# THE LIANA ASSEMBLAGE OF A CONGOLIAN RAINFOREST

## *Diversity, Structure and Dynamics*

*Corneille E.N. Ewango*

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Wageningen University

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**THESIS**
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To my parents for the best gift of life and ensuring my education
To Esse, Diane, Yannick, Simplice, Rhoda and Achilles for adding sense to life
To Nadine and Gaylord who have left us early
To my brothers and sisters for showing me love and affection

**This is it!!!**

# Abstract

This study analyzes the diversity, composition, and dynamics of the liana assemblage of the Ituri rain forest in northeastern DR Congo. I used data from two 10-ha plots of the Ituri Forest Dynamics Plots, in which all liana stems ≥2 cm diameter at breast height (dbh) were marked, mapped, measured and identified in 1994, 2001 and 2007. In addition, the plot topography and canopy structure were measured.

Chapter 2 analyzes the liana assemblage (in terms of species richness, abundance and diversity), characterizes liana functional traits and determines effects of forest structure, topography and edaphic variation on liana species composition. In 20 ha, 15008 liana individuals were found, representing 195 species, 83 genera and 34 plant families. Per hectare species number averaged 64, basal area was 0.71 $m^2$ and Fisher alpha, Shannon and Simpson diversity indices were 17.9, 3.1 and 11.4, respectively. There was oligarchic dominance of 10 plant families that represented 69% of total species richness, 92% of liana abundance and 92% of basal area, while ten dominant species accounted for 63% of abundance and 59% of basal area. Forty-one species (21%) were represented by one individual only. Most lianas were light-demanding, climbed their hosts by twining, and had conspicuous flowers, medium-sized leaves and animal-dispersed propagules. Liana abundance increased with abundance of medium-sized and large trees but was, surprisingly, independent of small-tree abundance. Canopy openness, soil moisture, and tree size were the most important environmental factors influencing abundance and distribution of lianas.

In Chapter 3 I investigate changes in structural characteristics, diversity, recruitment, mortality and growth of the liana community over the thirteen years (1994 - 2007). Liana density decreased from 750 (1994) through 547 (2001) to 499 (2007) stems $ha^{-1}$, with concomitant declines in basal area and above-ground biomass. Despite lower stem densities the species richness remained constant over time. Total liana recruitment rates decreased slightly from 8.6% per year in the first period to 6.6% in the second, but this decrease was not significant. Liana mortality rates decreased significantly from 7.2% to 4.4% per year over the two census intervals. Diameter growth rates and survival increased with liana stem diameter. Surprisingly, liana abundance in Ituri showed recent declines, rather than recent increases, as has been reported for tropical and temperate forests in the Americas. Interestingly, changes in overall liana community structure and composition were mostly driven by one species only: the dramatic collapse of superabundant *Manniophyton fulvum* between the first and the second census.

In chapter 4 I investigated species-specific dynamics of the 79 most abundant liana species, representing 13,156 of the stems (97% of total) in two 10-ha plots. I evaluated their demographic performance and the relation of the vital rates (growth, mortality, recruitment) to the species abundance and four functional traits (climbing strategy, dispersal syndrome, leaf size and light requirements) to determine across species variations and major strategies characterizing species. Vital rates shared a wide interspecific variation; species-specific recruitment rates varied from 0.0-10.9%, mortality rates from 0.43-7.89% over 13-year, and growth rates from -0.03-3.51 mm $y^{-1}$. Most species had low to moderate rates. Species that grew fast tended also to recruit and die fast, but recruitment and mortality rates were not directly related, suggesting that species shift in absolute abundance over the 13 year period. However, with the exception of the collapsing *Manniophyton fulvum* population, species maintained their rank-dominance over time. Species growth declined with abundance, but recruitment and mortality rates were not related to abundance. The demographic performance of liana species varied weakly with their climbing strategy and dispersal mode but was, surprisingly, not related to their lifetime light requirements. A principle components analysis of liana strategies in terms of functional traits and vital rates showed that light demand, and dispersal syndrome were the most determining traits. Based on the PCA three functional guilds were distinguished. I conclude that old-growth forest liana species show a large variation in abundance and vital rates, and that density-dependent mechanisms are insufficient to explain the species abundance patterns over time.

Lianas are thought to globally increase in density, but we have limited knowledge about the taxonomic patterns of change in liana abundance, and the underlying vital rates that explain changes in liana density. In chapter 5 the changes in abundance of 79 relatively abundant liana species are evaluated. The Ituri forest showed a pervasive change in liana population density in the last decade. 37 species changed significantly in their abundance over time: 12 (15% of total) species increased, and 25 (32%) species decreased. 42 (53%) species did not change. Of the 48 genera, 40% decreased and 52% stayed the same. Five of the 12 increasing species belonged to the Celastraceae, which also was the only significantly increasing family. Surprisingly, none of the four functional traits (lifetime light requirements, climbing mechanism, dispersal mechanism, and leaf size) was significantly associated with species change in population density. Many decreasing species, however, are associated with disturbed habitats and are short-lived. Many increasing species are late successional and longer-lived. Increasing species have a slightly higher recruitment, decreasing species a higher mortality. This study suggests that changes in the liana community result from forest recovery from past disturbances. Rising atmospheric $CO_2$ level was not a likely explanation for liana change: more species declined

than increased, and increasing species did not have higher growth rates. In the Ituri Forest local stand dynamics override more global drivers of liana change.

**Key words**: Liana assemblage, species composition, community, dynamics, canopy openness, *Manniophyton fulvum*, functional traits, population density, pervasive change.

# Contents

# Chapter 1

## General introduction

## DIVERSITY AND SPECIES RICHNESS OF LIANAS IN TROPICAL FOREST

Lianas are woody plants that begin life on the ground as small self-supporting shrubs and rely on other plants to reach the light-rich environment of the upper canopy (Darwin 1867, Putz 1984, Letcher & Chazdon 2009). Because lianas use other plants for support, they devote relatively little to structural support and instead allocate more resources to leaf production and stem/root elongation for rapid growth (Putz 1983, 1990). Lianas are important components of many forest communities across the world, and are especially conspicuous, diverse, and characteristic in tropical forest (Putz 1984, Phillips and Gentry 1994, Schnitzer *et al.* 2000). Lianas provide an important contribution to the physiognomy and species richness of tropical forests and are expected to play a vital role in ecosystem functioning as well (Putz & Mooney 1991, Schnitzer & Bongers 2002, Bongers *et al.* 2005, Phillips *et al.* 2005).

Lianas constitute around 25% of the woody species in lowland tropical forest, and on average 18% to the overall taxonomic diversity of tropical forests (Gentry 1991). Their importance decreases with increasing latitude, the average percentage of lianas in woody floras falling to c. 10% in temperate forests (Gentry 1991). Estimates of their contribution to the vascular plants species diversity of the community range from 12% in Puerto Rico, 25% in Upper Guinea, 31% in Ghana (Hall and Swaine 1981) and to over 40% in the Monogaga forest, Ivory Coast (Bongers *et al.* 2002). In Barro Colorado Island, Panama, 45% of all plant species >10 m tall are lianas (Croat 1978). In Neotropical and South-East Asian forests, 40–60% of all large (≥10 cm diameter) trees typically bear at least one liana of any diameter (Putz 1983, Putz and Chai 1987, Campbell and Newbery 1993, Pérez-Salicrup 1998). Liana diversity in Neotropical and South-East Asian forests is relatively well documented, but diversity in African forests lags behind, especially the central African rainforest of the Congo Basin. Lianas species account for one third of woody plant diversity in the Ituri Forest (Makana et al. 1998, 2004a, b), north-eastern part of the Congo Basin and our own study area. In the only other study I have found, Caballé and Martin (2001) have recorded 60 species of liana ≥ 5 cm diameter in a Gabonese rain forest. Lianas are characterized by a vegetative multiplication aptitude. Next to genets they can produce ramets and show extraordinary resprouting capacities (vegetative proliferation), a potential to increase their dominance (Nabe-Nielsen 2000, Parren & Bongers 2001, Parren 2003).

Lianas share a common growth strategy centered on ascending to the canopy using the architecture of other plants (Schnitzer & Bongers 2002). They display a variety of adaptations for attaching themselves to their host and climb towards the forest canopy

(Darwin 1867, Hegarty 1991). They come in a huge variety of climbing mechanisms (from hook/tendrils to twiners/adhesive), as well as seed sizes and leaf size (from small to large). In tropical rain forest they are predominantly animal-dispersed, while wind-dispersal has often been mentioned as important for the spatial distribution of lianas in tropical dry and temperate forests (Gentry 1991, Bullock 1995, Killeen *et al.* 1998). As structural parasites, lianas colonize trees and thus provide food and access between trees to arboreal animals (Emmons & Gentry 1983).

## LIANAS AND ECOSYSTEM FUNCTIONING

A number of studies documented the role of lianas for the ecosystem regulation and productivity. First, lianas contribute to canopy closure after tree fall, stabilizing the microclimate underneath (Schnitzer & Bongers 2002) and contributing to local evapo-transpiration (Meinzer *et al.* 1999). Second, lianas also play a role at the ecosystem level by contributing to the carbon budget of tropical forests, representing as much as 10% of fresh aboveground biomass (Putz 1984). Despite their size, lianas comprise an important structural component producing 5–7% of tropical forest biomass and up to 40% of leaf area and leaf productivity (Hegarty & Caballé 1991, Gerwing & Farias 2000), as well as large amounts of litter (up to 30%) that is incorporated in the nutrient cycle. More importantly, when lianas become abundant they can reduce the amount of carbon sequestered by a forest stand when the leaf area of highly productive trees is reduced due to liana shading (Schnitzer & Bongers 2002), suppress tree growth and regeneration (Grauel & Putz 2004, Peña-Claros *et al.* 2008, van der Heijden & Phillips 2009), increase tree mortality, and affect the competitive ability of trees for ecosystem function (Laurance *et al.* 2001, Phillips *et al.* 2002).

## LIANAS AND FOREST DYNAMICS

Lianas are considered to be drivers of a number of forest dynamics aspects. It is known that lianas may influence forest dynamics by increasing the size of tree fall gaps and thereby increasing tree turnover rate (e.g. Phillips & Gentry 1994, Putz 1984, Putz & Chai 1987, but see Parren & Bongers (2001) who did not find an effect of liana cutting on gap size) and by arresting forest development in tree fall gaps (Schnitzer *et al.* 2000). Liana removal in tree fall gaps, for instance, resulted in increased tree growth and recruitment (Schnitzer & Carson 2010). Large lianas compete with trees for light, water, soil nutrients, and space and may thus depress the growth and fecundity of trees and increase their mortality (Richard 1952, Putz 1984, Stevens 1987, Clark & Clark 1990, Schnitzer & Bongers 2002, van der Heijden *et al.* 2008, Nabe-Nielsen *et al.* 2009, Ingwell *et al.* 2010). The above- and below-ground competition is reason for reduced growth and regeneration of tree species (Dillenburg *et al.* 1993, Pérez-Salicrup & Bakker 2000, Schnitzer & Bongers 2002, Schnitzer *et al.* 2005, Peña-Claros *et al.* 2008, Villegas *et al.* 2009) co-occurring with lianas. In contrast to general belief, preliminary results show that below-ground competition is most important (Schnitzer *et al.* 2005, Toledo-Aceves & Swaine 2008).

## DRIVERS OF LIANA ABUNDANCE AND DISTRIBUTION IN TROPICAL RAIN FORESTS

Several factors have been suggested to influence the abundance, species richness and distribution of lianas in tropical forests, but these are not globally conclusive (see Londré & Schnitzer 2006, Toledo 2010, Schnitzer & Bongers 2002). Lianas, being disturbance-adapted life forms (Hegarty & Caballé 1991), are profiting to some degree from increasing forest disturbance by humans (Laurence *et al.* 2001). Lianas may be found almost everywhere, but their abundance increases in canopy gaps or forest edges (Putz 1984, Hegarty & Caballé 1991, Schnitzer & Carson 2001, Babweteera *et al.* 2000) because of elevated light intensities (Schnitzer *et al.* 2000). At local scale, both liana density and species richness have been found to be related to forest architecture and structure (Putz 1984, Nabe-Nielsen 2000), and to the successional stage of the forests (DeWalt *et al.* 2000). The abundance of liana in a forest is greater in recent tree fall gaps and their density is higher in regenerating secondary forest than in old-growth forest (DeWalt *et al.* 2000). Furthermore, tree fall dynamics together with host tree identity and host availability may be important factors determining the abundance and species composition of liana communities (Hegarty 1989, Ibarra-Manríquez & Martínez-Ramos 2002).

Lianas are light demanding species (Putz 1984) although some studies showed that lianas can proliferate along the whole light gradient of a forest (Hegarty 1991, Campbell & Newberry 1993), and are also tolerant to low light intensities on the forest understory (Nabe-Nielsen 2000). Consequently, lianas are more abundant in seasonal dry forest, where light intensity and penetration is high under the seasonally deciduous canopy (Gentry 1991, Toledo 2010). However, light availability seemingly does not affect liana abundance and distribution in temperate rain forests (Baars *et al.* 1998, Carrasco-Urra & Gianoli 2009, Gianoli *et al.* 2010). Moreover, contrasts in light availability among patches at different successional stages may permit the coexistence of groups of species defined by differential shade tolerance at the seedling stage (Denslow 1987, Clark & Clark 1992).

The patterns of species differentiation with respect to soil-borne resource availability, topography and forest canopy structure are less well known (but see Baars *et al.* 1998, Bond *et al.* 2001). In a study by Homeier *et al.* (2010) in Ecuador, elevation had less importance to liana abundance variation, and diameter size decreased with increasing altitude, but density and basal area were strongly correlated with host tree diameter and at little to soil fertility. For Amazonian and Malaysian forests, Putz & Chai (1987) and Gentry (1981) both found a positive relationship between soil fertility and density of lianas, but this was not the case in Mexico (Ibarra-Manríquez & Martínez-Ramos 2002). Lianas have been suggested to be less abundant and to have lower biomass on nutrient poor than on more fertile soils (DeWalt *et al.* 2006, Gentry 1991, Laurance *et al.* 2001, Putz & Chai 1987). However, recent studies have shown that the success of lianas may depend more on the availability of suitable host trees than on soil conditions (Phillips *et al.* 2005). In Neotropical forests, liana density may even be unrelated to soil fertility or to other soil gradients (van der Heijden & Phillips 2008), and Toledo (2010) showed that average liana infestation of trees is higher on more fertile soils, and the number of trees per hectare that have lianas (an indirect measure of liana density) was higher on more sandy soils.

Increased seasonality in rainfall is positively related to lianas abundance and species richness (Gentry 1991, Pérez-Salicrup *et al.* 2001, DeWalt *et al.* 2010, Toledo 2010), but Clinebell *et al.* (1995) also pointed out a negative association to species richness in Neotropical forests. Similarly, from their dry forest plot study in Ghana, Swaine & Grace (2007) reported an increase for the number of liana species as a proportion of total species related to forest rainfall gradient. Seen in conjunction, these results suggest that many abiotic and biotic environmental factors play a role in liana abundance, distribution, and maintenance of species richness; and most likely many of the variables are interrelated as well (Balfour & Bond 1993) to have a co- deterministic effect.

## **LIANA DYNAMICS AND CLIMATE CHANGE**

Recent investigations have shown that the abundance of lianas in tropical forests may increase (Phillips *et al.* 2002, Wright *et al.* 2004, Ingwell *et al.* 2010), possibly as a result of global climate change, probably promoted by a higher atmospheric $CO_2$ concentration and anthropogenic land use (Laurance *et al.* 2001). Raising atmospheric concentration of $CO_2$ might enhance density and dominance of lianas in western Amazonian rain forests, but failed to have a clear effect on their floristic composition, distribution, and compositional turnover rates (Phillips *et al.* 2002). Based on the Neotropical forests data from several unique, long-term, multi-regional studies of liana and tree populations, Phillips *et al.* (2002)

reported that lianas experienced enhanced growth, significant increases in the density, basal area and mean size of climbing woody plants, and that the dominance of large lianas relative to trees had increased by 1.7–4.6% a year over the last two decades of the 20th century. Similarly, Wright *et al.* (2004) observed an increase by 100% in the relative importance of large lianas for stems enumerated during the 1980s and 1990s surveys. They also noted that between 1986 and 2002 in the Barro Colorado Island, Panama the total liana leaf litter production and the proportion of liana matter in forest-wide leaf litter increased. More evidence continues to accumulate and recently, Ingwell *et al.* (2010) documented aggressive increase of tree infestation by lianas in Barro Colorado Island, while Allen *et al.* (2007) reported an increase in importance of lianas in the temperate floodplain forests of the southeastern United States. As lianas are increasing in density, proportion of woody stems and basal area, they are likely influencing tree species composition, growth, and mortality. Consequently, Gerwing & Farias (2000) argued that the role of lianas in forest stand development should be further explored and incorporated into stand development models of tropical forests.

## STUDYING LIANA DYNAMICS

Liana are taxonomically diverse (i.e. are found in many different plant families) and individual species differ widely in climbing mechanisms, light requirement, seed dispersal, etc., which influences life history across species (Darwin 1867). Approximately one-half of the families of vascular plants contain climbing species (Schenck 1892). In some families nearly all of the species are climbers, *Hippocrateaceae* and *Vitaceae* being examples. Little is known about the demography of liana species (but see Nabe-Nielsen 2002, 2004). Globally seen lianas appear to be increasing in importance, but looking only at liana demography, as seen in most studies of woody plants, is not providing a full understanding of the causes of liana community dynamics. The evolution of lianoid growth forms has occurred many times in the course of plant evolution, so that phylogenetic constraints on some characters, for example, is also expected to play a role in the demographic performance (Felsenstein 1985). Laurance *et al.* (2004) showed a pervasive alteration in tree communities in undisturbed Amazonian forests. However, no studies have so far taxonomically assessed the observed large-scale changes in liana communities. The high species richness and functional traits variation across species in relation to vital rates make it both necessary and advantageous to explore the demography and species composition changes on the basis of their taxonomic and phylogenetic considerations. Gerwing (2004) showed that different lianas employ different growth strategies in response to light and successional stage. Perhaps looking at the species phylogeny constrained to liana demographic performance and functional traits is an essential step toward understanding the observed general liana increases. It will enable us to detect commonalities in degree of change in population density and determinants for change among species that are members of particular functional or evolutionary groups based on both demographic apparent affinities and life history characteristics.

Although lianas are common in most of the world's rainforests, there is a paucity of information on their biology and ecology (Hegarty & Clifford 1991, Schnitzer & Carson 2000), although the last two decades the number of liana studies has increased drastically (S.A. Schnitzer, pers. com.). Up to now, most of the research was focused on lianas and liana assemblages of Neotropical rainforests. In contrast, this thesis analyses the liana assemblage of an African lowland tropical rain forest in the Congo basin, one of the largest tropical rain forest areas in the world. Richards (1973) referred to Africa as the odd man out because its tropical and other floras were considered taxonomically and structurally different from Neotropical and Indo-Malaysian ones. For lianas, the dominant Bignoniaceae family in the Neotropics is completely lacking and replaced by Apocynaceae in the Paleotropics (Gentry 1991). One of the major differences is also the relative poverty of the African rain forest flora. Specifically, it is time to ask whether the relationships found in the Neotropics and Australasian forests also hold in African forest ecosystems.

## OBJECTIVE AND RESEARCH QUESTIONS

In this thesis, I report on my studies on the liana assemblage of the Ituri rain forest in northeastern DR Congo. I describe, analyze and evaluate patterns of floristic composition and diversity, and changes therein, over a 13 year period. Specifically, I address the following questions:

(1) What is the overall diversity and structure of the liana assemblage in the mixed rain forest of Ituri?
(2) What are the dynamics in the liana assemblage of this forest?
(3) How do liana species vary in their demographic vital rates and how are these rates related to the liana species' abundance and their functional traits?
(4) Do lianas increase in abundance over the last 13 years?

## THESIS OUTLINE

This study deals with the long-term changes in species composition and vegetation structure of lianas in two paired 10-ha plots of mixed old-growth rain forest in Ituri, DR Congo. Three censuses (in 1994, 2000 and 2007) were realized. The main goal of this study is to provide insight in the dynamics of the Ituri Forest liana communities. It is composed of four core research chapters (chapter 2 to 5) apart from the general introduction (chapter 1) and the general synthesis (chapter 6). To examine the richness and diversity of lianas at a local scale, I used classic diversity indices (species richness, Fisher's alpha, Shannon-Wiener and Simpson's diversity) as they more relate either to abundance or species richness in the sampling size. I used a Principal Component Analysis (PCA) to detect the trends of changes in species composition and abundance in the liana community. Community-wide and species-specific demographic changes were assessed across the plots. Using the huge amount of available inventory data for these large plots in Ituri forest, DR Congo, collected over a comparatively long time-span, I disentangle the question: Do liana increase the last 13 years? It tests the hypothesis of Phillips *et al.* (2002) that the "composition of old-growth tropical forests is changing over large scales, and the prediction that lianas are benefiting and increase in abundance over the last two decades"

In CHAPTER 2 I evaluate the community structure of the liana assemblage of the mixed lowland Ituri forest. I first describe the floristics, diversity and structure of the liana assemblage in this old-growth forest. I then characterize liana functional traits (climbing mechanisms, regeneration guilds, leaf sizes, flower types and dispersal syndromes). I also determine the effects of forest structure, small-scale local topography and edaphic variation on liana species composition. I hypothesize that the forest tree canopy structure and composition (i.e. upper-canopy openness) affects the composition and structure of liana assemblages, and expect that liana abundance and diversity is lower in closed canopy forest parts, and that liana dominance is higher in forest parts with an open upper-canopy, parallel to light-demanding as most liana species are light loving and respond positively to forest disturbance (Webb 1958, Putz 1984, Laurance *et al.* 2001).

In CHAPTER 3 I describe the long-term dynamics in the liana community of this forest, based on liana inventories that took place in 1994, 2000 and 2007. I examine the changes in structural characteristics of lianas (size, density, growth, mortality, recruitment and above-ground biomass). I expect vital and dynamic rates (growth and survival) to be size dependent, and small-size stems to have faster growth and higher mortality compared to large-size stems that would have lower growth and higher survival in an old-growth forest liana community. I also analyze the liana assemblage in terms of species composition and test whether the change over time is directional (two periods of data available 1994-2000 and 2000-2007).

In CHAPTER 4 I analyze the species-specific patterns of liana recruitment, growth and mortality over the 13-year period. I predict that mortality, recruitment and growth rates will be highly variable across species. I expect common species to be more dynamic than rare species, twiners to be more dynamic than non-twiners, light demanding species to be more dynamic than shade tolerant ones, and large leaf size species to be more dynamic than the ones with small leaves. Additionally, I explore the relation between liana vital rates and species functional traits, how liana vital rates are associated one another and which general strategies do lianas have, based on their vital rates and functional traits.

In CHAPTER 5 I investigate the changes in population density and address whether the general prediction that "lianas increase in abundance over the last two decades" (Phillips *et al.* 2002), holds true for the Ituri Forest. For this I test whether liana abundance at different taxonomic levels (species, genera, families) increases or decreases more than expected by chance. Using demographic and functional traits-based comparisons, I test the hypothesis that species sharing particular ecological characteristics have undergone similar types of density shifts over time due to similar ecological constraints that determine their performance in local scale.

Finally, in CHAPTER 6 I summarize and synthesize the main findings of the different chapters and discuss the general research questions as well as ideas for future work on liana dynamics. Additionally, the implications of my results for forest management and conservation of liana diversity are discussed.

## STUDY SITES

### *Plot vegetation characteristics*

The two 10-ha mixed forest plots analyzed in this thesis form part of the Ituri Forest Dynamics Plot, that consist of four plots of 10-ha (200 x 500 m) each established by the Centre de Formation et de Recherche en Conservation Forestière (CEFRECOF) in 1994 in the central Ituri Forest at the Réserve de Faune à Okapis (RFO, 1˚25´N, 28˚35´E). The layout of the four plots is a replicated pair in two study areas with largely different forest communities, Edoro (mixed forest) and Lenda (monodominant forest). The distance between two 10-ha plots of a pair is 500 meters. The plots have a gentle undulating topography with occasional low hills of exposed patches of shallow rocky soils. Differences between the highest and lowest points between each pair are 24 m on Lenda and 14 m on Edoro plots. The most dominant species in the mixed forest are *Cynometra alexandri*, *Julbernardia seretii* (both legumes) and *Cleisthanthus michelsonii* (Euphorbiaceae), together representing about 30% of the canopy trees. The monodominant forest is strongly dominated by *Gilbertiodendron dewevrei* (legume): more than 90% of the canopy trees belong to this species. The forest canopy height varies between 35 to 40 m (based on the dominant species), with scattered emergents exceeding 45 m (Makana *et al.* 1998, 2004a, b). For my present study, I only used data of the Edoro mixed forest, and hence of a total of 20 ha.

### *Experimental design and data collection*

In 1994, the two 10-ha plots were surveyed and mapped to generate their topography. To facilitate the botanical inventory, each 1-ha subplot was divided again into 20 x 20 m subplots, and each free standing stem of shrubs and trees ≥1 cm diameter at breast height (dbh; at 1.30 cm above the ground) was measured, mapped, and tagged with a unique pre-numbered aluminum tag. Similarly, all lianas ≥2 cm dbh were included in the inventory. For both trees and lianas with several stems (clone individual) every stem received a single tag. The point of measurement was marked with a bright colored oil-based paint. Effort was made to identify each individual of tree and liana found in the plot to the species, genus or family level whenever possible. All unidentified individuals were assigned to morphospecies. A variety of herbarium collections has been made for both common species and unidentified ones to facilitate further botanical comparison and identification. Plant identification continued at the National Herbarium of the Netherlands - Wageningen branch (now Netherlands Centre for Biodiversity Naturalis – section NHN)) and the National Botanical Garden of Belgium (Meise). At least one good voucher for each species was selected and housed in the herbarium of CEFRECOF in Epulu; most of them have a duplicate deposited in the herbaria of Wageningen (The Netherlands) and Meise (Belgium). In 2000 and 2007/2008, all living stems were re-measured and new recruits mapped, tagged and identified. In this PhD study, we will use the liana data from all three 1994-2000-2007 censuses.

The Ituri Forest Dynamics Plots (IFDP) database includes the standard information of forest inventories and long-term dynamics studies data (largely following the worldwide CTFS protocol), but the IFDP differed to all other inventories in the network by adding lianas. Additional data include complementary topographical aspect (elevation) and mapping data of individuals within the plots. The database consists of three data sets containing sampling conducted from 1994 for initial inventories, and the first and second censuses that were undertaken in 2000 and 2007 respectively. The IFDP database includes observations on about 450 tree species from 300,000 stems of ≥1 cm dbh, and about 280 lianas species (30,000 stems) ≥2 cm dbh. Climatic data (rainfall and temperature) for each plot are collected from a station associated to each plot.

## THE ITURI FOREST IN THE CONGO BASIN AND TROPICAL FOREST NETWORK

This study is conducted within the framework of the Wildlife Conservation Society – Democratic Republic of Congo (WCS-DRC) & the Centre de Formation et de Recherche en Conservation Forestière (CEFRECOF) effort in partnership with the Center for Tropical Forest Science (CTFS). CEFRECOF aims to develop guidelines for conservation and sustainable management of forest resources and exploitation of botanical diversity within DRC, as an effort that complies to its national contribution to the Global Strategy of Plant Conservation (GSPC). Specifically, the current Ituri Forest Dynamics Plots is within the group of projects to provide knowledge on forest dynamics parameters and biodiversity in the context of climate change in the Congo Basin (Fig. 1.1). The biodiversity and demography of species are evaluated in this long-term ecological research. The overall objective of this IFDP is to contribute basic information to understand the processes leading to forest and biodiversity dynamics of this part of the Congo Basin forest. Such understanding is crucial for an effective management of tropical forest in general and the Ituri Forest in particular. Among the IFDP project output are: Lianas (this study), Forest structure, diversity of liana and understory treelets (Makana *et al.* 1998, 2004a, b; Makana 2004, Condit *et al.* 2006, Chave *et al.* 2008, Lewis *et al.* 2009, DeWalt *et al.* 2010).

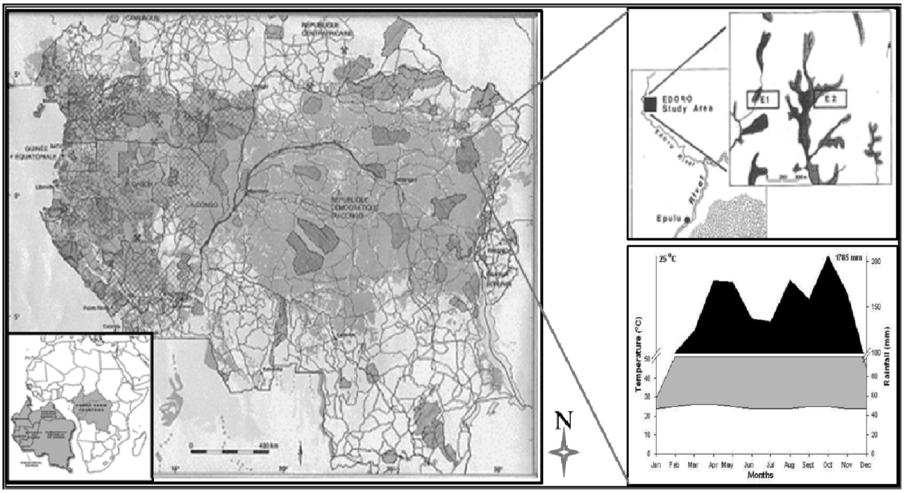

Figure 1.1. General overview of the study area. The Congo basin maps are taken from Central African Regional Program of Environment (CARPE) site. The inlet shows the Congo basin region. The upper right inset shows the location of the permanent sample plots, in which black areas in the inset represent swamps connected by rivers and streams; whereas the lower indicates climatic diagram in the site.

# *Chapter 2*

## *Structure and composition of the liana assemblage of a mixed rain forest in the Congo Basin*

*Corneille E.N. Ewango, Frans Bongers, Lourens Poorter, Jean-Remy Makana & Marc S.M. Sosef*

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## ABSTRACT

The Congo lowland forest represents one of the largest remaining tropical forest blocks in the world, but its liana assemblage has never been characterized. We evaluate liana floristics, diversity and structure in two 10-ha plots in Ituri Forest, characterize liana functional traits and determine effects of forest structure, topography and edaphic variation on liana species composition. In 20 ha, 15008 lianas (diameter ≥ 2 cm) were found, representing 195 species, 83 genera and 34 plant families. Per hectare species number averaged 64, basal area was 0.71 $m^2$ and Fisher's alpha, Shannon and Simpson diversity index values were 17.9, 3.1 and 11.4, respectively. Ten dominant plant families represented 69% of total species richness, 92% of liana abundance and 92% of basal area, while ten dominant species accounted for 63% of abundance and 59% of basal area. Forty-one species (21%) had one individual only. Most lianas were light-demanding, climbed their hosts by twining, had conspicuous flowers, medium-sized leaves and animal dispersed propagules. Liana abundance increased with abundance of medium-sized and large trees but was, surprisingly, independent of small-tree abundance. Canopy openness, soil moisture, and tree size were the most important environmental factors influencing abundance and distribution of lianas. We conclude that the liana assemblage of this Congo basin forest generally concurs with those of lowland tropical forests elsewhere.

