variations in wood structure visible to the naked eye (Fig. 4-2). However, microscopic observations were required to reliably detect anatomical features that mark growth-ring boundaries and distinguish them from e.g. intra-annual density variations. The main difficulties for the three study species was their low growth levels (average ring width of 1.13 to 1.65 mm) leading to frequently wedging or absent rings.

TABLE 4-1. Anatomical description of the wood and growth zones boundaries for the three study species.

Species	Main characteristics of the wood	Main characteristics of growth limits
A. ochroleuca	- vessels almost exclusively solitary - very thick-walled fibres - axial parenchyma diffuse and diffuse-in-aggregates - mix of uniseriate and larger 4- to 10-seriate rays with heterogeneous cellular composition characteristic for Rubiaceae (fusiform body of procumbent cells surrounded by over 4 rows of upright marginal cells)	- vessel frequency decreasing towards the end of the ring until a final vessel-less fibre band
C. paniculata	- vessels arranged in a radial pattern, in groups of 4 or more adjacent vessels of common occurrence - fibres thin- to thick-walled, with bordered piths on both radial and tangential walls - parenchyma cells diffuse - typical heterogeneous rays of Rubiaceae	- one or two lines of radially flattened fibres - very difficult to distinguish from density variations and often locally absent
X. wilwerthii	- vessels solitary or in radial groupings of 2 to 3 - axial parenchyma cells arranged in narrow bands forming a ladder-like pattern typical for Annonaceae (scalariform parenchyma) - rays homogeneous, 2-3 cells wide or rarely uniseriate	- increasing frequency of the parenchyma bands and 2 to 3 lines of very thick-walled latewood fibres with lumina almost completely closed

Ring widths were measured to the nearest 0.01 mm under a stereo-microscope coupled with a Lintab measuring device and TsapWin software (Rinn 2003), on two or three (for irregularly shaped samples) radii for each stem disc. Since the supposed growth season spans two calendar years (rainy season typically from October$_{n-1}$ to May$_n$), the year in which annual cambial activity is expected to stop (year n) was nominated to define the growth year and the corresponding ring-width value.

DENDROCHRONOLOGICAL ANALYSES

Tree-ring analyses were applied to all samples to show whether stem growth rate was synchronized over time for all trees. Crossdating, i.e. the matching of ring-width series, allows for the detection of missing rings (if one tree in the sample set did not form a ring in a particular year) or false rings (variations in the wood anatomy mistaken with ring boundaries) (Wils *et al.* 2009). Successful crossdating of ring-width series denotes consistent and synchronous patterns of variation (Cook and Kairiukstis 1992) and indicates that a common external factor controls ring formation in different trees (Pilcher and Gray 1982, Worbes 1995, Cherubini *et al.* 1998). Crossdating was performed visually in combination with a correlation analysis using Cofecha software (Holmes 1983). Starting with radii from the same tree, alignment of the ring-width series allowed the identification of anomalies that were then corrected after investigation on the stem discs. The series were then averaged per tree and the crossdating process was repeated between tree averages. The detection of pointer years, i.e. extreme years common within a site, served as an extra-check during the crossdating process (Schweingruber 1996).

Tree growth is affected by climatic fluctuations and by a wide array of non-climatic factors (Brookhouse 2008), e.g. canopy dynamics or individual size-related trends (Pilcher and Gray 1982). Tree-ring width series thus reflect a complex set of variations. To amplify the climate-induced signal, the series were standardized using Arstan software (Cook 1985) to remove low-frequency, most likely non-climatic trends. A smoothing spline (wavelength of 32 years) was first fitted to each raw series (Cook and Kairiukstis 1992), then each measure was divided by the corresponding value of the function to transform the original curves into stationary time-series (mean = 1 and homogenous variance). A ring-width index (RWI) series was created for each radius then tree. Autocorrelation (AC, year-to-year dependence of ring-width values due to the influence of a growth season on the next) was removed by applying an autoregressive model of the adequate order for each series. Eventually, the indexed curves were averaged to produce the final species chronologies.

Statistical information on the tree-ring measurements is summarised in Table 4-2. The mean sensitivity (MS) indicates the level of between-ring variability in the measured series and reflects the sensitivity of radial tree growth to a common external signal (Fritts 1976, Schweingruber 1996). Inter-series Pearson's correlations ($P < 0.05$) were calculated between radii of each tree, between trees and between species to express the level of affinity of the measured curves and evaluate the quality of the computed mean series. Student's t-values and coefficients of parallel variation (*Gleichäufigkeitskoeffizient* = Glk) were calculated between trees of each species to assess the quality of the final chronologies developed for climate-growth analysis (Baillie and Pilcher 1973).

TABLE 4-2. Descriptive statistics and quality control of the ring-width series contributing to the chronologies for three understory species of the Luki forest Reserve, DRC: *Aidia ochroleuca*, *Corynanthe paniculata* and *Xylopia wilwerthii*. SD, standard deviation; AC, autocorrelation (1-year lag); MS, mean sensitivity; Glk, *Gleichäufigkeitskoeffizient*. Average of Pearson's correlations, *t*-value ($P < 0.05$) and Glk or coefficient of parallel variation.

	Aidia ochroleuca	*Corynanthe paniculata*	*Xylopia wilwerthii*
Number of samples	5	5	5
Mean diameter (cm) *[range]*	21 *[18-25]*	24 *[17-40]*	16 *[14-17]*
Mean age (yr) *[range]*	55 *[39-85]*	97 *[69-112]*	39 *[26-49]*
Time span (yr)	1922-2006	1895-2006	1958-2006
Ring width (mean ± SD, mm) [a]	1.65 ± 1.14	1.13 ± 0.70	1.62 ± 0.98
AC [a]	0.61	0.54	0.19
MS [a]	0.42	0.42	0.50
Within-tree correlation [b]	0.70	0.60	0.72
Between-tree			
Correlation [b]	0.36	0.24	0.27
t-value (± SD) [b]	5.6 ± 0.7	5.9 ± 2.0	4.4 ± 1.7
Glk (± SD, %) [b]	72.3 ± 7.2	67.0 ± 4.9	73.2 ± 17.3

Values based on:

[a] Raw series.

[b] Detrended data.

ANALYSIS OF CLIMATIC EFFECTS

To investigate the link between the radial stem growth of understory trees and climate, we compared each species chronology with annual records of total rainfall, average temperature and average solar radiation from the Luki meteorological station. Moreover, to test whether the within-year timing of climate variation plays an important and differential role for the three species studied, Pearson's correlations ($P < 0.05$) were computed between the species chronologies and contemporary time-series of climate variables on a monthly basis and for groups of months (Fritts 1976). According to results from earlier studies on tree growth in a seasonal tropical climate (Couralet *et al.* 2005, Trouet *et al.* 2006) and high resolution measurements of radial growth (see below) the growing period was assumed to coincide approximately with the rainy season lasting from October to May. We calculated correlations for a 12-month period from September $_{\text{year n-1}}$ to August $_{\text{year n}}$, thus amply covering the rainy season.

In addition, the dbh of 10 trees per species was measured every month with graduated tape during 15 months (April 2006 - June 2007) to study seasonal growth dynamics of *Aidia*, *Corynanthe* and *Xylopia* in response to contemporary weather conditions. Since correlations with growth were found only with precipitation, the measurements were visually compared to contemporary monthly precipitation records to explore intra-annual climate-growth relationships and refine the results obtained from the ring-width chronologies.

RESULTS

STATISTICAL CHARACTERISTICS OF SINGLE RING-WIDTH SERIES AND CHRONOLOGIES

Mean ring width ranged from 1.13 mm for *C. paniculata* to 1.62 and 1.65 mm for *X. wilwerthii* and *A. ochroleuca*, respectively. The large standard deviations for this trait indicated a high variation in average ring width between trees of a same species (Table 4-2).

Within-tree correlations were high and allowed to merge the growth series into mean curves for each individual tree. Trees of the same species were also characterized by high values for mean series inter-correlations, t-values and Glk, thus providing robust chronologies per species. The rather high values of mean sensitivity indicated that ring width varied widely between years. The higher autocorrelation values in stem growth between successive years for *Aidia* and *Corynanthe* probably resulted in slightly lower values for mean sensitivity of these species. Overall, these results exhibit that trees of the same species synchronized their radial stem growth to the same external environmental factor. On the other hand, the correlations between species chronologies were low or very low (*Aidia-Xylopia*: 0.20, *Corynanthe-Xylopia*: 0.15, *Aidia-Corynanthe*: 0.03*)*, suggesting that the three species differ in response to climatic factors. This is visible when looking at the three chronologies that show almost no common variation (Fig. 4-3).

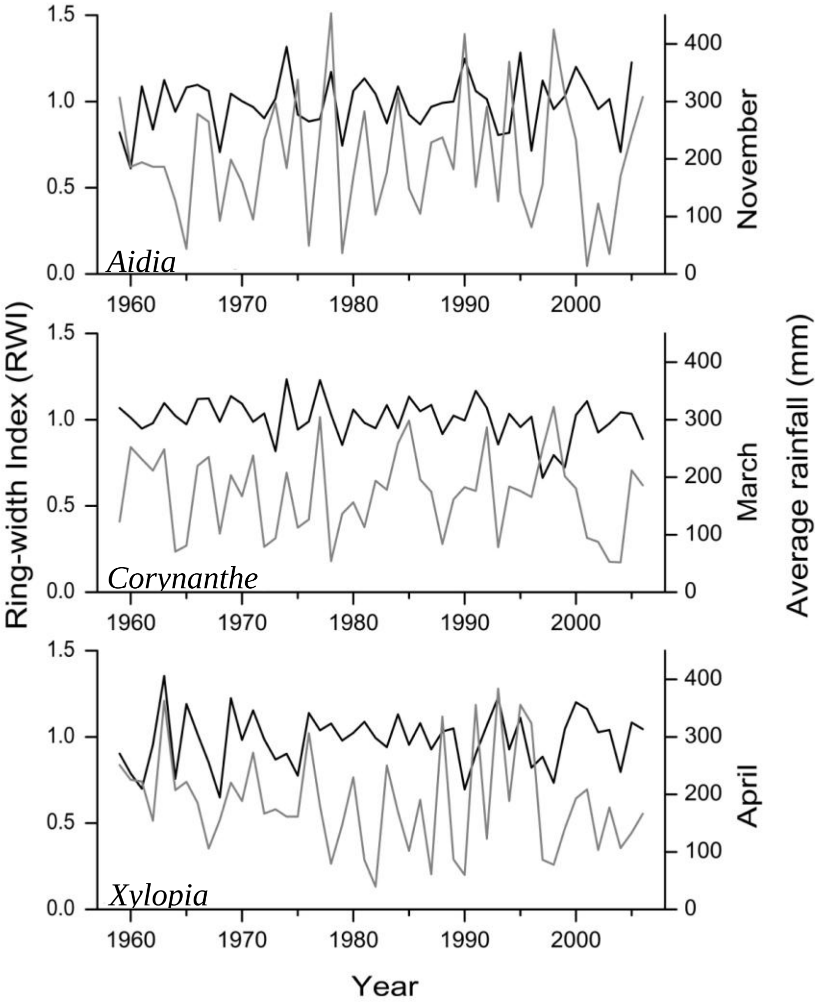

FIGURE 4-3. Illustration of the correlation ($P < 0.05$) between the RWI (ring-width index, black lines) of three understory tree species and single-month climatic records (grey lines) in the Reserve of Luki, DRC (1959-2006): *Aidia ochroleuca* and November rainfall ($r = 0.27$), *Corynanthe paniculata* and March rainfall ($r = 0.29$), *Xylopia wilwerthii* and April rainfall ($r = 0.34$).

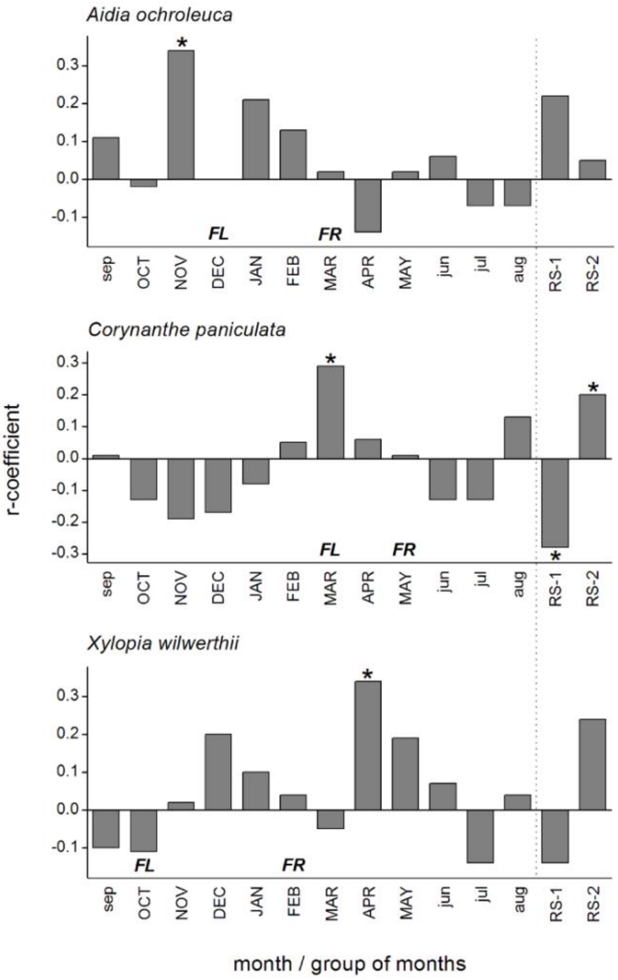

FIGURE 4-4. Correlations between the tree-ring chronologies of *Aidia ochroleuca, Corynanthe paniculata, Xylopia wilwerthii* and monthly average rainfall (1959-2006) in the Reserve of Luki, DRC. In addition we used rainfall averages over the first four (RS-1: October to January) and last four months (RS-2: February to May) of the rainy season, respectively.
* Significant correlation values ($P < 0.05$). Rainy season months appear in capital letters and dry season months in lower case. Flowering (*FL*) and fruiting (*FR*) are reported when most trees are found in these stages (Chapter 3 and Appendix 1).

CLIMATE-GROWTH RELATIONSHIPS

There was no significant correlation between the three species chronologies and annual total rainfall, average temperature or average solar radiation, indicating that radial growth of the study species was not controlled by long-term annual variation of these climate factors. Single-month temperature and solar radiation were also not associated with the annual variation in radial growth of the studied species. However, significant positive correlations appeared between ring width and single-month precipitation values for the three species.

Remarkably, the months for which significant values were found differed between species (Fig. 4-3). For *Aidia* the correlation between radial growth and rainfall was significant at the onset of the rainy season, in November, whereas for *Corynanthe* and *Xylopia* the correlation was significant at the end of the rainy season, in March and April respectively (Fig. 4-3 and 4-4).

These trends were supported by correlations between radial growth and monthly values of precipitation over the studied period, most clearly during the rainy season (Fig. 4-4). *Aidia* showed an overall positive growth response to rainfall in the early rainy season (September-February), culminating in November, and no specific trend in the late rainy season. Inversely, the radial growth of *Corynanthe* was negatively correlated to rainfall in the early rainy season (September-January) and positively correlated to rainfall in the late rainy season with a peak in March. For *Xylopia* there was no such clear pattern but the correlation between radial growth and rainfall was mostly positive over the whole rainy season and was strongest in the end, in April. Both types of analysis (Fig. 4-3 and 4-4) thus suggest that the amount of precipitation was critical for radial stem growth during the transition months from dry to wet season for *Aidia,* and from wet to dry season for *Corynanthe* and *Xylopia.*

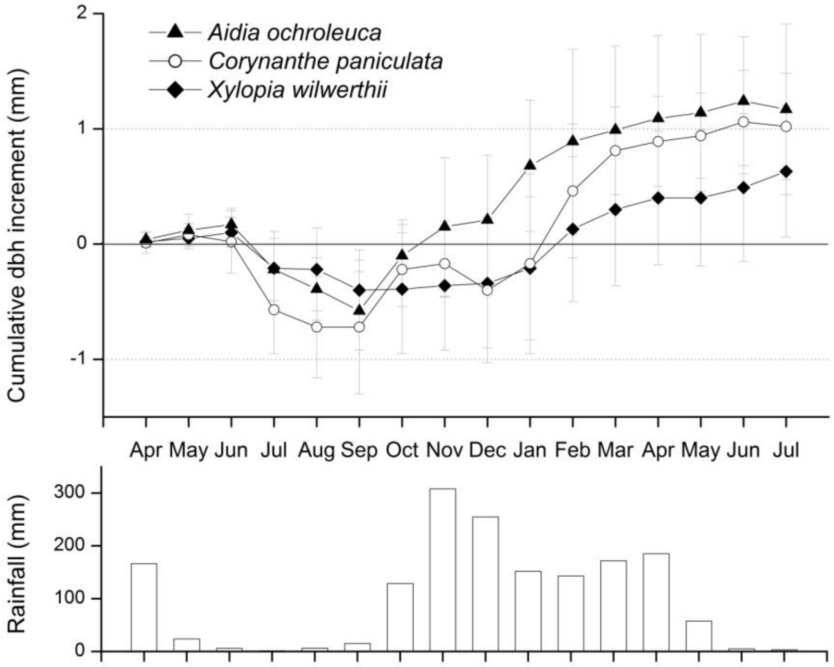

FIGURE 4-5. Cumulative diameter increments from monthly measurements at breast height on 10 trees of *Aidia ochroleuca*, *Corynanthe paniculata* and *Xylopia wilwerthii* for 15 consecutive months (April 2006-May 2007) and monthly precipitation for the corresponding period in the tropical rainforest of Luki, DRC. Error bars represent ± 1 SD.

INTRA-ANNUAL RADIAL STEM GROWTH

The 15-month long time series of monthly dbh measurements showed the nonlinear dynamics of radial growth and its association to seasonality in rainfall (Fig. 4-5). Stems exhibited shrinkage due to dehydration during the dry season (May-September). Subsequently, all trees returned to pre-dry season dbh values then showed substantial radial growth, although with variation in timing across species. *Aidia* trees regained previous stem diameter values rapidly after the onset of rains in October/November, while for *Corynanthe* and *Xylopia* this recovery occurred only three months later, in January/February. Moderate standard deviations (error bars) indicate high homogeneity of radial growth between trees of the same species.

DISCUSSION AND CONCLUSIONS

In the present study we investigated the relationships between radial tree growth and external environmental factors in the understory of a tropical rainforest, using three model species: *Aidia ochroleuca*, *Corynanthe paniculata* and *Xylopia wilwerthii*. While increasing empirical support has been found for the existence of annual rings in tropical trees in response to seasonal changes, primarily in rainfall (Worbes 2002), such evidence is restricted to deciduous canopy species growing in the upper canopy layer and fully exposed to external environmental factors (Pumijumnong and Park 1999, Worbes 1999, Brienen and Zuidema 2005). Moreover, the specific seasonal climate of the Mayombe region with a relatively low transpiration demand during the dry season, due to high air humidity as a consequence of cloud cover, does not seem prone to inducing a clear growth periodicity. Accordingly, missing rings, wedging rings and intra-annual zones of reduced growth (“false rings”) complicated the detection of growth rings in the investigated evergreen, understory species, as commonly seen for other tropical tree species (Ogden *et al.* 1981, Détienne 1989, Dünisch *et al.* 2003). Nevertheless, species-specific anatomical markers and crossdating techniques allowed for demonstrating the existence and annual nature of growth rings for the three study species. The presence of annual growth rings is thus proved for evergreen understory species, adding to successful tree-ring studies of deciduous canopy trees. As seen in Worbes *et al.* (2003) or Brienen *et al.* (2009), our results further substantiate the possibility to study the productivity, vitality and dynamics of whole communities of trees in tropical forests based on tree-ring analysis.

The successful cross-dating between tree-ring series of the same species denotes the shared influence of external environmental factors on seasonal wood formation. The chronologies of the three species, however, did not show common fluctuations over the past 50 years. This indicates that radial growth is determined by either differing external factors or by a differing timing of the factor(s). More specifically, the synchronized growth per species did not correlate significantly with annual variation in rainfall, temperature or radiation as observed in other studies on rainforest trees (Schöngart *et al.* 2006). However, the three species exhibited significant and distinct responses to rainfall during specific periods of the year. Increased growth of *Xylopia* occurred in response to high rainfall over the whole rainy season. In contrast, increased growth of *Aidia* and *Corynanthe* occurred mainly early and late in the rainy season, respectively.

The monthly diameter measurements supported these results. Cambium reactivation occurred at the onset of the rainy season for *Aidia*, while radial stem growth of *Xylopia* and *Corynanthe* resumed and peaked only later in the wet season. Towards the end of the rainy season the radial growth of all three species levels-off before showing an abrupt decline indicating stem shrinkage in July. Radial stem shrinkage due to loss of water from storage pools is a well-known phenomenon in seasonal tropics (Kozlowski and Winget 1964, Borchert 1994, Sheil 1995, Zweifel *et al.* 2007).

The features of *Aidia* growth are in line with several studies on stem growth of rainforest trees under seasonal climates. The role of rainfall has been stressed in the transition months between dry and wet season as a trigger for the initiation of cambial activity (Pumijumnong 1995, Dünisch *et al.* 2003, Brienen and Zuidema 2005, Pumijumnong and Wanyaphet 2006, Buckley *et al.* 2007) and in the early wet season as the determinant of ring width (Pumijumnong 1995, Dünisch *et al.* 2003, Fichtler *et al.* 2004, Brienen and Zuidema 2005). Late-season responses have been reported but to a lesser extent (Devall *et al.* 1995). The major known difference following this segregation is the above-ground morphology of the trees: *Aidia* has a ramified trunk from the base whereas stems of adult *Corynanthe* and *Xylopia* are mostly straight, with high branching. Roots depth and morphology may be linked to these features, with *Aidia* forming more shallow roots than the other two species. The phenology of trees is closely linked to seasonal changes in soil water status and depends on their water uptake and storage capacity (Borchert 1994). In the Reserve of Luki there is no proper aquifer layer in the subsoil (Donis 1948). Moreover, the superficial soil horizons are very permeable, with great surface runoff and leaching leading to rapid desiccation after the end of the rainy season (Donis 1948, Meulenberg 1949). Superficial roots of *Aidia* would allow the prompt reaction to the first rains that directly penetrate the upper soil layers after the dry months. Stem growth would mostly occur at the beginning of the wet season and slow down as the top soil gradually dries out. On the contrary, *Xylopia* and *Corynanthe* having a deeper, pivot-like root system would explain their delayed growth response, as long as the water did not reach deeper soil layers (Cao 2000). This would, however, enable growth towards the end of the rainy season and provide an explanation for the effect of late-season rains on ring width.

Our results showed that understory species can strongly differ in the periodicity of their wood production. The link between radial stem growth and tree phenology is fundamental yet poorly understood for tropical rainforest species (Borchert *et al.* 2002, O'Brien 2008). The phenology of wood production was compared to the reproductive phenology of the study species (Chapter 3). *Xylopia* trees produce flowers mostly in October at the onset of the rainy season, while radial stem growth is still minimal. For *Aidia* and *Corynanthe* however, blossoming and production of new wood seem to be synchronized. Matching radial stem increment, flowering occurs predominantly at the beginning of the rainy season for *Aidia* (December) and later in the rainy season for *Corynanthe* (March). The relation and potential tradeoffs between flower or fruit production and stem growth need to be further explored to evaluate the consequence of increased seasonality on species growth patterns and performances.

In this study it was proven that dendrochronology can be successfully applied for reconstructing radial growth patterns of tropical understory species in relation to climate. Hence it can be extended to the whole tropical tree community. Moreover, we uncovered significant interspecific differences in stem growth response to climate variations. This differential timing across the species studied is remarkable and implies that species at the same site and with seemingly similar life histories can vary widely in growth dynamics. Global climate change and deforestation influence the seasonality of climate in tropical forest areas. This may result in differential responses across species varying in phenology of radial stem growth and in the long term contribute to shifts in the species composition of tropical forests.

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CHAPTER 5

Heterogeneous growth patterns and responses to rainfall for canopy trees of the Central African rain forest

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ABSTRACT

In tropical regions with one distinct dry season most tropical tree species form growth rings and allow for dendrochronological studies and detailed analyses of growth at different time scales. *Terminalia superba* (Combretaceae) or “limba” and *Prioria balsamifera* (Fabaceae / Caesalpinioideae) or “tola” are important canopy species of West and Central African dense forests, both appreciated for domestic use and timber trade. Despite their value, few studies on the species’ growth variability have been conducted. This paper presents an investigation on the periodicity of radial growth and the influence of climate variations for these two species from the Reserve of Luki in the Democratic Republic of Congo. The tree-ring analyses are based on stem sections of 5 *T. superba* and 14 *P. balsamifera* and diameter increments are examined at the intra-annual level on 10 additional trees per species

Annual ring formation in relation to rainfall variations was proven for both species. The determination and measurement of tree rings was easy for *T. superba* but more problematic for *P. balsamifera* for which radiocarbon measurements had to confirm the dendrochronological results. Strong inter-specific, inter- and intra-individual heterogeneity of growth patterns were also exhibited among trees and within the trees themselves. Individual sensibilities to the type of substrate and fine plasticity of cambial activity in response to environmental changes have been suggested as possible causes for this growth variability.

Key words: Democratic Republic of Congo, Mayombe, annual ring formation, growth rates, radiocarbon dating, climate-growth relationships

INTRODUCTION

Dendrochronology is a direct and reliable way to fill this knowledge gap about ages and growth rates of tropical trees which currently hampers the establishment of sustainable forest management systems (Stahle 1999, Worbes *et al.* 2003). Climate/growth relationships can also be investigated through tree-ring analyses and proxy records for climate would allow predicting the consequences of future climate change on tropical vegetation (Clark 2004, Phillips *et al.* 2009). Reinforcing the network of tree species and regions with established growth series related to climate variations is thus of prime importance but tree-ring studies in Central and West Africa are still scarce (Détienne *et al.* 1998, Worbes *et al.* 2003).

Although the discrimination of growth rings on tropical wood is generally more complex than in temperate regions (Détienne 1989, Sass *et al.* 1995), dendrochronology has been successfully used on tropical tree species from various ecosystems including rain forests (Worbes *et al.* 2003, Fichtler *et al.* 2004, Brienen and Zuidema 2006a, Schöngart *et al.* 2006, Lisi 2008). Most tropical forests experience clear seasonality in rainfall, causing periodic rhythms in tree growth (Jacoby 1989, Schweingruber 1996, Borchert 1999, Worbes 1999). A dry season of at least two months with less than 60 mm of monthly precipitation results in annual ring formation for many tropical tree species, allowing the detailed study of growth time series (Worbes 1995). Large trees are usually the most suitable for dendrochronology because their rings, if present, are larger and clearer than in the wood of slow-growing understory trees.

Terminalia superba (Combretaceae) or “limba” and *Prioria balsamifera* (Fabaceae - Caesalpinioideae) or “tola” are two abundant canopy species in West and Central African forests and particularly in the Mayombe region. Their tall and straight trunks are very attractive for timber extraction, consequently they have long been overexploited and their populations are diminishing (Lubini 1997, De Ridder *et al.* 2010). Because of these issues the sustainable management of natural *T. superba* and *P. balsamifera* will require reliable information about long-term growth rates and associated climate/growth relationships. In this paper we report on a tree-ring study of these two species from the Reserve of Luki in the DRC (Democratic Republic of Congo). Because of the clear seasonality in the region with a distinct dry period of at least three months, tree growth was expected to be periodically limited by water shortage and year-to-year variation in precipitation to be reflected in the time series of tree-ring widths. The link between climate, phenology and distinctiveness of tree rings has been investigated for several tropical species. While most deciduous species form distinct rings, in brevi-deciduous or evergreen species phenology and cambial activity tend to be uncoupled from climate seasonality which prevents the formation of clear ring boundaries (Borchert 1999, Rao and Rajput 2001). Moreover, tree rings of slow-growing species are generally more difficult to discriminate and measure than the large ones of fast growers (Brienen and Zuidema 2006b). *T. superba* is a fast-growing and deciduous species that has already been shown to be a good candidate for successful tree-ring analyses (Mariaux 1969). No information exists yet about the potential of *P. balsamifera* for dendrochronology but being a brevi-decidous and slow growing species it is arguably a more difficult one. For tropical species with indistinct or problematic rings radiocarbon dating can be used to verify the annual nature of rings and the synchronisation of growth series (Worbes and Junk 1989, Wils *et al.* 2009). Bomb testing during the second half of the twentieth century produced a peak in global atmospheric ^{14}C concentrations that allows to date precisely wood samples produced in this period (Hua and Barbetti 2004). Using classic dendrochronological methods and radiocarbon dating as an additional tool, one aim of this work is thus to confirm that tree rings of *T. superba* can be used for dendroclimatological and dendroecological applied research and to evaluate if tree rings of *P. balsamifera* are suitable for this purpose. Specifically, for each study species we want to determine if ring formation is annual and if inter-annual growth variations are synchronised among trees. Furthermore, the monthly monitoring of diameter increments during 15 months on trees from the same forest allows us to complement the information generated by tree-ring analyses and to investigate the dynamics of radial growth both at the inter- and intra-annual levels.

In tropical climates with a clear dry season rainfall seems to be the primary climatic driving variable for tree development and cambial activity (Borchert 1999). For *T. superba* and *P. balsamifera* growing in Luki the relationship between tree growth and local rainfall is also investigated in this study to establish if annual wood growth varies with annual precipitation levels and if cambial activity is controlled by seasonal variations in rainfall.

MATERIALS AND METHODS

STUDY SITE

The Reserve of Luki is located in the south-western DRC (5°28’-5°42’ N, 13°4’-13°18’ E), 30 km north from the port city of Boma (Fig. 4-1). It is the southernmost remnant of the Mayombe forest, stretching along the Atlantic Ocean from the central coast of Gabon and renowned for its high floristic diversity and the presence of large timber trees (Monteiro 1962). The protected forest area covers 32.700 ha of hilly landscape (altitude between 150 and 500 m) on heterogeneous soils and with low levels of nutrients available for plants (Monimeau 1990). Records (1959-2007) of precipitation, air temperature, relative humidity and solar irradiance were available from the Luki meteorological station (Fig. 4-1). The climate is characterized by a mean annual temperature of 24.6°C with limited year-to-year variation and a mean annual rainfall of 1180 mm/yr. A distinct dry period lasts from June to September.

The forest in Luki can be generally classified as a tropical semi-deciduous rain forest of the Guineo-Congolian forest domain (Lebrun and Gilbert 1954, Lubini 1997, Whitmore 1998) but occurs in a mosaic landscape with patches of agricultural fields and settlements. It consists of a mixture of deciduous and evergreen tree species in the upper-stratum (e.g. *Hylodendron gabunense*, *Prioria balsamifera*, *Piptadeniastrum africanum*, *Terminalia superba*) and mostly evergreen species in the understory (e.g. *Aidia ochroleuca*, *Xylopia wilwerthii*, *Corynanthe paniculata*).

STUDY SPECIES

Terminalia superba Engl. & Diels (Combretaceae) is a frequent canopy species of the Guineo-Congolian lowland rain forests, naturally growing from Guinea to the western DRC (Lubini 1997). It is a long-lived heliophilous species growing fast in gaps after the establishment of the first colonizing vegetation and is strictly light-demanding, in all development stages (Mariaux 1969, Détienne *et al.* 1998). *T. superba* generally grows on clay soils and regenerates abundantly in forest gaps, most typically in ancient agricultural zones. It is a reference species for reforestation because of its good regeneration and fast growth (Nsenga 2004, De Ridder *et al.* 2010). It was extensively used for agro-forestry in the Mayombe region mostly in association with banana plantations (Fig. 5-2). The wood of *T. superba* is cream-white with no distinct heartwood (Fig. 5-3) except in the case of "black limba" presenting a black or brownish with black streaks core (Bauch 1982). The wood of *T. superba* is easy to cut and handle and has a rather low density (0.45 to 0.70 g/cm^3 at 12% of moisture content so it is used in many applications such as doors, flooring or furniture. Outdoor applications in ground contact are however not possible since *T. superba* belongs to the durability class IV and is easily attacked by fungi. Furthermore the species is susceptible to *Lyctus* beetles, which is relevant for many applications. In the forest of Luki *T. superba* sheds leaves at the end of the dry season (around September) and has a clear deciduous character with up to 50% of the trees being leafless simultaneously (Chapter 3).

FIGURE 5-1. Agroforestry system planted around 1940 and unmanaged since 1960, with *Terminalia superba* trees and banana plants (*Musa spp.*) in the Reserve of Luki, DRC. (photo M. De Ridder)

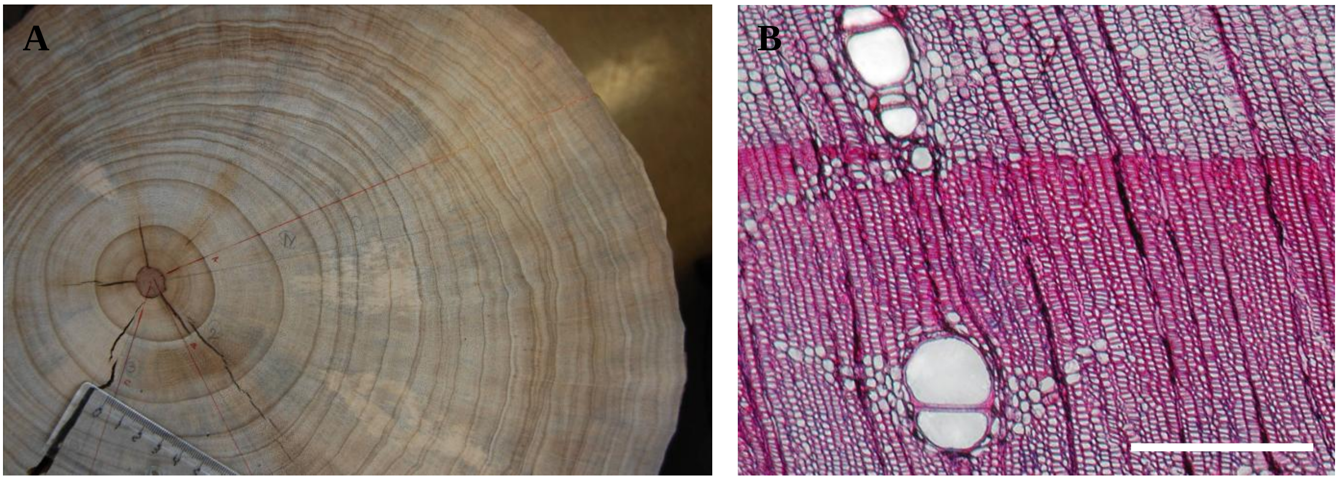

FIGURE 5-2. (A) Sanded surface of a stem section of *Terminalia superba* from the Reserve of Luki, DRC and (B) detail of a growth-zone boundary on a thin section (white scale bar = 1 mm).

Prioria balsamifera (Vermoesen) Breteler (Fabaceae, sub-family of Caesalpinioideae) is typically found in the upper-stratum of lowland (0-750 m) or mid-altitude (750-1500 m) humid forests of West and Equatorial Africa, preferably on deep and relatively wet soils but it can also be found on sandy soils rich in quartzite and mica-schist (Arno 2001). In its repartition area total annual precipitation varies between 1100 and 2200 mm and mean annual temperature between 24 and 26 °C. *P. balsamifera* has a great dispersal capacity because of a massive production of wind-disseminated seeds but a large number of seedlings only live for a few months because they are strictly light-demanding in this early development stage (Lubini 1997). However, from the sapling stage individuals are shade-tolerant and grow towards the upper canopy (Corbiez 2000). The adult tree has a straight, cylindrical and branch-free stem (Fig. 5-3) and a crown formed by vigorous and sinuous branches (Keay 1989, Arno 2001). *P. balsamifera* trees have brown heartwood and lighter, creamy white sapwood (Fig. 5-4). The wood is relatively light and its good mechanical characteristics allow a wide range of utilizations, mainly for construction (interior or exterior), boat decks, plywood and domestic furniture (Fouarge and Gérard 1964, Arno 2001).

Like *T. superba*, *P. balsamifera* trees in Luki shed leaves around September but are rarely totally leafless (Chapter 3) so the species is classified as brevi-deciduous (Sarmiento and Monasterio 1983).

Figure 5-3. Straight cylindrical trunk of *Prioria balsamifera* (photo J.-M. Maloti).

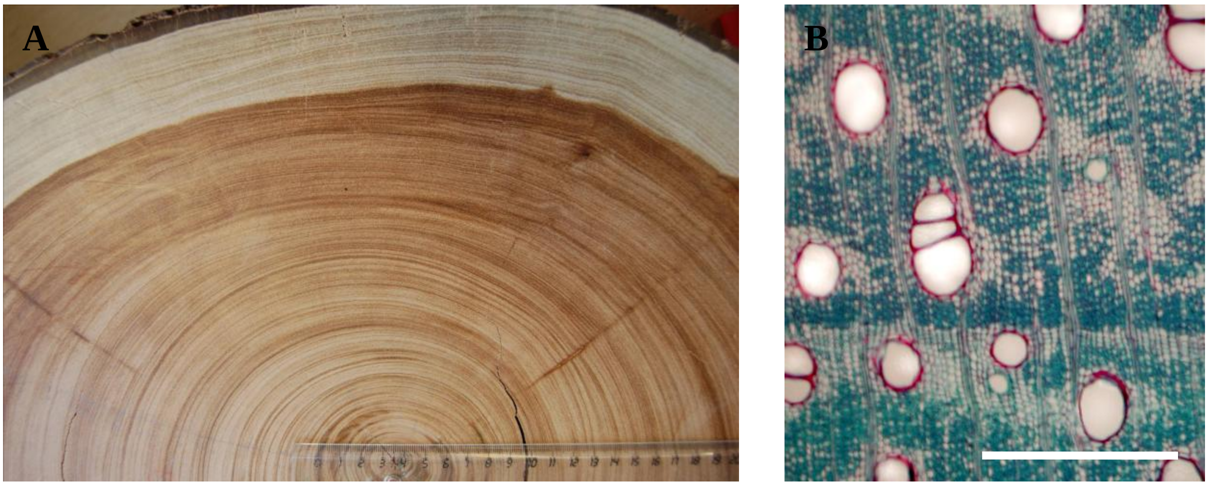

Figure 5-4. (A) Sanded surface of a stem section of *Prioria balsamifera* from the Reserve of Luki, DRC and (B) detail of a growth-zone boundary on a thin section (white scale bar = 1 mm).

SAMPLING AND SAMPLE PREPARATION

Tree-ring width data used in this study are derived from stem cross-sections of 5 *T. superba* (Tw58841 to Tw58845 in the Tervuren Wood reference collection) with diameters from 40.6 to 48.7 cm and 14 *P. balsamifera* (Tw58846 to Tw58850 and Tw58868 to Tw58876) with diameters from 16.3 to 57.7 cm from the Reserve of Luki. The sampled trees were between 14 and 22 m high and were all part of the dominant tree layer with their crowns fully in the canopy. The 5 *T. superba* samples and 5 of the 14 *P. balsamifera* samples were collected in 2005 from trees brought down by strong winds then a second series of nine *P. balsamifera* stem sections was collected in September 2007. All trees grew in dense forest stands inside the reserve but close to inhabited areas called Nkula (Fig. 1-2). The 4 to 6 cm-thick cross sections were taken approximately 1 m from the trunk base, to get a maximum amount of growth layers. After being deep-frozen for 2 weeks to eradicate insects possibly present in the wood, their surface was planed then progressively sanded with sandpaper until a grit-size of 1200.

DETECTION OF CONCENTRIC GROWTH LAYERS IN THE WOOD

Growth rings in tropical trees can be marked by various wood anatomical characteristics such as marginal parenchyma bands, alternate fibres and parenchyma, variation in the size or distribution of vessels, or a combination of those (Détienne 1989, Worbes 1995). In this study they were characterised according to the IAWA (International Association of Wood Anatomists) hardwood feature list (Wheeler 1989). Concentric growth zones were visible to the naked eye on all stem sections of *T. superba* and *P. balsamifera*. Thin sections were used to characterise their limits and for doubtful cases. Additionally, already existing thin sections of both species from the Mayombe forest were observed to refine the anatomical characteristics of growth rings (Xylarium of the Royal Museum of Central Africa, Tervuren, Belgium).

TREE-RING ANALYSES

For each tree growth rings were measured to the nearest 0.01 mm under an Olympus SZX 120 stereo-microscope coupled with a LINTAB measuring table associated to the software TSAP-Win (Rinn 2003). Two to four radii were selected depending on the regularity of the stem section (radii were added in case of extreme eccentricity or high number of problematic ring boundaries). First the raw measurements were compared visually to check if growth was synchronous between radii of the same tree. Statistical tests performed with TSAP-Win were used during the crossdating procedure (matching of ring-width series) to detect exceptional cases or measurement errors. For example growth limits that were not visible around the whole sample circumference (“missing rings”) and density variations or reaction wood looking like growth limits (“false rings”) were identified, investigated on the samples and the series were corrected accordingly. Tree-level mean series were calculated and compared to check the synchronicity of growth between trees of the same species. A good synchronicity between different average individual series indicates that the radial growth of these trees is influenced by a common external factor (Worbes 1995, Cherubini *et al.* 1998). Mean sensitivity (MS) and autocorrelation (AC) were also determined for each tree’s growth curve using the program Cofecha (Holmes 1983, Grissino-Mayer 2001). MS expresses the between-ring variability in the measured series and reveals the sensitivity of radial stem growth to external variables (Fritts 1976, Schweingruber 1996). AC indicates the year-to-year dependence of ring-width values due to the influence of a growth season on the next. It was removed using autoregressive models of the appropriate order for each individual series (standardisation) to highlight the influence of climate variations on radial tree growth. The crossdating accuracy was assessed by calculating Pearson’s correlation and TVBP (t-value from the Student’s t-test ($P < 0.05$) after a Baillie-Pilcher standardisation of the series) with the program Cofecha (Holmes 1983, Grissino-Mayer 2001).

ANALYSES OF CLIMATIC EFFECTS

The rainy and expected growth season in Luki spans over two calendar years (from October$_{n-1}$ to May$_{n}$). The year on which the cambial activity supposedly stopped and the growth limit was formed (year n) was chosen as the reference date for the observed growth zone. Moreover the sums of annual rainfall used in the analysis were calculated from October to September of year n.

The constructed master chronologies were first compared visually with contemporary records of total annual rainfall from the Luki meteorological station (data available from 1959). Then Pearson’s correlations were computed between the time series of radial growth and rainfall using monthly values, the sums of groups of months (first or last three months of the rainy season) and annual values.

^{14}C ANALYSES

Tree rings of *T. superba* were distinct and regular so the measurement was easy and straightforward. On the other hand, rings of *P. balsamifera* were smaller, less distinct and with various peculiarities (e.g. wedging or non-concentric) so the provisional dates inferred from measurement and crossdating were tested via a supplementary method.