**Key words:** Climbing mechanisms, Dispersal Types, Forest structure, Floristic composition, Ituri Forest Dynamics Plots, Lianas, Species diversity.

## INTRODUCTION

Lianas (woody climbers) are notoriously abundant in the tropics, forming up to 25% of the woody stem density (Gentry 1991a, Schnitzer & Bongers 2002) and contributing 12%-40% to the overall species diversity of tropical forests (Bongers *et al.* 2005, Gentry 1991a, Hall & Swaine 1981, Schnitzer & Bongers 2002, Smith 1970). Apart from their direct contribution to diversity, lianas help maintain diversity through their effects on forest structure and dynamics (Putz 1984, Schnitzer & Bongers 2002) and thus on species composition of both plants and animals. For some animals, such as phytophagous beetles, lianas even may be the preferential habitat (Ødegaard 2000). A number of studies have documented the functional aspects of lianas in tropical forests. First, lianas substantially contribute to canopy closure after tree fall, stabilizing the microclimate underneath, and contributing to whole-forest transpiration (Andrade *et al.* 2005, Schnitzer & Bongers 2002). Second, lianas contribute to the carbon budget of tropical forests (Lewis *et al.* 2009), representing as much as 10% of fresh above-ground biomass (Gehring *et al.* 2004, Phillips *et al.* 2002, Putz 1984) and accounting for up to 40% of leaf productivity (Gerwing & Farias 2000, Hegarty & Caballé 1991, Wright *et al.* 2004). When lianas become abundant they may reduce the amount of carbon sequestered by tropical forests (Laurance *et al.* 2001, Phillips *et al.* 2002, Schnitzer & Bongers 2002). Finally, by colonizing trees, lianas create structural stresses on their hosts, compete for light, water and soil nutrients, and reduce tree growth (Peña-Claros *et al.* 2008, Schnitzer *et al.* 2005, Villegas *et al.* 2009, Whigham 1984) and reproduction (Kainer *et al.* 2006, Nabe-Nielsen *et al.* 2009, Stevens 1987), and increase rates of tree fall and limb breakage (Lowe & Walker 1977, Putz 1984).

The varying species composition of lianas in different forest types demonstrates that there are large ecological and functional differences across species. Although lianas have a similar growth form and are generally thought to be light demanding (Putz 1984), species do differ in for example climbing mechanisms (Putz 1984, Putz & Holbrook 1991) and light requirements (Baars *et al.* 1998, Gianoli *et al.* 2010, Putz 1984). This enables occupation of a wide range of habitat types (Balfour & Bond 1993, Darwin 1867, Nabe-Nielsen 2001). Furthermore, flower size and diaspore type vary markedly across liana species (Bullock 1995, Cai *et al.* 2009, Gentry 1991b) and are connected to a wide range of pollinators and propagule distributers. Dispersal mechanisms are critical for plants to reach and colonize new locations while they influences patterns of seed predation, seedling establishment and survival, and determine the density and distribution of the next generation of adult individuals (Cain *et al.* 2000). Light requirements may determine the competitive ability of lianas and their power to infest tree crowns.

The abundance, species diversity and distribution of lianas depend upon several abiotic factors, including total rainfall, seasonality of rainfall, soil fertility, landscape topography, forest canopy structure, disturbance regimes and successional stage (DeWalt *et al.* 2000, 2006, 2010; Ibarra-Manriquez & Martinez-Ramos 2002, Poulsen *et al.* 2005, Schnitzer & Bongers 2002, Schnitzer *et al.* 2005, Toledo 2010). Putz (1984) and Balfour & Bond (1993) showed that trellis availability and canopy structure (i.e. canopy openness and tree architecture) together influence the distribution and abundance of lianas in different forest types. In addition, light availability and topographic positions differently affect liana growth, mortality and survival (Baars & Kelly 1996, Nabe-Nielsen 2002). Close associations between tree, Pteridophytes species and habitat (e.g. soil, topography) are shown at regional level (Clark *et al.* 1999, Harms *et al.* 2001, Pyke *et al.* 2001, Toledo 2010) as well as at local level (Duque *et al.* 2002, Itoh *et al.* 2003, Palmiotto *et al.* 2004, Svenning 1999, Tuomisto *et al.* 2002). Spatial variation in water availability may play an important role in these patterns and is often driven by topography, with higher soil moisture in valleys compared to slopes, ridges or plateaux (Brubaker *et al.* 1993, Enoki *et al.* 1997, Markesteijn *et al.* 2010, Roy & Singh 1994). Various growth forms have been analysed in these studies but none of them concern lianas (but see Kusumoto *et al.* 2008).

In Africa, liana community studies are available for South Africa (Balfour & Bond 1993), Upper Guinea (Addo-Fordjour *et al.* 2008, 2009; Bongers *et al.* 2002, 2005; Muoghalu & Okeesan 2005), western Lower Guinea (Caballé & Martin 2001, Parren 2003, Parren & Bongers 2001, Tchouto 2004), and East Africa (Babweteera *et al.* 2000, Eilu 2001, Senbeta *et al.* 2005). However, few studies have been performed in the vast Congo Basin (Lebrun 1937, Makana *et al.* 1998). In this study we evaluate the community structure of the liana assemblage of the mixed lowland Ituri forest, north-eastern Democratic Republic of Congo. Using data from two 10-ha forest plots we (1) describe the floristics, diversity and structure of the liana assemblage in this old-growth forest; (2) characterize liana functional traits (climbing mechanisms, regeneration guilds, leaf sizes, flower types and dispersal syndromes); and (3) determine the effects of forest structure, small-scale local topography and edaphic variation on liana species composition. We expect that the liana assemblage of this mixed old-growth forest concurs with those of lowland rain forests elsewhere.

## METHODS

### *Study site*

The study was carried out in the Okapi Faunal Reserve (Réserve de Faune à Okapis; RFO, 1°25’N, 28°35’E; Figure 2.1) in the central part of the Ituri Forest, north-eastern DR Congo. Two 10-ha permanent forest plots were established near the Edoro Field Research area of the Centre de Formation et de Recherche en Conservation Forestière and the Wildlife Conservation Society (hereafter referred as CEFRECOF/WCS). The Ituri Forest Dynamics Plots (IFDP) are part of the worldwide tropical forest network of the Center for Tropical Forest Science (CTFS; Condit 1998, Losos & Leigh 2004). The Edoro research area covers about 52 km$^2$ of primary mixed tropical lowland forest, and has an altitude of 700-850 m asl.

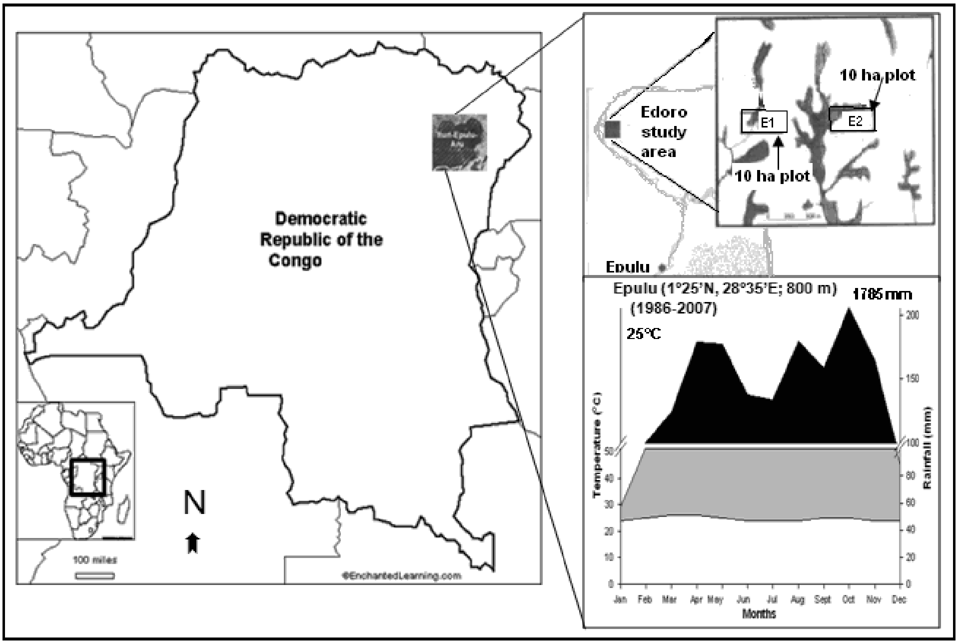

Figure 2.1. Location of the Edoro mixed forest dynamics plots (plots and swamps connected by streams) in the Ituri Forest and ombrothermic diagram from the Epulu site (Okapi Wildlife Reserve). Weather records collected from 1986-2007.

The climate of the region is classified as Köppen’s Am type (Gerard 1960), i.e. tropical megathermic with a severe dry season. Mean annual precipitation is 1785 mm, with a bimodal seasonal distribution: two wet seasons from March to June and August to November. In the dry season, December through February, rainfall is less than 100 mm and the two driest months, January and February, have less than 50 mm. Mean annual temperature ranges between 17.9°C to 25.5°C (Hart & Carrick 1996, Figure 1). The soils in the region consist mainly of highly weathered tropical oxisols, with texture ranging from sandy clay loam to sandy clay (Hart *et al.* 1989). Topography is gentle with only small differences in elevation: both plots have less than 20 m of internal elevation difference (Makana *et al.* 2004). For a more detailed description of the study area, soils and climate, see Hart (1985), Conway (1992) and Hart & Carrick (1996).

The vegetation in the area is classified as mixed tropical lowland forest (*sensu* White 1983). *Cynometra alexandri* C.H.Wright, *Julbernardia seretii* (De Wild.) Troupin (both Fabaceae), and *Cleistanthus michelsonii* J.Léonard (Phyllanthaceae) account for up to 30% of basal area and density of stems ≥10 cm dbh in the two plots (Hart 1985). The canopy is heterogeneous, 30-40 m in height, with frequent emergent trees.

### *Data collection*

Two permanent plots of 10-ha (200 × 500 m), 500 m apart and called Edoro-1 and Edoro-2, were established in mixed forest in December 1994. Botanical and topographic data were collected following the plot standards of the CTFS network (Condit 1998). In each 10-ha plot, a grid of 250 contiguous 20 × 20-m quadrats was demarcated with 286 cement stakes and each quadrat was subdivided into 16 sub-quadrats of 5 × 5 m. All individuals of lianas ≥ 2 cm dbh were identified, measured, mapped and marked with a pre-numbered aluminium tag. Most of the individuals of this size have their leaves in the forest canopy. Lianas were measured at 1.3 m height along the stem from their rooting point. To facilitate comparison with other liana studies, we only included true lianas species: climbing plants that produce true wood and that germinate on the ground but lose their ability to support themselves as they grow, so they have to rely on external physical support to ascend to the canopy (Gerwing *et al.* 2006). We distinguished genets from ramets for each individual liana, based on rooting location and underground stem connections. This was checked by removing litter. All multiple and non-rooted interconnected stems were assumed to belong to the rooted individual and were counted as an individual clone group. However, in some cases we could not reject with total certainty the possibility of below-ground connections. We adopted as a general rule, that stems were treated as genets unless it was evident that they had connections with other stems.

Major habitat types were defined using visual evaluation of superficial soil water permanence criteria. Tierra firme forest (TF) is non-inundated terrain with sandy to loamy soils and a thin layer of organic matter, and swamp forest (SF) is terrain with hydromorphic and alluvial soils along streambeds, regularly flooded during rainy periods. The canopy of SF is much lower, more open, and less homogeneous than that of TF. Elevation, convexity and slope were measured and calculated for each 20 × 20-m quadrat in the plot. Elevation was obtained from the mean elevations at the four corners of a quadrat (Harms *et al.* 2001). For each 5 × 5-m subquadrat we estimated canopy openness using a three-class semi-quantitative scale (0: cover = <25%, 1: cover =25%-50%, 2: cover = 50%-100%). This allows for a relative comparison of canopy structure across plots. Data were converted to their midpoint values for further analysis.

If possible, we identified lianas to species in the field. All botanical identifications were based on both reproductive (flowers or fruits) and vegetative (leaves, bark and trunks form) characteristics of specimens collected or observed in the field. In most cases, either fertile or sterile materials were collected for identifications at the reference Herbarium of CEFRECOF at Epulu. Collected materials were later compared with identified collections at international herbaria, notably the National Herbarium of the Netherlands-Wageningen branch (WAG), National Botanical Garden of Belgium (BR, Meise) and Missouri Botanical Garden (MO, St. Louis), where a set of voucher specimens was also deposited. Family nomenclature in the present study follows the Angiosperms Phylogeny Group (APG, Stevens 2001). Species nomenclature followed that of Lebrun & Stork (1991-1997).

### *Data analysis*

We characterized liana floristic and structural components at a fine scale (20 × 20-m quadrat), plot level (10 ha) and community level (20 ha). We used a conservative approach in calculating species numbers by lumping morphospecies into one group of higher taxa (i.e. genus or family) instead of considering them as several distinct species. All analyses in the present paper are based on identifications at different taxonomic ranks: species (with all subspecific taxa lumped under the parent species), genus and family. Morphogroups not identified to a named taxon (9.8% of all recorded stems) were excluded from further analyses.

To describe the liana community structure we calculated for each taxon the Importance Value Index (IVI), i.e. the average percentage of relative density, frequency and basal area (Ellenberg & Muller-Dombois 1974). The total number of species, genera and families were tallied for each plot (10 ha) and for the whole community (20 ha). We plotted each of the parameters following the method of Preston (1948), counting the frequency of each taxon in doubling classes of abundance and; species richness, stem abundance and basal area contribution in 2-cm interval of each size class distribution, respectively.

We used three indices, Fisher's alpha, Shannon-Wiener and Simpson diversity to calculate liana diversity in the 20-ha plot. These indices were selected based on their discriminant ability, sensitivity to sample size and popularity. For instance, Fisher's alpha is less sensitive to sample size and thus facilitates comparisons of diversity among sites that differ in abundance. The Shannon-Wiener diversity index emphasizes the contribution of rare species and the Simpson diversity index gives more weight to common species in a sample (Magurran 2004). We used EstimateS 8.0 (Colwell 2006) to compute the abundance-based coverage estimator (ACE), Chao1, Mao Tau (observed number of species) and Coleman non-parametric estimators of species richness from species abundance in the sample matrices (Chazdon *et al.* 1998, Colwell & Coddington 1994). For each estimator, we plotted the randomized mean species accumulation curve against the cumulative plot sample area. The Coleman and Mao Tau estimators are indicators of the site heterogeneity, while ACE and Chao1 reveal the fluctuation of species richness considering singletons (species presented by one individual in the plot) and doubletons (species represented by two individuals) as rare species components in the community.

We assigned functional attributes/ecological characteristics (climbing mechanism, leaf size, regeneration light requirements, flower type and primary dispersal syndrome) to each species, either by direct field observations and/or using data available in the primary literature (Evrard 1968, Gerard 1960). The climbing mechanism of all liana species were categorized as (1) stem twiner, (2) hook climber, (3) root climber, and (4) tendril climber (based on field observations). Leaf sizes were classified (Raunkiaer 1934) as lepto- (<0.2 $cm^2$), nano- (0.2-2 $cm^2$), micro- (2-20 $cm^2$), meso- (20-200 $cm^2$) and macrophyll (200-2000 $cm^2$). Regeneration light requirements were grouped into four classes (Evrard 1968): light demanding, partially light-demanding, partially shade-tolerant and shade tolerant. Flower types were classified (Gentry 1991) as conspicuous (with bright colour and flowers longer than 1 cm) and inconspicuous (with whitish-pale or green colour and flowers shorter than 1 cm). Three primary dispersal syndrome classes are used: anemochory (wind-dispersed fruits or seeds with plumose appendages or scarious wing-like appendages), zoochory (animal dispersed fruits with soft and fleshy outer layers or seeds with arils), and barochory (autochory or active seed dispersed by the plant itself, usually by explosive dehiscence, such as explosive pods).

In each 20 × 20-m quadrat the trees were categorized as small (1 cm $\leq$ dbh $\geq$ 10 cm), medium (>10 cm dbh $\leq$ 30 cm) and large trees (dbh >30 cm); and the lianas as small (dbh ≤ 5 cm) or large (dbh > 5 cm). We tested the hypothesis that tree abundance (in separate size classes) would affect the liana abundance (in separate size classes) using backward multiple regression analysis (SPSS 15.0 for Windows; SPSS Inc. Chicago, IL, USA).

Table 2.1. The ten most abundant species (A), genera (B) and families (C) of lianas in Edoro mixed rain forest in Ituri, Congo. Abundance, basal area and Importance Value in 20 ha of forest. Values between parentheses are percentages of abundances and basal area, and exponent values provide the rank order of taxa with decreasing abundance.

| **A. Species** | **Family** | **Stem abundance** | **Basal area ($m^2$)** | **Importance Value (%)** |
|---|---|---|---|---|
| *Manniophytum fulvum* | Euphobiaceae | 3299 (21.9)$^{1}$ | 2.2 (13.6) $^{1}$ | 14.3$^{1}$ |
| *Rourea thomsonii* | Connaraceae | 922 (6.1)$^{2}$ | 0.9 (5.6)$^{3}$ | 5.7$^{2}$ |
| *Dichapetalum staudtii* | Dichapetalaceae | 854 (5.7)$^{3}$ | 0.9 (5.3)$^{4}$ | 5.3$^{3}$ |
| *Agelaea pentagyna* | Connaraceae | 767 (5.1)$^{4}$ | 1.2 (6.3)$^{2}$ | 5.4$^{4}$ |
| *Combretum racemosum* | Combretaceae | 685 (4.6)$^{5}$ | 0.5 (3.2)$^{9}$ | 3.3$^{5}$ |
| *Dichapetalum heudelotii* | Dichapetalaceae | 638 (4.3)$^{6}$ | 0.7 (4.2)$^{7}$ | 3.8$^{6}$ |
| *Agelaea paradoxa* | Connaraceae | 636 (4.2)$^{7}$ | 0.5 (3.1)$^{10}$ | 3.9$^{9}$ |
| *Agelaea rubiginosa* | Connaraceae | 454 (3.0)$^{8}$ | 0.6 (3.7)$^{8}$ | 3.3$^{8}$ |
| *Combretum marginatum* | Combretaceae | 421 (2.8)$^{9}$ | 0.8 (4.9)$^{6}$ | 3.7$^{10}$ |
| *Millettia psilopetala* | Fabaceae | 390 (2.6)$^{10}$ | 0.9 (5.6)$^{5}$ | 3.7$^{7}$ |
| 10 most abundant | | 9066 (63.2) | 9.0 (59.2) | 55.8 |
| All other | | 5942 (36.8) | 7.2 (40.8) | 44.2 |
| Total for identified species | | 13534 (90.2) | 14.4 (89) | 88.2 |
| Total for non-identified morphogroups | | 1474 (9.8) | 1.8 (11) | 11.2 |
| Total (20 ha) | | 15008 (100) | 16.2 (100) | 100 |
| Number of identified species | | 195 | | |
| **B. Genera** | **Number of species** | | | |
| *Manniophytum* | 1 | 3299 (21.9)$^{1}$ | 2.2 (13.6)$^{2}$ | 14.8$^{1}$ |
| *Agelaea* | 3 | 2117 (14.1)$^{2}$ | 2.5 (15.3)$^{1}$ | 12.9$^{2}$ |
| *Dichapetalum* | 7 | 1821 (12.1)$^{3}$ | 1.9 (11.6)$^{3}$ | 10.8$^{3}$ |
| *Combretum* | 7 | 1506 (10.0)$^{4}$ | 1.8 (11.2)$^{4}$ | 9.3$^{4}$ |
| *Rourea* | 2 | 971 (6.5)$^{5}$ | 1.0 (6.1)$^{6}$ | 6.5$^{5}$ |
| *Millettia* | 1 | 583 (3.9)$^{6}$ | 1.4 (8.5)$^{5}$ | 5.6$^{6}$ |
| *Salacia* | 3 | 490 (3.3)$^{7}$ | 0.7 (4.5)$^{7}$ | 4.2$^{7}$ |
| *Strychnos* | 14?? | 480 (3.2)$^{8}$ | 0.4 (2.7)$^{9}$ | 3.4$^{8}$ |
| *Landolphia* | 13 | 303 (2.0$^{9}$ | 0.5 (2.9)$^{8}$ | 2.9$^{9}$ |
| *Cnestis* | 2 | 212 (1.4)$^{10}$ | 0.2 (1.0)$^{10}$ | 1.6$^{10}$ |

| | | | | |
|---|---|---|---|---|
| 10 most abundant | 40 (21) | 11782 (78.5) | 12.5 (77.5) | 72.2 |
| All other identified | 155 (79) | 3226 (21.5) | 3.7 (22.5) | 27.8 |
| Total for identified genera | 195 (100) | 14217 (94.7) | 15.2 (93.8) | 93.1 |
| Total for non-identified genera | | 791 (5.3) | 1.0 (6.2) | 6.9 |
| Total (20 ha) | | 15008 (100) | 16.2 (100) | 100 |

| **C. Family** | **# Genera** | **# Species** | **Stem abundance** | **Basal area (m$^2$)** | **Importance Value (%)** |
|---|---|---|---|---|---|
| Connaraceae | 5 | 13 | 3482 (23.2)$^{1}$ | 3.8 (23.5)$^{1}$ | 19.7$^{1}$ |
| Euphorbiaceae | 4 | 4 | 3420 (22.8)$^{2}$ | 2.34 (14.6)$^{2}$ | 16.3$^{2}$ |
| Dichapetalaceae | 1 | 7 | 1821 (12.1)$^{3}$ | 1.9 (11.6)$^{3}$ | 11.6$^{3}$ |
| Combretaceae | 1 | 7 | 1506 (10.0)$^{4}$ | 1.8 (11.2)$^{4}$ | 10.3$^{4}$ |
| Celastraceae | 10 | 22 | 1001 (6.7)$^{5}$ | 1.5 (8.9)$^{6}$ | 8.1$^{6}$ |
| Fabaceae | 6 | 15 | 820 (5.5)$^{6}$ | 1.8 (11.1)$^{5}$ | 8.1$^{5}$ |
| Apocynaceae | 11 | 30 | 654 (4.4)$^{7}$ | 0.7 (4.6)$^{7}$ | 5.2$^{7}$ |
| Loganiaceae | 1 | 14 | 480 (3.2)$^{8}$ | 0.4 (2.7)$^{8}$ | 4.1$^{8}$ |
| Annonaceae | 5 | 18 | 424 (2.8)$^{9}$ | 0.3 (1.8)$^{9}$ | 3.4$^{9}$ |
| Malvaceae | 3 | 5 | 245 (1.6)$^{10}$ | 0.2 (1.5)$^{10}$ | 2.1$^{10}$ |
| 10 most abundant | 47 | 135 | 13853 (92.3) | 14.9 (91.6) | 89.1 |
| All other identified | 36 | 60 | 1113 (7.7) | 1.3 (8.4) | 10.9 |
| Total for identified | | | 14966 (99.7) | 16.1 (99.4) | 99.5 |
| Total for non-identified | | | 42 (0.3) | 0.1 (0.6) | 0.5 |
| Total (20 ha) | | | 15008 (100) | 16.2 (100) | 100 |
| Number of identified taxa | 83 | 195 | | | |

A Principal Components Analysis (PCA, using CANOCO 4.5 for Windows, ter Braak & Smilauer 1997) was performed to describe the compositional pattern of the liana assemblages in 20 × 20-m quadrats. The main axes of variation were related to parameters of forest structure (density of trees in three size-class categories: small, medium, large -, canopy openness), and plot physiographic characteristics (habitat type, elevation, slope, convexity). Habitat type (TF or SF) was included as a binary variable. All variables were examined for collinearity, which was generally low (r between 0.002 and 0.941) and thus all variables were included in the analyses.

Table 2.2. Liana community floristic and structural attributes of Edoro mixed rainforest, Ituri, DR Congo (mean ± SD)

| Site | Edoro 1 | | Edoro 2 | | Edoro | |
|---|---|---|---|---|---|---|
| Attribute | 20 x 20 m | 1 ha | 20 x 20 m | 1 ha | 20 x 20 m | 1 ha |
| | N=250 | N=10 | N=250 | N=10 | N=500 | N=20 |
| ***Structural and taxonomic recorded characteristics*** | | | | | | |
| Abundance | 24.1 ± 13.7 | 603.6 ± 122.5 | 29.9 ± 15.1 | 749.8 ± 123.6 | 27.1 ± 0.7 | 676.7 ± 141.3 |
| Basal area (x10$^{-2}$ m²) | 2 ± 1 | 61 ± 10 | 3 ± 1 | 82 ± 10 | 3 ± 0. 1 | 71 ± 10 |
| Number of species | 9.1 ± 3.5 | 54.8 ± 7.8 | 11.6 ± 3.5 | 73.1 ± 2.1 | 10.2 ± 0.2 | 63.9 ± 10.9 |
| Number of genera | 8.4 ± 3.1 | 39.0 ± 3.9 | 9.4 ± 2.8 | 42.3 ±2.6 | 9.1 ± 0.1 | 40.6 ± 3.7 |
| Number of families | 7.6 ± 2.4 | 21.7 ± 1.7 | 7.9 ± 2.2 | 22.2 ± 1.7 | 8.4 ± 0.1 | 21.9 ± 1.7 |
| ***Species richness non-parametric estimators*** | | | | | | |
| ACE | 19.8 ± 11.7 | 78.6 ± 10.3 | 25.2 ± 14.9 | 100.3 ± 9.3 | 19.9 ± 12.7 | 90.4 ± 17.0 |
| Chao 1 | 18.8 ± 9.7 | 88.1 ± 24.4 | 25.4 ± 14.9 | 100.1 ± 14.8 | 20.5 ± 11.8 | 96.4 ± 21.9 |
| Coleman | 13.4 ± 2.6 | 62.8 ± 4.2 | 16.5 ± 2.9 | 85.9 ± 4.7 | 15.3 ± 2.9 | 80.1 ± 4.8 |
| Mao Tau (Spp Obs) | 9.1 ± 1.7 | 54.6 ± 4.3 | 11.6 ± 1.9 | 73.2 ± 4.8 | 10.4 ± 1.8 | 63.9 ± 5.0 |
| ***Species diversity*** | | | | | | |
| Fisher's Alpha | 6.2 ± 2.1 | 15.1 ± 1.2 | 8.4 ± 3.1 | 20.3 ± 1.4 | 7.4 ± 3.3 | 17.9 ± 1.3 |
| Shannon-Wiener | 1.9 ± 0.4 | 2.9 ± 0.1 | 2.1 ± 0. 3 | 3.2 ± 0.1 | 1.9 ± 0.4 | 3.1 ± 0.2 |
| ***Species dominance*** | | | | | | |
| Simpson | 6.9 ± 3.5 | 10.0 ± 1.6 | 8.7 ± 3.8 | 12.1 ± 1.7 | 8.4 ± 4.8 | 11.4 ± 1.9 |

## RESULTS

### *Floristic and taxonomic diversity*

A total of 15,008 stems was recorded in the two 10-ha plots. Of these stems, 90.2% (13,534 stems) were identified to species level and represented 195 species (see Appendix 2.1?? for a complete list), 83 genera and 34 families (Table 2.1). Edoro-2 (169 species, 76 genera and 33 families) was slightly richer than Edoro-1 (137 species, 72 genera and 31 families). The ten most abundant species together accounted for 63.2% (9066 stems) of the total number of stems and 59.2% (9.0 m²) of the total basal area. *Manniophytum fulvum* (Euphorbiaceae) had the highest Importance Value Index (14.3%): it accounted for 21.9% of all liana stems and 13.6% of the total basal area, and was distributed in 88.4% of the quadrats. The 10 most important genera harboured 40 species (21%) and contributed 78.5% to the number of stems and 77.5% to the basal area. *Manniophytum* (Euphorbiaceae) was the most abundant genus (21.9% of total number of stems), but *Agelaea* (Connaraceae) had the highest basal area (15.3%). *Landolphia* (13 species) was the most species-rich genus but contributed only 2% to the abundance and 2.9% to the basal area. Ten out of 34 families contained 47 genera, and contributed 92.3% to the number of stems, 91.6% to the basal area and 89.1% to the total Importance Value Index. The most species-rich families were Apocynaceae (30 species), Celastraceae (22) and Annonaceae (18). *Laccosperma secundiflorum* (Arecaceae) was the only palm liana in the IFDP liana assemblage.

### *Species richness and diversity*

An average of 63.9 species, 40.6 genera and 21.9 families were recorded per hectare (Table 2.2). Fisher α was 17.9, Shannon-Wiener index was 3.1 and Simpson dominance index was 11.4. Considering the whole community (20 ha), we found that the species estimates ranged between Mao Tau (63.9) and Chao1 (96.4), where Chao1 is 1.5 times the observed species number.

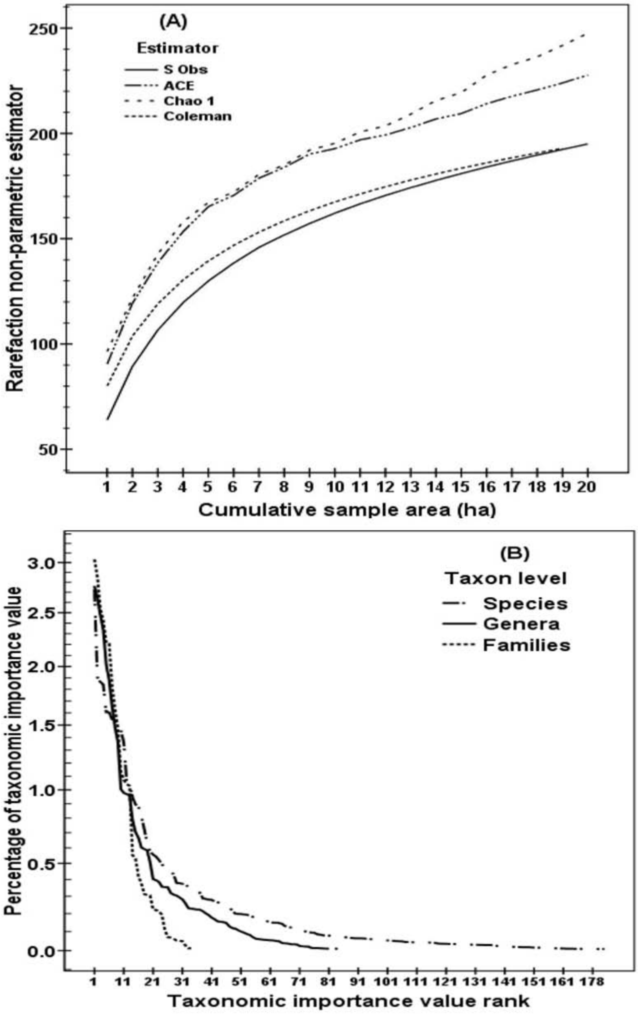

Figure 2.2. (A) Species area curves for observed species richness (S Obs) and species richness estimators Chao 1, ACE and Coleman for lianas in the Edoro mixed forest of Ituri, and (B) Rank-importance curves for species, genera and families for lianas in 20 ha of mixed rain forest in Ituri. Taxon importance is calculated as the percentage of the total community Importance Value Index and in the graph log-transformed.