All over the globe reference curves of atmospheric ^{14}C concentration show a peak due to nuclear bomb tests between 1945 and 1963, allowing the dating of wood formed after this period. Rings are dated by comparing the amount of ^{14}C that was sequestrated in the wood cellulose at the time of ring formation with the reference curve of ^{14}C atmospheric concentration (Worbes and Junk 1989, Hua and Barbetti 2004). The radiocarbon was not propagated instantly from the area of nuclear testing (Russia) to the rest of the atmosphere so different reference curves have been produced for the different regions of the globe. Luki is situated just under the Equator so the SH (Southern Hemisphere) reference curve was used for these analyses. In the Radiocarbon Laboratory of Poznan, Poland, ^{14}C concentrations were measured in selected growth rings of two *P. balsamifera* trees (Tw58849 and Tw58850) to verify the annual nature of ring formation and the crossdating process (Worbes 1995, Wils *et al.* 2009). From the alignment of growth series the formation years of the sampled rings were expected to be 1970, 1981 and 1990 for Tw58849 and 1958, 1963, 1973 and 1983 for Tw58850.

MONTHLY GROWTH RATES

In addition to tree-ring analyses, the dbh of 10 *T. superba* (T1 to T10) and 10 *P. balsamifera* (P1 to P10) was measured every month with graduated tape during 15 months (April 2006 - June 2007) to explore growth dynamics at the intra-annual level. These trees and the trees used for the tree-ring analyses were from the same forest stands. The measurements were also compared to contemporary monthly precipitation records to study intra-annual climate-growth relationships and complement the results obtained from the ring-width chronologies.

RESULTS

DISTINCTIVENESS OF GROWTH RINGS

For both species growth rings were visible to the naked eye on the wood surface of the stem sections (Fig. 5-2 and 5-4). They appeared most clearly for *T. superba*, being terminated by several lines of thick-walled fibres with reduced lumen. Vessels were surrounded by diamond-shaped parenchyma and became more numerous with winged aliform parenchyma at the end of the growth zones (Détienne 1989, Wheeler 1989). Moreover rings were large, almost merely concentric and present on the whole circumference of the sections (Table 5-1 and Fig. 5-2). Rings of *P. balsamifera* were less regular and their distinctiveness depended on ring width (Fig. 5-4). Ring boundaries of *P. balsamifera* were marked by a parenchyma band of 3 to 5-6 cells, typical for the Caesalpinioideae sub-family (Worbes 1989, Hohn 1999). Besides, growth zones often started with a band of thick-walled fibres with no vessel and no parenchyma cells, increasing the distinctiveness of ring limits. Wide rings were relatively easy to discriminate but thin rings had unclear limits and were often wedging out on some parts of the sections; moreover some rings were missing entirely. Missing and wedging rings were discovered during the crossdating process when assessing the synchronisation of the measured growth series and represented approximately 5% of all measurements.

CROSSDATING OF GROWTH SERIES

Mean ring width was significantly higher for *T. superba* (7.9 ± 1.2 mm) than for *P. balsamifera* (2.2 ± 0.7 mm) but *T. superba* trees were all very young (28 years on average) compared to *P. balsamifera* trees (91 years on average) (Table 5-1). The high or very high (for *T. superba*) intra-tree TVBP values (Table 5-2) revealed a good synchronization between the different radii of all stem sections and allowed the calculation of an average growth curve for each measured tree. The MS was relatively high for all samples of both species (0.48 on average) expressing important year-to-year variations in radial stem increment. As indicated by the high first-order AC values (except for Tw58843), these variations were greatly influenced by growth during the preceding year but were close to zero after correction of the series with appropriate autoregressive modelling (Table 5-2). For *T. superba* and most *P. balsamifera* samples the standardisation did not improve the intra-tree correlation, thus correlation values for raw series were higher. However for the *P. balsamifera* samples collected in 2005 and one collected in 2007 (Tw58846 to Tw58850 and Tw58874), the standardisation of the series significantly improved the accuracy of the crossdating between radii of each tree.

TABLE 5-1. Summary of tree-ring measurement results for five stem sections of *Terminalia superba* and 14 stem sections of *Prioria balsamifera* from the Reserve of Luki, DRC.

	Sample accession number (Tervuren wood)	Average diameter (cm)	Number of rings or age	Growth span	Number of radii	Annual radial growth (mm)	
						Mean	Range
T. superba	Tw58841	44.3	24	1982-2005	3	8.9	1.2-25.0
	Tw58842	40.6	21	1985-2005	3	9.2	2.0-31.3
	Tw58843	44.2	26	1980-2005	3	8.2	2.1-26.5
	Tw58844	41.3	31	1975-2005	3	6.5	1.6-50.7
	Tw58845	48.7	35	1971-2005	3	6.8	0.7-23.9
Average		43.8	28	-	-	7.9	1.5-31.5
P. balsamifera	Tw58846	56.6	228	1778-2005	4	1.4	0.1-3.8
	Tw58847	57.7	194	1812-2005	4	1.7	0.4-6.9
	Tw58848	43.9	77	1929-2005	4	2.8	0.8-5.3
	Tw58849	47.4	79	1927-2005	4	3.0	1.2-8.0
	Tw58850	50.7	83	1923-2005	3	3.2	0.8-10.9
	Tw60868	30.6	76	1932-2007	2	1.6	0.2-3.3
	Tw60869	25.1	75	1933-2007	2	2.4	0.5-6.3
	Tw60870	40.1	67	1941-2007	2	2.2	0.4-5.0
	Tw60871	33.4	58	1950-2007	2	2.0	1.3-9.7
	Tw60872	27.0	75	1933-2007	2	2.2	0.2-5.7
	Tw60873	34.8	59	1949-2007	2	1.2	0.1-2.9
	Tw60874	16.3	50	1958-2007	2	3.5	1.2-7.5
	Tw60875	40.8	82	1926-2007	2	2.0	1.1-6.5
	Tw60876	32.5	70	1938-2007	2	1.7	0.5-4.5
Average		38.4	91	-	-	2.2	0.6-6.2

For both species, although correlations between growth series of the same trees were high, values of TVBP and correlations between trees were very low, indicating that radial stem growth was not well synchronized between the measured trees of each species (Table 5-3). It was thus not possible to build accurate chronologies from all the study trees. The average growth curve of the 5 *T. superba* was however calculated to examine climate-growth relationships. For *P. balsamifera*, the growth series of two trees (Tw58849 and Tw58850) had a significantly higher correlation level than all other combinations (0.39 compared to a mean of 0.17 for all five trees). The average growth curve of these two samples was thus called a chronology and was used to explore relationships with rainfall.

TABLE 5-2. Descriptive statistics of 5 tree-ring series of *Terminalia superba* (limba) and 14 tree-ring series of *Prioria balsamifera* (tola) from the Reserve of Luki, DRC. Values were calculated for the raw series of measurements or after standardisation when indicated (std).

	Tree	1st order autocorrelation (AC)		Mean sensitivity (MS)	Mean intra-tree correlation (between radii)	TVBP (intra-tree)
		raw	std			
T. superba	T1	0.63	-0.02	0.66	0.73	19.9
	T2	0.93	-0.01	0.38	0.46	14.7
	T3	0.84	-0.03	0.38	0.31	7.5
	T4	0.82	-0.16	0.50	0.42	9.3
	T5	0.62	-0.03	0.46	0.64	16.6
	Average	0.77	-0.03	0.48	0.51	12.6
P. balsamifera	P1	0.31	-0.04	0.56	0.20 (std)	4.6
	P2	0.49	-0.01	0.47	0.19 (std)	3.8
	P3	0.11	-0.02	0.46	0.53 (std)	5.1
	P4	0.38	-0.04	0.42	0.58 (std)	4.1
	P5	0.33	-0.02	0.47	0.75 (std)	4.8
	P6	0.19	-0.2	0.49	0.55	5.7
	P7	0.31	-0.09	0.49	0.63	9.5
	P8	0.46	-0.29	0.38	0.48	4.6
	P9	0.55	-0.21	0.45	0.38	3
	P10	0.42	-0.19	0.53	0.42	2.8
	P11	0.47	-0.21	0.43	0.32	2.5
	P12	0.41	-0.04	0.47	0.51 (std)	4.8
	P13	0.51	-0.28	0.46	0.46	4.2
	P14	0.39	-0.27	0.61	0.45	3.1
	Average	0.38	-0.13	0.48	0.38	4.5

TABLE 5-3. Verification of the crossdating accuracy between the five *Terminalia superba* (limba) and the 14 tree-ring series of *Prioria balsamifera* (tola) from the Reserve of Luki, DRC. TVBP: t-value from the Student's t-test ($P < 0.05$) after a Baillie-Pilcher standardisation of the series.

	T. superba	*P. balsamifera*
TVBP	0.66	2.00
Pearson correlation	0.36	0.12

^{14}C ANALYSES

Although some of the dates given by the radiocarbon measurements contain some uncertainty the dates inferred by crossdating appear in the measurements results (Table 5-4). Moreover the time intervals between the different provisional dates are confirmed, which proves the annual character of growth ring formation.

CLIMATE-GROWTH RELATIONSHIPS

The average growth curve of the 5 *T. superba* trees was compared to rainfall records (Fig. 5-5). An important age trend was visible and correlations with contemporaneous records of rainfall (months, groups of months or annual values) were very low and not improved by standardisation of the series. The highest correlation value was between the raw average measurements and total annual rainfall (0.13). Synchronous positive peaks of total annual rainfall and tree growth were however remarkable in 1975, 1995, 1999 and 2004 and negative peaks in 1979, 1989, 1993 and 2003. For *P. balsamifera* no significant correlation was either found between the built chronology and precipitation series when considering months or groups of months. However figure 5-6 reflects the high positive correlation (0.55) between the *P. balsamifera* chronology and the time series of total annual rainfall. Like for *T. superba* both curves also shared some positive (1961, 1975, 1984, 1990, 1999 and 2005) and negative peaks (1965, 1968, 1982, 1996 and 2003). Eventually, although no significant correlation was found between *P. balsamifera* and *T. superba* series (r = 0.005) both species had common peaks of negative (1975 and 1999) and positive (2003) radial growth corresponding to exceptionally dry or wet years, respectively.

TABLE 5-4. Details of the radiocarbon dating for rings of two *Prioria balsamifera* trees from the Reserve of Luki, DRC. ^{14}C concentrations were measured on an accelerated mass spectrometer (AMS) at the Poznan Radiocarbon Laboratory, Poland. The two years given for the Tw58850 tree correspond to the dating uncertainty.

Sample reference number (Tervuren wood)	Lab number	^{14}C age	Error	Calibrated date (AD)	Provisional date (AD)
Tw58849	Poz-34712	-3166	26	1971	1970
	Poz-34713	-1833	24	1981	1981
	Poz-34714	-1237	25	1990	1990
Tw58850	Poz-29558	-336	24	1957-1958	1958
	Poz-29559	-1503	24	1962-1963	1963
	Poz-29560	-3002	22	1972-1973	1973
	Poz-29561	-1831	24	1982-1983	1983

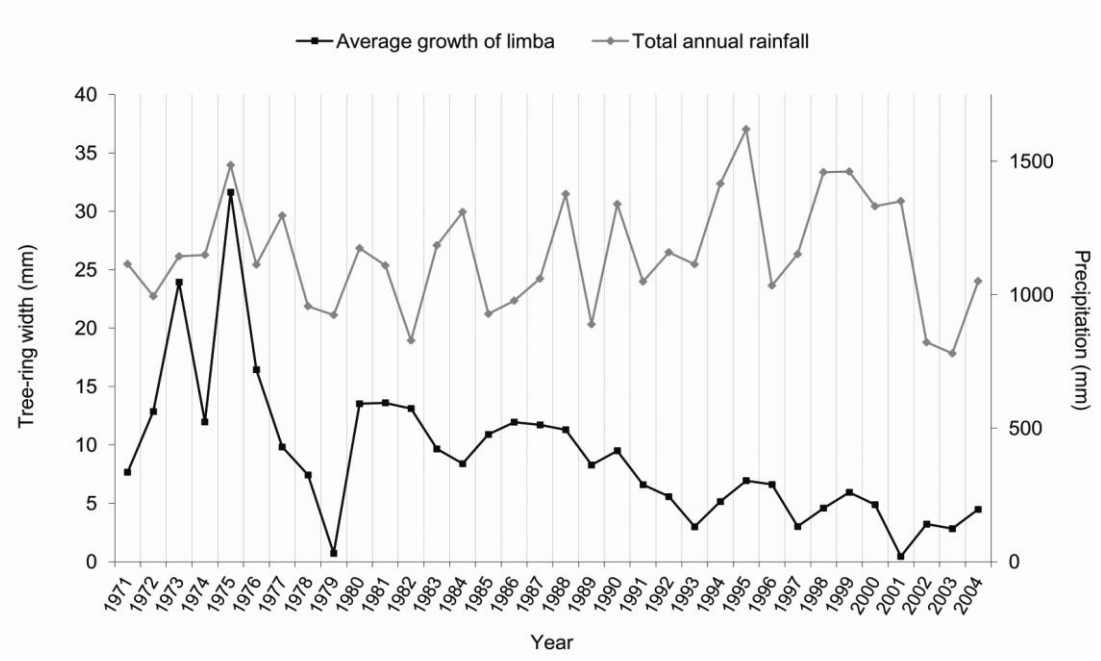

FIGURE 5-5. Average growth series of five *Terminalia superba* (limba) and contemporaneous total annual rainfall in the Reserve of Luki, DRC (Pearson's correlation = 0.13).

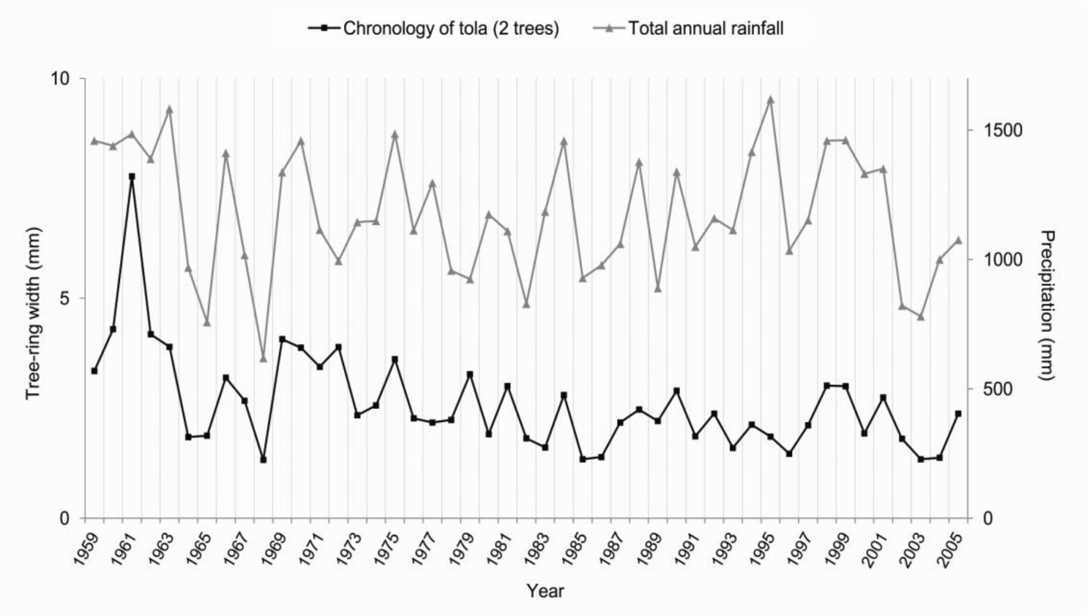

FIGURE 5-6. Chronology of two *Prioria balsamifera* (tola) and contemporaneous total annual rainfall in the Reserve of Luki, DRC (Pearson's correlation = 0.39).

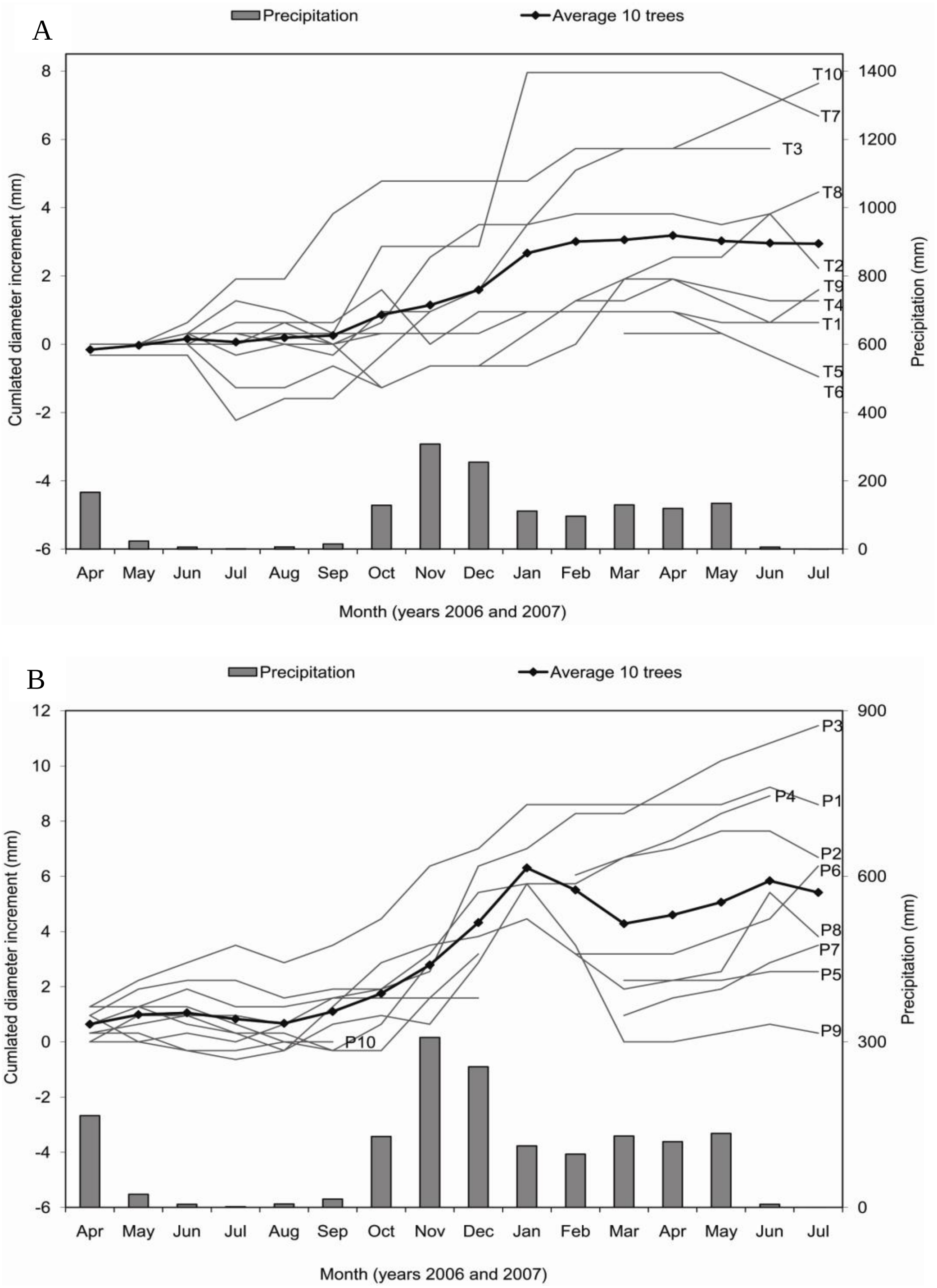

FIGURE 5-7. Cumulative diameter at breast height (dbh) increments from monthly measurements on (A) 10 *Terminalia superba* and (B) 10 *Prioria balsamifera* for 15 consecutive months (April 2006-July 2007) and monthly precipitation in the rain forest of Luki, DRC.

GROWTH RATES

The 15-month-long time series of cumulative diameter increments revealed the nonlinear dynamics of radial stem growth and its association to seasonality in rainfall (Fig. 5-7). The 10 growth patterns of *T. superba* were very heterogeneous. Several stems exhibited shrinkage due to dehydration during the dry season (June-September). Subsequently they all returned to pre-dry season dbh values then showed substantial radial growth, although with variations in timing and magnitude across species and individuals. It is also worth noting that stem shrinkage was particularly important for three *T. superba* trees that regained pre-dry season values only late in the rainy season (T4, T8 and T9). For *P. balsamifera* trees the patterns and growth rates were also heterogeneous but a general trend appeared more clearly. The radial stem increment of *P. balsamifera* globally started in the first months of the rainy season in October-November and continued until June-July, although with a little levelling-off in January-February (small dry season) for at least five trees (P1, P2, P3, P4 and P6).

DISCUSSION AND CONCLUSIONS

In the present study radial stem growth and its relationships with environment were investigated for two key canopy species of Central African rain forests, *Terminalia superba* and *Prioria balsamifera*. Increasing empirical support has been found for the occurrence of annual growth rings in tropical trees associated to seasonal changes, primarily in rainfall (Worbes 2002). Such evidence is mostly sustained for deciduous species growing in the upper-storey with their crowns fully exposed to external environmental factors (Pumijumnong and Park 1999, Worbes 1999, Brienen and Zuidema 2005). Accordingly, distinct growth rings were observed in the studied canopy trees growing under the seasonal climate of the Mayombe region and their formation was proved to be annual. This means that each year the trees experienced a resting period where cambial activity was stopped or strongly reduced, resulting in the formation of specific anatomical features around the tree circumference (a terminal band of thick-walled fibres for *T. superba* and several bands of parenchyma for *P. balsamifera*). The length of the growing season can however vary considerably from tree to tree, especially for *T. superba.* This most likely explains that ring-width series of *T. superba* trees could be crossdated but that huge differences in annual radial growth were observed within the species.