At the smaller scale of 20 × 20-m quadrats all of these values were considerably lower (Table 2). The estimated species number was up to twice as high as the observed number, but species dominance (Simpson) was rather similar. The species accumulation curves (Figure 2.2a) did not attain an asymptote, despite the 20 ha of sampling area. Rare species, defined as those found as singletons and doubletons remained numerous even in large samples.

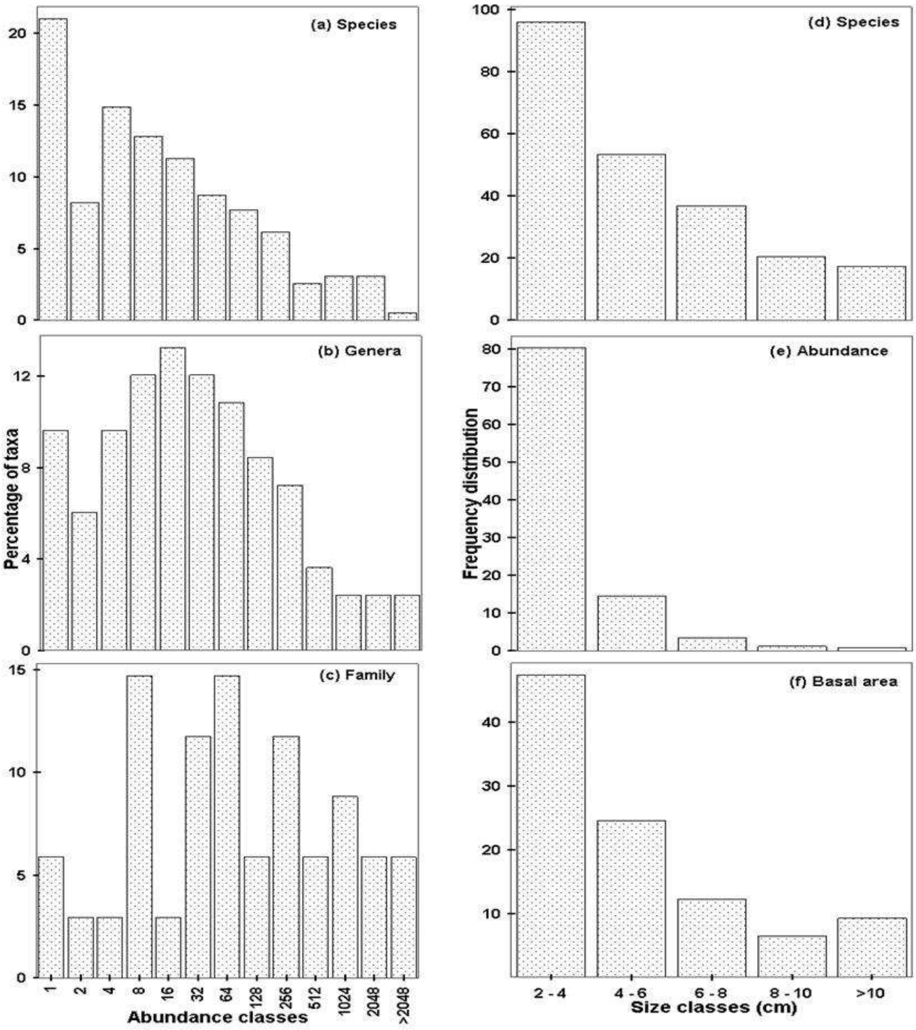

Figure 2.3. Frequency distributions of species (N=195), genera (N=83) and families (N=34) over abundance classes (a-c), and percentage of total species number (d), stem abundance (e) and basal area (f) of lianas of different size classes, in 20 ha of mixed rain forest in Ituri.

### *Liana assemblage structure*

Mean stem density was 677 stems ha$^{-1}$, and mean basal area was 0.71 m$^{2}$ ha$^{-1}$. The dominance-diversity curves showed strong dominance with few taxa being very abundant and many taxa being represented by only a few individuals (Figure 2.2b). Taxonomic abundances (Figure 2.3) at the 20-ha level varied greatly. Forty-one species (21%) were only known by a single individual, while 56.9% of the total stems were represented by species with less than eight liana stems (Figure 2.3a). In contrast, the genera and family taxa exhibited lognormal-like distributions (Figure 2.3b,c), indicating that taxa vary largely in their abundances. Most liana individuals were small: nearly 79% were smaller than 4 cm in diameter, while only 2% of stems were larger than >10 cm dbh (Figure 2.3e). On average stems measured 3.4 cm in dbh. The largest stem measured was 19.5 cm dbh (*Landolphia owariensis*, Apocynaceae). Species richness (Figure 2.3d), abundance (Figure 2.3e) and basal area (Figure 2.3f) decreased with increasing stem size. Large lianas (>10 cm dbh) contributed 16.5% to the total liana basal area.

Species stem abundance, basal area and frequencies were positively correlated (abundance versus basal area, $r = 0.95$; abundance versus frequency, $r = 0.89$; basal area versus distribution, $r = 0.93$; all $N = 195$ and $P < 0.001$, respectively).

### *Liana characteristics*

The functional and ecological characteristics are summarized for the total species assemblage as well as for the 10 most important families separately (Figure 2.4). Most liana species were stem twiners (69% of total), followed by tendril climbers (16%) and hook climbers (14%). Liana species were predominantly mesophyllous (55%) or microphyllous (43%) in leaf size. Most species were light demanding (82%); only few were either partially light-demanding or partially shade-tolerant. Just over half of the species had conspicuous flowers (53% vs. 46% inconspicuous flowers). The seeds of most species were animal dispersed (74%), followed by wind dispersed (22%). Only few species were barochorous (4%). With few exceptions the separate families generally exhibited similar trends in functional characteristics as the whole liana assemblage combined. Apocynaceae are mostly tendril-climbers and Loganiaceae are only hook climbers. Dichapetalaceae are only shade-tolerant. Annonaceae, Connaraceae, Loganiaceae, Dichapetalaceae, Lamiaceae and Rubiaceae species are entirely dispersed by animals, while Combretaceae are entirely wind-dispersed.

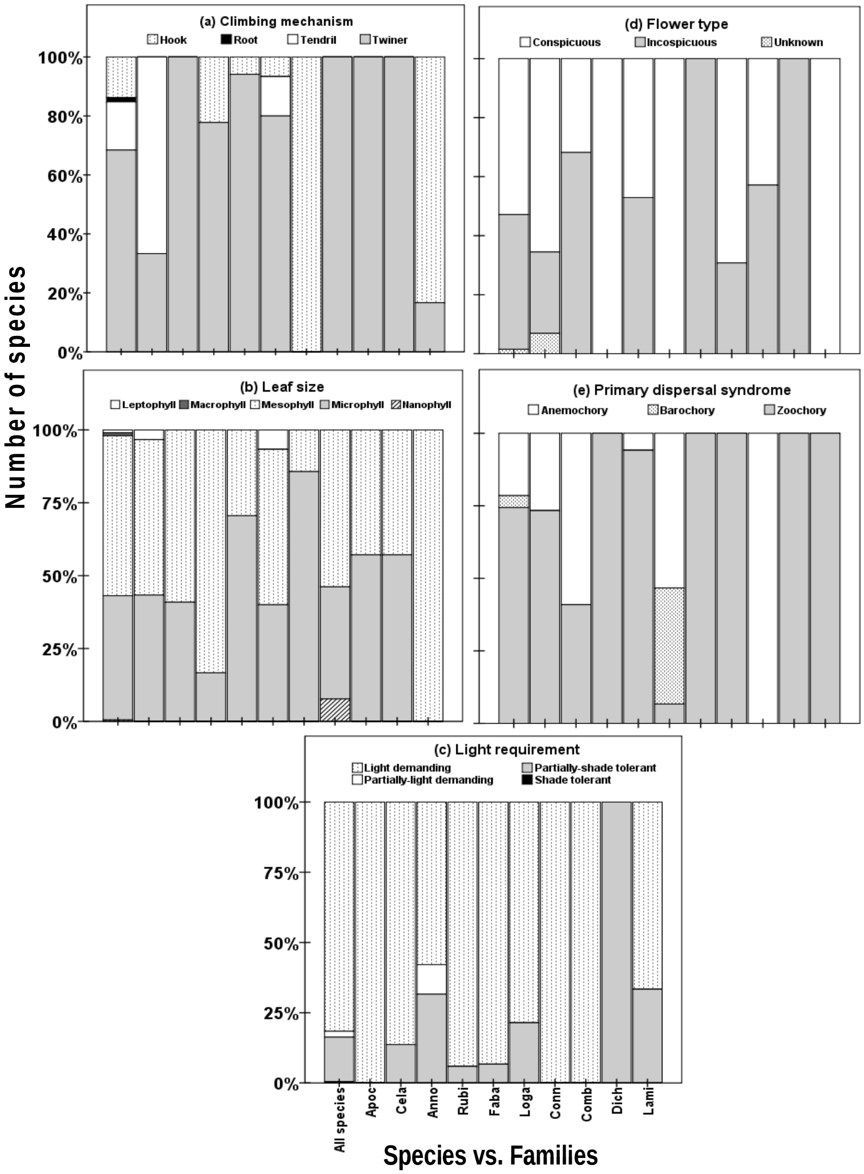

Figure 2.4. Proportion of species (N=195) with different (a) climbing mechanism, (b) leaf size, (c) life light requirement, (d) flower type, (e) primary dispersal syndrome for the 10 important families (Apoc = Apocynaceae (30 spp), Cela = Celastraceae (22), Anno = Annonaceae (18), Rubi = Rubiaceae (19), Faba = Fabaceae (15), Loga = Loganiaceae (14), Conn = Connaraceae (13), Comb = Combretaceae (7), Dich = Dichapetalaceae (7), and Lam = Lamiaceae (7).

### *Factors driving the abundance and distribution of lianas*

Species richness and abundance of lianas were positively related to richness and abundance of trees, although the explained variation was very low ($r^2 = 0.02$ and 0.01, $P < 0.01$ in both cases). Especially large-sized trees were important for liana abundance (Table 2.3); medium-sized trees had a large positive effect and, surprisingly, small trees had no effect at all.

Table 2.3. Pearson's correlations of liana abundance with abundance of trees in different stem diameter at breast height size classes in the Ituri mixed forest (N=500 quadrats). *r* is the Pearson coefficient of correlation, P is significance level (** $P < 0.01$, *** $P < 0.001$, ns = not significant).

| Stature category | Small trees (1-10 cm) | | Medium trees (> 10-30 cm) | | Large trees (> 30 cm) | |
|---|---|---|---|---|---|---|
| | r | P | r | p | r | P |
| Small lianas (2-50 cm) | 0.08 | ns | 0.15 | ** | 0.25 | *** |
| Large lianas (> 5 cm) | 0.04 | ns | 0.11 | ** | 0.09 | ns |
| All size-class lianas | 0.08 | ns | 0.16 | *** | 0.23 | *** |

The multivariate PCA showed that the two principal components together explained 50.3% of the multivariate variation in liana species abundances across the 500 quadrats. Axis 1 (32.1%) was strongly related to canopy openness and tree stature of the quadrats (forest structure) (Table 2.4) while axis 2 (18.2%) was also related to forest structure (canopy openness and medium-sized trees) but most importantly to the moisture (swamp versus tierra firme) and microtopography (elevation, convexity) of the quadrats (Figure 2.5a, b). Liana abundance and distribution reflect the mixed forest canopy structure in the ordination projection, in which many quadrats have an open canopy. The majority of species were aggregated in tierra firme habitat with open and comparatively low canopy stature. A limited number of species were associated either to swamp or to tierra firme areas and few were associated to medium-sized trees (Figure 2.5c, Table 2.4).

## DISCUSSION

The liana assemblage in the Ituri mixed lowland forest showed remarkable trends in floristic composition, structure and functional traits. Lianas were more abundant and diverse then reported for other forests, and the assemblage consisted of many small and only few large individuals. Twiners, zoochorous, light-demanding and meso- or microphyllous species dominated. Flower types were equally distributed among the two classes. Individual species differences in abundance and distribution were partly driven by micro-environmental variation in canopy openness, and to a lesser extent by habitat moisture.

Table 2.4. Summary of Principal Component Analysis (PCA) statistics for the liana species relationship to quadrats (N=500) and measured environmental variables in the mixed forest of Ituri. All eigenvalues and correlation coefficients were significant (P=0.002) as indicated by Monte Carlo simulations.

| Parameters/ Axes | 1 | 2 |
|---|---|---|
| Eigenvalues | 0.32 | 0.18 |
| Species-environment correlations | 0.32 | 0.69 |
| Cumulative percentage variance | | |
| of species data | 32.1 | 50.3 |
| of species-environment relation | 22.3 | 80.5 |
| *Inter set correlations of environmental variables* | | |
| Small trees | 0.11 | -0.10 |
| Medium trees | 0.05 | 0.25 |
| Large trees | -0.15 | -0.19 |
| Tierra firme | 0.12 | -0.63 |
| Swamp | -0.12 | 0.63 |
| Canopy openness | -0.20 | -0.37 |
| Elevation | 0.09 | -0.41 |
| Convexity | 0.06 | -0.19 |
| Slope | 0.01 | -0.13 |

### *Floristic composition*

Nearly all individuals (98.2% of all stems) were identified to family, genus or species level. This is generally well above the results reported in most other studies. For instance, in the Neotropics 62% of the individuals were identified in Colombian Amazonia (Duque *et al.* 2002), 65% in Peruvian Amazonia (Grandez *et al.* 2001), 74% in Ecuadorian Amazonia (Romero-Saltos *et al.* 2001), and 75% in Brazilian south-west Amazonia (Macia *et al.* 2007). In African forests, 94% of the individuals were identified in Ivory Coast (Kuzee & Bongers 2005).

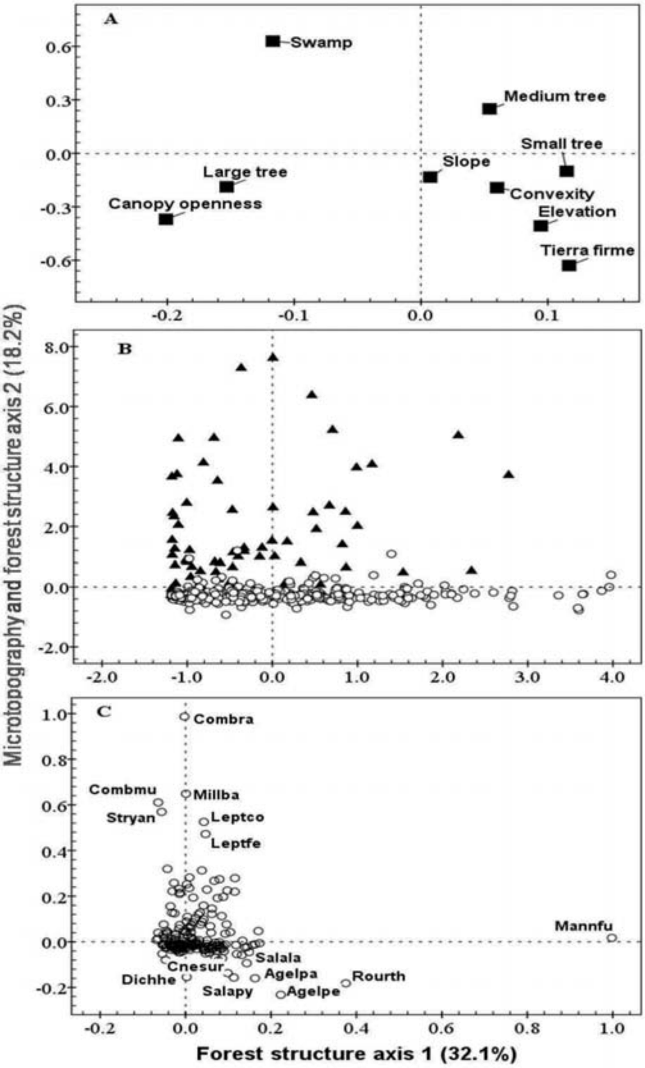

Figure 2.5

Ordination diagrams (Principal Component Analysis) showing the relationship between 195 liana species and environmental parameters in 500 quadrats. (a) environmental factors (note that tierra firme and swamp factors for quadrats are computed as presence/absence dummy variables), (b) scores of tierra firme (open circle) and swamp (triangle) plots and, (c) species scores in the Ituri mixed forest. Abbreviations of species names are based on the first four letters of the genus and the first two letters of the species names (for full species names see Appendix 2.1).

The liana flora in our study plots was dominated by only a few widespread and more generalist species, among them, *Manniophytum fulvum*. Such dominance may be the result of effective dispersal capacity, prolific vegetative sprouting, lack of specific habitat requirements and low abundance of seed predators, or combinations of these. Although this species is generally thought to be light-demanding, it is also found in shady environments. No apparent predator is known to attack its seeds.

Species composition and family dominance are largely the same as those found in most African tropical forests studied (West Africa: Jongkind & Hawthorne 2005, Ghana: Swaine *et al.* 2005; Cameroon: Parren 2003, Tchouto 2004; Ivory Coast: Kuzee & Bongers

2005, and Uganda: Eilu 2001). The IFDP liana community exhibits taxonomic characteristics (i.e. species, genera and families) also found elsewhere in the Guineo-Congolian liana flora. The most abundant species and families (Connaraceae, Euphorbiaceae, Dichapetalaceae, Combretaceae, Celastraceae, Fabaceae and Apocynaceae) are widely distributed in the Upper Guinea region (see Addo-Fordjour *et al.* 2008, Jongkind & Hawthorne 2005, Muoghalu & Okeesan 2005, Natta & Sinsin 2005, Swaine *et al.* 2005), suggesting that all West and Central African lowland forests are similar in the taxonomic composition of their lianas communities.

### *Diversity and community structure*

Lianas in the Ituri forest are abundant and diverse, and species diversity in our plot was high when compared to many other tropical forests (DeWalt *et al.* 2010, Parren 2003). The total number of liana species (195 species) in our dataset falls in the range of species numbers reported for other primary lowland forests in Africa and the Neotropics. Kuzee & Bongers (2005) recorded 156 liana species for 20-y-old and mature forest in Côte d'Ivoire, with on average 54 species per plot of varied forest structure and age. Liana community species richness in the Ituri Forest (on average 64 species $ha^{-1}$) is comparable to other tropical forests: 65 species $ha^{-1}$ in Panama (≥2 cm dbh, Putz 1984), 68 species $ha^{-1}$ in Cameroon (Parren 2003), and 70 species $ha^{-1}$ in Brazilian Amazonia (Laurance *et al.* 2001). Schnitzer & Bongers (2002) reported an average of 39 species $ha^{-1}$ for some African forests, and hence the Ituri Forest liana community can be placed among the richest in Africa.

Species richness (observed number of species, ACE and Chao 1; Figure 2) and species diversity (Shannon-Wiener and Fisher α) indices increased with sample sizes, as predicted. The continuous increase of richness and diversity, even after 20 ha, suggests that the total number of species would continue to increase with plot size, despite the plots being located in a rather homogeneous forest. The majority of species are rare, and therefore the probability of their occurrence still increases with plot size.

The IFDP contains a few highly abundant lianas. *Manniophytum fulvum* accounts for 22% of all liana stems, with 3299 individuals in 20 ha, and it is nearly threefold more important than the next species in line (*Rourea thomsonii*). This single species dominance (22%) is exceptional, compared to other studies of liana assemblages, even if these forests also had dominant liana species: *Moutabea aculeata* (Polygalaceae) accounted for 17% of the stems at La Selva (Burnham 2002, DeWalt *et al.* 2000, Nabe-Nielsen 2001), while *Strophanthus barteri* (Apocynaceae) accounted for 12% of the stems in Ghana (Addo-

Fordjour *et al.* 2008). *Machaerium cuspidatum* (Fabaceae) represented 11% of all stems censused in Yasuni National Park, Ecuador (Burnham 2002, Nabe-Nielsen 2001) while 11% of all stems in both secondary and primary forests in Panama belonged to *Maripa panamensis* (Convolvulaceae; DeWalt *et al.* 2000). Possibly, *M. fulvum*, a light-demanding species, is likely to have taken advantage of recent disturbances but the population is now declining due to gap closure. Family dominance, however, was in line with other studies in Africa, with Connaraceae, Euphorbiaceae, Dichapetalaceae, Combretaceae, Celastraceae, and Fabaceae being the most important families. The general dominance in the Ituri forest (10 out of 195 liana species represent 63.2% of the stems) may be characteristic of the Ituri forest, as also the tree assemblage shows a strong dominance (Hart 1985).

Small lianas account for the highest species richness, abundance and basal area (Figure 2.3d,e,f), and, compared to other tropical forests, Ituri forest is particularly poor in large lianas stems. The Ituri forest lianas had a relatively low basal area (0.7 $m^2$ $ha^{-1}$), comparable to southern Cameroonian forests (0.3 to 1.6 $m^2$ $ha^{-1}$, Parren 2003), and 1.1 $m^2$ $ha^{-1}$ in a Nigerian secondary forest (Muoghalu & Okeesan 2005). Richards (1952) advanced that Africa is typical for its high liana density, but we hypothetically argue that having many lianas individuals and few big ones may be because Ituri Forest is a dynamic forest with recent disturbances. It might even be that its high liana density is caused by the fact that the forest is relatively seasonal, and that only few big lianas are present because it is too wet.

Liana density in Ituri (mean 677 liana stems $ha^{-1}$, Table 1) is also high when compared to other African forests (DeWalt *et al.* 2010). Lowland tropical rain forest in Cameroon, for example, had 408 lianas $ha^{-1}$ (Parren 2003). Wet lowland Neotropical forests had, on average, higher number of lianas than Paleotropical forests (DeWalt *et al.* 2010). In four Neotropical forests liana stems ≥2.5 cm dbh averaged 605 $ha^{-1}$ (DeWalt & Chave 2004). However, Bolivian Amazon forests are known to be exceptionally liana-dense (mean of 2471 lianas $ha^{-1}$ ≥2 cm dbh) and in these forests lianas can constitute as much as 44% of the total woody species (Pérez-Salicrup *et al.* 2001). As most studies of floristic and structural characteristics of lianas are difficult to compare due to the lack of standardized methodology we welcome recent standardizations (Gerwing *et al.* 2006, Parren *et al.* 2005, Schnitzer *et al.* 2008). It is important to emphasize that lianas, despite their high abundance, have only low biomass in our study area compared to other tropical rain forests (e.g. in Brazil, Klinge & Rodriguez 1974; Venezuela, Putz 1983; Bolivia, Pérez-Salicrup *et al.* 2001, 2004; West Africa, Parren 2003). This is consistent with the observation that lianas in our studied plots are mainly of small size.

### *Functional characteristics of the liana community*

In Ituri, twining is the dominant climbing mode (70% of the species, figure 4a). Our findings corroborate with many others in the tropical forests. DeWalt *et al.* (2000) showed that both stem and branch twiners were more common in later successional forests in Panama. Twiners counted for more than half (63%) of the liana community of the semi-deciduous rain forest in Ghana (Addo-Fordjour *et al.* 2008). Twining featured prominently as climbing mechanism in the Xishuangbanna forests, southern China (Cai *et al.* 2009) and in Central Amazonian forest in Brazil (Laurence *et al.* 2001). Because of their ability to ascent trees directly via twining, twining species colonize indistinctively a wide range of trees and species. Herbivory in the understorey has been reported as an ecological factor inducing twining in climbing plant (Gianoli & Molina-Montenegro 2005). Families with tough and heavy stems tend to rely on safe. There seems to be an association between stems mechanical architecture and climbing mechanism; some families with heavy stem are entirely twiners (e.g. Celastraceae, Connaraceae, Combretaceae and Rubiaceae) or hook-climbing (e.g. Loganiaceae), while other families that tend to have flexible stems also rely on tendrils (e.g. Apocynaceae).

Herbaceous climbers are generally light-demanding, since they establish and grow well in large clearings (Putz 1984) while in contrast, woody lianas often occur in very heterogeneous light habitats such as in old gaps, forest margins and under irregular and broken forest canopies (Hegarty & Caballé 1991, Putz 1984). Our findings indicate that lianas are common in both deep shade and full-sun environments, and thus may possess a broad intraspecific physiological plasticity which strongly affects survival, growth and competitive ability (Cai *et al.* 2008). Most liana species can start their life as a seedling in the understorey, and wait for a long time until they find support and get access to the canopy. Liana abundance in old-growth forest is therefore not so much determined by light availability, but more by the availability of trellis trees (Table 2.3, cf. Carter & Teramura 1988). Most lianas in this study have been classified as light-demanders, because they need bright light in the adult stage (Figure 2.4c). Eighteen per cent of the liana species were classified as being (partially) shade tolerant. These species have the ability to remain self-supporting for a longer time, and they can grow several meters tall before they have to rely on trees for support. If they do not find support, they can flower and reproduce as a self-supporting plant in the shaded understorey, such as for instance the case for *Millettia psilopetala*, *Strychnos camptoneura*, *S. icaja*, *Trichoscypha reygaertii* and *Dichapetalum* spp.

About half of the species featured conspicuous flowers, while the other half featured inconspicuous flowers (Figure 2.4d). Species with conspicuous flowers are likely to be pollinated by birds, while species with inconspicuous flowers are likely to be pollinated by small insects such as bees and flies. The prevalence of zoochory and animal-mediated pollination confirms the faunal dependence of the majority of liana species, as is the case for most other rain-forest plants (Bawa 1980, Bullock 1995). This is important for conservation: lianas rely on animals for their seed dispersal and pollination, whilst animals rely on them for food and habitat (Ødegaard 2000, Schnitzer & Bongers 2002). Gentry (1991a) argued that animal dispersal is a characteristic feature of tropical rain-forest plants, as in such wind-still, closed-canopy forests seed dispersal is most effectively done by animals. In our study site we indeed found zoochory (74% of the species) to be the predominant dispersal mechanism of lianas, in line with other liana studies (Addo-Fordjour *et al.* 2008, Gentry 1991, Senbeta *et al.* 2005). In contrast, in semi-evergreen and dry evergreen forests, wind dispersal can be dominant, dispersal mechanism, and up to 60% of the species may be anemochorous (Cai *et al.* 2009, Muthuramkumar & Parthasarathy 2000, Parthasarathy *et al.* 2004). This can be explained by the fact that in dry forest with a seasonally open canopy, wind can disperse seeds more effectively.

### *Environmental effects on liana species composition*

Our results showed that abundance and distribution of most lianas were influenced by forest structure and micro-environmental variation in the plots (Figure 2.5). Openness of the canopy creates higher irradiance at the forest floor which is favourable for liana proliferation (Schnitzer & Carson 2001, Schnitzer *et al.* 2004). Lianas occurred in all quadrats, but their abundance was related to canopy openness, habitat moisture and elevation. These results are in accordance with Maestre & Cortina (2004), who showed that associations between plants and their habitat can give rise to a complex combination of positive and negative interactions, with a net outcome that depends on the abiotic and community contexts. The species richness and abundance of lianas was positively correlated with that of trees in the same quadrats (Table 2.3), which suggests that both trees and liana diversity and abundance are driven by the same local environmental conditions. Most liana species were found in open terra firme habitats (Figure 2.5). This small-scale pattern parallels observations done at larger spatial scales; that lianas tend to be most abundant in drier forests with a seasonally open canopy (DeWalt *et al.* 2010, Gentry 1991a, Schnitzer 2005).

In conclusion, this study shows that, in terms of structure and family composition, the liana community in IFDP is typical for a Guineo-Congolian old-growth forest, with prominent liana taxa being Dichapetalaceae, Connaraceae, Fabaceae, Apocynaceae and Loganiaceae. However, the Ituri Forest also differs from other Guineo-Congolian forests because it has a high liana abundance, basal area, and species richness, in the small size classes. In addition, the extreme dominance of one single liana species (*Manniophyton fulvum*) renders it unique compared to other forests worldwide.