Peaks of high or low radial increment corresponding to extremely wet or dry years showed that the growth of both species was associated to variations in rainfall. For *T. superba* the five growth curves presented high inter-variability and were not synchronised, because of strong individual growth trends due to the young age of the trees. Yet the clarity of growth zones did not induce measurement errors and the corresponding years of extreme growth and rainfall were strong indications for annual ring formation associated with precipitation. The growth series of two *P. balsamifera* trees were positively correlated and were also positively correlated with total annual rainfall. Radiocarbon measurements eventually confirmed that for *P. balsamifera* growth ring formation is annual and positively related to precipitation.

Although annual ring formation was verified for both species irregularities such as missing rings, wedging rings and unclear ring boundaries were commonly detected as seen for several other tropical tree species (Ogden *et al.* 1981, Détienne 1989, Dünisch *et al.* 2003, Brookhouse *et al.* 2008). In Luki there are at least 3 months with less than 50 mm of rainfall each year but the dense cloud cover resulting from oceanic influence and the hilly landscape maintain a constantly high level of air humidity. Water stress during the dry season may thus not always be strong enough to cause total cambial inactivation and the formation of clear ring boundaries. It has been shown that cambial activity, although presenting clear tendencies associated to rainfall variations, is rather plastic depending on individuals and micro-site conditions. This would explain the observed periodicity of radial growth with frequent irregularities. Growth ring discrimination was also more difficult with decreasing ring width. Consequently the measurement and alignment of series was straightforward for the young and fast-growing *T. superba* trees but more problematic and time-consuming for the older and slow-growing *P. balsamifera* trees.

Average growth rates were much higher for *T. superba* (7.9 mm/y) than for *P. balsamifera* (2.2 mm/y). This could be due to the young age of the *T. superba* sample trees (Table 1) but the growth rate found in this study is in line with the 9 to 11 mm/y calculated by Détienne (1998) on 35 trees of various ages (18 to 55 years). The difference in growth rates moreover remains when considering only the first 25 years of growth for both species (7.9 mm/y for *T. superba* and 2.7 mm/y for *P. balsamifera)*, which is in accordance with their life history traits. Even though *P. balsamifera* trees demand high light levels to pass from the seedling to the sapling stage, afterwards they can survive under the shade of a dense forest cover and slowly grow towards the canopy. On the other hand, *T. superba* is a heliophilous species with maximised growth efficiency during the first years of establishment in recent forest gaps. Growth rates can then be very high, commonly up to 3 or 4 cm/y of diameter growth. This exceptionally fast growth is one of the important reasons why *T. superba* is so appreciated for plantations (Mariaux 1969, Lubini 1997, Détienne *et al.* 1998). The results from dbh measurements on the living trees account for water storage and for wood growth so they are consequently higher than growth values inferred from ring measurements on the wood itself (Deslauriers *et al.* 2007).

High standard deviations expressed important heterogeneity in ring width among years and individuals. The high MS values indeed indicated that both tree species strongly react to year-to-year variations of environmental signals. Individual heterogeneity was also noticeable in the intra-year variability of growth patterns resulting from monthly dbh measurement. There was a general trend following the seasonality of rainfall: wood production slows down or stops during the dry season, starts again during the first rainy months and continues until the end of the rainy season. However, specific individual trends were observed resulting in a wide range of growth patterns. For example, three *T. superba* (T2, T3 and T4) exhibited more important stem shrinkage during or right after the dry season than the others. Those three trees were exposed to major environmental change by the time of the experiment, since the forest around them was cleared to settle agricultural fields. *T. superba* are sometimes kept in fields because they provide good micro-site conditions for cultures such as banana, taro or manioc and pleasant shade or protection for people working in the fields. Without the buffer effect of the vegetation, climate variations are more extreme in gaps than in closed forest. In open areas temperatures and evaporation rise fast and the absence of deep underground plant roots allows important desiccation. Moreover there is no proper aquifer layer in the subsoil of Luki and very permeable superficial horizons allow great surface runoff (Donis 1948, Meulenberg 1949). Consequently, while air and soil humidity remain almost constant inside the forest, in open areas they drop down as soon as rainfall stops. The apparent “negative growth” caused by remarkably low dbh values of three *T. superba* during the rainy season was presumably due to air and soil water shortage in their open environment, which can result in stem shrinkage (Kozlowski and Winget 1964, Borchert 1994, Sheil 1995, Zweifel *et al.* 2007).

Similarly, important low-frequency trends in the different radii of the five *P. balsamifera* sampled in 2005 were detected and removed by standardisation but were not present in the 14 samples from 2007 (except one). This indicates that in the 2005 trees growth series from different radii had common year-to-year variations but contrasted in longer time-scale trends. Low frequency trends can be used to describe (differences in) life-history traits (Brienen and Zuidema 2006a). Here at the intra-individual level they may indicate various micro-local environmental conditions around or in the trees themselves, which caused different growth patterns on different sides of the trees. Contrary to the ones cut in 2007, the five *P. balsamifera* from 2005 had grown in easily accessible and partly degraded forests exposed to frequent human influence. Trampling of the ground, wounding of the stem, branches or roots or variations in light and nutrient availability due to openings may have affected radial growth differently in different parts of the trees.

This heterogeneity of growth patterns may explain the difficulties in crossdating, although ring formation was proved to be annual. The misalignment of the different growth series prevented from building consistent species chronologies and using dendrochronological analyses efficiently. The plasticity of wood formation is however noteworthy and seems to be much more important than for temperate trees (Mellerowicz *et al.* 1992, Cherubini *et al.* 2003). The intra-annual variations in growth patterns indicate that cambial dormancy during the dry season may not be strict. Growth can be null but can also occur at different rates depending on the conditions, with a time-lag of a month or less. Likewise, cambial activity can vary inside the same tree depending on the micro-site environmental conditions, showing that the cambium can have various levels of activity around the same stem.

The two study species also exhibit varying patterns of leaf or reproductive phenology (Chapter 2), supporting the idea that trees react individually to the same environmental variations. Sensibility to the type of substrate can explain these individual reactions as suggested by Donis (1948) and Dubois (1959), who showed that refoliation could be shifted by several months depending on the substrate for *Terminalia superba*. Individual physiological responses to climate variations depending on micro-site differences arguably lead to a great variety of biological rhythms, including wood formation.

In line with this idea of individual responses to climate variations, we showed in the previous chapter that synchronised growth patterns of understory tree species were associated to precipitation during the rainy season, but in different months depending on the species. Inter- and intra-specific growth variabilities however, seem to be higher in the canopy than in the understory (Fig. 5-8). In the present study the substantial heterogeneity in growth levels and patterns of canopy trees is supported and is moreover highlighted at the intra-individual level. The size factor may explain this more important growth variability in canopy trees than in understory trees, since tall and large upper-storey trees are physically exposed to a wider range of environmental conditions. Moreover, the buffer effect of the canopy softens the effect of climate variations for understory trees. Direct and abrupt changes such as shifts in temperature or humidity first affect the upper forest storey then progressively reach the lower layers, resulting in homogenised environmental conditions in the understory. Important physiological reactivity may thus be beneficial for canopy trees, allowing them easy and fast adaptation to extreme and changing conditions.

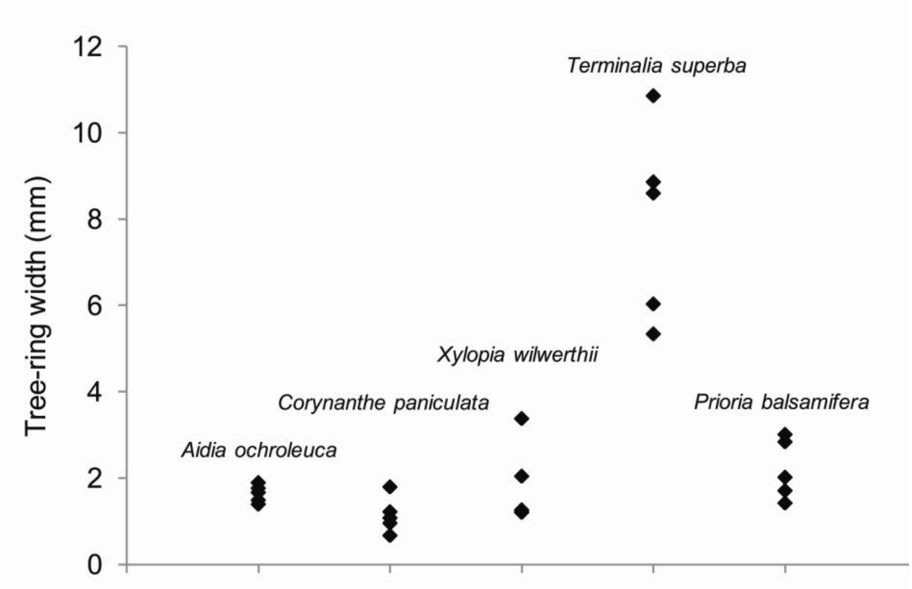

FIGURE 5-8. Comparison of average growth levels for trees of five species from the forest of Luki, DRC: three understory species (*Aidia ochroleuca*, *Corynanthe paniculata* and *Xylopia wilwerthii*) and the two canopy species studied here (*Terminalia superba* and *Prioria balsamifera*).

In this first dendroclimatological analysis of *Terminalia superba* and *Prioria balsamifera* annual ring formation associated with variations in rainfall is proven for both species. Since ring measurement was relatively fast and easy for *T. superba*, additional tree-ring studies are encouraged on older trees. For *P. balsamifera* accurate chronologies were also constructed from trees growing in open areas. With dense forest trees however, the discrimination of growth layers was extremely time-consuming and the synchronisation of growth series was not possible within or among trees. For this species growing in dense forests alternative methods to detect seasonal signals are thus recommended such as analyses of the isotopic composition of wood cellulose (McCarroll and Loader 2004, Poussart *et al.* 2004, Verheyden *et al.* 2005, Weigl *et al.* 2008, Wils *et al.* 2010) or non-destructive measurements based on X-ray tomography (Okochi *et al.* 2007).

ACKNOWLEDGEMENTS

We are grateful to all the staff in the Reserve of Luki, from INERA (Institut National pour l’Etude et la Recherche Agronomiques), MAB (Man And Biosphere program) and World Wide Fund-DRC and to Laurent Nsenga, Jean-Baptiste Loli Ndunga and Mbambi Ngoma in particular. We also thank Ilse Boeren, Maaike De Ridder and Marieke Vangoidsenhoven for their collaboration at different stages of this work.

CHAPTER 6

Intra-annual rhythms of radial growth in Central African rain forest trees

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ABSTRACT

Growth rhythms and modalities of cambial activity in relation to temperature and rainfall are not well known for tree species growing under tropical climates.

The present study aims to clarify xylem growth in five species of a natural semi-deciduous rain forest of the western Democratic Republic of Congo (DRC). Seasonal characteristics of wood formation were investigated using cambial pinning for *Prioria balsamifera* (Fabaceae/Caesalpinioideae), *Terminalia superba* (Combretaceae), *Xylopia wilwerthii* (Annonaceae), *Corynanthe paniculata* and *Aidia ochroleuca* (both Rubiaceae).

For the dominant canopy species *P. balsamifera*, cambial activity was important and positively associated to fluctuations in temperature and rainfall. For all other species however, xylem formation was low and did not appear to associate with climate variations. Cambial deactivation was not necessarily triggered by dry conditions and was always easily reversible. Wound-reaction wood after pinning was formed all year round, even when no normal wood production was observed away from the wound. Wound reaction and radial growth thus appeared to be independent from each other. Environmental conditions seemed to be always favourable for cambial activity; however radial growth was not always continuous. We conclude that cambial dormancy in tropical tree species is not strict but highly plastic and triggered by endogenous factors in addition to climate variations.

Key words: African rainforest; tropical wood anatomy; cambial activity; intra-annual growth rhythms; climate-growth relationships.

INTRODUCTION

Tropical forests have long been coveted for their most evident component: wood. For energy, construction or handicraft, wood provides multiple services and can be a major and durable source of income as long as wise forest exploitation prevents the decline of the resource. Wood is also a renewable energy source but rates of production and recovery must be known to allow sustainable use. The Congo Basin is the second largest stretch of tropical rain forest after the Amazon (Ruiz Perez *et al.* 2005, Laporte *et al.* 2007). 46 % of the African wood resources lie in the DRC (Democratic Republic of Congo) and are still relatively preserved because no large-scale deforestation has occurred since the middle of the twentieth century. At the extreme west of the country the Reserve of Luki is a patch of dense rain forest in a region with rapid demographic growth, calling for sound management plans to meet the needs of present and future generations (Nsenga 2004, Karsenty 2006). Knowledge on growth rhythms of trees in relation to the environment is prerequisite to be able to take up this challenge.

Dendrochronological studies focus on long timescales from decades to thousands of years and cannot precisely date anatomical variations within seasonal structures (Schweingruber 1996, Zweifel *et al.* 2006). Dendrometer measurements are a good alternative but do not discriminate wood growth from bark growth and trunk size variations due to temperature or humidity can cause important biases (Bormann and Kozlowski 1962, Fritts 1976, Zweifel *et al.* 2006). On the other hand, micro-sampling of the cambial zone (Deslauriers *et al.* 2003, Mäkinen *et al.* 2003) and cambial pinning (Wolter 1968, Kuroda and Kiyono 1997) are accurate ways to follow cambial activity of trees with a fine temporal resolution. The pinning method consists in injuring the cambium with a pin through the bark. As a consequence the cambium dies in the area close to the “pinning hole”, forming a distinct mark in the wood that records precisely the time of the traumatism: a cambial mark. The method is especially useful for the many tropical tree species for which wood anatomy is not well characterised (Yoshimura *et al.* 1981, Nobuchi *et al.* 1995, Dünisch *et al.* 2002, Verheyden *et al.* 2004, Seo *et al.* 2007).

In this study five species were selected for their wide distribution in Central Africa, because they are abundant and for their different biological characteristics. *Prioria balsamifera* (Fabaceae/Caesalpinioideae) and *Terminalia superba* (Combretaceae) are large canopy species. The first is shade-tolerant while the latter is a light-demanding pioneer mainly growing in gaps. On the contrary, *Xylopia wilwerthii* (Annonaceae), *Corynanthe paniculata* and *Aidia ochroleuca* (both Rubiaceae) are small-statured shade-tolerant species mostly growing in the understory. They all form growth rings that were proven to be annual but generally irregular (Couralet *et al.* 2010). The five species are exploited for their wood, the smaller ones mostly at a local scale and the two large ones also for international timber trade. Consequently it is necessary to include them in sound management plans or plantations, based on solid knowledge of their biology. This paper presents the first investigation on intra-annual patterns of wood formation in Central African rain forest trees, using periodic dbh measurement and cambial pinning. We tested the following hypotheses: (1) xylem production is seasonal and associated to climate variations (mostly rainfall) and (2) cambial activity is synchronous within species and among different species within a stand.

MATERIALS AND METHODS

STUDY SITE

The studied trees are from the Reserve of Luki (13°40’-13°18’ E, 05°28’-05°42’ N), approximately 30 km north from the port city of Boma in the south-western DRC (Fig. 1-2). The Reserve covers 32.700 ha of semi-evergreen rain forest of the Guineo-Congolean domain (Lebrun and Gilbert 1954, Lubini 1997, Whitmore 1998). It is a mixture of deciduous and evergreen tree species in the upper-stratum and mostly evergreen species in the understory. Except for the central zone of the Reserve, the forest occurs in a mosaic landscape with patches of agricultural fields and settlements. The mean annual temperature in Luki is 24.6 °C and the mean annual rainfall of 1180 mm/yr is characterized by a bimodal distribution (Donis 1948, Lubini 1997, Couralet *et al.* 2010). A distinct dry season (June to September) is followed by a long rainy season sometimes interrupted by a “smaller dry season” of one to two months around February. Monthly temperature and rainfall data were available from the Luki meteorological station from 1959 till 2007.

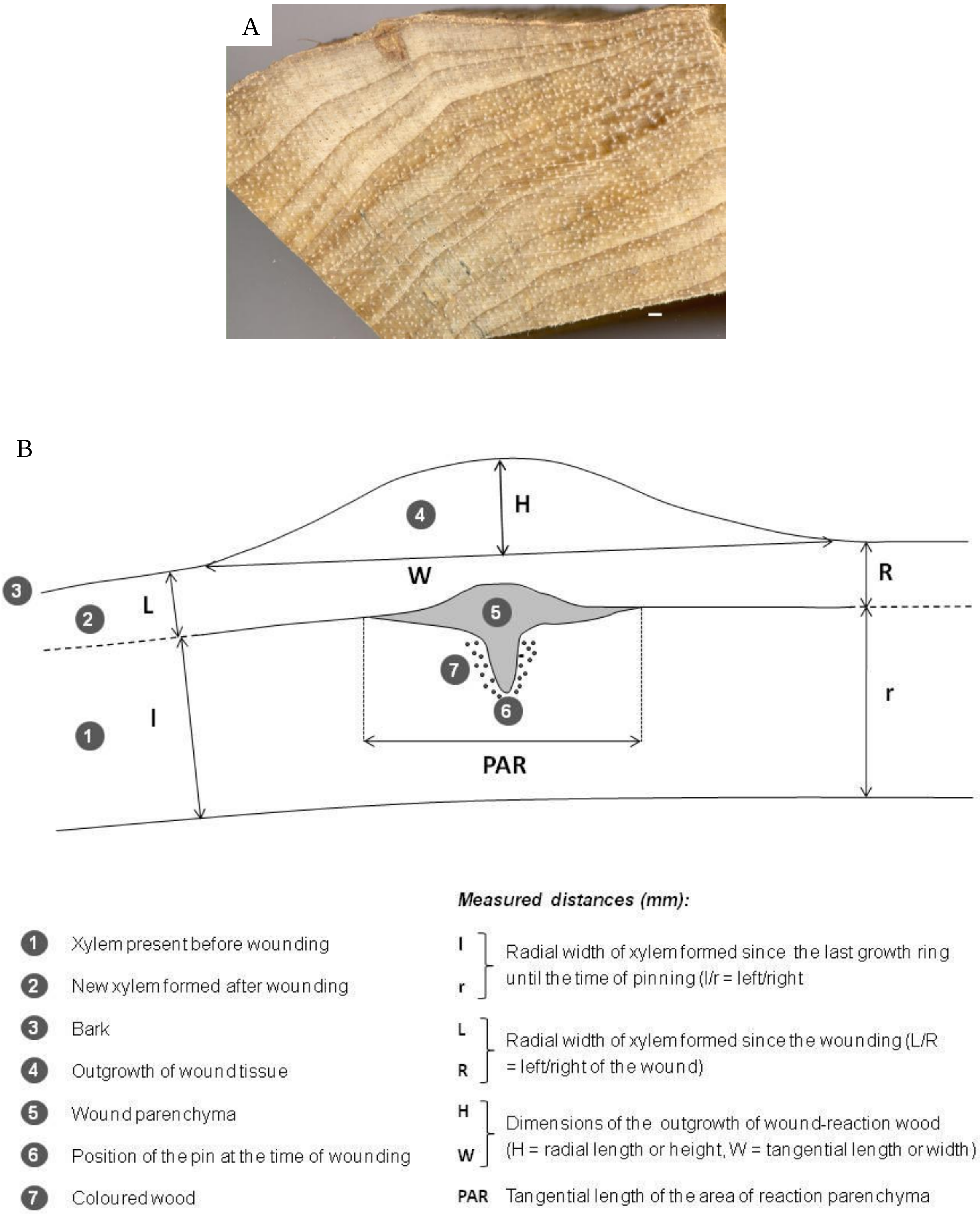

FIGURE 6-1. (A) Cambial mark visible on a cross-section of *T. superba* with eccentric growth rings. Scale bar = 1 mm. (B) Schematised representation of a cambial mark on a stem transverse section. All features are visible with the naked eye.

CAMBIAL MARKING AND SAMPLE PREPARATION

Ten trees of each study species *(Prioria balsamifera*, *Terminalia superba*, *Xylopia wilwerthii*, *Corynanthe paniculata* and *Aidia ochroleuca*) were selected in the Reserve of Luki. All *X. wilwerthii*, *C. paniculata* and *A. ochroleuca* trees grew in the same stand of closed rain forest, the Nkula forest (Fig. 1-2) and *P. balsamifera* and *T. superba* trees grew in other parts of the same forest type less than 1 km away. Trees were selected adult, healthy and within a medium size range for each species. Every first week of the month from April 2006 to August 2007, a cambial pinning was applied on each tree and stem girth at breast height (gbh) was measured with a graduated tape. The length of the experiment exceeded one year to ensure covering all possible climate seasons. If needed a thin portion of the bark was cut then the cambial zone was wounded with a surgical needle (0.2 mm of diameter) at breast height (Verheyden *et al.* 2004, Schmitz *et al.* 2008). The limited width of the wounding prevented pathogen attacks and important scar reactions that might complicate the interpretation of tissue production after pinning. Each new mark was made around the trunk circumference at the same height some 10 to 15 cm to the right. When a circumference was fully occupied, the next pinnings were made on a new circumference 20 cm higher. After 17 months i.e. 17 pricks, in the beginning of September 2007, all trees were felled. Stem sections were sawn at the level of the markings visible on the bark and signalled with paint. Samples were dried naturally then cut into small pieces, each containing one wound. Their surface was sanded until a grit size of 1200 and the different wood tissues were observed macro- and microscopically. Microscopic observations of the cross-sectional wood surface allowed detecting and characterising precisely wood tissues and new growth since the time of pinning. When more detailed examinations were needed transverse thin sections were cut with a sliding microtome and double-stained with Safranin and Fast Green. Furthermore, sanded surfaces of some wood blocks were additionally planed with a scalpel and observed without staining with a confocal microscope.

ANALYSES

Values of dbh (diameter at breast height) increment were averaged into 17-month-long series for each species. Correlation was calculated between the series and with monthly climate variables (temperature and rainfall). Several wound characteristics were measured on scanned pictures of the wood transverse sections of each scar using the image analysis software cell^A (® Olympus UK Ltd) via a camera connected to a stereomicroscope (Fig. 6-1). First, the nature of the reaction to pinning was studied. The tangential length of wound parenchyma formed around cambial marks (PAR, mm) was measured and an index for the area of wound tissue was calculated by multiplying the radial and tangential lengths of the outgrowth formed at the position of pinning (OUT = W x H). Xylem growth since the latest growth ring until time of pinning was also measured as the distance between the tangential band of wound parenchyma and the last-formed growth ring boundary, left and right of each scar (l and r). This was however possible only for some trees of the species with the clearest and widest rings, *T. superba*. For the other trees and species ring boundaries were indistinct and growth rings were irregular thus could not be identified from one scar to the other. Additionally, the radial width of new xylem formed after wounding was measured left and right of each scar, not at a fixed distance but at the end of the thin line of wound parenchyma marking the pinning (L and R). For each tree and each month left and right values were averaged into mean radial wood growth, in mm. Normal xylem production was examined right after the thin parenchyma line to avoid the zone of abnormal growth. Correlations were calculated between the time series of monthly PAR, OUT and radial wood growth of the different species. Trees were harvested in September, one month after the last pinning. Consequently time for tissue formation after the wounding was limited for the last measurements (June, July, and August). These data may thus only be a partial illustration of the trees’ reactions during these last months of experiment. To study the relationships between tissue production and climate, correlations were calculated between the time series of dbh increment, PAR, OUT, radial wood growth and monthly air temperature (T, °C) and rainfall (R, mm) in Luki during the 17 months of experiment (April 2006 - August 2007). All correlation coefficients reported are Pearson product-moment correlation coefficients.

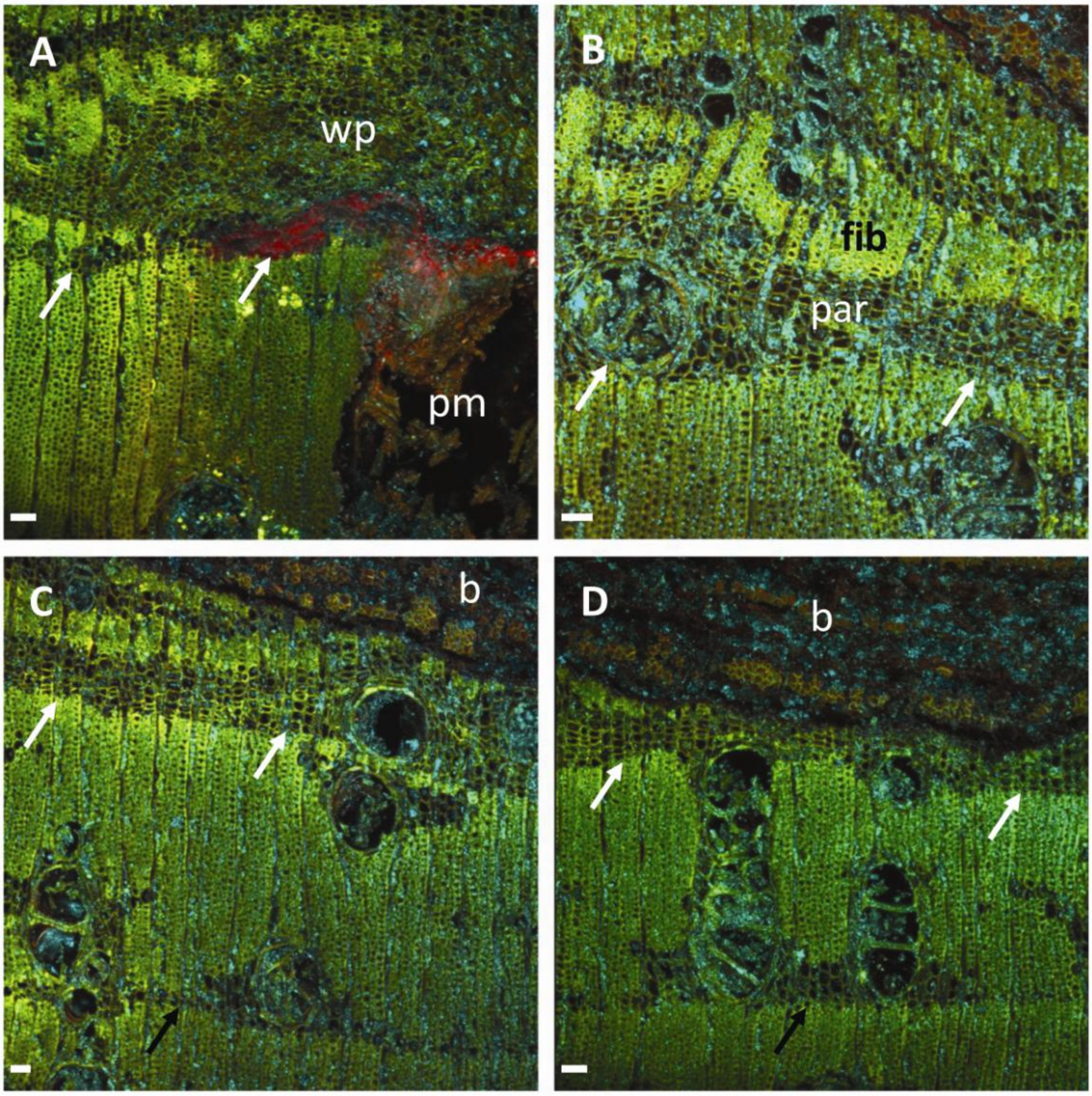

FIGURE 6-2. Details of the reaction to cambial pinning on a *T. superba* tree (sample T8, pinning in May 2006) observed with a confocal microscope (LSM, Carl Zeiss 510) using a single track, triple channel imaging with 405, 488, and 543 laser lines, and band-pass filters (BP 420-480; BP 505-530; BP 580-700). (A) An area around the pin mark (pm). The substance that fills the cavity of the pin mark is red (strong fluorescence in the red spectrum). Wound-reaction parenchyma (wp) covers the wound at the outer side. (B) An area adjacent to the wound. The direction of the wound is to the left. (C) and (D) are consecutive pictures in the tangential direction from the wound. White arrows indicate the parenchyma line marking the position of cambium at the time of pinning. Xylem growth after the pinning is above the white arrows and xylem before the pinning is below. Large cells in (B), (C), and (D) are vessels. Some of the vessels contain tyloses and a substance with blue fluorescence (possibly phenolics). Axial parenchyma cells (par) have brown-green walls and dark lumens. Fibres (fib) have green or orange walls and narrow lumens. Many of the cells are filled with a substance with strong blue fluorescence which is possibly phenolics. The bark (b) is at the top of the images. Black arrows point to axial parenchyma on the previous growth increment. All scale bars = 50 µm.

RESULTS

DBH INCREMENT

Values of dbh increment were different for the five study species (Table 6-1). During the 17 months of the experiment the slowest growing species was *X. wilwerthii* (cumulated increment of 0.63 mm) and the fastest was *P. balsamifera* (4.59 mm). After a moderate increment in the first two to three months of the experiment (April-June), dbh decreased during the dry season with a minimum in July. Stem shrinkage occurred for all species, most notably for understory trees. From September-October onwards dbh increase resumed, to diminish again from February-March. All species thus reacted positively to this rainy period but with some differences. *P. balsamifera* grew continuously from September on up to a steady drop in January-February, whereas the dbh growth of *T. superba, C. paniculata* and *A. ochroleuca* showed two peaks during the rainy season, in October and January-February. An intermediary pattern of dbh variations was observed for *X. wilwerthii.* Correlation values between the series confirmed these similarities (Table 6-1). The most dissimilar patterns were *T. superba* and *X. wilwerthii* and the most resembling were *C. paniculata* and *A. ochroleuca* or *X. wilwerthii.*

TABLE 6-1. Dbh at the time of felling, total cumulated dbh increment and correlation values between all species' time series of monthly dbh increment (ns = non significant, df = 15, $p < 0.05$) from April 2006 to August 2007 in the Reserve of Luki, DRC. Averages of ten trees per species.

	Average dbh (cm) mean *[range]*	***Cumulated dbh increment (mm)*** mean *[range]*		***P***	***T***	***X***	***C***
Prioria balsamifera	30 *[16-41]*	4.6 *[-5.4/19.1]*	***P***				
Terminalia superba	32 *[16-43]*	3.1 *[-1.0/7.6]*	***T***	**0.63**			
Xylopia wilwerthii	16 *[14-17]*	0.6 *[-0.3/1.42]*	***X***	**0.58**	**0.50**		
Corynanthe paniculata	24 *[17-40]*	1.0 *[0.5/1.8]*	***C***	ns	**0.64**	**0.76**	
Aidia ochroleuca	21 *[18-25]*	1.2 *[0.2/2.6]*	***A***	**0.69**	**0.67**	**0.60**	**0.76**

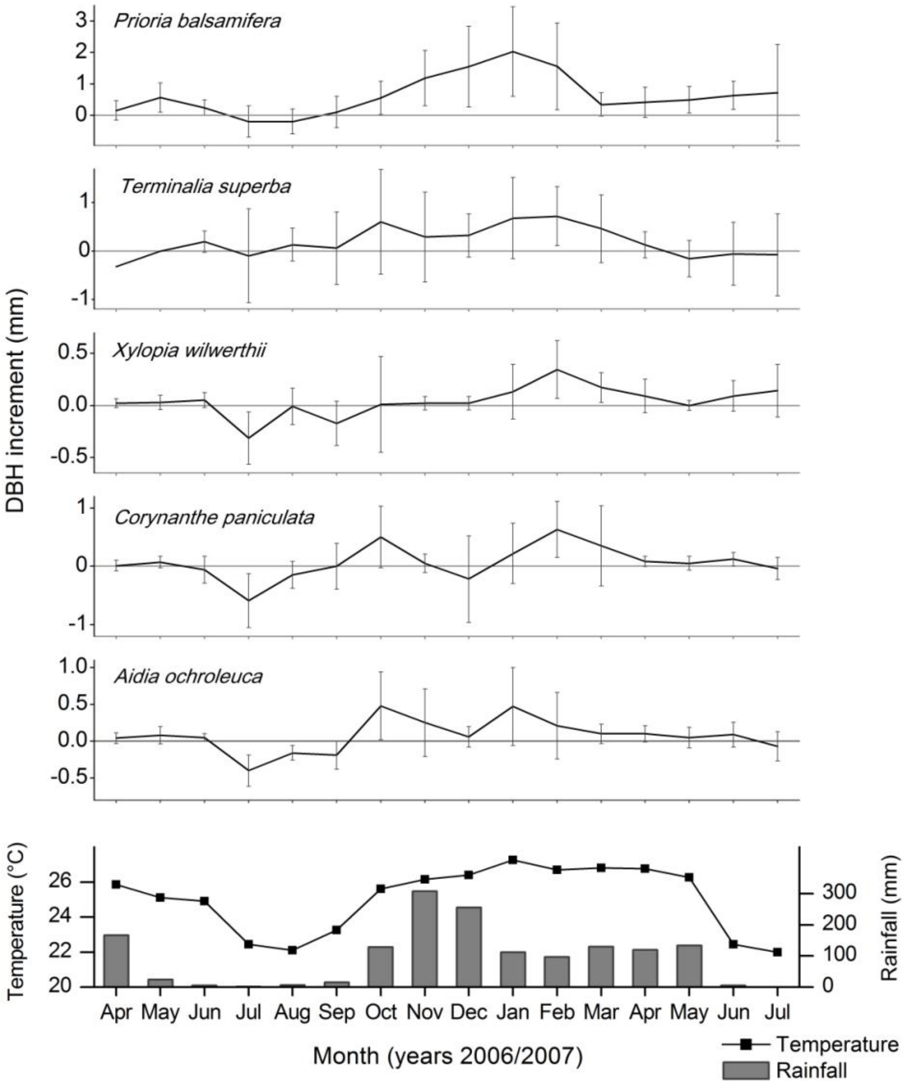

FIGURE 6-3. Time series of average monthly dbh increment for the five study species (ten trees per species) during 17 months (April 2006 - August 2007) in the Reserve of Luki, DRC.

WOOD ANATOMICAL DESCRIPTION OF THE CAMBIAL MARKS

All cambial pinnings provoked the formation of a visible scar in the wood. Most pin holes were encircled by an extra periderm formed under the bark and an outgrowth of wound-reaction wood was also frequently formed around the position of pinning (Fig. 6-4). Microscopically, the position of the cambial zone at the time of pinning was determined from a combination of wood anatomical characteristics (Fig. 6-1 and 6-2). In agreement with earlier reports, an area around the exact position of wounding was filled with reaction parenchyma, of variable extent according to individuals and months. A thin line of parenchyma also indicated the moment of the cambial marking for 86 % of the wounds (17 markings on 50 trees, *n* = 850) sometimes until 10 cm or more from the position of pinning, tangentially

(Nobuchi *et al.* 1995, Ohashi *et al.* 2005, Schmitz *et al.* 2008). Besides, a zone of protection wood stained by oxidation was observed inward to the pinning canal on 96 % of the scars (Schmitt *et al.* 2000, Carlquist 2001, Schmitz *et al.* 2008).

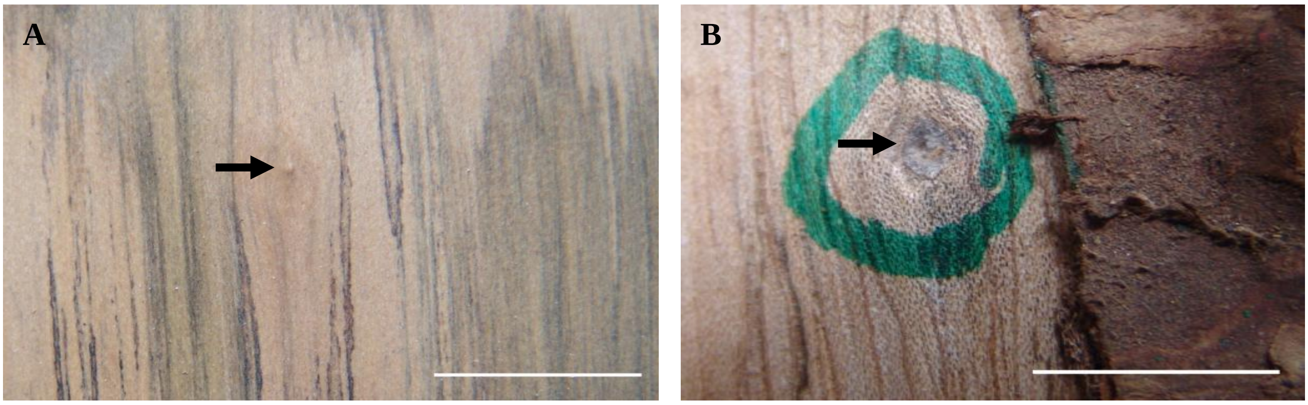

FIGURE 6-4. Scars 17 months after cambial pinning (indicated by black arrows) on the wood of *Corynanthe paniculata* (A, no bark) and *Prioria balsamifera* (B, scar marked with green pen, bark partly removed and extra periderm encircling the pin hole). Scale bars = 1 cm.

TISSUE PRODUCTION AFTER THE WOUNDING

Two main types of tissues were produced in reaction to cambial pinning: wound parenchyma and wound-reaction wood. An area around the position of pinning was always filled with wound parenchyma and an outgrowth of wound tissue was formed for the majority of the marks (Fig. 6-1). Besides, usual xylem was produced after the dated cambial marks. The production of these different tissues was quantified on an annual basis (May 2006 - April 2007) (Table 6-2).

All pinnings provoked the formation of specific wound features, of variable size according to individuals and months. The radial width of outgrown wood at the position of pinning (H) was more important than the radial xylem increment away from the scar, for all species except for *A. ochroleuca*. Trees of this species formed moderate amounts of outgrown wood but spread in wide and thin outgrowths. On average, *P. balsamifera* trees showed the highest production of wound parenchyma and outgrown wood (also the most variable among individuals) and *X. wilwerthii*, the lowest (Table 6-2 and Fig. 6-5). For all species rates of outgrown wood formation reached a maximum at the end of the first dry season (August-September 2006, Fig. 6-5). Regarding the production of wound parenchyma, the most noticeable pattern was a general increase in the late rainy season (May 2007) in all species except *P. balsamifera*.

TABLE 6-2. Tangential length of the reaction parenchyma (PAR, mm), index of the outgrown area of wood formed in response to pinning (OUT), radial length of outgrown wood (H, mm) and total radial wood growth (mm) measured on transverse sections of trees exposed to monthly cambial pinning. Mean annual values and ranges (in square brackets) for ten trees per species for the period May 2006 - April 2007 in the Reserve of Luki, DRC.

	PAR	**OUT**	**H**	**Radial wood growth**
P. balsamifera	8.5 *[4.0-19.4]*	28 *[0-126]*	12.2 *[0.0-21.1]*	3.7 *[1.4-8.4]*
T. superba	3.2 *[2.1-4.1]*	21 *[2-52]*	10.5 *[2.6-15.1]*	0.3 *[0.0-2.3]*
X. wilwerthii	3.0 *[2.1-3.6]*	3 *[0-12]*	6.4 *[0.5-9.6]*	0.4 *[0.0-1.3]*
C. paniculata	5.5 *[3.2-7.5]*	22 *[3-77]*	11.7 *[1.3-20.2]*	0.9 *[0.0-2.4]*
A. ochroleuca	5.2 *[2.9-8.6]*	25 *[1-97]*	1.3 *[0.4-2.1]*	1.8 *[0.0-4.0]*

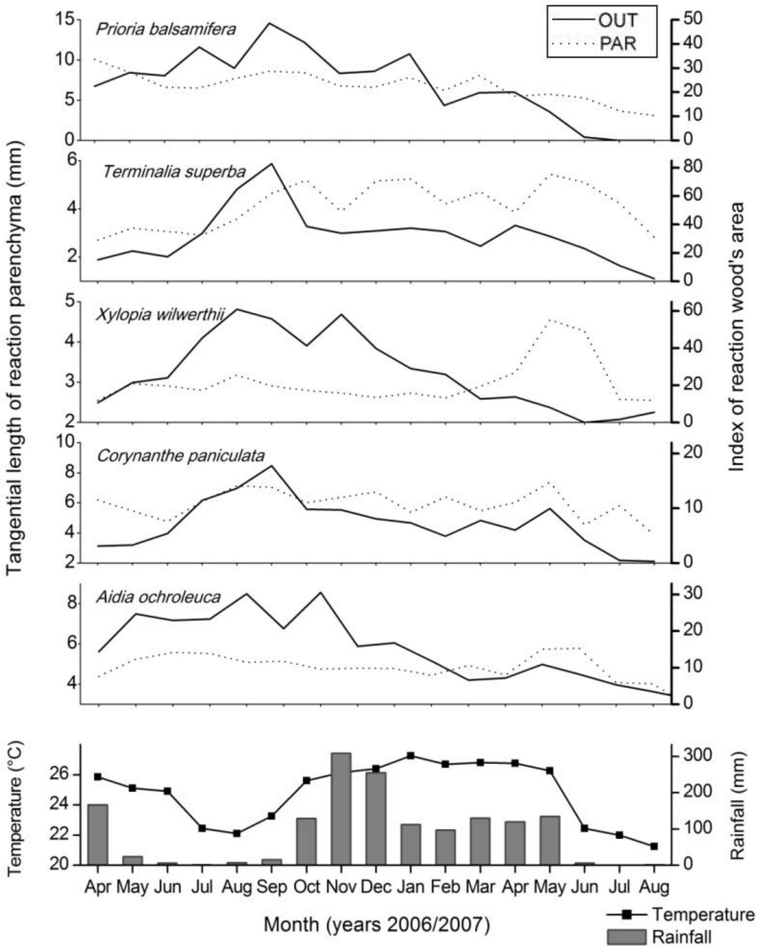

FIGURE 6-5. Tangential length of reaction parenchyma around the pinnings (PAR, mm) and index of the area of outgrown wood formed at the position of pinning (OUT). Average of ten trees per species from April 2006 to August 2007 in the Reserve of Luki, DRC.

In line with the dbh measurements, the study of wood sections confirmed that *P. balsamifera* trees had the most rapid and most variable radial wood growth among the five study species and *X. wilwerthii*, the slowest and less variable. Notably, the pioneer *T. superba* had the slowest annual radial growth while the shade-bearer *A. ochroleuca* grew 6 times faster (Table 6-2). These high values of radial increment for *P. balsamifera* and *A. ochroleuca* are mainly due to peaks of wood production at the very start of the rainy season, respectively in September and October (Fig. 6-6). No common pattern of radial wood growth was otherwise noted among species. On the contrary, individuals showed a high variability in the timing and magnitude of wood production, indicated by dissimilar growth curves and high standard deviations (Fig. 6-7). Apparently independent from temperature or rainfall, an individual tree of one particular species could show absolutely no radial wood growth while another tree of the same species could have a very high xylem production during the same month. Some trees even exhibited null cumulated radial growth after the 17 months of experiment (Table 6-2). For five *T. superba*, five *X. wilwerthii* and one *A. ochroleuca* no xylem was formed during 17 months, or so little that it was not visible under the stereomicroscope.