APPENDIX 2.1: Liana species (dbh ≥2 cm) recorded in the 20 ha plots in Ituri mixed forest, their species and family names, abundance; percentage of abundance, frequency and importance value index (IVI). Identified taxon name followed with Indet. or spp, and unknown are morphogroups.

| Species | Family | # Stem | % Abundance | % Frequency | IVI (%) |
|---|---|---|---|---|---|
| *Acacia pentagona* | Fabaceae | 6 | 0.04 | 0.06 | 0.06 |
| *Adenia cynanchifolia* | Passifloraceae | 17 | 0.11 | 0.13 | 0.16 |
| *Adenia lobata* | Passifloraceae | 2 | 0.01 | 0.03 | 0.02 |
| *Adenia* spp | Passifloraceae | 7 | 0.05 | 0.11 | 0.07 |
| *Agelaea paradoxa* | Connaraceae | 636 | 4.24 | 4.56 | 3.69 |
| *Agelaea pentagyna* | Connaraceae | 767 | 5.11 | 4.94 | 5.31 |
| *Agelaea rubiginosa* | Connaraceae | 454 | 3.02 | 3.17 | 3.65 |
| *Agelaea* spp | Connaraceae | 260 | 1.73 | 2.27 | 2.05 |
| *Alafia erythrophthalma* | Apocynaceae | 1 | 0.01 | 0.02 | 0.01 |
| *Alafia lucida* | Apocynaceae | 10 | 0.07 | 0.13 | 0.1 |
| *Alchornea cordifolia* | Euphorbiaceae | 84 | 0.56 | 0.23 | 0.58 |
| *Ancistrocarpus bequaertii* | Malvaceae | 134 | 0.89 | 0.99 | 1.06 |
| *Ancylobotrys amoena* | Apocynaceae | 1 | 0.01 | 0.02 | 0.01 |
| *Ancylobotrys scandens* | Apocynaceae | 26 | 0.17 | 0.30 | 0.22 |
| Annonaceae Indet. | Annonaceae | 71 | 0.47 | 0.89 | 0.55 |
| Apocynaceae Indet. | Apocynaceae | 7 | 0.05 | 0.11 | 0.08 |
| *Artabotrys congolensis* | Annonaceae | 6 | 0.04 | 0.10 | 0.06 |
| *Artabotrys insignis* | Annonaceae | 2 | 0.01 | 0.02 | 0.02 |
| *Artabotrys* spp | Annonaceae | 4 | 0.03 | 0.06 | 0.04 |
| *Artabotrys staudtii* | Annonaceae | 1 | 0.01 | 0.02 | 0.01 |
| *Artabotrys thomsonii* | Annonaceae | 1 | 0.01 | 0.02 | 0.01 |
| *Baissea axillaris* | Apocynaceae | 1 | 0.01 | 0.02 | 0.01 |
| *Baissea gracillima* | Apocynaceae | 5 | 0.03 | 0.08 | 0.05 |
| *Baissea leonensis* | Apocynaceae | 1 | 0.01 | 0.02 | 0.01 |
| *Baissea* sp1 | Apocynaceae | 1 | 0.01 | 0.02 | 0.01 |
| *Baissea* spp | Apocynaceae | 6 | 0.04 | 0.10 | 0.05 |
| *Baissea subrufa* | Apocynaceae | 2 | 0.01 | 0.03 | 0.02 |

| | | | | | |
|---|---|---|---|---|---|
| *Baphia spathacea* | Fabaceae | 43 | 0.29 | 0.36 | 0.33 |
| *Bequaertia mucronata* | Celastraceae | 28 | 0.19 | 0.31 | 0.27 |
| *Campylostemon angolense* | Celastraceae | 9 | 0.06 | 0.13 | 0.08 |
| *Campylostemon bequaertii* | Celastraceae | 18 | 0.12 | 0.28 | 0.17 |
| *Campylostemon* spp | Celastraceae | 3 | 0.02 | 0.03 | 0.02 |
| Celastraceae Indet. | Celastraceae | 412 | 2.74 | 3.09 | 3.09 |
| *Chrysophyllum welwitschii* | Sapotaceae | 2 | 0.01 | 0.03 | 0.02 |
| *Cissus aralioides* | Vitaceae | 1 | 0.01 | 0.02 | 0.01 |
| *Cissus barbeyana* | Vitaceae | 1 | 0.01 | 0.02 | 0.01 |
| *Cissus dinklagei* | Vitaceae | 44 | 0.29 | 0.48 | 0.40 |
| *Cissus louisii* | Vitaceae | 6 | 0.04 | 0.08 | 0.06 |
| *Cissus producta* | Vitaceae | 73 | 0.49 | 0.46 | 0.46 |
| *Cissus* spp | Vitaceae | 60 | 0.40 | 0.59 | 0.53 |
| *Clerodendron formicarum* | Lamiaceae | 2 | 0.01 | 0.02 | 0.02 |
| *Clerodendron melanocrater* | Lamiaceae | 1 | 0.01 | 0.02 | 0.01 |
| *Clerodendron rotundifolia* | Lamiaceae | 1 | 0.01 | 0.02 | 0.01 |
| *Clerodendron silvianum* | Lamiaceae | 1 | 0.01 | 0.02 | 0.01 |
| *Clerodendron sinuatum* | Lamiaceae | 1 | 0.01 | 0.02 | 0.01 |
| *Clerodendron* spp | Lamiaceae | 7 | 0.05 | 0.11 | 0.06 |
| *Clitandra cymulosa* | Apocynaceae | 78 | 0.52 | 1.09 | 0.54 |
| *Cnestis ferruginea* | Connaraceae | 3 | 0.02 | 0.05 | 0.03 |
| *Cnestis* spp | Connaraceae | 2 | 0.01 | 0.02 | 0.01 |
| *Cnestis urens* | Connaraceae | 207 | 1.38 | 1.91 | 1.58 |
| *Combretum cuspidatum* | Combretaceae | 46 | 0.31 | 0.44 | 0.42 |
| *Combretum fuscum* | Combretaceae | 8 | 0.05 | 0.10 | 0.08 |
| *Combretum marginatum* | Combretaceae | 421 | 2.80 | 3.14 | 3.31 |
| *Combretum mortehanii* | Combretaceae | 18 | 0.12 | 0.21 | 0.16 |
| *Combretum mucronatum* | Combretaceae | 273 | 1.82 | 2.06 | 1.82 |
| *Combretum parviflora* | Combretaceae | 6 | 0.04 | 0.02 | 0.06 |
| *Combretum racemosa* | Combretaceae | 685 | 4.56 | 2.14 | 3.98 |

| | | | | | |
|---|---|---|---|---|---|
| *Combretum* spp | Combretaceae | 49 | 0.33 | 0.49 | 0.42 |
| Connaraceae Indet. | Connaraceae | 126 | 0.84 | 1.28 | 0.98 |
| *Connarus griffonianus* | Connaraceae | 16 | 0.11 | 0.25 | 0.16 |
| *Craterosyphon louisii* | Thymelaeaceae | 4 | 0.03 | 0.06 | 0.04 |
| *Cremaspora triflora* | Rubiaceae | 4 | 0.03 | 0.06 | 0.04 |
| *Cuervea mannii* | Celastraceae | 2 | 0.01 | 0.02 | 0.02 |
| *Cyclocotyla congolensis* | Apocynaceae | 3 | 0.02 | 0.05 | 0.03 |
| *Dalbergia afzeliana* | Fabaceae | 3 | 0.02 | 0.05 | 0.03 |
| *Dalbergia bakerii* | Fabaceae | 2 | 0.01 | 0.03 | 0.02 |
| *Dalbergia ealaensis* | Fabaceae | 3 | 0.02 | 0.05 | 0.03 |
| *Dalbergia florifera* | Fabaceae | 4 | 0.03 | 0.05 | 0.04 |
| *Dalbergia holstii* | Fabaceae | 2 | 0.01 | 0.03 | 0.02 |
| *Dalbergia saxatilis* | Fabaceae | 4 | 0.03 | 0.06 | 0.04 |
| *Dalbergia* spp | Fabaceae | 6 | 0.04 | 0.06 | 0.05 |
| Dichapetalaceae Indet. | Dichapetalaceae | 75 | 0.50 | 0.72 | 0.57 |
| *Dichapetalum affine* | Dichapetalaceae | 39 | 0.26 | 0.46 | 0.31 |
| *Dichapetalum fructuosum* | Dichapetalaceae | 85 | 0.57 | 0.64 | 0.64 |
| *Dichapetalum heudelotii* | Dichapetalaceae | 638 | 4.25 | 3.47 | 3.98 |
| *Dichapetalum librevillense* | Dichapetalaceae | 102 | 0.68 | 1.13 | 0.74 |
| *Dichapetalum mombuttense* | Dichapetalaceae | 27 | 0.18 | 0.23 | 0.22 |
| *Dichapetalum staudtii* | Dichapetalaceae | 854 | 5.69 | 4.90 | 5.45 |
| *Dichapetalum zenkeri* | Dichapetalaceae | 1 | 0.01 | 0.02 | 0.01 |
| *Dictyophleba lucida* | Apocynaceae | 1 | 0.01 | 0.02 | 0.01 |
| *Dictyophleba ochracea* | Apocynaceae | 1 | 0.01 | 0.02 | 0.01 |
| *Dovyalis macrocalyx* | Salicaceae | 1 | 0.01 | 0.02 | 0.01 |
| *Efulensia clematoides* | Passifloraceae | 4 | 0.03 | 0.05 | 0.04 |
| *Entada gigas* | Fabaceae | 10 | 0.07 | 0.11 | 0.09 |
| *Entada pursaetha* | Fabaceae | 4 | 0.03 | 0.06 | 0.04 |
| Fabaceae Indet. | Fabaceae | 53 | 0.35 | 0.62 | 0.54 |
| *Friesodielsia enghiana* | Annonaceae | 12 | 0.08 | 0.18 | 0.13 |

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|---|---|---|---|---|---|
| *Grewia malacocarpoides* | Malvaceae | 9 | 0.06 | 0.13 | 0.08 |
| *Grewia seretii* | Malvaceae | 59 | 0.39 | 0.51 | 0.45 |
| *Grewia* spp | Malvaceae | 32 | 0.21 | 0.21 | 0.21 |
| *Grewia ugandensis* | Malvaceae | 2 | 0.01 | 0.03 | 0.02 |
| *Helictonema velutina* | Celastraceae | 3 | 0.02 | 0.03 | 0.03 |
| *Hippocratea myriantha* | Celastraceae | 7 | 0.05 | 0.08 | 0.07 |
| *Hugonia platysepala* | Linaceae | 44 | 0.29 | 0.62 | 0.38 |
| *Illigera pentaphylla* | Hernandiaceae | 20 | 0.13 | 0.26 | 0.18 |
| *Iodes africana* | Icacinaceae | 1 | 0.01 | 0.02 | 0.01 |
| *Jasminum bakeri* | Oleaceae | 5 | 0.03 | 0.08 | 0.05 |
| *Keetia gueinzii* | Rubiaceae | 3 | 0.02 | 0.05 | 0.03 |
| *Keetia mannii* | Rubiaceae | 5 | 0.03 | 0.08 | 0.05 |
| *Keetia molundensis* | Rubiaceae | 15 | 0.10 | 0.11 | 0.15 |
| *Keetia multiflora* | Rubiaceae | 2 | 0.01 | 0.03 | 0.02 |
| *Keetia ornata* | Rubiaceae | 1 | 0.01 | 0.02 | 0.01 |
| *Keetia* spp | Rubiaceae | 3 | 0.02 | 0.05 | 0.03 |
| *Keetia venosa* | Rubiaceae | 7 | 0.05 | 0.11 | 0.07 |
| *Laccosperma secundiflorum* | Arecaceae | 117 | 0.78 | 0.31 | 0.78 |
| *Landolphia angustisepala* | Apocynaceae | 1 | 0.01 | 0.02 | 0.01 |
| *Landolphia eminiana* | Apocynaceae | 3 | 0.02 | 0.05 | 0.03 |
| *Landolphia forestiana* | Apocynaceae | 16 | 0.11 | 0.18 | 0.16 |
| *Landolphia glabra* | Apocynaceae | 7 | 0.05 | 0.10 | 0.07 |
| *Landolphia incerta* | Apocynaceae | 82 | 0.55 | 1.05 | 0.58 |
| *Landolphia landolphioides* | Apocynaceae | 6 | 0.04 | 0.05 | 0.06 |
| *Landolphia ligustrifolia* | Apocynaceae | 10 | 0.07 | 0.11 | 0.09 |
| *Landolphia mannii* | Apocynaceae | 12 | 0.08 | 0.13 | 0.13 |
| *Landolphia owariensis* | Apocynaceae | 121 | 0.81 | 1.64 | 0.87 |
| *Landolphia* sp1 | Apocynaceae | 25 | 0.17 | 0.33 | 0.21 |
| *Landolphia* sp2 | Apocynaceae | 14 | 0.10 | 0.20 | 0.14 |
| *Landolphia* sp3 | Apocynaceae | 1 | 0.01 | 0.02 | 0.01 |
| *Landolphia villosa* | Apocynaceae | 5 | 0.03 | 0.08 | 0.05 |

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|---|---|---|---|---|---|
| *Leptoderris congolensis* | Fabaceae | 36 | 0.24 | 0.38 | 0.30 |
| *Leptoderris ferruginea* | Fabaceae | 54 | 0.36 | 0.33 | 0.43 |
| *Leptoderris glabrata* | Fabaceae | 4 | 0.03 | 0.03 | 0.04 |
| *Leptoderris* spp | Fabaceae | 3 | 0.02 | 0.05 | 0.03 |
| *Loeseneriella africana* | Celastraceae | 4 | 0.03 | 0.06 | 0.04 |
| *Loeseneriella apiculata* | Celastraceae | 11 | 0.07 | 0.15 | 0.11 |
| *Loeseneriella clematoides* | Celastraceae | 1 | 0.01 | 0.02 | 0.01 |
| *Macaranga angolensis* | Euphorbiaceae | 26 | 0.17 | 0.13 | 0.21 |
| Malvaceae Indet. | Malvaceae | 6 | 0.04 | 0.08 | 0.05 |
| *Manniophytum fulvum* | Euphorbiaceae | 3299 | 21.91 | 7.22 | 14.21 |
| *Manotes expensa* | Connaraceae | 40 | 0.27 | 0.51 | 0.32 |
| *Millettia barteri* | Fabaceae | 187 | 1.25 | 0.62 | 1.44 |
| *Millettia psilopetala* | Fabaceae | 390 | 2.60 | 2.88 | 3.31 |
| *Millettia* spp | Fabaceae | 6 | 0.04 | 0.08 | 0.05 |
| *Monanthotaxis barteri* | Annonaceae | 1 | 0.01 | 0.02 | 0.01 |
| *Monanthotaxis cauliflora* | Annonaceae | 27 | 0.18 | 0.26 | 0.22 |
| *Monanthotaxis diclina* | Annonaceae | 4 | 0.03 | 0.05 | 0.04 |
| *Monanthotaxis elegans* | Annonaceae | 7 | 0.05 | 0.10 | 0.07 |
| *Monanthotaxis ferruginea* | Annonaceae | 28 | 0.19 | 0.31 | 0.24 |
| *Monanthotaxis foliosa* | Annonaceae | 40 | 0.27 | 0.49 | 0.32 |
| *Monanthotaxis lucidula* | Annonaceae | 23 | 0.15 | 0.31 | 0.18 |
| *Monanthotaxis schweinfurthii* | Annonaceae | 12 | 0.08 | 0.10 | 0.13 |
| *Monanthotaxis seretii* | Annonaceae | 1 | 0.01 | 0.02 | 0.01 |
| *Monanthotaxis* spp | Annonaceae | 65 | 0.43 | 0.91 | 0.55 |
| *Monanthotaxis vogelii* | Annonaceae | 1 | 0.01 | 0.02 | 0.01 |
| *Mormodica jeffreyana* | Cucurbitaceae | 1 | 0.01 | 0.02 | 0.01 |
| *Mussaenda arcuata* | Rubiaceae | 1 | 0.01 | 0.02 | 0.01 |
| *Mussaenda elegans* | Rubiaceae | 4 | 0.03 | 0.06 | 0.04 |

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|---|---|---|---|---|---|
| *Neostenanthera myristicifolia* | Annonaceae | 2 | 0.01 | 0.02 | 0.02 |
| *Neuropeltis acuminata* | Convolvulaceae | 6 | 0.04 | 0.08 | 0.05 |
| *Neuropeltis alnifolia* | Convolvulaceae | 2 | 0.01 | 0.03 | 0.02 |
| *Neuropeltis* spp | Convolvulaceae | 10 | 0.07 | 0.15 | 0.11 |
| *Orthopichonia seretii* | Apocynaceae | 44 | 0.29 | 0.61 | 0.38 |
| *Pararistolochia triactina* | Aristolochiaceae | 7 | 0.05 | 0.10 | 0.07 |
| Passifloraceae Indet. | Passifloraceae | 8 | 0.05 | 0.11 | 0.07 |
| *Phyllanthus muellerianus* | Phyllanthaceae | 7 | 0.05 | 0.06 | 0.06 |
| *Piper guineensis* | Piperaceae | 44 | 0.29 | 0.38 | 0.33 |
| *Plukenettia conophora* | Euphorbiaceae | 11 | 0.07 | 0.16 | 0.10 |
| *Pristimera andongensis* | Celastraceae | 4 | 0.03 | 0.06 | 0.04 |
| *Pristimera plumbea* | Celastraceae | 1 | 0.01 | 0.02 | 0.01 |
| *Pyrenacantha klaineana* | Icacinaceae | 38 | 0.25 | 0.56 | 0.30 |
| *Reissantia indica* | Celastraceae | 7 | 0.05 | 0.11 | 0.06 |
| *Rhaphiostylis beninensis* | Icacinaceae | 3 | 0.02 | 0.05 | 0.03 |
| *Rhaphiostylis ferruginea* | Celastraceae | 4 | 0.03 | 0.05 | 0.04 |
| *Ritchiea capparoides* | Capparaceae | 9 | 0.06 | 0.15 | 0.08 |
| *Rourea coccinea* | Connaraceae | 8 | 0.05 | 0.11 | 0.08 |
| *Rourea erythrocalyx* | Connaraceae | 5 | 0.03 | 0.06 | 0.04 |
| *Rourea minor* | Connaraceae | 4 | 0.03 | 0.06 | 0.03 |
| *Rourea obliquifoliolata* | Connaraceae | 8 | 0.05 | 0.13 | 0.07 |
| *Rourea parviflora* | Connaraceae | 21 | 0.14 | 0.33 | 0.18 |
| *Rourea* spp | Connaraceae | 3 | 0.02 | 0.05 | 0.03 |
| *Rourea thomsonii* | Connaraceae | 922 | 6.13 | 5. 41 | 5.72 |
| Rubiaceae Indet. | Rubiaceae | 72 | 0.48 | 0.89 | 0.59 |
| *Rutidea dupuisii* | Rubiaceae | 1 | 0.01 | 0.02 | 0.01 |
| *Rutidea smithii* | Rubiaceae | 1 | 0.01 | 0.02 | 0.01 |
| *Rytigynia nigerica* | Rubiaceae | 3 | 0.02 | 0.05 | 0.03 |
| *Saba comorensis* | Apocynaceae | 3 | 0.02 | 0.05 | 0.03 |
| *Sabicea dewevrei* | Rubiaceae | 1 | 0.01 | 0.02 | 0.01 |

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|---|---|---|---|---|---|
| *Salacia alata* | Celastraceae | 1 | 0.01 | 0.02 | 0.01 |
| *Salacia cerasifera* | Celastraceae | 14 | 0.10 | 0.16 | 0.13 |
| *Salacia elegans* | Celastraceae | 34 | 0.23 | 0.49 | 0.28 |
| *Salacia kivuensis* | Celastraceae | 10 | 0.07 | 0.08 | 0.08 |
| *Salacia laurentii* | Celastraceae | 91 | 0.61 | 0.92 | 0.72 |
| *Salacia lebrunii* | Celastraceae | 6 | 0.04 | 0.10 | 0.05 |
| *Salacia pyriformioides* | Celastraceae | 330 | 2.20 | 3.04 | 2.89 |
| *Salacia pyriformis* | Celastraceae | 2 | 0.01 | 0.03 | 0.02 |
| *Salacia staudtiana* | Celastraceae | 2 | 0.01 | 0.02 | 0.01 |
| *Sherbournia ailarama* | Rubiaceae | 1 | 0.01 | 0.02 | 0.01 |
| *Sherbournia batesii* | Rubiaceae | 11 | 0.07 | 0.16 | 0.10 |
| *Sherbournia bignoniiflora* | Rubiaceae | 4 | 0.03 | 0.05 | 0.03 |
| *Sherbournia* spp | Rubiaceae | 11 | 0.07 | 0.16 | 0.09 |
| *Simiretris tisserantii* | Celastraceae | 1 | 0.01 | 0.02 | 0.01 |
| *Strophanthus hispidus* | Apocynaceae | 1 | 0.01 | 0.02 | 0.01 |
| *Strychnos aculeata* | Loganiaceae | 5 | 0.03 | 0.08 | 0.04 |
| *Strychnos angolensis* | Loganiaceae | 79 | 0.53 | 0.61 | 0.57 |
| *Strychnos camptoneura* | Loganiaceae | 4 | 0.03 | 0.06 | 0.03 |
| *Strychnos congolana* | Loganiaceae | 7 | 0.05 | 0.08 | 0.06 |
| *Strychnos dale* | Loganiaceae | 2 | 0.01 | 0.03 | 0.01 |
| *Strychnos densiflora* | Loganiaceae | 1 | 0.01 | 0.02 | 0.01 |
| *Strychnos icaja* | Loganiaceae | 9 | 0.06 | 0.15 | 0.08 |
| *Strychnos longicaudata* | Loganiaceae | 278 | 1.85 | 2.11 | 1.86 |
| *Strychnos malchairii* | Loganiaceae | 3 | 0.02 | 0.05 | 0.03 |
| *Strychnos phaeotricha* | Loganiaceae | 26 | 0.17 | 0.34 | 0.21 |
| *Strychnos scheffleri* | Loganiaceae | 3 | 0.02 | 0.05 | 0.03 |
| *Strychnos spinosa* | Loganiaceae | 1 | 0.01 | 0.02 | 0.01 |
| *Strychnos* spp | Loganiaceae | 28 | 0.19 | 0.26 | 0.20 |
| *Strychnos urceolata* | Loganiaceae | 32 | 0.21 | 0.44 | 0.28 |
| *Stychnos nigritana* | Loganiaceae | 2 | 0.01 | 0.03 | 0.01 |

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|---|---|---|---|---|---|
| *Syrrheonema fasciculata* | Menispermaceae | 1 | 0.01 | 0.02 | 0.01 |
| *Tabernaemontana eglandulosa* | Apocynaceae | 159 | 1.06 | 1.64 | 1.25 |
| *Tetracera alnifolia* | Dilleniaceae | 24 | 0.16 | 0.38 | 0.20 |
| *Tetracera poggei* | Dilleniaceae | 1 | 0.01 | 0.02 | 0.01 |
| *Tetracera potatoria* | Dilleniaceae | 9 | 0.06 | 0.15 | 0.08 |
| *Tetracera* spp | Dilleniaceae | 8 | 0.05 | 0.11 | 0.07 |
| *Tiliacora mayumbensis* | Menispermaceae | 1 | 0.01 | 0.02 | 0.01 |
| *Trichoscypha reygaertii* | Anacardiaceae | 71 | 0.47 | 0.54 | 0.46 |
| *Triclisia dictyophylla* | Menispermaceae | 4 | 0.03 | 0.05 | 0.03 |
| *Triumphetta cordifolia* | Malvaceae | 3 | 0.02 | 0.03 | 0.02 |
| *Uncaria africana* | Rubiaceae | 60 | 0.40 | 0.46 | 0.45 |
| Unknown (spp) | xxx | 42 | 0.28 | 0.48 | 0.37 |
| *Urera camerooniana* | Urticaceae | 174 | 1.16 | 1.51 | 1.41 |
| *Urera trinervis* | Urticaceae | 12 | 0.08 | 0.11 | 0.12 |
| *Uvaria platyphylla* | Annonaceae | 1 | 0.01 | 0.02 | 0.01 |
| *Uvaria pulchra* | Annonaceae | 86 | 0.57 | 1.12 | 0.68 |
| *Uvaria* spp | Annonaceae | 29 | 0.19 | 0.38 | 0.23 |
| *Ventilago diffusa* | Rhamnaceae | 20 | 0.13 | 0.30 | 0.18 |
| *Vernonia andohii* | Asteraceae | 5 | 0.03 | 0.05 | 0.04 |
| *Vitex thyrsiflora* | Lamiaceae | 12 | 0.08 | 0.10 | 0.11 |

# Chapter 3

## Thirteen years of dynamics of the liana assemblage in a Congo Basin rain forest

*Corneille E.N. Ewango, Lourens Poorter, Marc S.M. Sosef, Jean-Remy Makana & Frans Bongers*

(Submitted to Biotropica)

## ABSTRACT

Lianas are important components of tropical rain forests having a large impact on forest functioning, and their importance may even increase with global climate change. We evaluated changes in structural characteristics, diversity, recruitment, mortality and growth of the liana community over thirteen years period in the Ituri rain forest, Democratic Republic of Congo. We used data from three censuses conducted in two 10-ha plots, comprising 17,653 liana stems. Liana density decreased from 750 (1994) through 547 (2001) to 499 (2007) stems ha$^{-1}$, with concomitant declines in basal area and above-ground biomass. Despite lower stem densities the species richness remained constant over time. Total community recruitment rates decreased slightly from 8.6% per year in the first period to 6.6% in the second, but this decrease was not significant. Liana community mortality rates decreased significantly from 7.2% to 4.4% per year over the two census intervals. Diameter growth rates and survival increased with liana stem diameter. Changes in liana community structure and composition were driven by one species only, the dramatic collapse of superabundant *Manniophyton fulvum* between first and second period of censuses. In contrast to what has been reported for tropical forests elsewhere, liana abundance in Ituri showed recent declines, rather than the increases reported earlier. This questions the generality of liana responses to global climate change. In conclusion, lianas are extremely dynamic in this forest, but this community level dynamism is fully driven by one strongly dominant species. This is, as far as we know, the first documented liana collapse.

**Key words:** Iutri rain forest, liana, species populations, community-wide dynamics, *Manniophyton fulvum*, Congo basin**.**

## INTRODUCTION

Old-growth tropical forests have long been considered as steady-state communities that have passed all successional phases and are now stable in their community and population characteristics (Richards, 1952; Whitmore, 1984). This view however, has been challenged (Connell, 1978; Sheil, 2001) and the forest community may be seen as the result of continuously changing species populations (Connell and Slatyer, 1997). Lianas are characteristic components of tropical forests comprising up to 25% of woody plant stems and species (Gentry, 1991; Schnitzer & Bongers, 2002) and contributing up to 40% of forest leaf biomass (Wright et al., 2004). Lianas are considered as drivers (Putz, 2001; Parren and Bongers, 2001) or inhibitors (Schnitzer et al., 2000; Schnitzer and Carson, 2010) of forest dynamics, and their importance may even be increasing under global climate change scenarios (Phillips et al., 2002).

Recent studies have shown that in the Americas lianas are in general increasing in abundance and productivity (Phillips et al., 2002; Wright, 2004; Allen et al., 2007, but see Londré and Schnitzer, 2006), but evidence for similar patterns in African forests is scarce (Caballé and Martin, 2001). If lianas are increasing in abundance and basal area, then they are likely to influence tree species composition, growth, and mortality. Long-term and persistent increase in the density and distribution of lianas may also imply shifts in the composition of plant functional traits (Allen et al., 2005). Consequently, we argue that the structure, dynamics and functioning of lianas in forest stand development should be explored and incorporated into stand dynamics models of tropical forests.

Increases in liana abundance have been associated with increased small-scale disturbance (Laurance et al., 2001; Zagt et al., 2003; Bongers et al., 2005) with succession after shifting cultivation (DeWalt et al., 2000, Guariguata and Ostertag, 2001) and with large-scale disturbances such as hurricanes (Vandermeer et al., 2000; Allen et al., 2005). The changes in the liana communities have been related to changes in environmental conditions, notably increasing light availability (Avalos and Mulkey, 1999; Guariguata and Ostertag, 2001) but changes in response to increasing drought have been suggested as well (Schnitzer, 2005; Dewalt et al., 2010). Nonetheless, successional patterns of lianas in undisturbed old-growth forest have hardly been studied (Phillips et al., 2005). Long-term dynamics in natural old-growth forests may be driven by small-scale tree death, resulting in individual-tree replacement patterns through natural-gap dynamics. Small-scale species loss and gain due to mortality and recruitment of individual trees can serve as an inherent factor that drives successional change within old-growth forests: community change being then the result of individual species population dynamics (Harper, 1977). Although lianas are said to be extremely dynamic, only few quantitative data are available to evaluate these claims and growth and turnover rates are rarely reported (Phillips et al., 2005; Nabe-Nielsen, 2002), let alone size-dependent patterns therein. For tree community and tree populations many studies are available (e.g., Dallmeier and Comiskey, 1998; Losos and Leigh, 2004 for more details) but for lianas such information is scarce (Phillips et al., 2002, 2005; Wright et al., 2004). Additionally, as liana populations strongly interact with trees (Van der Heijden and Phillips, 2009; Peña-Claros et al., 2008; Ingwell et al., 2010, Schnitzer & Carson, in press) and crucially depend on forest structure (Toledo, 2010); the magnitude and impact of liana long-term changes need examination.

Although lianas have been the focus of a growing number of studies in tropical forests in the last two decades, questions on their constituent floristic, structural and dynamics patterns at a detailed level have hardly been explicitly addressed (but see Caballé and Martin, 2001; Mascaro et al., 2004; Nabe-Nielsen, 2002, 2004). Their richness and abundance differ greatly from one forest to another and between forest locations, climate seasonality being one of the major driving factors at least for abundance (Swaine and Grace, 2007; DeWalt et al., 2010). These differences have been demonstrated at a continental scale (Rollet, 1974; Gentry, 1993) and at a regional scale (Van der Heijden et al., 2008, 2009), but less so at smaller, more local scales (but see Burnham, 2002, 2004; Mascaro et al., 2004).

In African forests, most studies have concentrated in the western Upper and Lower Guinea phytochoria (White, 1979, reviewed in Bongers et al., 2005) reflecting typologies and dynamics of these forests. In contrast, few long-term studies have been conducted on liana diversity and corresponding population dynamics elsewhere in Africa (but see Caballé and Martin, 2001; Parren, 2003) despite their undisputed importance in the forest. In this paper we analyze community-wide dynamics of lianas in tropical old-growth forest in the Congo Basin. We use long-term data from three censuses (1994, 2001 and 2007) conducted in the Ituri Forest Dynamics plots, Democratic Republic of Congo for two 10-ha plots, in which we monitor 17,653 liana stems. We evaluate the structural characteristics, and recruitment, mortality and growth of the liana community over time. We specifically address the following questions: (1) How does the liana community change over time in abundance, basal area, stem size, aboveground biomass, recruitment and mortality? (2) Are the patterns in vital rates (mortality and growth) size-dependent? and (3) How does the species composition of the liana assemblage change over time? We have the following corresponding predictions: ($H_1$) Given the recently reported increase in liana abundance in the Neotropical forests (Phillips et al., 2002), we expect that lianas also become more dominant in this old-growth African forest and population changes to be mainly driven by increased recruitment rates and stem densities; ($H_2$) Considering small-size stems as fragile individuals, we expect vital and dynamic rates (growth and survival) to be size dependent, and small-size stems to have faster growth and higher mortality compared to large-size stems that would have lower growth and higher survival rates in the old-growth forest liana community; and ($H_3$) Assuming that lianas are highly dynamic, and that they have recently increased in abundance (Phillips et al., 2002, 2005), we expect large directional changes in liana species community composition.

## MATERIAL AND METHODS

### *Study sites*

The long-term plot is located in the Réserve de Faune à Okapi (RFO) in the Ituri Forest, Democratic Republic of the Congo, at the northeastern edge of the Congo Basin forest. Two 10-ha plot are studied, Edoro 1 (NE corner: 01°33’44”N 028°31’02”E; SW corner: 01°33’37”N 028°30’45”) and Edoro 2 (NE corner: 01°33’46”N 028°31’34”E; SW corner: 01°33’38”N 028°31’18”), both 500 x 200 m, with a comparatively flat topography and a natural mixed old-growth forest between the Edoro and Afarama rivers. The climate is seasonal, with a 4 to 5 months dry season (with rainfall <50 mm/month in the two driest months, January and February) from December through March/April. Mean annual rainfall is 1785 mm. Detailed descriptions of the climate, vegetation, and fauna of the Edoro Field Research can be found elsewhere (Hart, 1985, 1986; Makana et al., 1998). The plots contain some swampy areas but the large majority is dry-land forest. Mean altitude is 750 m. Upon establishment of the plots there were no large gaps. The floristic composition of the mixed forest in both plots is similar; the canopies are characterized by *Cynometra alexandri*, *Julbernardia seretii*, and *Cleistanthus michelsonii*. The 10 most abundant liana families in this forest (Connaraceae, Euphorbiaceae, Dichapetalaceae, Combretaceae, Celastraceae, Fabaceae, Apocynaceae, Loganiaceae, Annonaceae and Malvaceae) account for 69% of the liana species and 92% of the basal area (Ewango et al., submitted). *Manniophyton fulvum* is by far the most abundant liana species in the mixed forest comprising 24% of the stems.

### *Field sampling*

The two plots were established in 1994-1996, and were re-censused during 2000/2001 and again in 2007, thus providing three censuses over a 13-year period. In each plot, all liana stems ≥ 2 cm dbh (diameter at breast height) were identified, labelled and mapped, and their dbh was measured. All stems were marked with paint at 1.3 m height. During re-censuses all stems were checked, re-measured and re-painted. New recruits reaching 2 cm dbh were added in the same way (see Makana et al., 1998 for details of the measuring protocol). Throughout re-censuses, individuals were classified as being alive, recruit or dead if a tag was found or if no vital sign (e.g. resprouting, survival basal part of a damaged stem) could be established. We differentiated and individually marked resprouts; if the main stem died or was broken below the point of measurement and a new stem was emerging, this stem was marked as a new individual in the subsequent censuses.

### *Forest dynamic analysis*

Liana community dynamics was calculated from a total of 17,653 stems over the 13-years period, recorded in two 10-ha plots. Stem abundance (density), species numbers, mortality, recruitment, and biomass were calculated by summing the total of each species and all individuals recorded in a given census.

We analyzed liana changes in recruitment, mortality and basal area growth for the whole community and for three size classes separately (2-5 cm, > 5-10 cm and > 10 cm dbh), using the derived exponential model (the natural logarithm equations of dynamics) of population changes over time.

Annual liana recruitment (R) and mortality (M) rates (in % year$^{-1}$) are calculated as: $R = [\ln(N_0 - N_m + N_r) - \ln(N_0 - N_m)/t] \times 100$ (Phillips et al., 1994), and $M = [\ln(N_0) - \ln(N_0 - N_m)/t] \times 100$ (Lewis et al., 2004); where $N_0$ is the number of stem at the initial census, $N_m$ and $N_r$ are the individuals that died or were recruited during the time interval of first and second census (t), respectively. Individual liana basal area (BA in $m^2 = \pi(dbh)^2/4*10{,}000$) was calculated for all individuals that survived one or both of the monitoring periods, and was translated into above ground biomass using the standardized liana stem biomass allometric equation of Schnitzer et al. (2006): $AGB = \exp[-1.484 + 2.657 \ln(D)]$, where D is diameter at breast height in centimeter. Total above ground biomass for all lianas was then calculated for each of the 20 one-ha plots, for each of the census years.

Diameter growth (in mm year$^{-1}$) was calculated as the slope of the linear regression between individual's dbh and the two measurement dates of census intervals 1 (1994-2001) and 2 (2001-2007). Survivorship of liana individuals across these stem size diameters was calculated as $P(S) = 1 - P(M)$, where $P(M)$ is the probability of mortality in a diameter size class for a given census interval.

We quantified the relative importance of each species (i.e. species rank-abundance) on the basis of the number of individual of a given species to the total number of individuals recorded in the community for each census. To describe the nature of changes of species dominance over time we regressed all relative abundances of the species at the first census against relative abundances at the second census. Based on the abundance in the 1994 census, we classified species as being dominant (total abundance ≥300 individuals), abundant (60-299 individuals), frequent (15-59 individuals), and rare (<15 individuals); and also differentiated doubletons (species exactly known by two records) and singletons (recorded only by a single individual).

A principal component analysis (PCA) was used to analyze community changes in liana composition over time. For every single one-ha plot data on species abundance for each of the three censuses (1994, 2001 and 2007) was used in a composite PCA. Changes in species composition of each one-ha plot over time are reflected in the trajectories of each plot in PCA space (cfr. Austin and Greig-Smith, 1968; Verburg and Van Eijk-Bos, 2003).

### *Statistical analysis*

Temporal changes in numbers of individuals, recruitment, mortality, basal area and biomass per ha (n = 20) and in diameter size classes between 1994 and 2001 and between 2001 and 2007 were tested using a paired *t*-test. To detect how structural characteristics and vital rates vary with census interval and liana size classes we did a repeated-measures ANOVA with censuses year as a within-factor and size class as a between-factor. We used a Sidak *post hoc* test in the ANOVA analyses to evaluate differences between classes (Zar, 1999). In this repeated-measures ANOVA, the Mauchley's W statistic tested for sphericity (i.e. equality of variances of the differences between census years). If sphericity was not met, Greenhouse-Geisser values were considered and where needed data were $\log_{10}$-transformed prior to analysis. All statistical analyses were conducted using SPSS 15 for windows (SPSS Inc., 2006).

In addition, we calculated diversity (Fisher alpha, Shannon-Wiener and Simpson diversity index) per ha (n = 20) for each of the three censuses and evaluated temporal changes using repeated-measures ANOVA.

## RESULTS

### *Dynamics in the liana assemblage: density, biomass, mortality and recruitment*

Mean liana density decreased from 750 (1994) through 547 (2001) to 499 (2007) stems per hectare and similar changes were found in basal area and above-ground biomass (Figure 3.1).

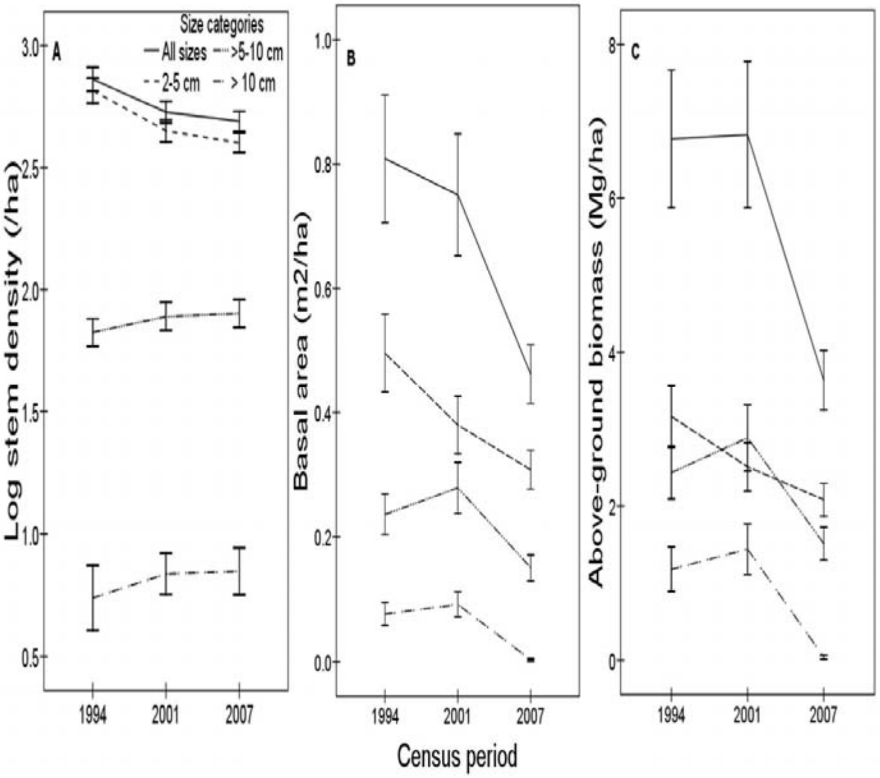

Figure 3.1. Change in stem density (A), basal area (B), and above-ground biomass (C) of liana stems during a 13-year period in the Ituri mixed forest. Dynamics parameters are grouped according to whole community and size class categories. Values correspond to the mean ± 1 SE for 20 one-ha plots.

These changes were not paralleled by changes in total species number (192, 195 and 197 per 20-ha census respectively). The community-wide mean stem density of lianas decreased significantly over both census periods (paired *t*-test; $t_{94\text{-}01} = 16.18$ and $t_{01\text{-}07} = 6.06$, df = 19, $P < 0.001$ in both cases). The census year changes of density violated the assumption of sphericity ($\chi^2_{(2)} = 27.4$, $P < 0.05$), therefore we used the corrected Greenhouse-Geisser estimates for degree of freedom, and found no effect of census year on mean stem density (repeated-measures ANOVA, $F_{1.4,82.2} = 0.197$, $P > 0.05$), but size class ($F_{2,57} = 908.2$, $P < 0.001$) and the interaction census year × size class ($F_{2.9,82.2} = 22.41$, $P < 0.001$) strongly affected density. The Sidak pairwise comparisons showed that all size classes significantly lost stems, where the changes in the small size class (2-5 cm) were larger than that in the medium size class (>5-10 cm) and the largest size (>10 cm) class.

Mean basal area (BA) of the liana assemblage declined significantly over time (paired *t*-test; $t_{94\text{-}01} = 4.9$ for the first interval, $t_{01\text{-}07} = 11.1$ at the second interval; df =19 and $P < 0.001$ in both cases), being 0.81, 0.75 and 0.46 $m^2\ ha^{-1}$ in 1994, 2001 and 2007 respectively. This reduction led to concomitant reductions in overall liana biomass (6.8, 6.8 and 3.6 Mg $ha^{-1}$) in which the biomass in 2007 was nearly half of the biomass in 2001. Surprisingly, biomass did not change significantly in the first interval ($t_{94\text{-}01}$ =-0.5, d f=19, $P > 0.05$) but it decreased sharply during the second interval ($t_{01\text{-}07}$ =11.0; df =19, $P < 0.001$). This difference is caused by the significantly higher relative growth and recruitment rates in the first interval compared to the second interval (Figure 3.2, 3.3). Surprisingly, there was only little change in basal area and biomass during the first census interval while lots of change occurred during the second; this contrasts with the changes in density.

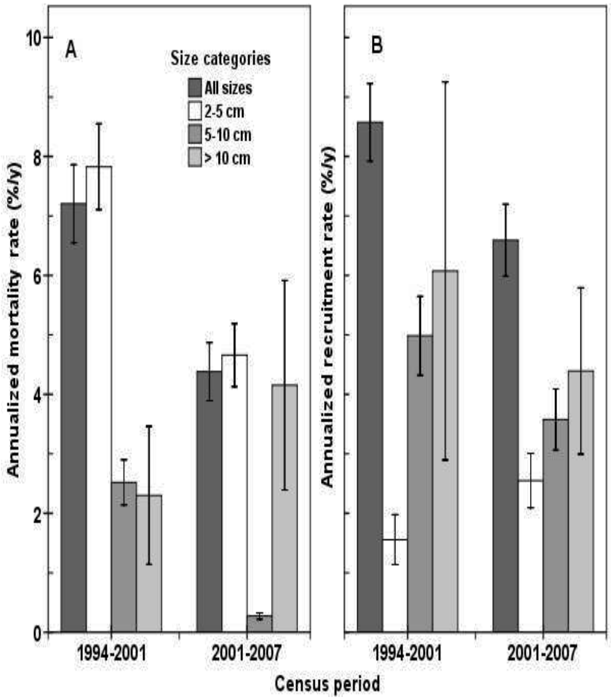

Figure 3.2.
Mean annualized mortality (A) and recruitment (B) rates of lianas community of the Ituri mixed forest plots. Different census periods (1994-2001, 2001-2007), the whole community and separate size class intervals (2-5 cm, 5-10 cm, and > 10 cm dbh) are shown. Each bar represents the mean ± 1 SE for 20 one-ha plots.

Total community recruitment rates decreased slightly from 8.6% per year in the first period to 6.6% in the second, but this decrease was not significant (Figure 3.2b; paired t-test: t = -0.64, df = 19, $P > 0.05$). Recruitment rates in size classes varied significantly over census year (repeated-measures ANOVA, $F_{2,76} = 32.6$, $P < 0.001$) and with size class ($F_{2,38} = 507.1$, $P < 0.001$), but not their interaction ($F_{2,76} = 2.89$, $P > 0.05$). Small sized lianas increased slightly

(1.56 to 2.55%) while medium sized (4.98 to 3.58 %) and large lianas (6.08 to 4.39%) decreased markedly over time.

Total liana mortality rates decreased significantly from 7.2% per year over the first interval to 4.4% over the second (Figure 3.2a; paired t-test: $t = 10.6$, $df = 19$, $P < 0.001$). Annual mortality rates of lianas differed between census intervals ($F_{2,114} = 13.3$, $P < 0.001$), among size classes (repeated-measures ANOVA, $F_{2,57} = 737.5$, $P < 0.001$) and there was also a strong interaction between size class and census interval ($F_{2,114} = 37.9$, $P < 0.001$). The Sidak *post hoc* pairwise comparisons estimated average mortality of 2.3% and 1.0% per year for each interval and there were significant differences between small (2-5 cm; 7.8 to 4.7% of mortality), medium (5-10 cm, 2.5 to 0.3%) and large (>10 cm, 2.3 to 4.1%) lianas stems.

### *Size-dependent growth and survivorship*

Annual size-growth differed significantly among diameter size classes (repeated-measures ANOVA, $F_{1,18.5} = 39.21$, $P < 0.001$), but did not between census intervals (paired t-test, $t = 1.95$, $df=8$, $P > 0.05$). Liana growth was size-dependent and increased from 0.5 mm/y for the smallest size class to 1.50 mm/y for the largest size class (Figure 3a). Growth of lianas in the middle size classes (50-70 mm) was twice as fast in the first census period compared to the second period, although this was not the case for smallest and largest size classes. Survival differed significantly amongst size classes (repeated-measures ANOVA, $F_{1.1,8.5} = 21.04$, $P < 0.001$), but did not differ between the census intervals (paired t-test, $t = -0.94$, $df = 8$, $P > 0.05$). Size-dependent survival differences were large during the first interval, but less so during the second interval. Larger lianas survived better that smaller ones (Figure 3.3b). Liana survival probability over census period ranged from 0.57 to 0.94 over the liana size range, with a continuous increase up to 50 mm, a maximal survivorship probability at 70 mm, and a somewhat declining probability with bigger sizes for the first interval. Survival of lianas in the lower size classes (20-40 mm) was substantially higher in the second period compared to the first period (Figure 3.3b), and fast growth in large-sized stems was, surprisingly, coupled with their decline in survivorship.

### *Community diversity and rank-abundance changes*

During our 13-year study period there were significant temporal changes in Fisher's $\alpha$ (repeated-measures ANOVA, $F_{1.2,23.5} = 78.4$, $P < 0.001$), Shannon-Wiener ($F_{1.3,25.5} = 116.3$, $P < 0.001$), and Simpson ($F_{1.2,22.3} = 45.6$, $P < 0.001$) diversity indices. All three measures increased during the first period (especially Simpson's diversity) after which they remained more or less constant during the second interval (Table 3.1). Simpson's diversity was low (51.6) in the 1994 census when *Manniophyton fulvum* strongly dominated, and was high in 2001 (92) and 2007 (90) after *M. fulvum* collapsed. No significant change was observed between the censuses in 2001 and 2007 as the 10 next-dominant species were fairly stable over time (Figure 4).

Table 3.1. Summary of liana changes in the mixed forest permanent plot at Ituri Forest, Okapi Faunal Reserve, DR Congo, for the period 1994–2007. We used 20 one-ha plots, and all tests are based on annual average or census interval. We used paired t-test to compare how liana parameters vary between census intervals (1994-2001, 2001-2007). To detect how structural characteristics and diversity measures vary with census interval and liana size classes we did a repeated-measures ANOVA with censuses year as a within factor and size class as a between factor.

| | **Year of survey** | | | **Results and significance levels** |
|---|---|---|---|---|
| **Parameter** | **1994** | **2001** | **2007** | |
| Density ($ha^{-1}$) | 750.4 | 547.2 | 499.1 | $t_{94-01}$ = 16.18, $t_{01-07}$ = 6.06, df = 19, P < 0.001 |
| Basal area ($m^2ha^{-1}$) | 0.81 | 0.75 | 0.46 | $t_{94-01}$=4.9, $t_{01-07}$=11.1; df=19, P<0.001 |
| ABG (kg $ha^{-1}$) | 6.8 | 6.8 | 3.6 | $t_{94-01}$ =-0.5,P=0.6 ; $t_{01-07}$ =11.0;df=19, P<0.001 |
| Fisher α | 27.48 | 29.62 | 30.51 | $F_{1.2,23.5}$ = 78.4, P < 0.001 |
| Shannon-Wiener | 4.15 | 4.47 | 4.44 | $F_{1.3,25.5}$ = 116.3, P < 0.001 |
| Simpson | 51.55 | 91.55 | 89.69 | $F_{1.2,22.3}$ = 45.6, P < 0.001 |
| Mortality rates (%/y) | 7.2 | | 4.4 | $t_{1-2}$=10.6; df=19, P<0.001 |
| Recruitment rates (%/y) | | 8.7 | 6.6 | $t_{1-2}$=-0.64; df=19.06, P>0.05 |
| Growth rates (mm/y) | | 0.5 | 1.5 | $F_{.1,18.5}$ = 39.21, P < 0.001 |
| Survivorship | | 0.57 | 0.94 | $F_{1.1,8.5}$ = 21.04, P < 0.001 |

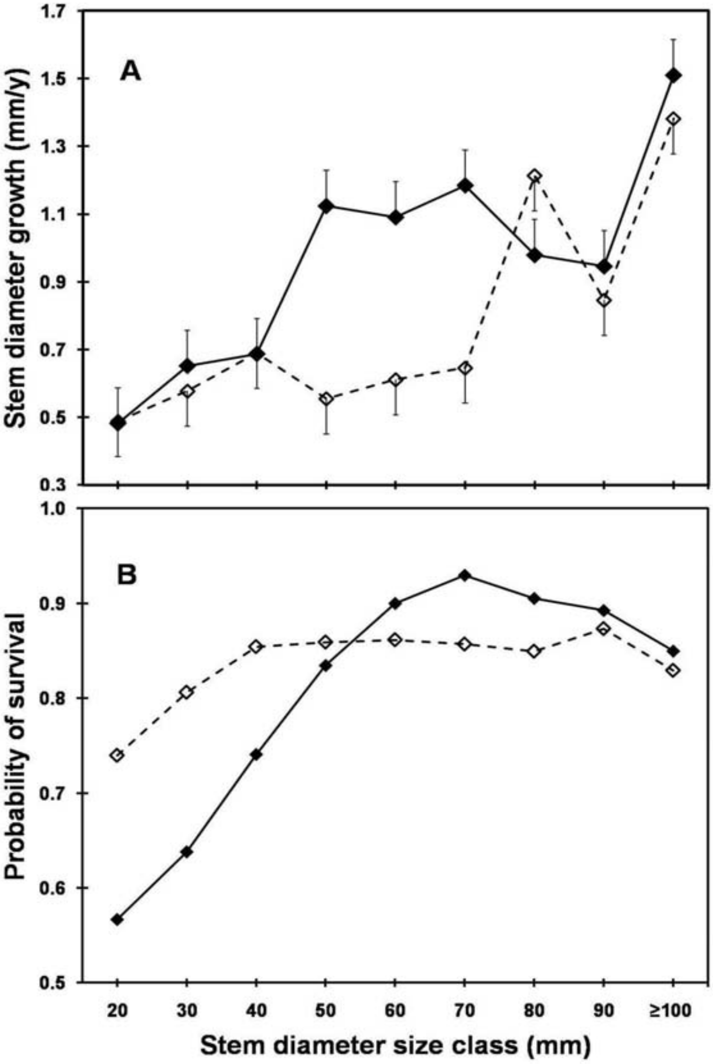

Figure 3.3. Size-dependent diameter growth (A) and survivorship (B) of liana individuals for two census intervals in the lowland Ituri rainforest. Census interval 1:1994-2001 (dark diamond symbols); census interval 2: 2001-2007 (open diamond symbols). Size classes are 10 mm wide (20 means 20 ≤ size < 30mm). Standard errors are shown for diameter growth.

Species rank-abundance patterns differed significantly amongst census years (repeated-measures ANOVA, $F_{1.4,292.7} = 20.18$, $P < 0.001$). This difference is probably driven by *M. fulvum*, which was very dominant in 1994 (24% of all individuals) and collapsed thereafter (comprising 0.6% of all individuals). The relative abundance of species in 2001 is moderately correlated with their relative abundance in 1994 when *M. fulvum* is included (Pearsons r = 0.57), but strongly correlated (Pearsons r = 0.99) when *M. fulvum* is excluded (Figure 3.4a). The relative species abundance in 2007 is, in turn, also highly correlated with the relative abundance in 2001 (Figure 3.4b). Models that exclude the *M. fulvum* collapse describe therefore nicely the relatively constant ranks of the other species over time (Figure 3.4a, b).

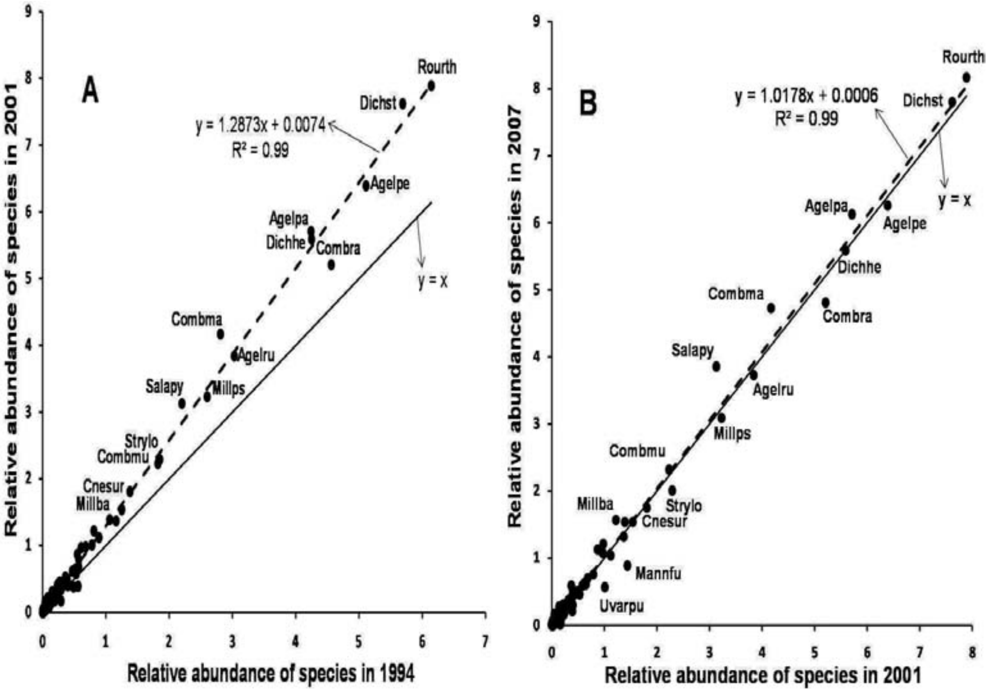

Figure 3.4. Ranking of dominance of liana species between different census periods. (A): Relative abundance of species in 2001 versus 1994 (B): Relative abundance of species in 2007 versus 2001. Regression line (dotted line) and coefficients of determination ($R^2$) are given. The continuous line indicates the relationship where y=x. Only the label for the most common species are shown (Agelpa: *Agelaea paradoxa*, Agelpe: *A. pentagyna*, Agelru: *A. rubiginosa*, Dichhe: *D. heudelotii*, Dichst; *Dichapetalum staudtii*, Cnesur: *Cnestis urens*, Combma: *Combretum* marginatum, Combmu: *C. mucronatum*, Combra: *C. racemosa*, Mannfu: *Manniophyton fulvum*, Millba: *Millettia barteri*, Millps: *M. psilopetala*, Rourth: *Rourea thomsonii*, Salapy: *Salacia pyriformioides*, Strylo: *Strychnos longicaudata*, Uvarpu: *Uvaria pulchra*).

Table 2.2. Liana species richness during three census years (1994, 2001, 2007) in the Ituri Forest Dynamics Plots. Species are grouped according to abundance categories in the 20 ha plot. The minimum and maximum of species relative abundance is given in parentheses.

| | **1994** | **2001** | **2007** |
|---|---|---|---|
| | | **# Spp (% range)** | |
| Total # spp | 192 | 195 | 197 |
| Dominant ( ≥300) | 11 (2.2-24.1%) | 10 (3.13-7.89%) | 10 (3.09-8.17%) |
| Abundant (60-299) | 20 (0.4-1.85%) | 18 (0.58-2.29%) | 16 (0.61-2.32%) |
| Frequent (>15-59) | 33 (0.1-0.39%) | 36 (0.14-0.53%) | 40 (0.15-0.59%) |
| Rare (≤15) | 128 (0.01-0.9%) | 131 (0.01-0.13%) | 131 (0.01-0.15%) |
| # Doubletons | 16 (0.01%) | 39 (0.02%) | 19 (0.02%) |
| # Singletons | 40 (0.01%) | 38 (0.01%) | 40 (0.01%) |
| # Disappeared spp | | 5 (0.01%) | 10 (0.01-0.03%) |
| # Appeared spp | | 8 (0.01-0.03%) | 12 (0.01-0.03%) |
| # Reappeared spp | | | 2 (0.01-0.02%) |

There were cases in which populations increased first and then declined afterwards, or vice versa, specifically for frequent and rare species, such as the doubletons (species recorded twice), that increased from 16 species in the first census, to 39 in the second census, and fell back to 19 species in the third census (Table 2.2). Only two species present in 1994 disappeared in 2001 and reappeared in 2007 (Table 2.2), but it is unclear if this might have been due to identification problems during censuses.

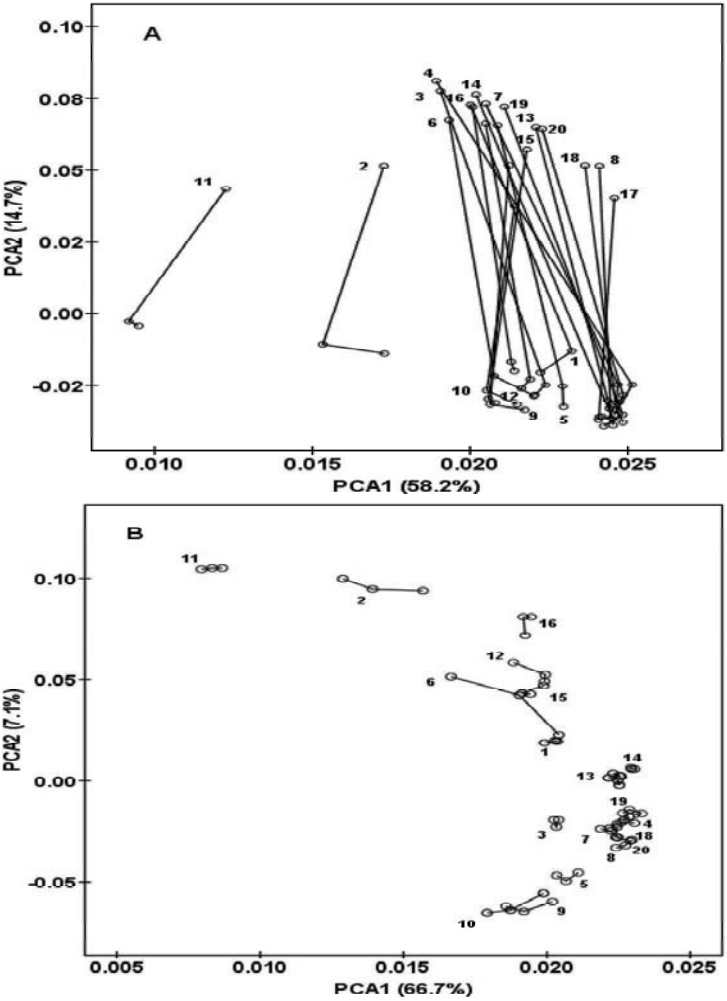

Figure 3.5. Changes in the abundance weighted community composition of lianas over time, for 20 1-ha plots of a mixed forest in the Ituri dynamics plot. A: Ordination with all recorded species, and B: ordination excluding the strongly dominating *Manniophyton fulvum*. Census dates are: 1994, 2001 and 2007. Circle represents each 1-ha plot. The number near each circle indicates the plot number.

The results of the PCA analyses show that the community composition of all 20 one-ha plots changed strongly in the first period and weakly in the second (Figure 3.5a). Two plots separated from the rest, both with *M. fulvum* and *Combretum racemosum* as co-dominant species. In all other plots *M. fulvum* was strongly dominant. Because of this overall strong dominance of *M. fulvum* we recalculated the PCA after excluding this species (Figure 3.5b). Then most plots were stable in their composition over time, and only five plots showed small temporal changes. This indicates that *M. fulvum* alone is accounting for virtually all changes in the liana assemblage of this old-growth mixed forest.

## DISCUSSION

In this study we analyse community-wide dynamics of lianas and showed how a super-dominant species, *M. fulvum*, drives changes of the community over time in this tropical old-growth forest in the Congo Basin. Most changes occurred during the first census interval, and over the 13 years evaluated, the liana abundance decreased, rather than increased over time.

### *Dynamics in the liana assemblage: individuals and biomass*

Given the recently reported increase in liana abundance in Neotropical forests (Phillips et al., 2002), we expected that lianas would also become more dominant in this old-growth African forest and that population changes would mainly be driven by increased recruitment rates and stem densities. Our results clearly show that this was not the case. Lianas were extremely dynamic in our Ituri Forest Dynamics Plots (Table 3.1, 3.2). Liana density, basal area and biomass generally decreased during the course of our study, especially for density during the first period (Figure 3.1). The number of small-sized lianas decreased considerably due to low recruitment, high mortality and growth into the next size class. Concomitantly, liana basal area and aboveground biomass decreased over the thirteen-year monitoring period. The decrease in density does agree with the results of Caballé and Martin (2001) who, in a 13-year study in Gabonese rainforests, found that both species richness and density of lianas decreased. Liana basal area, however, did not decrease in their study.

Our results are in contrast to findings of several studies in the Americas on recent increase in liana abundance. For example, over the last two decades, the relative abundance of large lianas has increased by 1.7 - 4.6 % year$^{-1}$ in Neotropical forests (Phillips et al., 2002). Similarly, Wright et al. (2004) reported a 100% increase in liana density between 1980s and 1990s surveys on Barro Colorado Island, Panama. They also found that between 1986 and 2002 the total liana leaf litter production and the contribution of lianas to forest-wide leaf litter production increased. Ingwell et al. (2010) showed that liana infestation in trees of 30 species in Panama increased drastically over the last decades, and also noted the extreme variation on a per tree basis during the last 10 years. Recently, Allen et al. (2007) showed an increasing importance of lianas in term of abundance in temperate floodplain forests of the southeastern USA. They suggested that the observed increase is primarily caused by atmospheric $CO_2$ increase and regional severe drought effect of El Niño, as a global signal of climate change. However, the African rain forest including the Ituri region, is recovering from past disturbance (Richards, 1952; Maley 1996; Van Gemerden et al., 2003) and past drought (a phase ending 2,500 yr BP; Maley, 2001). These forests are characterized by high abundance of liana in the re-colonization and building phase, but some species are now decreasing with the age of the forest. Specifically in the Ituri Forest, Hart et al. (1996) found evidence of small widespread fires associated with increased human activities during the last two millennia; and storm tracks in the form of corridors of fallen trees are also relatively common in the central Ituri Forest, which is the reason for the occurrence of old secondary forest scattered in the forest. These storm tracks in addition to the intermittent canopy structure provide suitable habitats to the development and high abundance of lianas, because of their high light intensities. Therefore, disturbance-related changes in canopy structure may regulate the abundance and species composition of the liana community.

### *Are growth and mortality size-dependent?*

We expected vital and dynamic rates (growth and survival) to be size-dependent and small-sized stems to show faster growth and higher mortality compared to large-sized stems. Our results show that vital rates indeed were stem size dependent. Mortality rates were high, both at community level and for each of the size classes, especially during the first interval (Figure 3.2a). Recruitment to larger size classes was generally high but little recruitment occurred in the smallest size class (Figure 3.2b). As a result, recruitment was not sufficient to counterbalance the high mortality rates of lianas in the smallest size class. This pattern may be explained by a wave of high recruitment, possibly as a result of high disturbance in the past (e.g. fire, storm treefall gaps, and drought) and followed by reduced recruitment in later post-disturbance stages due to canopy closure.