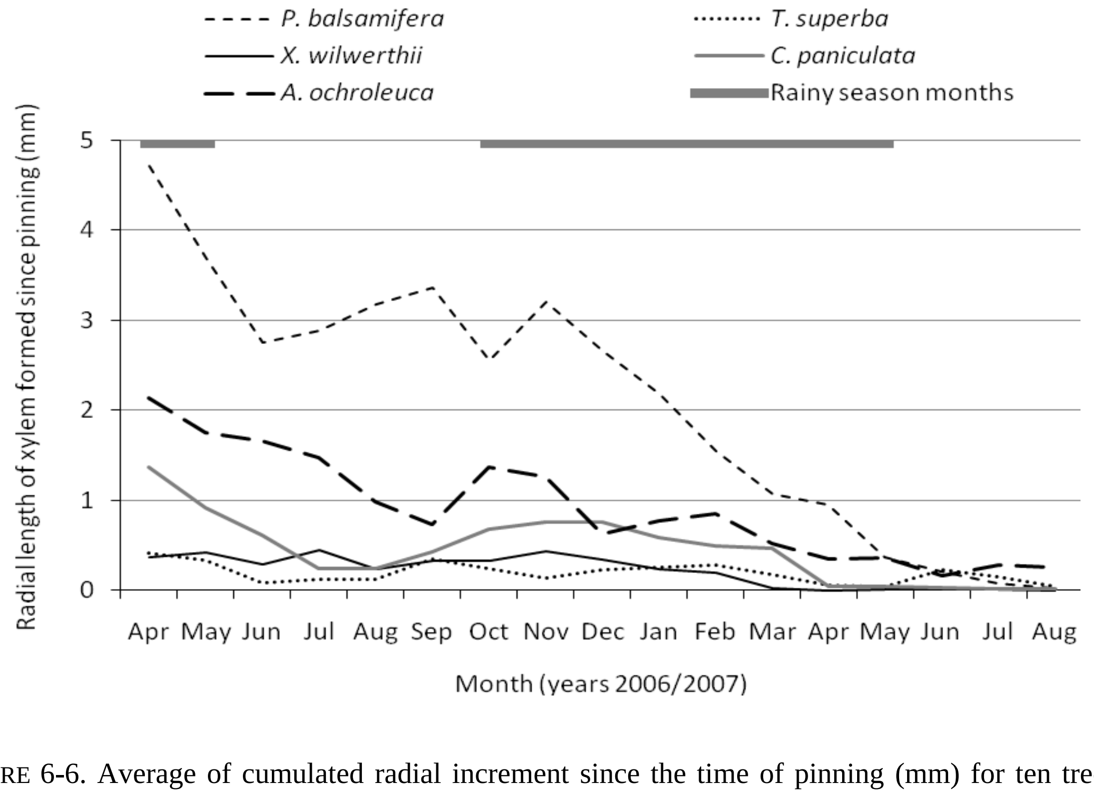

FIGURE 6-6. Average of cumulated radial increment since the time of pinning (mm) for ten trees of five species from the Reserve of Luki, DRC (April 2006 - August 2007).

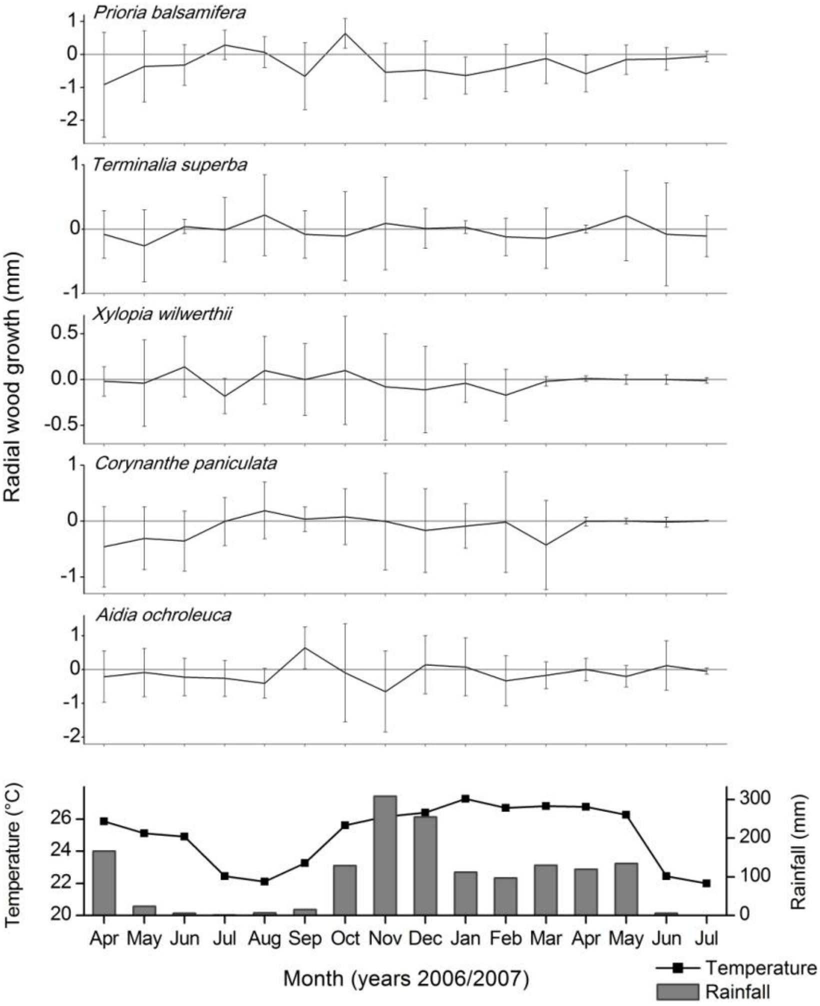

FIGURE 6-7. Average monthly radial increment since the time of pinning (mm) for ten trees of five tree species from the Reserve of Luki, DRC (April 2006-August 2007). Vertical bars indicate standard deviation.

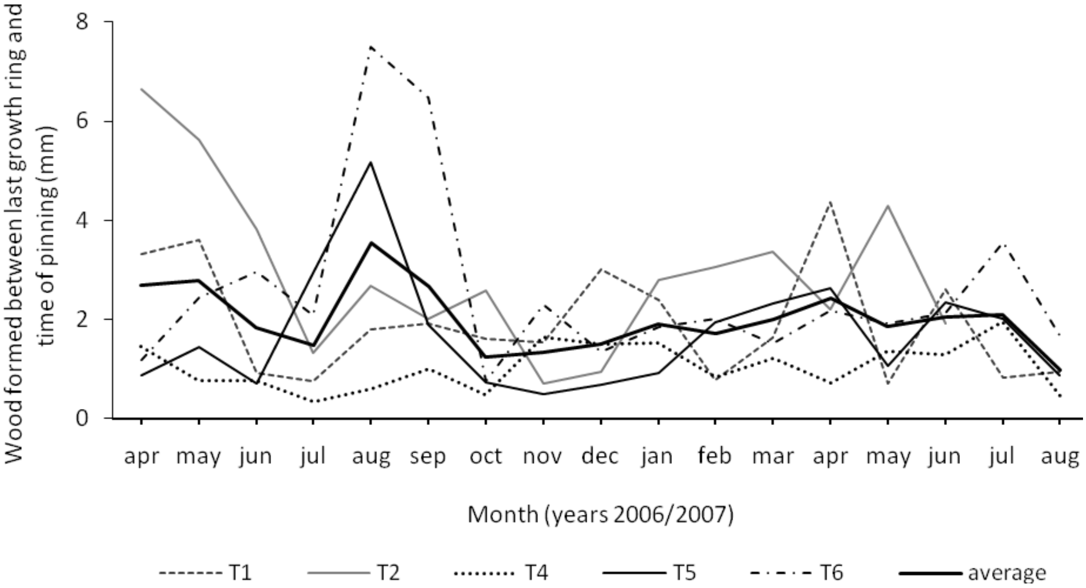

FIGURE 6-8. Radial wood growth from the last growth ring until the position of pinning (mm) for five *T. superba* trees (T1, T2, T4, T5 and T6) from the Reserve of Luki, DRC (April 2006-August 2007).

Measurements of wood formed since the last growth ring until the time of pinning for five *T. superba* trees showed no specific trend. The variability between individuals is noticeable, with no apparent influence of seasonal climate variations (Fig. 6-8).

CLIMATE-GROWTH RELATIONSHIPS

The relationships between tissue formation in the studied trees and climate were investigated using correlation analysis. The chosen climate variables were rainfall (mm) and air temperature (°C) in Luki from April 2006 until August 2007 (correlation coefficient between these two variables = 0.71). The dbh increment measured with tape around the stem circumferences of living trees was positively associated with temperature and rainfall for the canopy species *P. balsamifera* and with temperature only for the pioneer species *T. superba* (Table 6-3). No other significant correlation was found between tissue production and climate variations.

TABLE 6-3. Pearson correlation values between series of monthly dbh increment (mm) measured with tape, tangential length of reaction parenchyma around the pinnings (PAR, mm), index of the area of wound-reaction wood (REAC), radial wood growth (mm) measured on transverse wood sections and monthly temperature (T, °C) and rainfall (R, mm) in Luki (ns = non significant correlation, df = 15, $p < 0.05$). Averages of ten trees per species between May 2006 and April 2007 in the Reserve of Luki, DRC.

	Dbh increment		**PAR**		**REAC**		**Radial wood growth**	
	T	**R**	**T**	**R**	**T**	**R**	**T**	**R**
P. balsamifera	**0.56**	**0.49**	**0.44**	ns	ns	ns	ns	ns
T. superba	**0.50**	ns	ns	ns	ns	ns	ns	ns
X. wilwerthii	ns	ns	ns	ns	ns	ns	ns	ns
C. paniculata	ns	ns	ns	ns	ns	ns	ns	ns
A. ochroleuca	ns	ns	ns	ns	ns	ns	ns	ns

DISCUSSION AND CONCLUSIONS

The pinning method is based on the assumption that wounding the cambium of trees generates a datable scar in the wood (Larson 1994). In line with this hypothesis all pinnings applied in this study provoked a visible mark. Outgrowths of wood formed in response to the mechanical strength of the pinning and wound parenchyma around the exact position of cambial pinning were observed and usual xylem production was tracked with a monthly resolution away from the scars. An important finding of this study is that the cambium of most study trees was never completely dormant. Moreover, amounts of reaction tissues and of normal xylem were variable among species, individuals and even within the same tree, revealing the plasticity of cambial activity.

Fluctuations in trunk diameter were positively correlated to variations in rainfall and temperature for the canopy species *P. balsamifera* and to variations in temperature for *T. superba*, probably due to the direct exposition of their crowns to the atmosphere. Our results confirmed radial trunk shrinkage or swelling in relation to climate for canopy trees (Kozlowski and Winget 1964, Borchert 1994a, Borchert 1994b, Sheil 1995, Zweifel *et al.* 2006). On the other hand, understory trees grow in a buffered environment where external climate variations are softened by the upper vegetation layers. That is why for the three dominated species changes in stem size were moderate and did not associate with temperature or rainfall. Besides, except for *P. balsamifera* there was no correlation between these dbh variations and internal xylem growth, suggesting two things. Variations in radial stem size are either mostly located in the bark or due to variations of water content in the tissues regardless of cambial activity. Consequently, this reaffirms that direct cambial monitoring is more accurate than circumference measurements to study radial wood growth (Kuroda and Kiyono 1997).

According to their biological guild the two canopy species grew faster than the three understory species during the 17 months of experiment. Understory species generally have their crowns fully in the shade thus grow extremely slowly (Swaine and Whitmore 1988, Gourlet-Fleury 2005). Among the canopy species the pioneer *T. superba* grew slower than the shade-tolerant *P. balsamifera*, which contradicts the average growth rates commonly known for both species (Mariaux 1969, Lubini 1997, Breteler 1999). These rates are calculated based on all life stages whereas the studied trees were adult trees, moreover growing in a dense forest. Pioneers establish in full light where they can grow very fast, but once they are surrounded by other trees and light levels are lower their growth rates are moderate. On the other hand, adult shade-tolerant trees that have reached the canopy are “climax” trees, with spread crowns receiving high amounts of light and extensive root networks accessing water and nutrients in large areas (Hallé *et al.* 1978, Oldeman and van Dijk 1991, Lubini 1997). Consequently, in a dense forest and at the adult life stage shade-tolerant trees like *P. balsamifera* are likely to grow faster than light-demanding pioneers like *T. superba*.

P. balsamifera and *X. wilwerthii* also had the highest and lowest amount of wound tissues, respectively. It could suggest that productions of standard xylem and of reaction tissues are correlated, but this proved only true for *P. balsamifera*. For this species radial wood growth is associated to the formation of wound parenchyma and of wound-reaction wood ($r^2 = 0.83$ and 0.75 respectively) and all tissues productions are positively correlated to temperature and rainfall. Intensive cambial activity can be explained by optimal growth conditions in the canopy. Besides, direct exposition to external environment can account for the strong reactivity to climate variations. At the intra-annual level all study species have common patterns of wound tissue production, indicating that they must be influenced by common external factors (Schweingruber 1996). The production of wound-reaction wood was maximal at the end of the first dry season suggesting that it may be associated with periods of growth stress. The minimal growth measured at the same period the following year is probably due to the limited time after the last pinnings. Low correlation values between the production of wound tissues and climate variations also suggest that other factors may be influential. Different reactions to wounding were observed among species, trees and from one month to the other within trees but did not identify any pattern or correlated variable.

Nevertheless, the formation of parenchyma or wound-reaction wood regardless of the season indicates that the cambium was never completely dormant. For all species except *P. balsamifera* the production of reaction tissues often provided evidence for cambial activity although sometimes no xylem growth was observed after wounding. It means that the cambium is potentially active in all seasons but that radial growth is not automatic even in favourable conditions. On the other hand, healing a wound is necessary for the tree survival and may demand cambial activation in all cases. In Luki it was assumed that some trees remained alive but suppressed for very long times with extremely low or null growth rates, especially in the understory (Lubini 1997). *X. wilwerthii* or *C. paniculata* trees that had been marked in 1948 as being under 20 cm of circumference were still under this size in 2006 meaning they had grown less than 20 cm in 58 years, equivalent to less than 1 mm of annual dbh increment on average. This study confirmed this observation and suggests that variables other than climatic trigger xylem formation. In understory trees and some *T. superba* several trees showed no xylem growth even when the cambium was active. This was not observed for *P. balsamifera* where tissue production was correlated to climate variations. It indicates that for dominant trees growing in favourable conditions cambial activity is triggered by climate variations, equivalent to observations for temperate species (Cha and Bonga 1974, Larson 1994). The cambium is dormant during the least favourable periods (winter or dry season) and is reactivated when conditions are more favourable (spring or rainy season). The particularity of the tropical *P. balsamifera* is that xylem formation is not stopped during the dry season but only slowed down. On the other hand, for understory species or light-demanding species in low light levels, cambial activity may be influenced by other variables than climate. As shown by the wound reactions the cambium is always potentially active but trees do not automatically produce normal wood thus radial increment can be null during more than a year.

Noticeably, wood growth was very irregular with regard to time and position of pinning. Important eccentricity of the rings and frequent ring discontinuities were observed on the surface of the samples and exhibited by the results from measurements. Radial growth was highly variable between trees of the same species. Moreover within the same trees growth levels appeared to vary greatly from one scar (or month) to the other. We studied in detail the samples from some *T. superba* trees, which had the largest and clearest rings. However, even with precise “timers” represented by the cambial pinnings, the irregularities of wood anatomy and of cambial activity between trees and around the circumference of each tree did not allow us to highlight any specific growth trend. For other species with less clear rings, the task seems to be even more challenging. In the five study species from the Reserve of Luki radial cambial divisions seem to have different dynamics around the stem circumferences, which did not allow for the interpretation of cambial scars.

This study revealed that cambial activity in tropical trees is variable from one species to the other, among trees of the same species and around the stem circumference of individuals, seemingly regardless of the large-scale climate variations. It suggests that cambial activity is highly plastic and may be influenced by small-scale environmental conditions in each tree. Moreover the definition of cambial dormancy used in temperate climates (Savidge and Wareing 1981, Catesson 1994) may need to be refined for tropical tree species in which growth inhibition appears to be more plastic than in temperate regions and controlled by other variables than temperature, humidity or day length. Cambial functions are not deactivated during the dry season but they are in an easily reversible rest state that for example a mere needle pinning can invert.

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Maloti ma Songo, Fils Mbungu Phaka, Luyeye Vangu Nsadi and Lupeta Mamana Mbambifor their precious assistance at various stages of this work. Anouk Verheyden, Nele Schmitz and Valérie Trouet are also acknowledged for the valuable advice provided for this study.


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CHAPTER 7

General conclusion

The objective of this study was to gain knowledge about several ecological aspects of trees growing in the Central African rain forest that remain poorly known and to get a better understanding of tree community dynamics. We wanted to value the information contained in ancient datasets from the Reserve of Luki in the DRC and to complement it using new analyses, with the following specific aims:

1. Evaluate the present state of the forest and assess the changes of the ligneous community in response to major disturbances.

2. Draw rhythms of leaf and reproductive cycles for species and groups of species, highlight possible associations with climate variations and assess the level of heterogeneity of these patterns.

3. Determine whether tree species in the Central African rain forest form annual rings and study the influence of climate variations on tree growth for species of different forest strata.

4. Characterize the cambial reactions to pinning and the intra-annual patterns of cambial activity in relation with climate variations among species and among individuals of the same species.

In Chapter 2 we showed that the forest in Luki has moderate species diversity and moderate biomass content, typical for African rain forests (Parmentier *et al.* 2007). We also highlighted that in 2006 these parameters were augmenting in a plot that was subject to a major silvicultural treatment 58 years before, and that both values were higher than in undisturbed parts of the Reserve. The floristic composition proved that the abundance of light-demanding species was higher, but also of shade-bearer canopy species more typical of mature forests. The size-structure of the tree community moreover indicated good general fitness. We concluded that the forest had an important resilience capacity and suggested that an intermediate level of disturbance seems to promote local species diversity. If logging is controlled in the reserve so that it does not reach intensive levels, the forest may gain biomass and species diversity. Forest management plans supporting this idea must however rely on sound ecological knowledge of the most harvested species. An important question in community ecology is to determine the level of heterogeneity of responses to environmental variations within the same community.

In the third chapter we investigated the leaf and reproductive cycles of the community of trees in Luki to evaluate how heterogeneous, or plural, species were in terms of phenological patterns. This type of study requires long-term and extensive monitoring usually very difficult to achieve but we could analyse a unique dataset summarising observations of 3750 African rain forest trees from 1948 until 1957. Most studied tree species and functional groups of species were found to have annual rhythms of leaf and reproductive phenology. A wide array of phenological patterns was however highlighted, from synchronous annual peaks to continuity. Positive association between leaf phenology and rainfall was shown for the group of canopy species and for the canopy and heliophilous study species. For the heliophilous and understory groups and for the understory study species however, positive correlation with rainfall was found for reproductive phenology (flowering and fruiting). Only one environmental variable (rainfall) has been examined but other important drivers of tree water status such as air temperature, soil moisture or vapour pressure deficit should be studied more detailedly to understand the variety of phenological rhythms (Borchert 1999).

For a set of species selected for their abundance and because they are sought after for harvest, we performed dendroclimatological analyses (Chapter 4 and 5). Annual ring formation was proven for all species: the small-statured, understory *Aidia ochroleuca*, *Corynanthe paniculata* and *Xylopia wilwerthii* and the tall canopy, shade-tolerant *Prioria balsamifera*, the long-lived, pioneer *Terminalia superba*. Association with variations in rainfall was also highlighted, with different magnitude and timing depending on the species. For the understory species associations were found with rainfall with clear inter-specific differences. The radial growth of each species was positively correlated to variations in rainfall but in different months of the rainy season. For *P. balsamifera* and *T. superba* a positive association was found between radial growth and the annual sum of precipitations. Ring determination was however laborious and time-consuming because of various growth irregularities. In this study we experienced some limits of the classical methods of ring-width measurements and of dendrochronology in general when applied to tropical tree species. Cross-dating relying on the experience and subjectivity of the researcher may not be adapted to the numerous peculiarities of radial tree growth in the tropics. Possible alternative solutions could be to study periodic signals in high-resolution time series of wood anatomical variables (Verheyden *et al.* 2005, Weigl *et al.* 2008) or to measure stable isotopes more systematically (Farquhar *et al.* 1982, Evans and Schrag 2004, McCarroll and Loader 2004, Hietz *et al.* 2005). Automated devices to extract portions of wood at regular intervals or non-destructive methods such as measurements based on X-ray tomography might also be adequate (Okochi *et al.* 2007).

To unravel these growth irregularities and possible inter- and intra-specific differences in growth, additional investigations were performed on the intra-annual rhythms of cambial activity using monthly cambial pinnings (Chapter 6). Irregularities were again highlighted and differences between species, between individuals and even within individuals were also stressed. Consequently, even with the time marks left in the wood by the cambial pinnings important growth eccentricity and frequent ring discontinuities did not allow us to uncover precise growth trends. This chapter revealed that cambial activity in tropical tree species from different functional types commonly varies among species, among trees of the same species and around the stem circumference of individuals, seemingly regardless of the large-scale climate variations. It suggests that cambial activity is highly plastic in trees growing under tropical climates, even with distinct seasonality of rainfall. Micro-site environmental conditions may trigger cambial activation or deactivation, like we observed subsequently to small wounding by surgical needles. Growth inhibition known to be induced in temperate climates by low temperatures, dry conditions and short photoperiod or a combination of those, seems to be of different nature in the tropics. It appears to be highly reversible, and possibly on very short notice due to fine changes in environmental conditions or to minor physical alteration of the cambial zone.

The climate of the Mayombe region is seasonal with at least 3 months of limited rainfall but the relative air humidity is always high because of the Oceanic influence combined to the hilly landscape (Senechal *et al.* 1989, Pendje and Baya ki 1992, Lubini 1997). Consequently, the forest differs from other seasonal tropical forests where periodical dry conditions determine tree growth and phenological patterns of the different tree species. It is likely that these features are at least partly responsible for specific phenological and growth patterns.