This past wave of recruitment in smaller size classes continued in the larger sizes classes during the course of our study (Figure 3.1, 3.2b). Nabe-Nielsen (2002, 2004) and Nabe-Nielsen and Hall (2002) pointed out that large canopy openness facilitates the penetration of high light intensity to the understory and together with micro-topographic conditions led to drastic increase in abundance and growth of *Machaerium cuspidatum*, a dominant liana species in most Amazonian forests. This may be congruent to what we observed for *M. fulvum* in the Ituri Forest. The population structure of *M. fulvum* thus may be controlled by the age and structure (e.g. canopy openness, light availability) of the forest. *M. fulvum* is a generalist species, widely distributed in West and Central Africa. There should have been large disturbance in the past (but not that too long ago) that the forest is now "recovering from"; alternatively the collapse of only this one species seems more likely associated with a specific pathogen. It is relatively shade tolerant, and as a result it can be found in a wide range of environments (also in the plot), although it requires high light conditions for a fast growth. The ability of *M. fulvum* to combine shade tolerance (i.e. survival in seedling stage) with faster growth in areas of high-light intensities is probably crucial to its establishment and abundance in old-growth mixed forest with potential disturbances in the future.

In general, liana growth was size dependent, and varied from 0.5 to 1.5 mm for the two census periods (Figure 3.3a). Growth increased with stem diameter, with the largest increases in stems from 40 mm (first period) or 70 mm onward (second period). Similarly, Gilbert et al. (2006) showed for a Neotropical rainforest community that all liana and tree species showed an increased growth and survival with size. Large lianas may realize fast radial growth because of their larger leaf area and better access to light compared to small lianas. Larger lianas also survive better because they are more robust against environmental hazards. Surprisingly, individuals in the largest size class (>100 mm diameter) combine fast growth with a decline in survivorship (Figure 3.3), possibly because these largest individuals die from hazards (drought, windthrow by storms), or because they have attained their maximal age.

*Do liana diversity and community composition change over time?*

Assuming that lianas are highly dynamic, and that they have recently increased in abundance (Phillips et al., 2002, 2005), we expected that recruitment would increase overall liana population size and that there would be large directional changes in liana community composition. The liana community species abundance in all plots changed drastically from 1994 to 2001 and only slightly thereafter (Figure 3.5). This change was mainly due to the collapse of the dominant *M. fulvum*, while other abundant species changed only insignificantly in their population size. As far as we know this is the first time such a drastic one-species-only collapse is reported in the literature. This phenomenon needs further investigation, for instance of the particularities (e.g. seedlings autoecology) of this dominant species. Possibly, the significant collapse of *M. fulvum* was due to either the combined effect of forest regrowth and canopy closure, or to drought effects, specifically between 1994 and 2001.

There was a non-directional change in the community composition as a whole, and the ten most abundant species remained rather constant over the 13 year period that we analyzed (Figure 3.4). However, species richness slightly increased despite a decrease in abundance, and all these new species entered the community through new recruits. Our local large-scale and long-term study illustrates three main patterns: (1) long-term trends in which liana density, basal area and biomass consistently decreased; with poor recruitment being unable to balance the strong increase in liana mortality over time in our study plots; (2) the size class structure suggests a population with very little recruitment over time; small lianas that die or that recruit into larger size classes are not being replaced (Figure 3.2b), so there is a continuous trend of declining stem density, basal area and correlated biomass likely to continue for a long time if recruitment and growth are not enough to balance losses; (3) the species richness and diversity remained constant over time, despite the continuous decrease of liana abundance.

In conclusion, our study is the first to show a strong decrease of the liana population in old-growth forest. This general decrease is in contrast with the widely documented increase of lianas over the last decades. Our study is also the first to document that this community level dynamics is completely driven by the dynamics of one species only. Future studies on liana communities in old-growth forests are needed to test whether or not such single dominant species driven community dynamics is a general phenomenon in tropical old-growth forests. We also showed that changes in liana dynamics and composition differed dramatically between the first and the second census interval, despite the fact that these census intervals spanned a relatively long time (6-7 years), in which year-to-year fluctuations are expected to average out. Conclusions on liana increase or decrease thus depend heavily on the time-window used. Therefore, we argue that long-term and large scale studies are needed to evaluate the direction of community changes and to predict the eventual consequences of climate change.

# Chapter 4

## *Thirteen years of species-specific dynamics of lianas in a Central African rain forest*

*Corneille E.N. Ewango, Lourens Poorter, Marc S.M. Sosef & Frans Bongers*

## ABSTRACT

Demographic rates of liana species are expected to be related to their functional traits. We investigated over a 13 years period species-specific dynamics of the 79 most abundant lianas species in the evergreen Ituri rain forest of Congo. We evaluated their demographic performance and the relation of vital rates to abundance and to four functional traits (climbing strategy, dispersal syndrome, leaf size and light requirements) to determine across species variation and to characterize their major strategies. Vital rates varied widely: species-specific recruitment rates varied from 0.0-10.9%, mortality rates from 0.43-7.89%, and growth rates from -0.03-3.51 mm $y^{-1}$. Most species had low to moderate rates. Fast growing species tended to recruit and die fast, but recruitment and mortality rates were not related, suggesting that species shift in absolute abundance. However, with the exception of the collapsing *Manniophyton fulvum* population, species maintained their rank in abundance over time. Species growth declined with abundance, but recruitment and mortality rates were not significantly related to abundance. Liana demographic performance varied weakly with climbing strategy and dispersal mode but was, surprisingly, not related to lifetime light requirements of the species. Liana strategies in terms of functional traits and vital rates were summarized using a principle components analysis. Light demand, and dispersal syndrome were the most determining traits. Three functional guilds were distinguished.  We conclude that old-growth forest liana species show a large variation in abundance and vital rates, and that density-dependent mechanisms are insufficient to explain the species abundance patterns over time.

**Key words:** species-specific dynamics, lianas, growth, mortality, recruitment, functional traits

## INTRODUCTION

A community assemblage is the product of the dynamics of the individual species that compose the assemblage. Therefore, knowledge of the dynamics of individual species (recruitment, growth and mortality rates) helps to understand the dynamics of the whole assemblage (Haper 1977, Begon *et al.* 1996). The first step to understand liana dynamics is to characterize their species' vital rates and relate this to their functional traits. Until recently, hardly any studies exist dealing with the vital rates of individual liana species (but see Caballé & Martin 2001; Nabe-Nielsen 2002, 2004, Mascaro *et al.* 2004), and none has tried to relate those to their functional traits. Community-level long-term demographic studies on lianas are nearly non-existing (but see Caballé & Martin 2001; Phillips *et al.* 2002; Wright *et al.* 2004; Allen *et al.* 2005). Here we report on the demography and vital rates of a highly diverse assemblage of liana species in an old-growth lowland rainforest in the Congo Basin, where the liana community appears to be extremely dynamic and decreasing in overall abundance (Ewango *et al.* submitted). This decrease contrasts with the generally found increase in earlier liana studies, notably in the Neotropics (Phillips *et al.* 2002; Wright *et al.* 2004; Allen *et al.* 2007).

Changes in abundance of a species are the result of the recruitment, growth, and mortality rates. These vital rates are not only affected by the environment, but also by the species-specific functional traits. Empirical studies have shown that species traits such as seed size, leaf size, adult height and wood density influence species vital rates (Ackerly *et al.* 2002; Cornwell, Schwilk & Ackerly 2006, Poorter *et al.* 2008, Kooyman *et al.* 2010). In addition, for liana species also their climbing mechanism affects their vital rates (Darwin 1867; Putz and Mooney 1991, Currasco-Urra & Gianoli 2009).

Determining the causes of commonness and rarity of individual species in ecological communities is essential for our understanding of how communities are structured and has important implications for biodiversity conservation (Kunin & Gaston 1997; Hubbell & Foster 1986). Identifying the determinants of species abundance has been particularly challenging in tropical forests, which are characterized by both high species richness and high rarity.  Although Rabinowitz (1981) outlined the seven causes of species rarity, a number of more recent studies neglected the importance of vital rates trade-offs to explain and understand species relative abundance. Density-dependent decline in growth and survival is thought to keep the most abundant species under control (Janzen 1970, Connell 1978,), and hence, maintain species diversity. It has also been shown that vital rates of tree species are related to their abundance (Comita & Hubbell 2009), but it is not known yet whether the same applies for lianas as well.

Most previous studies on liana dynamics strongly relied on community dynamics and hardly determined how species-specific performances contribute to species population maintenance within a community. For the present paper we use the existing long-term, standardized datasets from the Ituri Forest Dynamics Plots, Democratic Republic of Congo, which is part of the global network of large forest dynamics plots coordinated by the Center for Tropical Forest Science (CTFS). We examine the demography of lianas over 13 years (1994–2007) for 15,008 stems belonging to 195 species showing a wide range of functional traits. We address five specific questions: (1) How variable are liana species in demographic performance (i.e. their vital rates)? (2) How are liana vital rates associated with each another? (3) What is the relation between liana vital rates and species abundance? (4) What is the relation between liana vital rates and species functional traits? and (5) Which general strategies do lianas have, based on vital rates and functional traits? We formulate the following corresponding hypotheses: First, species mortality, recruitment and growth rates are highly variable across species, considering that lianas are a taxonomically diverse group. Second, liana vital rates are closely associated in a fast-slow continuum, in which species with a high recruitment rate will also have high growth and mortality rates. Third, species growth, survival and recruitment will be lower in common species than in rare species because of negative density-dependent effects (Connell *et al. 1984*, Comita *et al.* 2010). Fourth, vital rates will be higher for species that are light demanding, twine, and have large leaves (Bonsall *et al.* 2004, Gerwing 2004, Gilbert *et al.* 2006). Fifth, we expect that competition for light will be the major process characterizing species.

## MATERIAL AND METHODS

### *Study site and plot sampling*

We conducted this research in the Réserve de Faune à Okapis (RFO; 1°25’N, 28°35’E), a protected area in the Ituri Forest, north-eastern Democratic Republic of Congo. For this paper, we use two 10-ha plots established in mixed tropical rain forest. Each plot was divided into 250 20 × 20 m contiguous subplots. In 1994, all lianas ≥ 2 cm dbh (diameter at breast height, measured at 130 cm from the rooting point) were tagged, mapped, identified and their diameter measured to the nearest mm in 1994 (Makana *et al.* 1998). In 2001 and 2007, these plots were recensused, and all individuals alive from the previous censuses were re-measured and newly recruited individuals were recorded and measured following the same methods used in 1994.

The two 10-ha plots are floristically and topographically homogenous. *Cynometra alexandri* C.H.Wright, *Julbernardia seretii* (De Wild.) Troupin and *Cleistanthus michelsonii* J.Léonard are the most common and dominant canopy trees. The canopy is 30-40m in height and irregular. The altitude reaches 700-850 m *asl* and topography in the study plots is fairly insignificant: the surface is only slightly undulating and the difference between the highest and lowest point is only 14 to 21 m for each plot, respectively (Makana *et al.* 2004). Temperatures are quite uniform year-round (with daily minimum reaches 17.9°C and 25.5°C at maximum), but rainfall (mean annual precipitation of c. 1785 mm) is seasonal, with the driest months January and February receiving less than 50 mm of rain. More details for climate, vegetation, and fauna in the area of the two plots can be found in Hart (1985, 1986) and Makana *et al.* (1998).

In the field, the most common and readily identifiable species were directly named and plant material was collected of all other species and for fertile herbarium material. A total of nearly 10000 vouchers were collected during the survey. The vouchers were processed at the Centre de Formation et de Recherche en Conservation Forestière: CEFRECOF Herbarium (Epulu) and part of duplicates deposited to the Nationaal Herbarium Nederland (Wageningen University Branch), Meise (Brussels), and Missouri Botanical Garden (St. Louis, USA) for identification by specialists. Vouchers collected were identified using major regional floras/ taxonomic literature, mainly Flore d'Afrique centrale [Congo-Rwanda-Burundi], Flore du Cameroun, Flore du Gabon, Flora of East (FTEA) & West Tropical Africa (FTWA), and either by comparisons with identified herbarium materiel or assisting by plant taxonomists in Wageningen, Meise and Missouri. Nomenclature follows the Angiosperm Phylogeny Group (APG) and for taxonomic group with unreliable classification, we referred to Lebrun et al. (1991–1997).

### *Species functional traits*

We selected four species functional traits from literature (Evrad 1968, Bongers *et al.* 2005) that are thought to be important for liana dynamics. Dispersal syndrome is an indicator of the dispersal and colonization potential of species, and was derived from diaspore types and included anemochory (wind-dispersed), barochory (e.g. explosive) and zoochory (animal-dispersed). The climbing strategy indicates how fast and efficient species grow to the canopy, and it was categorized based on their anchorage structures as hook, tendril, twiner, and root climbers. Light requirements for species recruitment and growth were classified into light-demanding or shade-tolerance, based on information on species life history (Evrard 1968). Leave size is important for the light capture and heat balance of the plant, and leaf size was classified as being small ($< 20\ cm^2$) or large ($\geq 20\ cm^2$), based on information from Raunkiaer (1934) on leaf size categories and adopted in Evrard (1968).

*Species-specific vital rates*

For each species we calculated the relative abundance as the percentage of number of individuals of that species over the total individuals of all the species, and changes therein over time. We calculated recruitment, mortality and annual growth rates during the intercensus period (1994 to 2007) for all species with ≥ 10 individuals in 1994. Demographic rates were defined for the recruitment rate over 13-year for a species calculated as $r = 100\times[\ln N_{t1} - \ln N_{t2}/t]$, and mortality rate as $m = 100\times[\ln (N_{t2}) - \ln (N_{t1})]/(t_2 - t_1)$, in which $N_{t1}$ *is* the total number of lianas present at the initial census, $N_{t2}$ is the number of lianas of this cohort still alive at the second census, and $t_1$ and $t_2$, are the initial and final census dates (i.e., species-specific time varied from 11-13 years), respectively (Condit *et al.* 1999). The annual diameter growth was calculated as $D = (dbh_2 - dbh_1)/(t_2 - t_1)$, where $dbh_1$ and $dbh_2$ refer to the diameter of the individuals at the initial and final census. The time interval spanned by a species was defined as the arithmetic mean time between censuses for individuals of that species, based on the census data of each 20 x 20 m quadrat in the plots.

*Statistical analysis*

First, we performed the Shapiro-Wilk test to assess whether liana species show a normal distribution of their vital rates. Relationships between demographic vital rates on the one hand, and functional traits, and species abundances in 1994 and 2007 on the other hand, were analyzed using linear regressions. From this analysis we excluded 3 species (*Entada gigas* for growth, *Laccosperma secundiflorum* as palm, and *Urera* trinervis for recruitment) that were clear outliers with very extreme rates. To test whether species with different functional traits differed in demographic vital rates and in their abundance (i.e. commonness/rarity) we used one-way ANOVA, with Tukey's HSD significant difference *post hoc* test. We used a t-test for light requirement and leaf size (Zar 1999). In all these analyses, only species with at least 10 individuals in total were used, and where necessary population data were transformed using a logarithmic transformation ($\log_{10}(x)$), to conform to assumptions of normality and homogeneity of variance.

To summarize lianas species strategies, we performed a Principal Component Analysis (PCA) ordination to detect potential species guilds based on the combination of their demographic vital rates and functional traits. Finally, to estimate species concordance in species rank-abundance across time, we used the non-parametric Kendall's tau correlation (Field 2009). All statistical analyses were done using SPSS for Windows 17.0.

## RESULTS

### *Floristics*

The two 10-ha plots contained 15,008 stems ≥2 cm dbh in 1994 and 9,982 stems in 2007 representing a total of 195 and 198 species, respectively. Of these, 79 species (41% of the total) were selected that had sufficient individuals (≥10 stems in the 20 ha) in 1994 to calculate their vital rates. These 79 species represent together 13,156 of the stems (97% of total) in 1994 and 8,749 stems (95%) in 2007, and belong to 23 families and 44 genera (Table 4.1). The Apocynaceae (12 species), Celastraceae and Connaraceae (8), Annonaceae (7), Dichapetalaceae and Fabaceae (6) were the most speciose families. *Manniophyton fulvum* (Euphorbiaceae) alone accounted for 24% of the stems.

### *Species-specific performance*

Most species are rare; the species frequency distributions over abundance classes was not normal and strongly skewed to the right (1994 census, Shapiro-Wilk test = 0.24, $P < 0.001$, $n = 195$, Figure 4.1A; 2007 census, Shapiro-Wilk test = 0.39, $P < 0.001$, $n = 198$, Figure 4.1B). Recruitment rates of the 79 analyzed species varied from 0.0-10.9% per year with an average (mean ± SE) of 1.29 ± 0.16. Most species had a low recruitment rate (Figure 4.1C; Shapiro-Wilk test = 0.61, $P < 0.001$, $n = 79$). Mortality rates varied from 0.43-7.89% per year with an average of 2.78 ± 0.18. Its distribution was not normal (Shapiro-Wilk test = 0.92, $P < 0.001$, $n = 79$, Figure 4.1D) but most species had intermediate mortality. Growth rates varied from -0.03-3.51 mm $y^{-1}$ with an average of 0.67 ± 0.54, its distribution being not normal (Shapiro-Wilk test = 0.77, $P < 0.001$, $n = 79$, Figure 4.1E). Most species had intermediate growth rates. Few species, however, grow extremely fast. For example, *Urera trinervis* had the highest recruitment (10.9% $y^{-1}$) of all species, and *Entada gigas* had the highest (3.51 mm $y^{-1}$) growth rate.

Table 4.1. Total abundance (1994 and 2007), demography over 13-year period and functional traits of liana species. Dispersal syndrome: Anemo-, baro-, and zoochory. Light requirement: light demanding (LD) and shade tolerant (ST), leaf size: large leaves (LL) and small leaves (SL). The species list is alphabetically ordered by family and species scientific names.

| Family | Species name | # Ind. 1994 | # Ind. 2007 | Vital rates | | | Average time ($y^{-1}$) | Functional traits | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Growth (mm/ y) | Mortali -ty rate (%) | Recruit-ment rate (%) | | Climbing strategiy | Dispersal syndrome | Light requi-rement | Leaf size |
| Anacardiaceae | Trichoscypha reygaertii | 71 | 63 | 0.56 | 2.49 | 0.99 | 12 | Twiner | Zoo- | ST | LL |
| Annonaceae | Friesoldielsa enghiana | 12 | 13 | 0.33 | 2.56 | 1.91 | 11 | Twiner | Zoo- | LD | LL |
| | Monanthotaxis cauliflora | 27 | 17 | 0.33 | 3.42 | 0.50 | 11 | Twiner | Zoo- | LD | LL |
| | M. ferruginea | 28 | 26 | 0.70 | 2.20 | 0.99 | 12 | Twiner | Zoo- | LD | LL |
| | M. foliosa | 40 | 48 | 0.52 | 2.69 | 2.28 | 12 | Twiner | Zoo- | LD | LL |
| | M. lucidula | 23 | 33 | 0.27 | 2.34 | 2.88 | 11 | Twiner | Zoo- | LD | LL |
| | M. schweinfurthii | 12 | 7 | 0.37 | 3.85 | 0.61 | 11 | Twiner | Zoo- | ST | LL |
| | Uvaria pulchra | 86 | 76 | 0.41 | 2.33 | 0.90 | 11 | Twiner | Zoo- | LD | LL |
| Apocynaceae | Alafia lucida | 10 | 8 | 1.04 | 3.85 | 1.84 | 11 | Twiner | Anemo- | LD | LL |
| | Ancylobotrys scadens | 26 | 12 | 0.59 | 4.14 | 0.00 | 12 | Tendril | Zoo- | LD | LL |
| | CLitandra cymulosa | 78 | 61 | 0.75 | 2.86 | 0.82 | 12 | Tendril | Zoo- | LD | LL |
| | Landolphia forsterii | 16 | 20 | 1.11 | 1.44 | 1.59 | 12 | Tendril | Zoo- | LD | LL |
| | L. incerta | 82 | 113 | 0.51 | 0.56 | 1.49 | 12 | Tendril | Zoo- | LD | SL |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | L.ligustrifolia | 10 | 7 | 0.70 | 3.08 | 0.62 | 11 | Tendril | Zoo- | LD | SL |
| | L. mannii | 12 | 11 | 0.78 | 0.64 | 0.00 | 11 | Tendril | Zoo- | LD | LL |
| | L.owariensis | 121 | 157 | 0.94 | 1.40 | 1.73 | 12 | Tendril | Zoo- | LD | SL |
| | Landolphia sp | 25 | 13 | 1.03 | 4.31 | 0.61 | 12 | Tendril | Zoo- | LD | SL |
| | Landolphia sp4 | 14 | 9 | 0.58 | 2.75 | 0.00 | 12 | Tendril | Zoo- | LD | LL |
| | Orthopichonia seretii | 44 | 29 | 0.64 | 3.15 | 0.39 | 12 | Twiner | Zoo- | LD | SL |
| | Tabernaemontana eglandulosa | 159 | 154 | 0.27 | 3.00 | 1.77 | 11 | Twiner | Zoo- | LD | LL |
| Arecaceae | Laccosperma secundiflorum | 117 | 57 | -0.03 | 5.06 | 1.35 | 11 | Hook | Zoo- | LD | LL |
| Celastraceae | Bequaertia mucronata | 28 | 17 | 0.47 | 3.02 | 0.00 | 11 | Twiner | Anemo- | LD | SL |
| | Campylostemon bequaertii | 18 | 29 | 0.63 | 0.43 | 2.09 | 11 | Twiner | Anemo- | LD | SL |
| | Loeseneriella apiculata | 11 | 14 | 0.91 | 0.70 | 1.29 | 11 | Twiner | Anemo- | LD | LL |
| | Salacia cerasifera | 14 | 31 | 0.97 | 0.55 | 3.38 | 11 | Twiner | Zoo- | LD | SL |
| | S. elegans | 34 | 52 | 0.81 | 1.81 | 2.67 | 11 | Twiner | Zoo- | ST | SL |
| | S. kivuensis | 10 | 14 | 1.10 | 0.77 | 1.66 | 12 | Twiner | Zoo- | LD | LL |
| | S. laurentii | 91 | 108 | 0.57 | 1.35 | 1.42 | 11 | Twiner | Zoo- | LD | LL |
| | S.pyriformioides | 330 | 385 | 0.41 | 1.59 | 1.50 | 11 | Twiner | Zoo- | ST | LL |
| Combretaceae | Combretum cuspidatum | 46 | 46 | 0.90 | 2.68 | 1.65 | 11 | Twiner | Anemo- | LD | LL |
| Combretaceae | Combretum marginatum | 421 | 472 | 1.03 | 1.85 | 1.47 | 11 | Twiner | Anemo- | LD | SL |
| | Combretum mortehanii | 18 | 20 | 0.72 | 1.71 | 1.43 | 11 | Twiner | Anemo- | LD | SL |
| | Combretum multiflorum | 273 | 232 | 0.46 | 2.70 | 1.03 | 11 | Twiner | Anemo- | LD | SL |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Combretum racemosum | 685 | 480 | 0.27 | 4.22 | 1.71 | 11 | Twiner | Anemo- | LD | LL |
| Connaraceae | Agelaea paradoxa | 636 | 612 | 0.38 | 1.69 | 0.79 | 12 | Twiner | Zoo- | LD | LL |
| | Agelaea pentagyna | 767 | 625 | 0.51 | 2.15 | 0.46 | 12 | Twiner | Zoo- | LD | LL |
| | Agelaea rubiginosa | 454 | 372 | 0.60 | 2.29 | 0.60 | 11 | Twiner | Zoo- | LD | LL |
| | Cnestis urens | 207 | 175 | 0.29 | 1.97 | 0.47 | 12 | Twiner | Zoo- | LD | SL |
| | Connarus griffonianus | 16 | 16 | 0.19 | 1.44 | 0.81 | 11 | Twiner | Zoo- | LD | LL |
| | Manotes expensa | 40 | 43 | 0.48 | 0.96 | 0.78 | 12 | Twiner | Zoo- | LD | LL |
| | Rourea parviflora | 21 | 22 | 1.31 | 1.10 | 0.79 | 11 | Twiner | Zoo- | LD | LL |
| | Rourea thomsonii | 922 | 816 | 0.38 | 2.15 | 0.78 | 11 | Twiner | Zoo- | LD | LL |
| Dichapetalaceae | Dichapetalum afzelii | 39 | 39 | 0.46 | 1.58 | 0.92 | 11 | Twiner | Zoo- | ST | SL |
| | Dichapetalum fructuosum | 85 | 70 | 0.28 | 1.99 | 0.38 | 12 | Twiner | Zoo- | ST | SL |
| | Dichapetalum heudelotii | 638 | 558 | 0.24 | 1.92 | 0.57 | 12 | Twiner | Zoo- | ST | LL |
| | Dichapetalum librevillense | 102 | 121 | 0.42 | 0.68 | 0.98 | 12 | Twiner | Zoo- | ST | LL |
| | Dichapetalum mombuttense | 27 | 24 | 0.36 | 2.56 | 1.13 | 11 | Twiner | Zoo- | ST | LL |
| | Dichapetalum staudtii | 854 | 779 | 0.38 | 1.90 | 0.74 | 11 | Twiner | Zoo- | ST | SL |
| Dilleniaceae | Tetracera alnifolia | 24 | 21 | 0.34 | 2.56 | 1.02 | 12 | Twiner | Zoo- | LD | LL |
| Euphorbiaceae | Alchornea cordifolia | 84 | 21 | 1.29 | 6.23 | 1.07 | 11 | Twiner | Zoo- | LD | LL |
| | Macaranga angolensis | 26 | 20 | 0.95 | 2.96 | 0.85 | 11 | Twiner | Zoo- | LD | LL |
| | Manniophyton fulvum | 3299 | 94 | 0.32 | 7.59 | 2.46 | 12 | Twiner | Baro- | ST | LL |
| | Plukkenettia conophorum | 11 | 5 | 1.11 | 5.59 | 1.85 | 12 | Twiner | Baro- | LD | SL |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Fabaceae | Baphia spathacea | 43 | 26 | 0.40 | 3.04 | 0.00 | 11 | Twiner | Baro- | LD | LL |
| | Entada gigas | 10 | 11 | 3.51 | 4.62 | 4.06 | 11 | Tendril | Baro- | LD | SL |
| | Leptoderris congolensis | 36 | 49 | 0.71 | 1.92 | 2.31 | 11 | Twiner | Anemo- | LD | LL |
| | Leptoderris ferrugineus | 54 | 46 | 0.41 | 1.99 | 0.55 | 11 | Twiner | Anemo- | LD | LL |
| | Millettia barterii | 187 | 154 | 0.89 | 2.43 | 0.74 | 11 | Twiner | Baro- | LD | LL |
| | Millettia psilopetala | 390 | 308 | 0.26 | 1.95 | 0.21 | 12 | Twiner | Baro- | ST | LL |
| Hernandiaceae | Illigera pentaphylla | 20 | 7 | 1.81 | 5.38 | 0.60 | 11 | Twiner | Anemo- | LD | LL |
| Icacinaceae | Pyrenacantha klaineana | 38 | 37 | 0.55 | 2.83 | 1.64 | 11 | Twiner | Zoo- | ST | LL |
| Lamiaceae | Vitex thyrsiflora | 12 | 6 | 0.58 | 3.85 | 0.00 | 12 | Twiner | Zoo- | LD | LL |
| Linaceae | Hugonia platysepala | 44 | 30 | 0.44 | 3.50 | 0.85 | 11 | Hook | Zoo- | LD | SL |
| Loganiaceae | Strychnos angolense | 79 | 59 | 0.45 | 2.82 | 0.65 | 11 | Hook | Zoo- | LD | SL |
| | Strychnos longicaudata | 278 | 201 | 0.35 | 2.74 | 0.44 | 11 | Hook | Zoo- | LD | SL |
| Loganiaceae | S. phaeotricha | 26 | 21 | 0.20 | 1.78 | 0.18 | 12 | Hook | Zoo- | LD | SL |
| | Strychnos urceolata | 32 | 36 | 0.47 | 0.48 | 0.71 | 11 | Hook | Zoo- | LD | SL |
| Malvaceae | Ancistrocarpus bequaertii | 134 | 104 | 0.33 | 2.18 | 0.29 | 12 | Twiner | Zoo- | LD | LL |
| | Grewia seretii | 59 | 51 | 0.57 | 2.22 | 0.77 | 11 | Twiner | Zoo- | LD | LL |
| Passifloraceae | Adenia cinanchyfolia | 17 | 4 | 0.94 | 6.33 | 1.09 | 11 | Tendril | Zoo- | LD | LL |
| Piperaceae | Piper guineensis | 44 | 4 | 0.18 | 7.34 | 2.63 | 11 | Root | Zoo- | ST | LL |
| Rhamnaceae | Ventilago diffusa | 20 | 25 | 1.06 | 2.31 | 2.12 | 12 | Twiner | Zoo- | LD | LL |
| Rubiaceae | Keetia molundensis | 15 | 6 | 0.82 | 5.13 | 0.71 | 11 | Twiner | Zoo- | LD | LL |
| | Sherbournia batesii | 11 | 17 | 0.18 | 2.80 | 3.42 | 11 | Twiner | Zoo- | LD | SL |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Uncaria africana | 60 | 30 | 1.16 | 4.74 | 0.97 | 12 | Hook | Anemo- | LD | SL |
| Urticaceae | Urera camerooniana | 174 | 132 | 1.35 | 3.89 | 1.57 | 12 | Root | Zoo- | LD | LL |
| | Urera trinervis | 12 | 30 | 1.48 | 6.41 | 10.93 | 11 | Root | Zoo- | LD | LL |
| Vitaceae | Cissus dinkglagei | 44 | 59 | 1.10 | 2.10 | 2.40 | 11 | Tendril | Zoo- | LD | LL |
| | Cissus producta | 73 | 34 | 1.00 | 4.43 | 0.33 | 12 | Tendril | Zoo- | LD | LL |

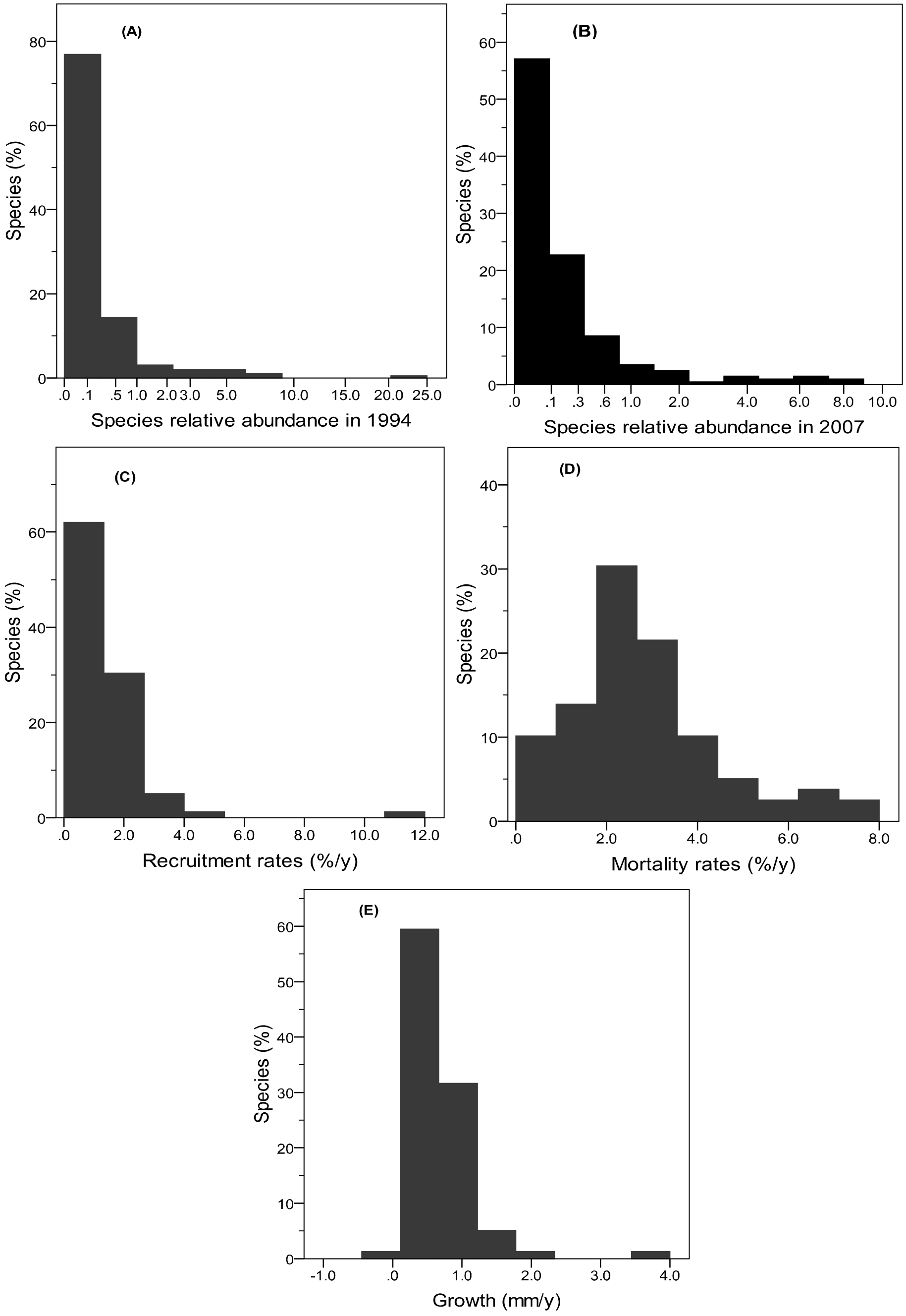

Figure 4.1. Frequency distribution of species (in %) over abundance size classes (for 1994 and 2007), recruitment, mortality and growth.

### *Correlations among liana species vital rates*

Among the 79 species, *Urera trinervis* had the highest recruitment (10.9%) and mortality (6.4%), *Entada gigas* had highest growth (3.51 mm $y^{-1}$) and high recruitment (4.1%), and five species with high mortality (*Piper guineensis* 7.3%, *Adenia cynanchifolia* 6.3%, *Alchornea cordifolia* 6.2%, *Illigera pentaphylla* 5.4%, and *Keetia molundensis* 5.1%) had low recruitment

We examined correlations between species vital rates for 76 liana species (Figure 4.2, Table 4.2), after excluding one palm liana species that did not show secondary growth, and 2 outlying species with extreme rates of growth or recruitment. Annual growth increased significantly with both mortality (linear regression, F = 5.4, P = 0.02; $R^2$ = 0.07, Figure 4.2A) and recruitment (F = 10.0, P = 0.002; $R^2$ = 0.12, Figure 4.2B). Annual mortality was not related to recruitment rates (F = 0.5, P = 0.50; $R^2$ = 0.006, Figure 4.2C).

Table 4.2. Results of linear regressions assessing relationships between species-specific demographic parameters and abundance in 20 ha of Ituri Forest Dynamics Plots. The F-value, coefficient of determination, and significance levels are given. The first parameter mentioned in the demography column is independent and the second is dependent in the regression: species with ≥10 stems (N = 76-78), ≥ 20 stems (N = 58), ≥ 40 stems (N = 40), while the palm and extreme outlier's recruitment and mortality species are ecluded, respectively.

| **Demography** | **Spp ≥ 10 stems** | | | | **Spp ≥ 20 stems** | | | **Spp ≥ 40 stems** | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | **F** | **$R^2$** | **P** | **N** | **F** | **$R^2$** | **P** | **F** | **$R^2$** | **P** |
| Mortality-Recruitment | 4.31 | 0.23 | 0.04 | 78 | 1.33 | 0.02 | 0.25 | 5.88 | 0.13 | 0.02 |
| | 0.45 | 0.01 | 0.50 | 76 | | | | | | |
| Growth-Recruitment | 10.02 | 0.12 | 0.002 | 77 | 0.53 | 0.01 | 0.47 | 1.13 | 0.03 | 0.29 |
| | 0.93 | 0.12 | 0.34 | 76 | | | | | | |
| Growth-Mortality | 5.38 | 0.07 | 0.02 | 78 | 2.59 | 0.44 | 0.11 | 0.92 | 0.02 | 0.34 |
| | 4.10 | 0.05 | 0.05 | 77 | | | | | | |
| Growth-Abundance 1994 | 8.50 | 0.02 | 0.005 | 76 | 5.04 | 0.08 | 0.03 | 3.15 | 0.08 | 0.08 |
| Mortality-Abundance 1994 | 0.02 | 0.00 | 0.89 | 77 | 0.16 | 0.003 | 0.69 | 0,11 | 0.003 | 0.74 |
| Recruitment-Abundance 1994 | 1.84 | 0.02 | 0.18 | 76 | 0.03 | 0.00 | 0.88 | 0.001 | 0.00 | 0.97 |

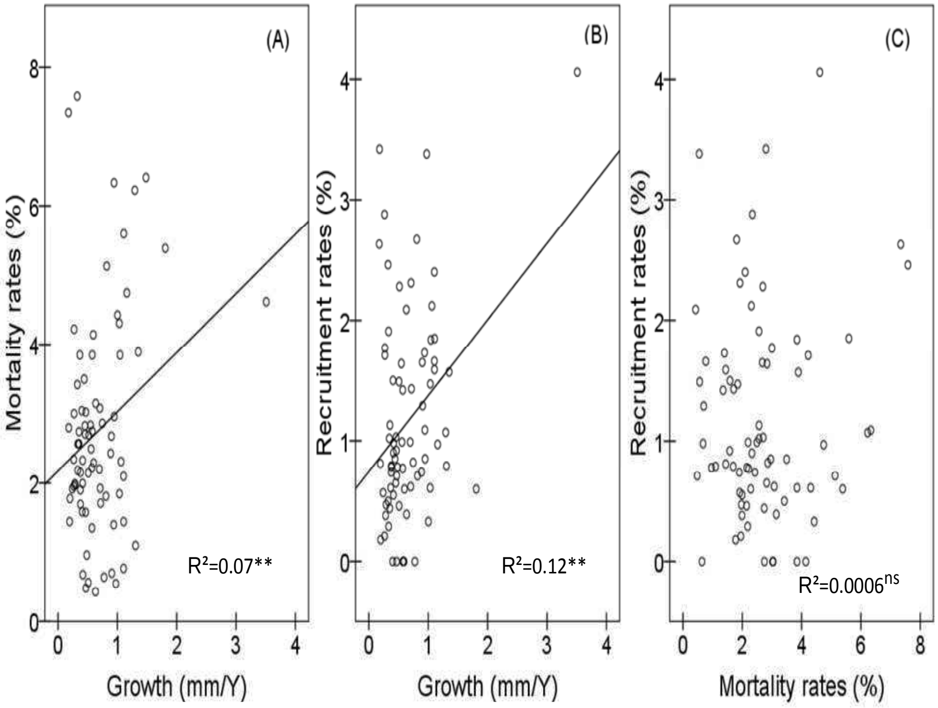

Figure 4.2. Relationships between mortality, diameter growth, and recruitment of 79 liana species in the Ituri Forest. Each point represents a species; the regression lines corresponding coefficient of determination ($R^2$), and significance levels are shown as ** $P < 0.001$, ns = no significant. Species-specific mortality and recruitment are investigated over a 13 years period.

*Abundance and vital rates*

Of the species vital rates only growth was negatively related to abundance (linear regression, $F = 8.5$, $P = 0.005$; $R^2 = 0.02$; Table 4.2, Figure 4.3B). This relation disappeared, however, when only species with ≥20 (n = 58 species) or ≥40 (n = 40 species) stems were considered (data not shown). Species mortality (linear regression, $F = 0.002$, $P = 0.09$; $R^2 = 0.00$; Figure 4.3A) and recruitment ($F = 1.84$, $P = 0.18$; $R^2 = 0.02$; Figure 4.3C) were independent of species abundance. This lack of density-dependence remained when only species with ≥20 or ≥40 stems were considered (data not shown).

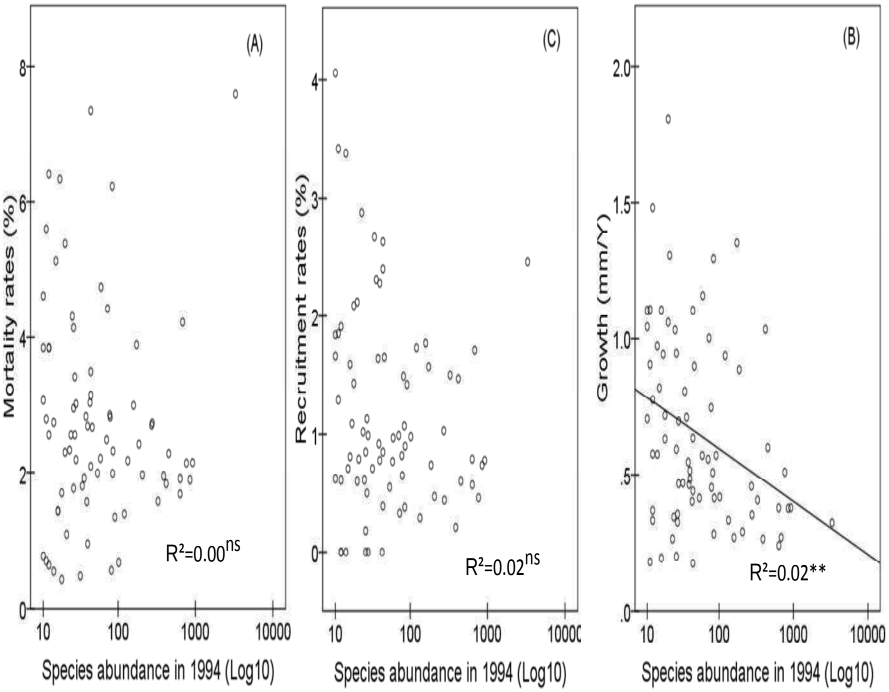

Figure 4.3. Relationship between mortality, diameter growth and recruitment and abundance in 1994 of 79 liana species in the Ituri Forest. Each point represents a species; the regression line, corresponding coefficient of determination ($R^2$), and significance levels are shown as ** $P < 0.001$, ns = no significant. Species-specific mortality and recruitment are investigated over a 13 years period.

Over the 13-year study period, 48% of the liana stems died. However, species maintained their abundance over time (n=211, $R^2 = 0.98$, Figure 4.6B) when the dominant species *Manniophyton fulvum* was excluded. Although the species-dominance rank order was significantly concordant between the 1994 and 2007 censuses (Kendal tau, $\tau = 0.77$; n = 212, P = 0.01; Figure 4.6A), rare species tended to have more rank crossovers during that period than common species.

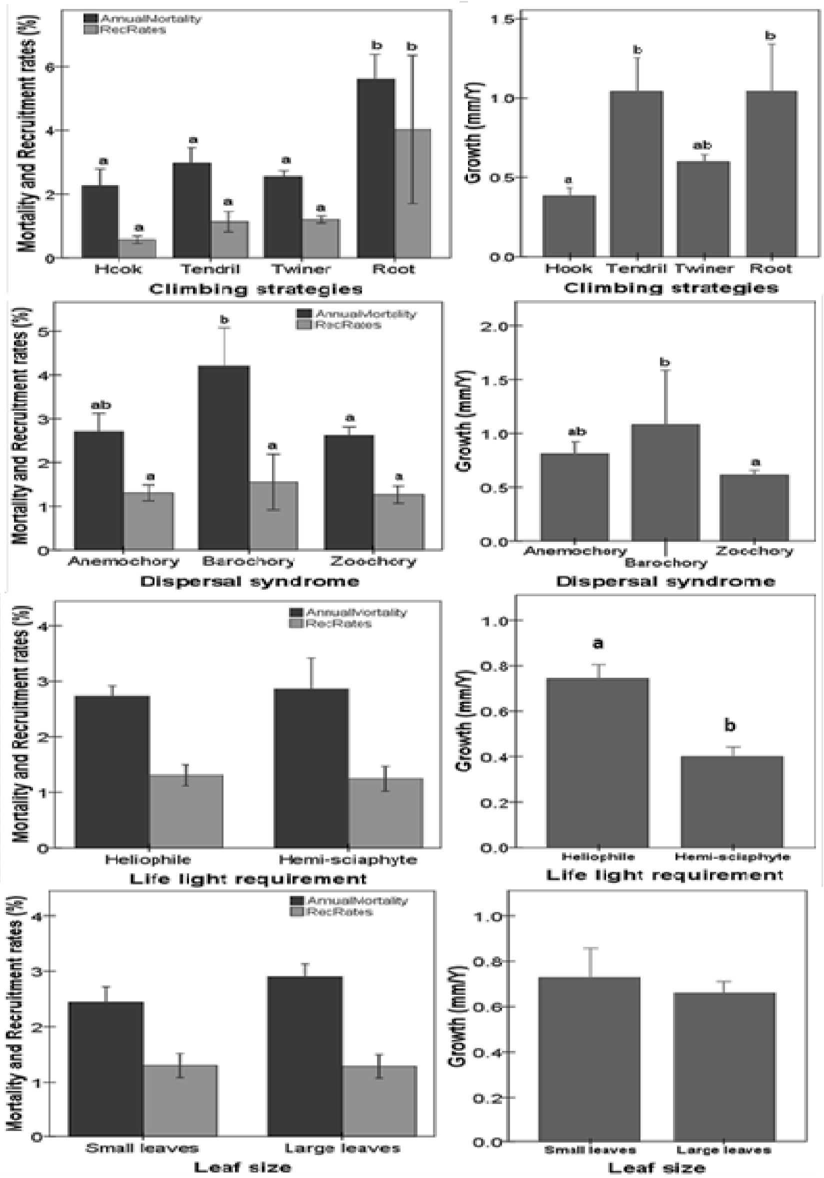

Figure 4.4. Mean (±SE) mortality, recruitment, and growth rates for four functional traits (climbing strategy, dispersal syndrome, life light requirement, and leaf size) of 79 Ituri Forest liana species. Columns accompanied by a different letter are significantly different (ANOVA (climbing and dispersal) and *t*-test (light requirement and leaf size), $P<0.05$).

Table 4.3. Results of the ANOVA (with Tukey' HSD test) and t-test comparing liana demographic attributes between functional traits in 20 ha of Ituri Forest Dynamics plots. Values between brackets in the first column indicate number of species with that trait: ANOVA test results are given for species [i] excluding palms and [ii] excluding palm and extreme demographic rate species. The F-value of ANOVA test, significance P levels, and mean ± standard errors are given. Significant differences in Tukey post-hoc comparisons between functional traits with demographic attributes are indicated by different letters in the same column

| **Functional traits vs. Demography** | | **Growth** | | | **Mortality** | | | **Recruitment** | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | **Mean ± SE** | **F** | **P** | **Mean ± SE** | **F** | **P** | **Mean ± SE** | **F** | **P** |
| **Climbing mechanism** | [i] | 0.68±0.05 | 5.19 | 0.01 | 2.76±0.18 | 5.80 | 0.001 | 1.29±0.16 | 6.89 | 0.000 |
| | [ii] | 0.64±0,04 | 3.46 | 0.02 | 2.74±0.18 | 3.58 | 0.018 | 1.07±0.08 | 2.07 | 0.11 |
| Hook (5) | | 038±0.1$^{a}$ | | | 2.26±0.52$^{a}$ | | | 0.57±011$^{a}$ | | |
| Tendril (13) | | 1.04±0.21$^{b}$ | | | 2.97±0.48$^{a}$ | | | 1.13±0.32$^{a}$ | | |
| Twiner (56) | | 0.60±0.05$^{ab}$ | | | 2.55±0.19$^{a}$ | | | 1.20±0.11$^{a}$ | | |
| Root (4) | | 1.04±0.30$^{b}$ | | | 5.59±0.78$^{b}$ | | | 4.03±2.33$^{b}$ | | |
| **Dispersal syndrome** | [i] | 0.68±0.05 | 3.41 | 0.04 | 2.76±0.18 | 2.88 | 0.06 | 1.29±0.16 | 0.14 | 0.89 |
| | [ii] | 0.63±0.04 | 2.16 | 0.12 | 2.68±0.17 | 2.52 | 0.09 | 1.13±0.09 | 0.37 | 0.69 |
| Anemochory (13) | | 0.81±0.11$^{ab}$ | | | 2.71±0.42$^{ab}$ | | | 1.30±0.18$^{a}$ | | |
| Barochory (6) | | 1.08±0.50$^{b}$ | | | 4.80±0.88$^{b}$ | | | 1.55±0.63$^{a}$ | | |
| Zoochory (59) | | 0.61±0.04$^{a}$ | | | 2.62±0.19$^{a}$ | | | 1.40±0.16$^{a}$ | | |
| | | **Mean ± SE** | **t** | **P** | **Mean ± SE** | **t** | **P** | **Mean ± SE** | **t** | **P** |
| **Life light requirement** | [i] | 0,34±0.14 | 2.54 | 0.01 | -0.13±0.47 | -0.28 | 0.78 | 0.06±0.42 | 0.14 | 0.89 |
| | [ii] | 0.29±0.09 | 3.02 | 0.003 | -0.22±0.45 | -0.48 | 0.63 | -0.14±0.24 | -0.59 | 0.56 |
| Light demanding (64) | | 0.74±0.06$^{a}$ | | | 2.73±0.18$^{a}$ | | | 1.30±0.19$^{a}$ | | |
| Shade tolerant (14) | | 0.40±0.04$^{b}$ | | | 2.86±0.56$^{a}$ | | | 1.24±0.22$^{a}$ | | |
| **Leaf size** | [i] | 0.07±0.12 | 0.58 | 0.56 | -0.46±0.38 | -1.20 | 0.22 | 0.01±0.34 | 0.40 | 0.97 |
| | [ii] | -0.03±0.08 | -0.38 | 0.70 | -0.48±0.37 | -1.29 | 0.20 | 0.08±0.20 | 0.42 | 0.67 |
| Small leaves (25) | | 0.73±0.13$^{a}$ | | | 2.44±0.27$^{a}$ | | | 1.30±0.22$^{a}$ | | |
| Large leaves (53) | | 0.66±0.05$^{a}$ | | | 2.90±0.23$^{a}$ | | | 1.54±0.21$^{a}$ | | |

### *Liana functional traits and demography*

Liana demographic performance varied with functional traits (Table 4.3, Figure 4.4). Lianas with different climbing strategy varied in growth (One-way ANOVA, F = 5.19, P = 0.01), mortality (F = 5.80, P = 0.001) and recruitment (F = 6.89, P = 0.0001) rates (the palm species were excluded). When considering climbing strategies, hook species had a lower mean growth compared to the tendril and root climbing species, and root climbing species show a higher mean mortality and recruitment rate compared to the other three strategies (Tukey's HSD test, P<0.05). Dispersal syndrome had a significant effect on growth and mortality rate (One-way ANOVA, F = 3.41, P = 0.04; excluding palm), in which barochorous species had a significantly faster growth rate than zoochorous species (Tukey's HSD test, Figure 4.4D). Light demanding species had significantly higher growth rate than shade tolerant species (t = 3.02, P = 0.003; removing palm and two species with extreme demographic values), but the two groups did not differ in mortality and recruitment rates. Leaf size did not have a significant effect on any of the demographic vital rates (Table 4.3).

### *Characterizing species variation*

Species were characterized using a PCA including all functional traits and all vital rates. Categorical variables (light demanding, shade tolerant, large leaves, small leaves, hook, tendril, twiner, root-climber, animal-dispersed, explosive dispersal, and wind-dispersed) were entered as dummy variables. The PCA of the eleven functional traits explained 36% of the total trait variation with the first two axes. Axis 1 (20%) can be characterized as an axis of variation in light demand with light-demanding species at the left and shade-tolerant species at the right. Axis 2 (16%) can be characterized as an axis of variation in dispersal (Figure 4.5A) with wind-dispersed species at the top and animal-dispersed species at the bottom. The species showed a nice spread on the first two axes of the PCA. A few species had unique trait and rate combinations (*Manniophyton fulvum*, *Millettia psilopetala*, and *Uncaria africana*; Figure 4.5B), but generally three clusters show up in the figure, indicating species with similar characteristics of vital rates and functional traits. Species in cluster (a) are characterized by wind-dispersal species in cluster (b) are root climbers and intermediate mortality and recruitment species in cluster (c) are characterized by hooks or tendrils and animal dispersal. Interestingly, most families and genera with >2 species had their species in a single cluster; only Combretaceae, Connaraceae and Celastraceae had species in two clusters.

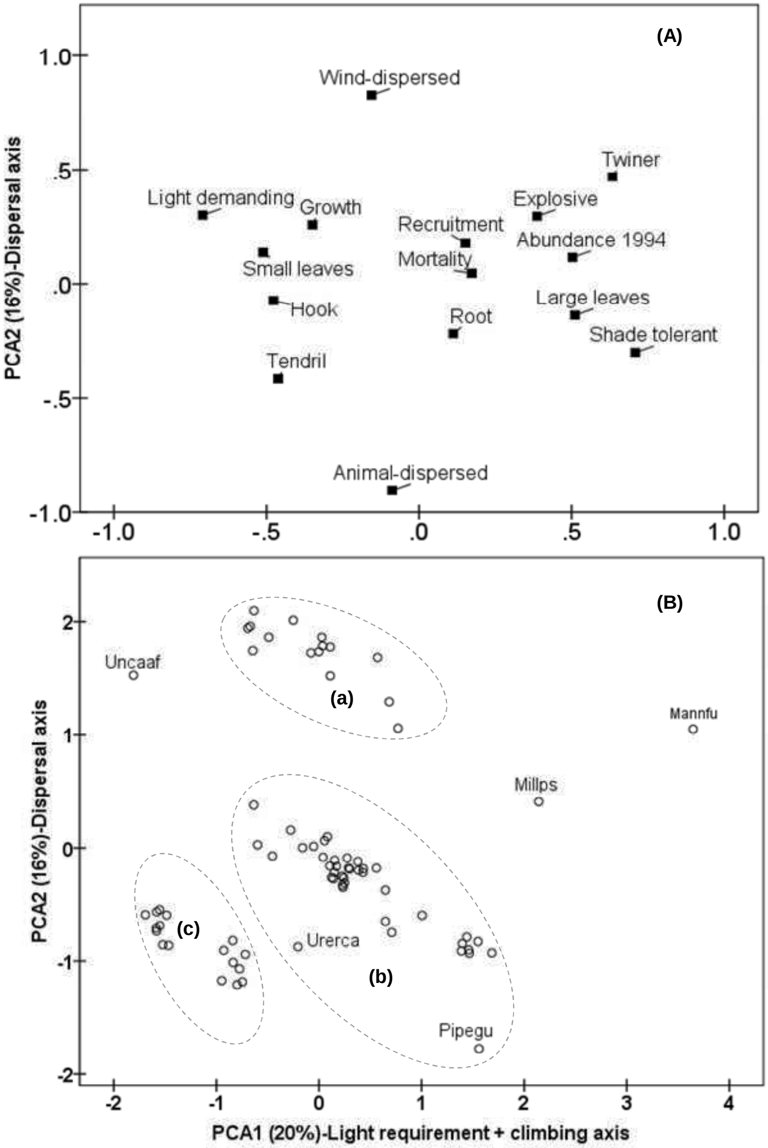

Figure 4.5. PCA ordination of 76 liana species based on three vital rates (growth, mortality, and recruitment) and four functional traits. (A) trait loadings. The functional traits relate to climbing strategy (hook, tendril, twiner, root climber), dispersal syndrome (animal, explosive, wind), life light requirement (light-demanding, shade-tolerant), and leaf size (small, large). (B) species regressions cores, with (a) wind-dispersal species, (b) root climbers and intermediate mortality and recruitment, (c) hooks or tendrils climbers and animal-dispersed cluster.

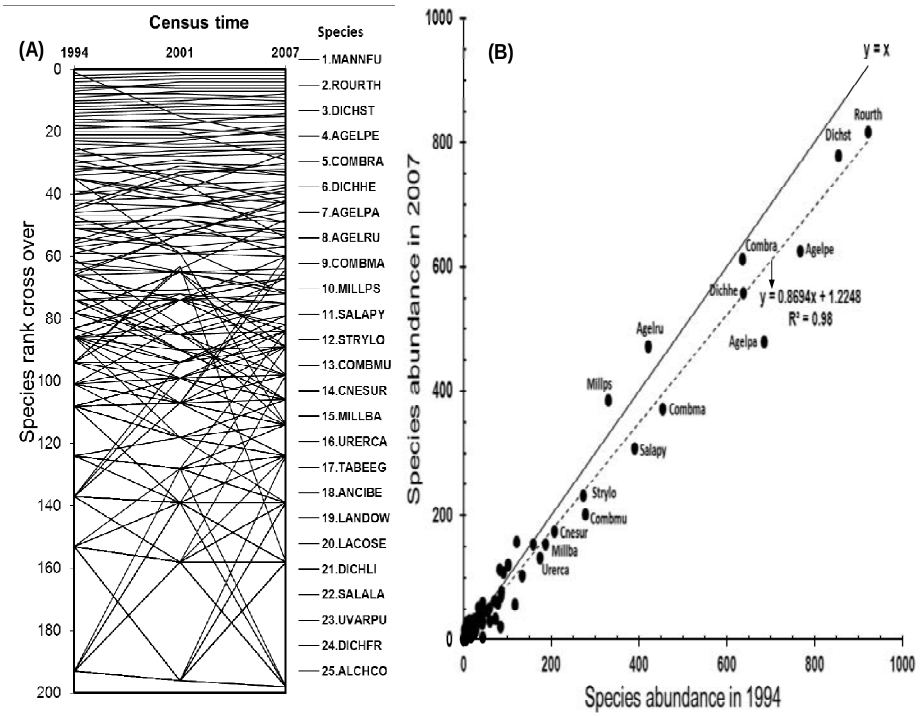

Figure 4.6. (A) Species abundance ranks in 1994, 2001 and 2007, and changes therein. Each line connects the rank of one species over time. (B) Relationship between abundance in 1994 and 2007 of 211 liana species in Ituri Forest (*Manniophyton fulvum* is excluded).

## DISCUSSION

This study analyzed the dynamics of liana species in a Congolese tropical mixed lowland forest. Although the whole liana population drastically declined over the 13-year period, responses appear to be very species specific. There was a wide interspecific variation in recruitment, growth and mortality rates, although most species had low to moderate rates. Recruitment and mortality rates were independent of density, but growth rates decreased with density. With the exception of the collapsing *Manniophyton fulvum* population, species maintained their rank-dominance over time. Based on demographic vital rates and selected functional traits species can be grouped into three functional guilds.

### *Patterns in species performance*

We expected that species would be normally distributed with respect to their abundance, and vital rates. However, none of these rates were normally distributed, and recruitment and mortality were clearly skewed to the right (Figure 4.1). In 2007, there is an increase of species in some of the intermediate abundances classes due to growth to higher size classes, and as a consequence, the number of rare species (i.e. with low abundance) decreased. Most common species tended to remain their relative rank in the community, with the exception of the initially strongly dominant *Manniophyton fulvum*. That declined tremendously in its absolute and relative abundance (Figure 4.6B).

We hypothesized that species mortality, recruitment and growth rates would be highly variable across species. Most of the species had low recruitment (<2%) and growth (<1 mm/ y), while mortality showed a peak between 2 and 3% (Figure 4.1D). Changes in species richness are affected by a number of demographic factors. Among such factors, recruitment and growth have a decisive influence to counterbalance populations and species richness in many cases (Harper 1977). This study has some similarities with other tropical forests, suggesting that our findings that liana diameter growth rates are typically low but variable among species corroborates with results reported in the Neotropical forests. In a 8-year monitoring of 15 species, Putz (1990) recorded an average annual species diameter growth rate of 1.4 mm in a Panamanian forest. Considering large lianas (dbh >10 cm), Ewers *et al*. (1991) registered on average 1.8 mm $y^{-1}$, but with many species represented only by single stem, over 13 year period in a Costa Rican forest. Putz (1990) also found that for a 3-year study period, species diameter growth ranged between 0.2 and 5.8 mm per year. Gerwing (2004) reported a mean annual diameter growth rate of 1.3 mm for the six species he studied, varying from 0.3 mm for the late successional *Memora* to 2.2 mm for the pioneer *Croton*. In a temperate forest, Allen *et al.* (1997) found a mean annual diameter increment of 1.3 mm for five liana species. Data on mortality rates are scarce. Putz (1990) reported mean annual mortality rates of 1.5% for climbing ramets and 0.3% for climbing genets of 15 species studied over 8 years. Gerwing (2004) found 6.7% mortality for ramets and 3.1% for genets. Mortality rates in the Ituri forest were substantially higher (average across species mean annual stem mortality rate of 2.76%; range 0.43–11%, with a maximum of 11% for *Urera*), may be because we did not differentiate between genets and ramets. Gerwing (2004) and Gilbert *et al.* (2006) concluded that lianas and trees exhibit broadly overlapping ranges in survival and relative growth rates. They also found large interspecific variation in liana mortality rates, and high diversity in life history strategies.

### *Are vital rates correlated?*

We hypothesized that the species vital rates would be highly correlated and that fast-growing species would die and recruit fast as well. Species growth was indeed positively, albeit weakly correlated to mortality and recruitment rate. Similarly, Gilbert *et al.* (2006) found for 22 Panamanian liana species a positive relation between growth and mortality rate, both at the seedling and the sapling stage. This relationship, also known as the growth-survival trade-off, has been widely found across tropical and temperate tree communities (e.g., Hubbell & Foster 1992, Kitajima 1992, Kobe 1996, Poorter & Bongers 2006), and is thought to represent an important demographic axis of variation, shaping the life history strategies of liana and tree species. It should be said that this trade-off is strongest in the smallest size classes, and disappears when plants grow taller, perhaps because they acquire all similar beneficial high light conditions, or because taller individuals are more robust against environmental hazards and show less mortality. The relatively weak growth-survival trade-off that we found in our study can be explained by the fact that vital rates have been calculated for relatively large individuals (between 2-10 cm dbh), of which most are already exposed to full light in the canopy.