Overall this study highlighted the extreme complexity of phenological and growth patterns of tree species growing in African rain forests, which may explain the strong resilience capacity of tree communities to disturbances that was also pointed here. This heterogeneity of responses to environmental changes also supports the idea that plurality rather than neutrality is a key concept in species-rich rain forests, as recently suggested by Newbery and Lingenfelder in Borneo (2009). As a consequence, studying the diverse components of this heterogeneous mix remains extremely challenging and will require repeated efforts on the long run. Protecting this natural resource that is so far from being understood is therefore of utmost importance.

APPENDIX 1. List of tree species from the Reserve of Luki, DRC. Functional groups are CAN (canopy shade-bearers), HEL (long-lived heliophilous and semi-heliophilous), PIO (pioneers) and UND (understory shade-bearers). Inventories were performed in the UH48 plot in 1948 before (UH48pre) and after (UH48post) the transformation thinning and in 2006 (UH48-2006), and in the Central Zone of the Reserve in 2007 (CZ-2007). Phenology in the Nkula forest stand was monitored between 1948 and 1957. The five study species are in bold.

Functional group	*Species name*	Family or Family/Subfamily	Inventories in the UH48 plot: basal area (m^2/ha)				Phenology				
			UH48pre	UH48post	UH48-2006	CZ-2007 (gbh>60cm)	Observed trees	Maximum			
								DEF	FL	FR	DISS
CAN	*Afzelia bipindensis*	Fabaceae/Caesalpinioideae					6	jan	jun	nov	feb
CAN	*Albizia coriaria*	Fabaceae/Mimosoideae			0.037		-				
CAN	*Albizia ferruginea*	Fabaceae/Mimosoideae					97	oct	dec	sep	oct
CAN	*Albizia gummifera*	Fabaceae/Mimosoideae	0.271	0.065	0.019		-				
CAN	*Albizia sp.*	Fabaceae/Mimosoideae					7	oct	nov	sep	oct
CAN	*Allanblackia floribunda*	Clusiaceae/Guttiferaceae	0.039	0.039	0.139	0.010	29	-	feb	may	dec
CAN	*Allophyllus africanus*	Sapindaceae					11	aug	may	apr	dec
CAN	*Alstonia boonei*	Apocynaceae			0.003		-				
CAN	*Alstonia congensis*	Apocynaceae	0.026				1	-	may	-	-
CAN	*Amphimas ferrugineus*	Fabaceae/Caesalpinioideae	0.053	0.001	0.026		4	sep	jan	feb	mar
CAN	*Amphimas pterocarpoides*	Fabaceae/Caesalpinioideae			0.026		-				
CAN	*Annickia chlorantha*	Annonaceae			0.020	0.002	-				
CAN	*Annickia lebrunii*	Annonaceae	0.011	0.011			-				
CAN	*Anthonotha macrophylla*	Fabaceae/Caesalpinioideae	0.008	0.008	0.006	0.003	5	dec	dec	mar	sep
CAN	*Anthonotha pynaertii*	Fabaceae/Caesalpinioideae			0.002	0.004	-				
CAN	*Antiaris toxicaria*	Moraceae	0.173	0.094	0.128	0.132	29	oct	nov	nov	nov
CAN	*Antrocaryon micraster*	Anacardiaceae	0.369	0.096			-				
CAN	*Antrocaryon nannanii*	Anacardiaceae			0.316	0.033	35	sep	nov	feb	jun
CAN	*Autranella congolensis*	Sapotaceae	0.041		0.002	0.036	4	jul	feb	jan	jan
CAN	*Baikiaea insignis*	Fabaceae/Caesalpinioideae					9	-	nov	feb	feb
CAN	*Barteria dewevrei*	Passifloraceae	0.027	0.027	0.029	0.002	13	apr	nov	jan	jan
CAN	*Berlinia grandiflora*	Fabaceae/Caesalpinioideae	0.083	0.005			-				
CAN	*Blighia welwitschii*	Sapindaceae			0.050		9	feb	oct	jan	jan

CAN	*Bombax buonopozense*	Bombacaceae			0.028	0.005	-				
CAN	*Canarium schweinfurthii*	Burseraceae	0.109	0.017	0.068	0.003	15	oct	apr	aug	feb
CAN	*Celtis gomphophylla*	Ulmaceae			0.245		-				
CAN	*Celtis mildbraedii*	Ulmaceae	0.372	0.281	0.422	0.019	109	may	nov	mar	may
CAN	*Celtis sp.*	Ulmaceae					4	oct	nov	feb	jun
CAN	*Celtis tessmannii*	Ulmaceae			0.001		-				
CAN	*Chrysophyllum africanum*	Sapotaceae	0.126	0.100	0.003	0.164	14	-	sep	feb	feb
CAN	*Coelocaryon botryoides*	Myristicaceae			0.099	0.074	25	-	feb	aug	sep
CAN	*Coelocaryon preussii*	Myristicaceae	0.040	0.040			-				
CAN	*Cynometra lujae*	Fabaceae/Caesalpinioideae	0.262	0.194	0.192	0.990	4	apr	feb	apr	may
CAN	*Dacryodes pubescens*	Burseraceae	0.791	0.224			-				
CAN	*Daniellia pynaertii*	Fabaceae/Caesalpinioideae			0.033		-				
CAN	*Desbordesia glaucescens*	Irvingiaceae				0.129	-				
CAN	*Dialium excelsum*	Fabaceae/Caesalpinioideae	0.020	0.008	0.001	0.003	13	mar	oct	jan	apr
CAN	*Dialium gossweileri*	Fabaceae/Caesalpinioideae			0.009	0.005	-				
CAN	*Dialium pachyphyllum*	Fabaceae/Caesalpinioideae	0.524	0.453			45	oct	dec	feb	apr
CAN	*Dialium tessmannii*	Fabaceae/Caesalpinioideae	0.074	0.074	0.133	0.037	4	-	jan	feb	mar
CAN	*Dichostemma glaucescens*	Euphorbiaceae					2	-	jan	jan	may
CAN	*Discoglypremna caloneura*	Euphorbiaceae			0.015	0.007	18	oct	jan	feb	mar
CAN	*Dracaena arborea*	Liliaceae			0.102		13	aug	oct	jan	feb
CAN	*Elaeis guineensis*	Arecaceae	0.048	0.048	0.048	0.007	-				
CAN	*Entandrophragma angolense*	Meliaceae	0.020	0.020	0.016	0.012	5	aug	nov	jan	sep
CAN	*Entandrophragma candollei*	Meliaceae			0.010		-				
CAN	*Entandrophragma utile*	Meliaceae	0.002	0.002	0.001		4	oct	nov	jun	oct
CAN	*Eriocoelum microspermum*	Sapindaceae	0.120		0.073	0.006	41	jan	may	aug	dec
CAN	*Erythrophleum suaveolens*	Fabaceae/Caesalpinioideae					9	feb	apr	sep	jan
CAN	*Erythrophleum suaveolens*	Fabaceae/Caesalpinioideae		0.161	0.160	0.012	-	feb	apr	sep	jan
CAN	*Ficus exasperata*	Moraceae			0.004	0.007	1	aug	-	-	-
CAN	*Ficus mucuso*	Moraceae			0.000		5	sep	may	feb	feb
CAN	*Ficus sp.*	Moraceae	0.040				2	-	-	sep	nov
CAN	*Ficus variifolia*	Moraceae	0.003	0.003	0.021	0.031	21	sep	dec	jan	jan
CAN	*Fillaeopsis discophora*	Fabaceae/Mimosoideae	0.002	0.002	0.052	0.031	2	-	-	mar	-
CAN	*Funtumia africana*	Apocynaceae	0.094	0.094	0.235	0.024	-				
CAN	*Ganophyllum giganteum*	Sapindaceae	0.361	0.155	0.887	0.019	44	jan	nov	jan	feb
CAN	*Gilbertiodendron dewevrei*	Fabaceae/Caesalpinioideae			0.016		-				

CAN	*Gilbertiodendron mayombense*	Fabaceae/Caesalpinioideae			0.046		-				
CAN	*Gilletiodendron kisantuense*	Fabaceae/Caesalpinioideae			0.410	0.002	-				
CAN	*Guarea cedrata*	Meliaceae	0.136	0.136	0.089	0.011	9	jun	sep	jan	jan
CAN	*Guarea thompsonii*	Meliaceae			0.055	0.171	-				
CAN	*Hexalobus crispiflorus*	Meliaceae	0.086	0.045	0.159	0.038	28	nov	mar	feb	feb
CAN	*Holoptelea grandis*	Ulmaceae			0.004		5	oct	nov	nov	dec
CAN	*Hylodendron gabunense*	Fabaceae/Caesalpinioideae	1.419	1.419	1.564	0.020	99	oct	nov	feb	may
CAN	*Irvingia gabonensis*	Irvingiaceae					3	-	oct	jan	feb
CAN	*Irvingia grandifolia*	Irvingiaceae	0.055	0.003	0.049		15	oct	sep	jan	jan
CAN	*Irvingia smithii*	Irvingiaceae			0.001		-				
CAN	*Irvingia sp.*	Irvingiaceae			0.001		-				
CAN	*Julbernardia arnoldiana*	Fabaceae/Caesalpinioideae					12	-	dec	mar	apr
CAN	*Julbernardia brieyi*	Fabaceae/Caesalpinioideae				0.459	-				
CAN	*Julbernardia seretii*	Fabaceae/Caesalpinioideae			0.307	0.496	-				
CAN	*Khaya anthotheca*	Meliaceae				0.062	-				
CAN	*Klainedoxa gabonensis*	Irvingiaceae	0.099	0.009	0.028	0.102	8	oct	mar	jan	jan
CAN	*Lannea welwitschii*	Anacardiaceae	0.071	0.059	0.075	0.043	35	sep	nov	feb	feb
CAN	*Letestua durissima*	Anacardiaceae			0.010	0.093	-				
CAN	*Lovoa trichilioides*	Meliaceae	0.032	0.032	0.047	0.031	10	feb	jan	feb	feb
CAN	*Maesopsis eminii*	Rhamnaceae	0.010	0.010	0.004		2	sep	feb	mar	jul
CAN	*Mammea africana*	Clusiaceae/Guttiferaceae					1	-	jan	jan	jan
CAN	*Margaritaria discoidea*	Euphorbiaceae			0.054		1	oct	nov	-	-
CAN	*Milicia excelsa*	Moraceae	0.067	0.067	0.001		31	sep	oct	may	oct
CAN	*Millettia drastica*	Fabaceae/Faboideae	0.042	0.042	0.047	0.014	3	nov	jan	-	-
CAN	*Monodora angolensis*	Annonaceae	0.408		0.135		37	-	oct	jan	feb
CAN	*Monodora myristica*	Annonaceae	0.272		0.036	0.021	23	nov	dec	apr	apr
CAN	*Morinda lucida*	Rubiaceae			0.002		1	-	-	-	-
CAN	*Nauclea diderrichii*	Rubiaceae			0.015		-				
CAN	*Neoboutonia melleri*	Euphorbiaceae	0.003	0.003			-				
CAN	*Nesogordonia leplaei*	Tiliaceae/Sterculioideae	0.418	0.418	0.599	0.390	22	feb	feb	jun	aug
CAN	*Newtonia glandulifera*	Fabaceae/Mimosoideae	0.159	0.070	0.305	0.285	-				
CAN	*Newtonia leucocarpa*	Fabaceae/Mimosoideae			0.179	0.167	28	feb	jul	oct	jan
CAN	*Omphalocarpum sankuruense*	Sapotaceae					7	sep	jan	feb	mar
CAN	*Ongokea gore*	Olacaceae	0.183	0.050	0.111	0.015	16	oct	mar	oct	nov
CAN	*Parkia bicolor*	Fabaceae/Mimosoideae			0.004		-				

CAN	*Parkia biglobosa*	Fabaceae/Mimosoideae	0.016	0.001			-				
CAN	*Pauridiantha callicarpoides*	Rubiaceae	0.000	0.000			-				
CAN	*Pausinystalia pynaertii*	Rubiaceae				0.002	-				
CAN	*Pausinystalia sp.*	Rubiaceae			0.080		-				
CAN	*Pentaclethra macrophylla*	Fabaceae/Mimosoideae	0.535	0.319	0.770	0.234	50	dec	mar	sep	jan
CAN	*Petersianthus macrocarpus*	Lecythidaceae	0.117	0.067	0.288	0.019	29	oct	dec	jan	feb
CAN	*Piptadeniastrum africanum*	Fabaceae/Mimosoideae	0.587	0.182	0.718	0.168	39	feb	jul	jan	feb
CAN	*Pouteria superba*	Sapotaceae			0.002		-				
CAN	***Prioria balsamifera***	**Fabaceae/Caesalpinioideae**	0.811	**0.811**	**0.940**	**0.585**	**192**	**sep**	**dec**	**feb**	**feb**
CAN	*Prioria oxyphylla*	Fabaceae/Caesalpinioideae	0.077	0.077	0.100	0.410	50	oct	jan	oct	jan
CAN	*Pseudospondias microcarpa*	Anacardiaceae	0.057	0.031	0.026	0.065	25	-	mar	jan	jan
CAN	*Pteleopsis hylodendron*	Combretaceae	0.297	0.078	0.180	0.044	91	sep	mar	jun	jul
CAN	*Pterocarpus tinctorius*	Fabaceae/Faboideae	0.521	0.241	0.733		38	oct	may	aug	oct
CAN	*Pterygota bequaertii*	Combretaceae			0.002		-				
CAN	*Ricinodendron heudelotii*	Euphorbiaceae	0.260	0.067	0.372	0.158	46	aug	oct	feb	may
CAN	*Spathodea campanulata*	Bignoniaceae					3	nov	apr	jul	oct
CAN	*Staudtia kamerunensis*	Myristicaceae	0.213	0.213	0.435	0.199	31	sep	may	jul	nov
CAN	*Sterculia bequaertii*	Sterculiaceae	0.140	0.087		0.106	38	sep	jan	jun	jul
CAN	*Strombosia pustulata*	Olacaceae	0.002	0.002	0.027	0.201	3	-	feb	jan	feb
CAN	*Strombosiopsis tetrandra*	Anacardiaceae			0.066	0.038	-				
CAN	*Symphonia globulifera*	Clusiaceae	0.027	0.027	0.035	0.007	6	-	may	jan	jan
CAN	*Tieghemella heckelii*	Sapotaceae					1	-	-	-	-
CAN	*Trilepisium madagascariense*	Moraceae	0.023	0.023	0.076	0.005	23	sep	sep	dec	dec
CAN	*Vitex madiensis*	Verbenaceae			0.132		-				
CAN	*Wildemaniodoxa laurentii*	Sapotaceae			0.001		-				
CAN	*Chrysophyllum subnudum*	Sapotaceae			0.173		-				
CAN	*Garcinia kola*	Clusiaceae			0.043	0.128	-				
HEL	*Ceiba pentandra*	Bombacaceae	0.191	0.010	0.026	0.039	11	sep	sep	jan	jan
HEL	*Pycnanthus angolensis*	Myristicaceae	0.089	0.037	0.208	0.073	21	jul	feb	jun	oct
HEL	*Albizia adianthifolia*	Fabaceae/Mimosoideae			0.004		-				
HEL	*Berlinia giorgii*	Fabaceae/Caesalpinioideae				0.007	-				
HEL	*Bikinia durandii*	Fabaceae/Caesalpinioideae			0.005		-				
HEL	*Chrysophyllum beguei*	Sapotaceae			0.018		-				
HEL	*Chrysophyllum lacourtianum*	Sapotaceae			0.033	0.031	-				
HEL	*Cola ballayi*	Sterculiaceae	0.001	0.001			-				

HEL	*Dialium corbisieri*	Fabaceae/Caesalpinioideae			1.837	0.306	-				
HEL	*Funtumia elastica*	Apocynaceae					147	nov	dec	jul	sep
HEL	*Holarrhena floribunda*	Apocynaceae	0.031	0.005	0.000		-				
HEL	*Hymenocardia ulmoides*	Euphorbiaceae	0.277		0.020		23	sep	feb	jun	aug
HEL	*Julbernardia sp.*	Fabaceae/Caesalpinioideae			0.034		-				
HEL	*Millettia versicolor*	Fabaceae/Faboideae	0.011	0.011			17	sep	jan	jun	oct
HEL	*Pentadesma grandifolia*	Clusiaceae	0.001	0.001			-				
HEL	*Picralima nitida*	Apocynaceae			0.007	0.005	-				
HEL	*Pseudospondias longifolia*	Anacardiaceae			0.053	0.020	-				
HEL	*Sterculia tragacantha*	Sterculiaceae			0.105	0.007	-				
HEL	***Terminalia superba***	**Combretaceae**	0.395	**0.395**	**0.035**	**0.003**	**184**	**sep**	**nov**	**jun**	**sep**
HEL	*Tessmannia africana*	Fabaceae/Caesalpinioideae			0.013	0.254	-				
HEL	*Trichilia sp.*	Meliaceae	0.067	0.067		0.020	-				
HEL	*Trichilia welwitschii*	Meliaceae					-				
HEL	*Uapaca brieyii*	Euphorbiaceae	0.014	0.014			-				
HEL	*Ximenia americana*	Olacaceae	0.000	0.000			-				
HEL	*Afzelia bella*	Fabaceae/Caesalpinioideae	0.010	0.010	0.001	0.003	1	oct	sep	jan	feb
PIO	*Cleistopholis patens*	Annonaceae			0.005	0.043	-				
PIO	*Croton congensis*	Euphorbiaceae	0.010	0.010			-				
PIO	*Harungana madagascariensis*	Clusiaceae	0.001	0.001			7	sep	feb	apr	jun
PIO	*Musanga cecropioides*	Cecropiaceae	0.153	0.111	0.072	0.084	10	sep	jan	feb	mar
PIO	*Myrianthus arboreus*	Moraceae	0.046		0.011	0.025	13	feb	apr	sep	nov
UND	***Aidia ochroleuca***	**Rubiaceae**	1.880	**1.880**	**1.573**	**0.046**	**19**	**-**	**nov**	**may**	**aug**
UND	*Annona senegalensis*	Annonaceae					5	oct	jan	feb	aug
UND	*Anthocleista djalonensis*	Loganiaceae	0.009	0.009			-				
UND	*Blighia unijugata*	Sapindaceae	0.013	0.013	0.023	0.004	-				
UND	*Brenania brieyi*	Rubiaceae					4	-	apr	jan	mar
UND	*Brenania sp.*	Rubiaceae				0.031	-				
UND	*Carapa procera*	Meliaceae	0.066		0.060	0.012	34	-	nov	jan	feb
UND	*Chytranthus macrobotrys*	Sapindaceae			0.001		-				
UND	*Chytranthus mortehanii*	Sapindaceae	0.001	0.001			-				
UND	*Cola griseiflora*	Sterculiaceae			0.044	0.779	-				
UND	*Cola mahoundensis*	Sterculiaceae	0.352		0.400	0.030	57	-	-	-	-
UND	*Cola nitida*	Sterculiaceae					2	-	aug	jan	jan
UND	*Cola sp.*	Sterculiaceae					1	-	nov	-	-

UND	***Corynanthe paniculata***	**Rubiaceae**	1.559	**1.506**	**1.356**	**0.057**	**117**	**oct**	**mar**	**may**	**nov**
UND	*Craterispermum cerinanthum*	Rubiaceae	0.005	0.005			-				
UND	*Croton sylvaticus*	Euphorbiaceae			0.015	0.003	11	aug	nov	feb	mar
UND	*Dacryodes buettneri*	Burseraceae			1.034	0.238	69	feb	feb	sep	jan
UND	*Dacryodes edulis*	Burseraceae					5	-	oct	jan	feb
UND	*Deinbollia acuminata*	Sapindaceae			0.164	0.006	-				
UND	*Deinbollia laurentii*	Sapindaceae	0.121	0.121			21	oct	may	sep	nov
UND	*Dialium zenkeri*	Ebenaceae				0.119	-				
UND	*Dictyandra arborescens*	Rubiaceae			0.000		-				
UND	*Diospyros heterotricha*	Ebenaceae					1	-	jan	feb	mar
UND	*Diospyros macrocarpa*	Ebenaceae					1	-	oct	-	-
UND	*Diospyros mannii*	Ebenaceae			0.013		-				
UND	*Diospyros pseudomespilus*	Ebenaceae			0.009		-				
UND	*Diospyros sp.*	Ebenaceae	0.183		0.023	0.153	16	sep	nov	feb	apr
UND	*Diospyros vermoesenii*	Ebenaceae	0.032	0.032			-				
UND	*Dracaena mannii*	Liliaceae	0.120	0.068	0.050	0.005	-				
UND	*Enantia affinis*	Annonaceae					9	-	oct	jan	feb
UND	*Erythrina droogmansiana*	Fabaceae/Faboideae			0.006		5	sep	nov	feb	jun
UND	*Garcinia epunctata*	Clusiaceae	0.262		0.040	0.002	11	-	oct	jan	jan
UND	*Garcinia punctata*	Clusiaceae			0.082	0.006	-				
UND	*Garcinia sp.*	Clusiaceae				0.003	-				
UND	*Heinsia crinita*	Rubiaceae			0.002		-				
UND	*Hua gabonii*	Huaceae	0.004	0.004		0.126	9	-	nov	jan	feb
UND	*Isolona dewevrei*	Annonaceae			0.066	0.007	79	feb	oct	jan	feb
UND	*Lijndenia jasminoides*	Melastomataceae			0.003		-				
UND	*Macaranga monandra*	Euphorbiaceae		0.001			6	feb	dec	feb	mar
UND	*Macaranga spinosa*	Euphorbiaceae			0.002		1	-	feb	feb	-
UND	*Mallotus oppositifolius*	Euphorbiaceae		0.007	0.006		5	oct	nov	jun	jun
UND	*Manilkara sp.*	Sapotaceae	0.119	0.119	0.262	0.053	12	feb	oct	jan	feb
UND	*Maranthes glabra*	Rosaceae	0.352	0.181	0.301	0.530	8	oct	may	nov	dec
UND	*Markhamia tomentosa*	Bignoniaceae	0.053	0.053	0.015	0.007	17	nov	mar	jul	sep
UND	*Melia bambolo*	Meliaceae			0.005		1	sep	oct	jun	jun
UND	*Microdesmis puberula*	Euphorbiaceae	0.055		0.041		45	oct	nov	feb	feb
UND	*Millettia laurentii*	Fabaceae/Faboideae			0.006		-				
UND	*Nauclea latifolia*	Rubiaceae					2	-	apr	sep	oct

UND	*Olax gambecola*	Olacaceae			0.004		-				
UND	*Oncoba dentata*	Flacourtiaceae	0.006	0.006	0.002		2	sep	oct	jan	feb
UND	*Oncoba welwitschii*	Flacourtiaceae	0.137	0.137	0.153		49	nov	oct	feb	feb
UND	*Oxyanthus speciosus*	Rubiaceae	0.013	0.013	0.003		-				
UND	*Parkia filicoidea*	Fabaceae/Mimosoideae					8	nov	jan	feb	mar
UND	*Paropsia braunii*	Passifloraceae	0.014	0.014			17	oct	oct	oct	nov
UND	*Paropsia sp.*	Passifloraceae			0.018	0.002	-				
UND	*Passiflora foetida*	Passifloraceae			0.000		-				
UND	*Pausinystalia macroceras*	Rubiaceae	0.004	0.004			12	nov	feb	may	nov
UND	*Pentaclethra eetveldeana*	Fabaceae/Mimosoideae	0.406		0.116	0.042	125	feb	mar	oct	nov
UND	*Placodiscus resendeanus*	Sapindaceae					14	sep	oct	jan	jan
UND	*Plagiostyles africana*	Euphorbiaceae			0.027	0.014	-				
UND	*Platysepalum chevalieri*	Fabaceae/Faboideae	0.010	0.010			6	-	apr	jan	-
UND	*Polyalthia suaveolens*	Annonaceae	0.205	0.205	0.633	0.030	42	oct	mar	oct	jan
UND	*Psychotria dermatophylla*	Rubiaceae	0.057		0.033	0.010	36	feb	mar	jul	oct
UND	*Psydrax palma*	Rubiaceae	0.222		0.002		20	feb	jun	aug	oct
UND	*Quassia undulata*	Simaroubaceae	0.038	0.013	0.030	0.018	18	-	oct	jan	jan
UND	*Rothmannia urcelliformis*	Rubiaceae			0.004		-				
UND	*Santiria trimera*	Burseraceae					5	mar	oct	feb	feb
UND	*Schrebera trichoclada*	Olacaceae	0.005	0.005			3	oct	jan	jun	nov
UND	*Scorodophloeus zenkeri*	Fabaceae/Caesalpinioideae			0.016		-				
UND	*Scottellia klaineana*	Flacourtiaceae	0.088	0.088			26	sep	feb	mar	apr
UND	*Sorindeia africana*	Anacardiaceae			0.002		-				
UND	*Sorindeia gilletii*	Anacardiaceae			0.100	0.074	-				
UND	*Sorindeia mayumbensis*	Anacardiaceae			0.082	0.011	-				
UND	*Sorindeia ochracea*	Anacardiaceae	0.011	0.011			-				
UND	*Sorindeia sp.*	Anacardiaceae			0.008		-				
UND	*Spondias monbin*	Anacardiaceae					6	aug	nov	mar	apr
UND	*Strombosia grandifolia*	Olacaceae	0.022			0.007	53	-	oct	nov	dec
UND	*Synsepalum stipulatum*	Sapotaceae			0.010		-				
UND	*Syzygium sp.*	Myrtaceae					1	-	jun	sep	nov
UND	*Tabernaemontana crassa*	Apocynaceae			0.001		11	-	feb	jun	sep
UND	*Tapura fischeri*	Dichapetalaceae	0.069		0.048		-				
UND	*Tetrapleura tetraptera*	Fabaceae/Mimosoideae	0.037	0.037	0.023		7	dec	jan	jun	sep
UND	*Tetrorchidium didymostemon*	Euphorbiaceae			0.001		7	may	oct	may	jul

UND	*Thomandersia congolana*	Acanthaceae	0.001	0.001			-				
UND	*Treculia africana*	Moraceae	0.030	0.030	0.024	0.011	3	-	apr	jan	jan
UND	*Trema orientalis*	Celtidaceae	0.001	0.001	0.005		-				
UND	*Tricalysia crepiniana*	Rubiaceae			0.006		3	oct	jun	nov	dec
UND	*Trichilia dregeana*	Meliaceae			0.000		-				
UND	*Trichilia gilgiana*	Meliaceae			0.112	0.755	55	oct	apr	aug	nov
UND	*Trichilia monadelpha*	Meliaceae	0.000	0.000	0.089	0.007	9	feb	nov	jan	feb
UND	*Trichilia prieureana*	Meliaceae	0.160	0.160	0.031	0.122	27	-	mar	jul	aug
UND	*Trichilia rubescens*	Meliaceae				0.031	-				
UND	*Trichoscypha acuminata*	Anacardiaceae	0.013	0.013	0.013	0.011	7	-	sep	oct	oct
UND	*Trichoscypha oddonii*	Anacardiaceae	0.006	0.006			7	-	nov	jan	jan
UND	*Uapaca guineensis*	Euphorbiaceae			0.004	0.002	-	-	mar	sep	dec
UND	*Vernonia conferta*	Asteraceae					7	-	aug	sep	dec
UND	*Vitex welwitschii*	Verbenaceae	0.123	0.123		0.028	26	dec	feb	may	aug
UND	*Xylopia aethiopica*	Annonaceae	0.040	0.040	0.001		45	sep	jan	nov	dec
UND	*Xylopia chrysophylla*	Annonaceae					51	oct	may	jul	oct
UND	*Xylopia cupularis*	Annonaceae			0.040	0.013	-				
UND	*Xylopia hypolampra*	Annonaceae			0.360		-				
UND	*Xylopia parviflora*	Annonaceae	0.456	0.456	0.055		-				
UND	*Xylopia sp.*	Annonaceae			0.003		-				
UND	*Xylopia toussaintii*	Annonaceae			0.250		-				
UND	***Xylopia wilwerthii***	**Annonaceae**	1.640	**1.640**	**1.518**		**120**	**jul**	**oct**	**feb**	**mar**
UND	*Zanha golungensis*	Sapindaceae					21	oct	dec	dec	jan
UND	*Zanthoxylum gilletii*	Rutaceae	0.156	0.156	0.136	0.105	40	mar	nov	jan	feb
UND	*Zanthoxylum rubescens*	Rutaceae	0.003	0.003			-				
UND	*Zanthoxylum sp.*	Rutaceae					3	oct	jan	mar	apr
UND	*Zanthoxylum welwitschii*	Rutaceae					5	nov	jan	apr	apr

APPENDIX 2. Methodological details on tree-ring analyses.

1. Crossdating

Crossdating aims at dating a tree ring curve of unknown age by comparing it to a dated reference tree ring chronology (Stokes and Smiley 1968, Schweingruber 1996). In most tropical regions (including the DRC) no exactly dated reference chronologies are available so cross-dating consists of comparing growth curves of different trees visually and statistically to bring ring-width series in a synchronous position (Cook and Kairiukstis 1992, Worbes 1995). Successful cross-dating indicates the influence of an external growth factor on tree growth in a site (Eckstein *et al.* 1981). The reliability of mean tree-ring chronologies generally depends on the number of trees averaged and on how well the series fit together (Fritts 1976). Consequently, several parameters have been developed to estimate the signal strength of mean chronologies (Esper *et al.* 2001).

- *t-value Baillie and Pilcher (TVBP)*

Baillie and Pilcher (1973) developed a cross-correlation algorithm to calculate Student's t-values for all positions of overlap of two series:

$$\textit{Student's } t = r \cdot \frac{\sqrt{n-2}}{\sqrt{1-r^2}}$$

(n = number of cases; r = Pearson's correlation coefficient)

The t-value expresses the degree of affinity of two time series, while incorporating the number of observations (Baillie and Pilcher 1973). In dendrochronology, t-values of 3.5 or higher are desirable ($P < 0.0001$).

- *Gleichäufigkeitskoeffizient (Glk)*

In addition to the t-test, the "Gleichläufigkeitskoeffizient" (Glk) is used in dendrochronology to investigate the success of cross-dating. It calculates the proportion of synchronous year-to-year increasing (positive) and decreasing (negative) trends in two chronologies, expressed by the following equations (Eckstein and Bauch 1969):

$$\Delta_i = (x_{i+1} - x_i) \quad \text{when} \quad \begin{array}{l} \Delta_i > 0 : Glk_{ix} = +\frac{1}{2} \\ \Delta_i = 0 : Glk_{ix} = 0 \\ \Delta_i < 0 : Glk_{ix} = -\frac{1}{2} \end{array}$$

$$\textit{for two curves x and y, } Glk_{(x,y)} = \frac{100}{n-1} \sum_{i=1}^{n-1} \left| Glk_{ix} + Glk_{iy} \right|$$

with n = number of values; x, y = series and Δ_i = difference in tree ring width between two consecutive years.

In general, a 70% threshold (meaning that 70% of the increasing or decreasing slopes between two series are equal) is accepted for Glk to indicate successful cross-dating.

2. Standardisation

The juvenile period of a tree's life is usually characterized by large increments and large local variance, which both decrease with age to a typical level for each species. The growth tendency in each growth series, if not treated, would import unwanted trends into dendroclimatological studies. Therefore, the variance is usually stabilized by a power transformation. A flexible cubic spline is the most appropriate detrending method for trees from closed-canopy stands (Cook and Kairiukstis 1992) and the flexibility of the cubic spline determines the amount of variation removed from the growth trend (Grissino-Mayer 2001). The aim of this procedure is to remove the long-term growth trends and to filter out low frequency variation that might be caused by e.g. canopy-dynamics. After fitting a cubic spline curve to a tree ring series the residuals are calculated by dividing each raw value by the value of the fitted spline (Brienen and Zuidema 2005).

3. Characterisation of tree ring chronologies

A number of parameters provide a basis for the characterisation and comparison of tree ring series. Parameters commonly used to define the characteristics of tree ring series include mean sensitivity and correlation coefficients (Schweingruber 1996).

- *Mean sensitivity (MS)*

The sensitivity of a tree ring series to environmental factors (climate variability in particular) can be determined by calculating values of mean sensitivity (MS) (Schweingruber 1996). The MS is a measure of relative difference in width from one ring to the next, expressed as one average value for each series. It indicates whether the samples are sensitive or complacent, and thus, more or less suitable for dendroclimatology. A complacent ring-width series has a small variability, which theoretically suggests that growth is relatively unaffected by variations of ecological factors such as climate. In contrast, a sensitive tree-ring series is usually affected by such factors and exhibits high-frequency variance.

MS values can be calculated as the average of the absolute values of individual sensitivities in a series:

$$\overline{S} = \frac{\sum_{i=1}^{n-1} \left| S_i + 1 \right|}{n-1} \text{ with } S_i = \frac{\left(x_i - x_{i-1}\right) \cdot 2}{\left(x_i + x_{i-1}\right)}$$

where xi is the observed value of the tree ring series x at moment I, n the number of observations (number of rings in the series) and S_i the sensitivity in interval i.

- *Autocorrelation (AC)*

The mean first-lag autocorrelation (AC) is a measure of association between the series lagged in time (one year). A comparison of the autocorrelation before and after the standardization helps to control the quality of the detrending technique applied (Cook and Kairiukstis 1992). The autocorrelation coefficient is calculated as the Pearson's correlation coefficient between a series and the same series displaced in time over one year. It can be used as a measure for the strength of the growth trend in a tree ring series. Pearson's correlation coefficients are calculated as follows:

$$r = \pm \frac{\sum(x_i - \overline{x})(y_i - \overline{y})}{\sqrt{\sum(x_i - \overline{x})^2 \sum(y_i - \overline{y})^2}}$$

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SUMMARY

The tropical forest of Central Africa is the second largest and probably the best preserved stretch of rain forest on Earth, yet the least known. Increasing demographic growth and economic interests are major threats to this ecosystem. Accurate knowledge on community dynamics and on the ecology of tree species growing in this forest is thus urgently needed to underpin conservation and management practices.

The Reserve of Luki at the extreme West of the Democratic Republic of Congo was a privileged site to study this ecosystem, moreover concealing spectacular biological collections and datasets. From the community level to the minute anatomy of wood this dissertation gives an overview of the ecology of trees of the Central African rain forest from 1948 until today. First, the history of community dynamics in a 200 ha forest plot was studied to highlight tendencies in the variations of species diversity and biomass content. Then the biological rhythms of five selected tree species and functional groups of species were examined to get a better understanding of natural ecosystem processes in relation with climate variations.

Long-term inventory data revealed 58 years of forest dynamics after an initial transformation thinning treatment and continuous forest use until today. Perturbations maintained at a moderate level by the protected status of the Reserve seem to have favoured species diversity and biomass sequestration in this forest. Besides, most tree species were found to have annual rhythms of leaf and reproductive phenology but in a wide array of patterns, from synchronous annual peaks to continuity. Direct and indirect associations with intra-annual and supra-annual climate variations suggest that changes in environmental conditions will affect the phenological rhythms of tropical trees. Dendrochronological analyses proved annual ring formation for the five study tree species and positive correlation between growth and rainfall. For the three understory species radial growth was found to associate with precipitation during the rainy season but in a different month for each species. For canopy species strong heterogeneity of growth patterns was found, between species and between individuals of the same species. A more detailed study of radial wood growth by use of cambial marking experiments showed that individual sensibilities to the type of substrate and fine plasticity of cambial activity in response to environmental changes are possible causes for this growth variability. Cambial dormancy in tropical trees may not be strict like in trees of temperate regions, but highly plastic and triggered by endogenous factors as well as climate variations.

This heterogeneity of responses to environmental changes between species and between individuals of the same species growing in the same site supports the idea that plurality is a key concept in species-rich rain forests. As a consequence, studying the diverse components of this heterogeneous mix remains extremely challenging and requires repeated efforts on the long run. Protecting this natural resource that is so far from being understood is therefore of utmost importance.

RÉSUMÉ

La forêt d'Afrique Centrale est la deuxième plus grande étendue de forêt tropicale humide au monde et probablement la mieux préservée, mais elle est aussi la plus mal connue. La croissance démographique et les intérêts économiques sont des menaces majeures pour cet écosystème. Une connaissance solide de la dynamique des communautés et l'écologie des espèces d'arbres qui composent cette forêt est donc un besoin urgent pour sous-tendre les pratiques de conservation et de gestion.

La Réserve de Luki à l'extrême Ouest de la République Démocratique du Congo est un site privilégié pour étudier cet écosystème, qui de plus recèle de spectaculaires collections et bases de données biologiques. De la communauté d'espèces à l'anatomie microscopique du bois cette dissertation dresse un panorama de l'écologie des arbres de la forêt tropicale humide d'Afrique Centrale de 1948 à aujourd'hui. Tout d'abord, l'histoire de la dynamique de communautés a été étudiée dans une parcelle de forêt de 200 ha pour dégager les tendances en termes de diversité floristique et de biomasse. Ensuite les rythmes biologiques de cinq espèces d'arbres et de groupes fonctionnels d'espèces ont été examinés afin de mieux comprendre les processus en jeu dans les écosystèmes naturels en relation avec les variations du climat.

Des données d'inventaire anciennes ont permis de révéler 58 ans de dynamique forestière après un traitement initial d'uniformisation par le haut et une utilisation continue de la forêt jusqu'à aujourd'hui. Les perturbations maintenues à un niveau modéré grâce au statut de la Réserve semblent avoir favorisé la biodiversité et le stockage de biomasse dans cette forêt. En outre, pour la plupart des espèces d'arbres un rythme annuel a été mis en évidence pour la phénologie de la formation des feuilles et de la reproduction, avec une grande variabilité entre espèces allant de la présence de pics annuels synchrones jusqu'à la continuité. Les associations directes et indirectes avec les variations intra-annuelles et supra-annuelles du climat suggèrent que des changements de conditions environnementales peuvent affecter les rythmes phénologiques des arbres tropicaux. Les analyses dendrochronologiques ont démontré la formation de cernes annuels pour les cinq espèces étudiées ainsi que des corrélations positives entre la croissance et la pluviosité. Pour les trois espèces de sous-bois une association positive entre la croissance et les précipitations pendant la saison pluvieuse a été dégagée, mais pendant un mois différent pour chaque espèce. Pour les espèces de canopée une forte hétérogénéité des rythmes de croissance a été montrée, entre espèces et entre individus de la même espèce. Une étude plus détaillée de la croissance radiale grâce à la technique des marquages cambiaux a révélé que des sensibilités individuelles au type de substrat et une plasticité fine de l'activité cambiale en réponse aux changements environnementaux sont des causes possibles pour cette variabilité de croissance. La dormance cambiale des arbres tropicaux ne semble pas être stricte comme pour les arbres des climats tempérés, mais au contraire très plastique et contrôlée par des facteurs endogènes aussi bien que par les variations climatiques.

Cette hétérogénéité de réponses aux changements environnementaux, entre espèces et entre individus d'une même espèce au sein du même site, supporte l'idée que la pluralité est un concept clé dans les forêts tropicales humides abritant une forte biodiversité. Ainsi, l'étude des multiples composantes de ce mélange hétérogène est un défi qui requiert des efforts répétés sur le long terme. En conséquence, la protection de cette ressource naturelle qui est si loin d'être comprise reste d'une extrême importance.

SAMENVATTING

Het tropisch bos in Centraal Afrika omvat het op een na grootste en waarschijnlijk het best geconserveerde aaneengesloten stuk regenwoud ter wereld; desondanks tevens het minst bekende. Toenemende bevolkingsdruk en economische belangen bedreigen het ecosysteem. Om beheersmaatregelen te bekrachtigen is het derhalve van groot belang accurate kennis te verwerven over veranderingen in de bosecologie en over de ecologie van boomsoorten in het betreffende woud.

Het Luki Reservaat in het uiterste westen van de Democratische Republiek Congo, bood een vruchtbare locatie om het ecosysteem te onderzoeken. Daarnaast onthulde de plek spectaculaire biologische collecties en datasets. Deze verhandeling geeft een overzicht van de boomecologie van het Centraal-Afrikaanse regenwoud tussen 1948 en heden, daarbij een veld bestrijkend van (bos)gemeenschapsniveau tot de minutieuze aspecten van houtanatomie. Allereerst werden de veranderingen in bosdynamiek in de tijd onderzocht op een bosareaal van 200 ha; zodoende werden patronen in soortvariatie en inhoud van de biomassa onderlijnd. Vervolgens werden de biologische ritmes van vijf geselecteerde boomsoorten en functionele groepen geanalyseerd. Dit leidde tot een beter begrip van de natuurlijke processen in een ecosysteem in relatie tot klimaatvariaties.

Lange-termijn inventarisatie gegevens onthulde 58 jaar aan bosdynamiek die zich voor deed na een eerste transformatie als gevolg van uitdunningsmaatregelen en een constant bosgebruik tot op heden. Verstoringen, die beperkt waren gezien de beschermde status van het gebied, lijken de soortdiversiteit en de vastlegging in biomassa van dit bos ten goede te zijn gekomen. Daarnaast blijken de meeste boomsoorten een jaarlijkse cyclus te hebben in de verschijningsvorm van het blad en reproductieve delen. Deze cyclus vertoont evenwel veel variatie: van synchrone jaarlijkse pieken tot continue ontwikkeling. Directe en indirecte relaties met klimaatvariaties binnen en tussen de jaren duiden erop dat veranderingen in omgevingsfactoren het fenomenologische ritme van tropische bomen beïnvloeden. Dendrochronologische analyses tonen aan dat de vijf onderzochte soorten jaarlijks ringen vormen en wijzen op een positieve correlatie tussen groei en regenval. Bij drie soorten uit de ondergroei blijkt de radiale groei in relatie te staan met de neerslag tijdens het regenseizoen. Deze groei vindt bij elk van de soorten echter plaats in een andere maand. Bij soorten van het kronendak werd een sterke heterogeniteit in groeipatronen vastgesteld; zowel tussen soorten onderling als tussen individuen van eenzelfde soort. Uitvoeriger onderzoek naar de radiale houtgroei door middel van cambiummarkeringen toonden aan dat individuele gevoeligheid voor de aard van de ondergrond en de fijne plasticiteit van de cambiale activiteit als reactie op veranderingen in de omgeving mogelijke oorzaken zijn voor de genoemde verscheidenheid in groei. Dit wijst erop dat groeistilstand in tropische boomsoorten niet vastomlijnd is zoals bij soorten in gematigde gebieden, maar juist in hoge mate plastisch is en teweeggebracht wordt door zowel endogene factoren als klimaatsvariatie.

De genoemde verschillen in de reactie op omgevingsveranderingen tussen zowel soorten onderling als individuen van eenzelfde soort (groeiend op eenzelfde locatie), bevestigt het idee dat verscheidenheid een sleutelbegrip is in een soortenrijk regenwoud. Als gevolg hiervan blijft het onderzoeken van de diverse componenten van deze heterogene mix lastig; het vergt herhaaldelijke onderzoeksinspanningen op de lange termijn. Het beschermen van deze natuurlijke bron, die wij verre van volledig begrijpen, is derhalve van groot belang.


Bud


PPRD

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