Species co-occurring within a community often show a wide variation in demographic vital rates, as demonstrated by long-term community dynamics studies in permanent tropical forests plots (e.g. Condit *et al.*1995, Gerwing 2004, Nascimento *et al.* 2005, Swaine *et al.* 1987). In our study, species mortality rate was not related to recruitment rate (Figure 4.2C), indicating that individual species populations are not in equilibrium, and that some species should be increasing in abundance, while others decrease. Yet, given that the majority of the species have low to intermediate recruitment and mortality rates, these changes should go relatively slow. In our forest the species populations were quite stable: species abundances were constant over time and species ranks were concordant for the two periods of this study (Figure 4.6A). The only species showing dramatic changes is the single, most dominant species, *Manniophyton fulvum*, comprising as much as 24% of the stems in the liana community, and without that one, species populations are in equilibrium (Figure 4.6B).

### *Are vital rates dependent on species abundance?*

We predicted that density-dependence processes would keep the most abundant species under control in this forest, and that survival, growth, and recruitment should be lower in common (here relatively abundant) species compared to rare ones. Species growth indeed declines with species abundance, while recruitment and mortality rates were not significantly related to abundance, although abundance may set an upper limit to the recruitment and mortality rates that are possible (i.e., the upper right corners in the graphs are empty, Figure 4.3). This is a slightly counterintuitive result, because one might expect that if density-dependence is important, that it first should affect survival (Comita & Hubbell 2009) and recruitment (Harms *et al.* 2000), rather than growth. The trade-off between vital rates and abundance can therefore not explain dynamics in species abundance over time. Although we analyzed a relatively long time window (13 years), vital rates may still change over time, and the initial abundance values may be the result of different vital rates in the past. For example, current low recruitment values may results from dispersal limitation in the recent past (Tilman 1994, Hurtt and Pacala 1995, Hubbell 1997). Such discordance over time may lead to the absence of correlations between current recruitment and current abundance of older stages (Connell *et al*. 1977, Connell 1978, Warner and Hughes 1988).

### *Do functional traits matter?*

We further predicted that groups of liana species that differed in functional traits would also differ in their demographic vital rates. Some functional traits were indeed found as being characteristic for species with certain vital rates and thus to drive species dynamics. Dispersal groups differed in mortality and growth, but not in recruitment. Climbing strategies showed such relationships, but leaf size and, surprisingly, light requirements, did not. Our results suggest that for larger individuals of old-growth forest lianas their climbing strategies are more important in terms of reaching the canopy than their light requirements: from 2 cm dbh onwards most species were adult and exposed in the canopy already and thus do not compete for light anymore (C.E.N. Ewango, unpublished data). Light seems to be more important for seedling establishment, growth and mortality (Welden *et al.* 1991; Nabe-Nielsen 2002).

Based on the fifteen demographic and functional variables we evaluated, liana species are separated along two main axes of variation: one axis characterized by light requirement and one axis by seed dispersal (Figure 4.5A). In fact, having tendrils appeared to be correlated to high growth rates, while being a root climbing is correlated to mortality. Our PCA analyses discriminated species into three relatively discrete clusters, based on the first two axes. Thus, our results reflects the importance of the joined influences of the dispersal mechanisms and light requirement in which individuals are found, and not so much with vital rates in different environments. Furthermore, there is a variation among species in growth and mortality rates of climbing stems that may correlate with habitat affinity. For instance, later successional species of lianas appear to have lower growth and mortality rates than those associated with early successional forest in the eastern Brazilian Amazon old-growth forest (Gerwing 2004). Such trade-offs in life history strategies can contribute to species coexistence and the maintenance of local diversity (Bonsall *et al.* 2004).

### *Concluding remarks*

In conclusion, old-growth tropical forest lianas show a wide variation in species-specific abundance: most species are rare and only few are very common. Except for one extremely abundant species, the Ituri forest liana species are relatively stable in their dominance ranking. Only three species entered the community over a 13-year period. The liana stand as a whole is indeed highly dynamic, which is in line with earlier studies in the Neotropics (Phillips *et al.* 2005, Wright *et al.* 2004, Ingwell *et al.* 2010). However, in contrast to the strong increase in lianas in other forests, overall liana abundance in the Ituri forest collapsed. Individual species may respond differently to such environmental changes, and further research should examine species' vital rates across environments.

Density-dependent mechanisms regulating the dynamic equilibrium in dominance across common and rare lianas are insufficient to explain species abundance. Other factors, such as disturbance, habitat association, canopy structure and topography, and soil pathogens (Nabe-Nielsen 2002, Mangan *et al. 2010*) also determine species performance and need to be considered to explain the high diversity and dynamics of old-growth tropical forest lianas.

# Chapter 5

## Pervasive decline in density of liana species in a Congolese rainforest

*Corneille E.N. Ewango, Frans Bongers & Lourens Poorter*

## ABSTRACT

Lianas are thought to increase globally in density, but we have limited knowledge about the taxonomic patterns of change in liana abundance, and the underlying vital rates that explain changes in liana density. In this study the abundance of 79 relatively abundant liana species has been monitored for 13 years in 20 ha of undisturbed old-growth forest in the Ituri Forest, in the northeastern Congo basin in DR Congo. Here we show that the Ituri forest experienced a pervasive change in liana population density in the last decade. We found that 37 species changed significantly in their abundance over time; 12 (15% of total) species increased and 25 (32%) species decreased. 42 (53%) species did not change significantly. Of the 48 genera, 40% decreased, 8% increased and 52% stayed the same. Five of the 12 increasing species belonged to the Celastraceae, which also was the only significantly increasing family, and 39% of the families decreased. Surprisingly, none of the four functional traits analyzed (lifetime light requirements, climbing mechanism, dispersal mechanism, and leaf size) was significantly associated with species change in population density. A close examination at species level, however, revealed that many of the decreasing species are associated with disturbed habitats and that many of the increasing species are late successional and short-lived. Our results suggest that the liana community is recovering from past disturbances. Rising atmospheric $CO_2$ level is not a likely explanation for liana change, because more species were declining than increasing, and increasing species did not have higher growth rates. In this forest local stand dynamics override more global drivers of liana change.

**Key words:** Lianas, Population change, Growth, Mortality, Recruitment, Functional traits, Ituri Forest, Random drift

## INTRODUCTION

Recent studies suggest that tropical forests have become more dynamic over the past decades, with an increase in tree growth, mortality, and turnover (Phillips and Gentry 1994, Wright 2005, Lewis et al. 2009) and directional changes in genus composition (Laurence et al. 2004). Such changes have been attributed to global increases in atmospheric $CO_2$ concentrations (Lewis et al. 2009, Rozendaal et al. 2010), fire-derived nutrient deposition (Artaxo et al. 2003), reduced cloud cover (Graham et al. 2003) and increased forest disturbance (Laurance *et al.* 2001). If true, such changes in tree communities may have large consequences for ecosystem productivity and carbon storage, and cascading effects on pollinators, herbivores, and symbiotic fungi that are often highly specialized on these tree species.

In documenting these changes, lianas or woody climbers have often been overlooked, despite the fact that they are a conspicuous component of tropical forest ecosystems, typically comprising between 15% and 45% of the woody individuals and species (Gentry 1991, Pérez-Salicrup *et al.* 2001, Schnitzer 2005) and contributing up to 40% of forest leaf area and leaf productivity (Hegarty & Caballé 1991, Wright *et al.* 2004). Lianas have often been overlooked, perhaps because they are more difficult to measure (Gerwing *et al.* 2004, Parren *et al.* 2005)), and good long-term data are lacking. This is surprising, as especially lianas are thought to respond to increased atmospheric $CO_2$ concentrations because of their fast inherent growth rates, and to respond to increased disturbance because of their high light requirements (Hegarty & Caballé 1991, Laurance *et al.* 2001), although the putative increase of lianas in forest ecosystems and the potential influence of $CO_2$ in explaining it are both controversial (Mohan *et al.* 2006).

Recent increases in stand-wide liana density and basal area (Phillips *et al.* 2002) and liana litter production (Wright *et al.* 2004) have been reported for tropical forests in Latin America and for temperate forests in North America (Allen *et al.* 2007, but see Londré & Schnitzer 2006). However, comparable studies for African forests are near to absent (there is only one study); despite the fact that African forests represent one-third of the remaining tropical forest blocks in the world. The Congo Basin rainforests is the world's second largest expanse of forest (with an estimated total area of 200 million hectares) accounting for 26% of the world's tropical rainforest. Caballé and Martin (2001) found that liana density in a Gabonese rainforest declined over a 13 year period, which suggests that the Neotropical findings can not easily be extended to other continents, or that this African forest is a special case. Many authors have suggested that African old-growth forests are undergoing recovery of past natural and large-scale anthropogenic disturbances (Richards 1952, Fairhead & Leach 1998, van Gemerden *et al.* 2003, Lewis *et al.* 2009). Most studies that documented changes in liana abundance did so at the stand level, and evaluated the largest individuals (>10 cm in stem diameter) only (e.g., Phillips et al. 2002), or inferred liana abundance from leaf litter production (Wright et al. 2004). However, no studies have examined so far whether changes in liana abundance are pervasive and occur among many distant taxa, what liana species are changing in abundance and why. Such changes in liana abundance are not readily attributable to a single cause, and life-history features, vital rates, and functional traits may shape species responses to environmental change and give insight into the ecological determinants of species change.

Despite increasing attention from researchers, the ecology of lianas is in many aspects still poorly understood. Particularly limited is our knowledge about taxonomic patterns of liana change in abundance and dynamics. In this study the abundance of 79 most numerous liana species has been monitored for 13-year in 20 ha of mixed old-growth forest in the northeastern Congo basin forest. We examined population trends of species and changes in liana abundance were related to their underlying vital rates (growth, recruitment, mortality) and functional traits (i.e., light requirements, climbing mechanism, dispersal mechanism, and leaf size). We hypothesized that there are pervasive changes in population density of lianas, and that these changes occur across many different taxa (i.e., species, genera, and families). We also expect increases in liana density to be driven by recruitment and mortality rather than growth, as these vital rates have a direct impact on population size. We predicted that increasing species will have larger leaf size as large leaves are more efficient in terms of light capture, and will have a twining climbing mechanism, as twining species reach the canopy faster and thus have faster access to favourable high light conditions. Decreasing species are expected to be light demanding as with time forests generally get darker.

## MATERIALS AND METHODS

### *Study area and data collection*

The study was carried out in lowland tropical forest on the Ituri Forest Dynamics Plots of Edoro Field Research Station, northeastern Democratic Republic of Congo. Detailed descriptions of the vegetation, fauna, and climate of Edoro terrain can be found in Hart (1985), Makana *et al.* (2004), and Ewango *et al.* (subm.: chap II of this thesis). Two 10-ha plot in old-growth mixed forest where established in 1994 (Makana *et al.* 1998, 2004). All liana ≥ 2 cm diameter at breast height (dbh) were tagged, mapped, identified. The diameter of each stem was measured at diameter at breast height, i.e. at 130 cm or from a rooting point unless there were trunk irregularities at the measurement point, in which case the measurement was taken at a nearest lower/upper point where the stem was cylindrical (Makana *et al.*1998, see also Gerwing *et al.* 2006). In 2001 and 2007 these plots were recensused, and all individuals alive from the previous censuses were re-measured and newly recruited individuals were recorded and measured following the same criteria as used in 1994. For the present paper, we use data from the first (1994) and last (2007) census, to provide a long-term (13 years) perspective on population change.

### *Species selection and functional traits*

Only those taxa were included that had at least 10 stems in 1994, to ensure robust statistical power, and to have a sufficient sample size to estimate mortality and growth rates. We thus calculated annualized recruitment, mortality and growth rates for the period 1994 to 2007 for 79 species (38% of all species) with ≥ 10 individuals.

To get insight what species are changing in abundance and why, we described the species based on four functional traits that are important for liana performance and were compiled from a variety of published primary literature (Evrard 1968, Bongers *et al.* 2005). The climbing mechanism (hook, tendril, twiner and root), indicates how quickly and with what investment species access the canopy. The life light requirement (light demanding and shade tolerant) indicate whether species need disturbances or not for the completion of their life cycle. The dispersal syndrome (animal-dispersed: zoochory, explosive: barochory, and wind-dispersed: anemochory) is an indicator of the potential dispersal distance. Leaf size (small: $\leq 20\ \text{cm}^2$ or large: $> 20\ \text{cm}^2$) is important for light capture and the regulation of the heat balance of the plant.

### *Calculation of vital rates*

To estimate the dynamics underlying population change, we calculated species vital rates in terms of growth, mortality, and recruitment. The annual diameter growth D was calculated as: $D = (dbh_2 - dbh_1) / (t_2 - t_1)$, where dbh and t refers to the diameter of the individuals and time at the initial and the final census, respectively.

The annualized mortality rate was calculated as $m = (\ln N_1 - \ln S_2) / (t_2 - t_1)$, while recruitment rate $r = (\ln N_1 - \ln S_2) / (t_2 - t_1)$ is the number of individuals recruiting in the interval between 1994 and 2007; in which N and S refers to number of individuals and survivors at each census period t, and *ln* stands for the natural logarithm (Harper 1977, Swaine & Lieberman 1987, Condit 1999). The time interval spanned by a species was defined as the arithmetic mean time between censuses for individuals of that species, based on the census data of each 20 x 20 m quadrat in the plots. To examine the change in population density and trend for each taxon (species, genus, or family) we calculated the ratio ($\lambda$) of species abundance in 2007 ($N_2$) over abundance in 1994 ($N_1$). Thus, a ratio > 1 indicates an increase, < 1 a decrease, whereas a ratio equal to one indicates a constant population.

### *Statistical analyses*

We estimated confidence limits for $\lambda$ of each species using bootstrapping. The census plots were divided in 20 1-ha plots. Randomly (with replacement) 20 1-ha plots were drawn from these 20 plots and the cumulative abundance of these plots in 2007 were divided by the cumulative abundance in 1994. This value represents the bootstrapped $\lambda$ of the species. We repeated this procedure a thousand times, which gives the confidence interval for that species (the 25th and 975th ranking values of $\lambda$ give the 95% confidence interval. If the confidence interval does not include $\lambda = 1$ then the species significantly changed in abundance. Additional to 95% confidence limits also 99% confidence limits were determined (the 5th and 995th ranking value of $\lambda$) to have a more conservative evaluation of species level changes in abundance. We used a one-way ANOVA to test whether decreasing, constant, and increasing species differed in their vital rates, and used $\chi^2$ tests to test whether increasing and decreasing taxa differed in their functional traits. All analyses were performed with PASW Statistics 17 (SPSS 17) for windows (SPSS Inc.).

## RESULTS

### *Taxonomic changes in abundance*

We recorded 13391 stems (in 1994) for the 79 relatively abundant identified liana species, taxonomically distributed among 48 genera and 23 families (Appendix 5.1). The average $\lambda$ across species was 0.70, and ranged from 0.03 for *Manniophyton fulvum* to 2.77 for *Monanthotaxis lucidula*. Of the 79 species considered, 37 species changed significantly in their abundance over time, which is nine times higher than expected by chance (using a P level of 0.05 we expected that 4 of the 79 species would show a significant change). 12 (15% of total) species increased, 25 (32%) species decreased and 42 (53%) species did not change significantly. Five of the 12 increasing species belonged to the Celastraceae. Typical decreasing species were *Manniophyton fulvum* (0.03) and *Piper guineensis* (0.09). The more conservative P level of 0.01, still resulted in 23 species (29% of the total) with a significant change in abundance; 6 increasing species and 17 decreasing species (Table 5.1).

Table 5.1. Increasing or decreasing liana taxa (species, genus, or family) in Ituri forest, with the ratio of change between 1994 and 2007, expressed as density in 2007 over the density in 1994. The level of significance (P) indicates whether the ratio differs from 1, as determined by bootstrap tests. * P<0.05, ** P <0.01.

| **Liana density increasing over time** | | | | **Liana density decreasing over time** | | | |
|---|---|---|---|---|---|---|---|
| ***Species*** | ***Family*** | ***Ratio*** | ***P*** | ***Species*** | ***Family*** | ***Ratio*** | ***P*** |
| Monanthotaxis lucidula | Annon- | 2.77 | * | Bequaertia mucronata | Celastr- | 0.94 | ** |
| Salacia cerasifera | Celastr- | 2.21 | ** | Rourea thomsonii | Connar- | 0.93 | ** |
| Campylostem bequaertii | Celastr- | 1.61 | ** | Landolphia sp | Apocyn- | 0.87 | ** |
| Salacia elegans | Celastr- | 1.56 | * | Agelaea rubiginosa | Connar- | 0.85 | ** |
| Landolphia owariensis | Apocyn- | 1.43 | ** | Agelaea pentagyna | Connar- | 0.83 | ** |
| L. incerta | Apocyn- | 1.40 | ** | Clitandra cymulosa | Apocyn- | 0.81 | * |
| Salacia kivuensis | Celastr- | 1.40 | * | Millettia psilopetala | Fabaacea | 0.8 | ** |
| Leptoderris congolensis | Fabaceae | 1.39 | ** | Illigera pentaphylla | Hernandi- | 0.8 | * |
| Salacia laurentii | Celastr- | 1.22 | ** | Ancistrocarpus bequaertii | Malvaceae | 0.78 | * |
| Salacia pyriformioides | Celastr- | 1.20 | * | Combretum racemosum | Combret- | 0.75 | * |
| Combretum marginatum | Combret- | 1.17 | * | Ancylobotrys scandens | Apocyn- | 0.75 | ** |
| Dichapetalum librevillense | Dichapetal- | 1.10 | * | Hugonia platysepala | Linaceae | 0.7 | * |
| | | | | Landolphia sp4 | Apocyn- | 0.64 | * |
| | | | | Strychnos longicaudata | Logani- | 0.6 | ** |
| | | | | Baphia spathacea | Fabaceae | 0.6 | ** |
| | | | | Cnestis urens | Connar- | 0.59 | ** |
| | | | | Plukenetia conophorum | Euphorbi- | 0.55 | ** |
| | | | | Vitex thyrsiflora | Lamiaceae | 0.55 | * |
| | | | | Laccosperma secundiflorum | Arecaceae | 0.52 | ** |
| | | | | Uncaria africana | Rubiaceae | 0.52 | ** |
| | | | | Cissus producta | Vitaceae | 0.48 | ** |
| | | | | Orthopichonia seretii | Apocyn- | 0.43 | ** |
| | | | | Sherbournia bignoniiflora | Rubiaceae | 0.36 | * |
| | | | | Piper guineensis | Piperaceae | 0.09 | ** |
| | | | | M. fulvum | Euphorbi- | 0.03 | ** |

| ***Genus*** | ***Ratio*** | ***P*** | ***Genus*** | ***Ratio*** | ***P*** |
|---|---|---|---|---|---|
| Baissea | 2.90 | ** | Rourea | 0.94 | * |
| Salacia | 1.29 | ** | Cnestis | 0.91 | ** |
| Landolphia | 1.18 | ** | Agelaea | 0.89 | ** |
| Leptoderris | 1.12 | ** | Strychnos | 0.82 | ** |
| | | | Clitandra | 0.81 | * |
| | | | Millettia | 0.81 | ** |
| | | | Ancistrocarpus | 0.78 | * |
| | | | Hugonia | 0.73 | * |
| | | | Orthopichonia | 0.66 | ** |
| | | | Bequaertia | 0.61 | ** |
| | | | Baphia | 0.6 | ** |
| | | | Plukenetia | 0.55 | ** |
| | | | Ancylobotrys | 0.52 | ** |
| | | | Laccosperma | 0.52 | * |
| | | | Uncaria | 0.52 | * |
| | | | Vitex | 0.5 | * |
| | | | Illigera | 0.4 | * |
| | | | Piper | 0.09 | ** |
| | | | Manniophyton | 0.03 | ** |
| ***Family*** | ***Ratio*** | ***P*** | ***Family*** | ***Ratio*** | ***P*** |
| Celastraceae | 1.25 | ** | Connaraceae | 0.91 | ** |
| | | | Fabaceae | 0.85 | ** |
| | | | Loganiaceae | 0.82 | ** |
| | | | Malvaceae | 0.79 | ** |
| | | | Linaceae | 0.73 | * |
| | | | Arecaceae | 0.52 | ** |
| | | | Hernandiaceae | 0.4 | * |
| | | | Piperaceae | 0.09 | ** |
| | | | Euphorbiaceae | 0.04 | ** |

Of the 48 genera evaluated, 8% increased significantly in abundance, 40% decreased and 52% stayed the same (Figure 5.1A, Table 5.1). *Baissea* (2.90) was the strongest increasing and *Manniophyton* (0.03) was the strongest decreasing genus. Of the 23 families evaluated, 4% increased significantly in abundance, 37% decreased and 59% stayed the same.

Celastraceae was the only increasing family, and Euphorbiaceae (0.04) and Piperaceae (0.09) were the strongest decreasing families.

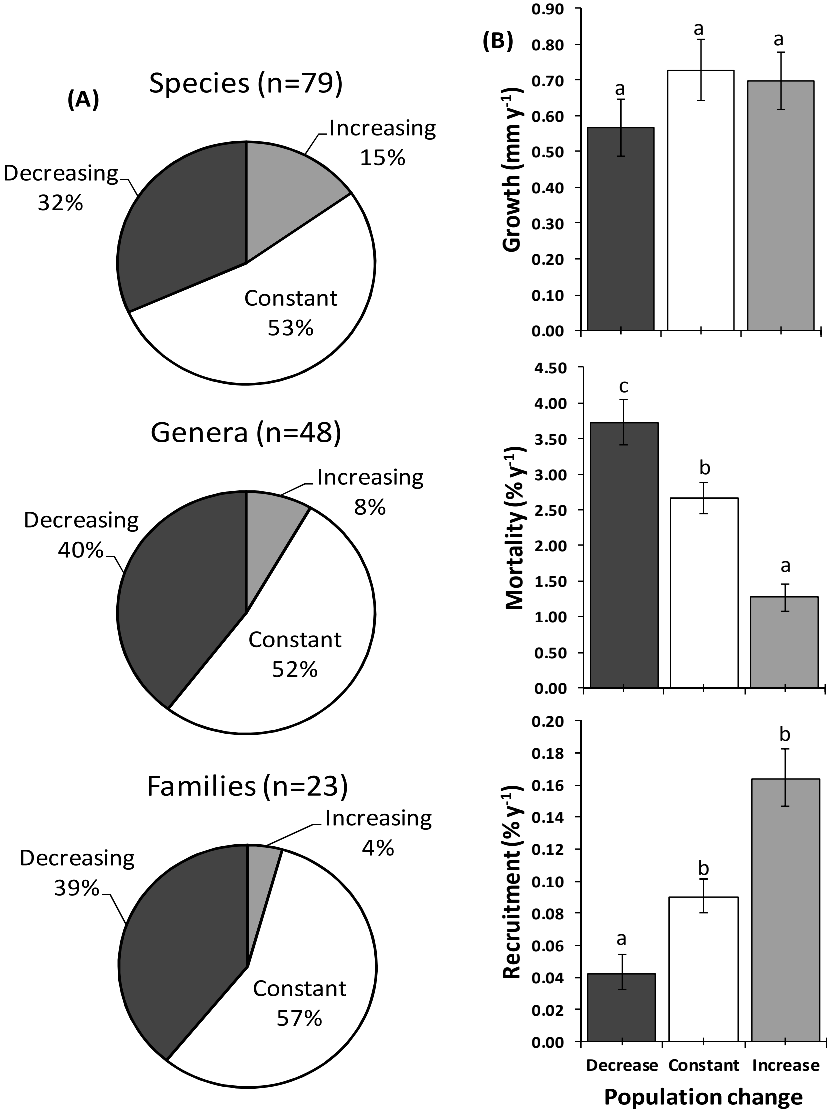

Figure 5.1. Frequency distribution of change (decreasing-, constant, increasing) in population size of liana taxa (species, genera, and families) during a 13 years period (A), vital rates (growth, mortality, recruitment) for species with decreasing, constant, and increasing populations (B). Bars represent means and standard errors. Bars accompanied by a different letter are significantly different at a P level of 0.05 (Tukey HSD post-hoc test).

### *Population change as function of species characteristics*

Increasing, decreasing, and constant species differed in their recruitment rates ($F_{2,76}$ = 10.32, P = 0.001) and mortality rates ($F_{2,76}$ = 13.05, P = 0.001), but not in their growth rates ($F_{2,76}$ = 0.89, P = 0.41). Increasing- (on average 0.16%/y) and constant species (0.09) had much higher recruitment rates than decreasing species (0.04, Figure 5.1). In contrast, decreasing species had much higher mortality rate (on average 3.73%/y) than constant (2.66) and increasing (1.27) species (Figure 5.1B).

None of the four functional traits (Table 5.2) was associated with species change (at P = 0.05) in population density ($\chi^2$<4.68, and P>0.19 in all cases). However, at a more conservative significance level of 0.01, the dispersal syndrome differed significantly between increasing and decreasing species ($\chi^2$ = 9.09, df = 4, P = 0.05): anemochorous species increased more than expected (2 increasing species observed versus 1 expected) and barochorous species decreased more than expected (4 observed versus 1.3 expected). Leaf size ($\chi^2$ = 5.26, df = 2, P = 0.07) was only weakly associated with species change.

Table 5.2. Results of contingency $\chi^2$ tests of number of species that have increased, decreased or stay equal against functional traits of these species. Species changes are based on conservative estimates of change (P < 0.05) and on very conservative estimates of change (P < 0.01). Climbing mechanisms are divided in four classes (Hook, tendril, twiner, root), dispersal syndrome in 3 classes (anemochory, barochory, zoochory), leaf size in 2 classes (large leaves, small leaves), and light requirement in 2 classes (light demanding and shade tolerant). $\chi^2$, degree of freedom (df) and significance level (P) are shown.

| Variables | $\chi^2$ | df | P |
|---|---|---|---|
| **Species changes (based on** P<0.05) against | | | |
| Climbing mechanisms | 4.24 | 6 | 0.64 |
| Dispersal syndrome | 4.68 | 4 | 0.32 |
| Leaf size | 3.28 | 2 | 0.19 |
| Light requirement | 1.05 | 2 | 5.59 |
| **Species change (based on** P<0.01) against | | | |
| Climbing mechanisms | 4.34 | 6 | 0.63 |
| Dispersal syndrome | 9.09 | 4 | 0.06 |
| Leaf size | 5.26 | 2 | 0.07 |
| Light requirement | 1.43 | 2 | 0.49 |

## DISCUSSION

This study set out to examine the abundance of 79 most representative liana species monitored for 13-year in 20 ha census plot in an old-growth forest. We found pervasive changes in population density for almost half of the species examined. Changes in liana abundance were related to their mortality and recruitment rates, and weakly to dispersal syndrome and leaf size.

### *Pervasive decreases in liana density in Ituri forest*

Our working hypothesis was that there would be pervasive changes in population density of lianas, and that these changes would occur across many different taxa. Our results support this hypothesis. The Ituri old-growth forest showed drastic changes in abundances of many species. Nearly half of the species (47%) showed a significant change in density, which is nine times higher than expected by chance. In contrast to one expectation, only 15% of all species increased in density, whereas 32% of the species decreased. A closer examination of the individual species reveals that nearly two-third of the changing species were associated with disturbed habitat types (e.g. old gaps and open canopy patches in the plots). Ecologically, decreasing species tend to be pioneers or early successional species (e.g., *Rourea thomsonii*, *Ancistrocarpus bequaertii*, *Cnestis urens*, *Hugonia platysepala*, *Manniophyton fulvum*), characterized by high mortality and low recruitment rates. These species do not regenerate anymore, suggesting that the forest is in a transition from an early- towards a later successional stage. These pioneer and late-successional species were distributed in different genera and or families recorded in the plots. Five of the 10 significantly changed families are among the most important liana families in African tropical forest (Jongkind & Hawthorne 2005), and may be changing in abundance all over Africa.

The evidence for pervasive changes is not only found at the species level, but also at the genus and family level (Figure 5.1). We expected changing taxa to be driven by recruitment and mortality rather than growth, as these vital rates have a direct impact on population size. Indeed, high mortality and low recruitment are the main causes of population changes for the increasing species, and vice versa for the decreasing species. Increasing and decreasing liana taxa did not have clear biological differences: their functional traits did not differ much. Decreasing barochorous species might have faced limitation in seed dispersal towards their suitable recruitment habitats. Surprisingly, lifetime light requirement was not of importance for population changes trends. Carrasco-Urra & Gianoli (2009) argued that climbing host characteristic, rather than light availability are important for liana success in old-growth forest. As species mortality and recruitment depend on many other environmental factors (e.g. topography, moisture, soil, and drought) it is perhaps difficult (if not elusive) to show strong links between rather soft species traits and population change.

Collectively observed trends suggest that the changing species and genera reflect two ecological patterns that are biologically distinct: 1) increasing species belong to a late successional group, with low growth and high persistence, and 2) decreasing species include many pioneers that are adapted to disturbances and are generally fast-growing and mass-dying. The growth rates of the two groups were not significantly different, maybe because most individuals of the species reached their maximum size, with overall slowed growth. In line with our findings, it is likely that species' dynamics and successional position would at least partially drive the observed changes in population density.

### *What are the external drivers of liana change?*

Lianas in the Neotropics and North America have been reported to increase (Phillips *et al.* 2002, Wright *et al.* 2004, Allen *et al.* 2007), while this study in Congo and the study by Caballé and Martin (2001) in Gabon show that lianas are decreasing in Africa. We believe that this observation is crucial for hypotheses regarding the generality of the drivers of pervasive changes in liana density.

Changes in liana density could be due to global increases in atmospheric $CO_2$ concentrations (Phillips *et al.* 2002) fire-derived nutrient deposition (Asner *et al.* 1997, Chen *et al.* 2010), droughts (Condit *et al.* 1995, Engelbrecht *et al.* 2005), forest disturbance (Laurance et al. 2001), global dimming (Stanhill & Cohen 2001, Feeley *et al.* 2007) or changes in liana density may also simply be a result of random drift (Hubbell 2001). The combined effects of increasing $CO_2$ and increasing N-depositions is likely to lead to high fertilization of lianas, and thus rapid growth and reproduction, resulting in increased liana abundance. This growth fertilization hypothesis is not likely to explain the observed changes, as growth did not differ among species groups (Fig. 1), and because liana populations are decreasing, not increasing. Global changes in liana density could also be due to global changes in rainfall patterns and increasing El Niño droughts (Holmgren *et al.*2001, Condit *et al.* 2004). Yet, neither this hypothesis is likely to explain our results, as the Ituri Forest did not experience strong droughts in the last two decades, and as lianas in our forest decreased rather than increased, as expected based upon their high abundance in drier regions (DeWalt et al. 2010, Toledo 2010) and their dry season growth advantage (Schnitzer 2005). Neutral theory and random drift are neither a likely explanation, as random changes would imply a similar amount of increasing and decreasing species, whereas in our community changes are clearly directional at all taxonomic levels: there are far more decreasing than increasing taxa at the species-, genus-, and family level (Figure 5.1).

Based on our results we believe that at least two phenomena more likely may account for the liana changes and the massive decline of the strongly dominant species. First, the observed changes might reflect more cloudy weather. Graham *et al.* (2003) argued that cloud cover, and thus reduced irradiance, limits net $CO_2$ uptake and growth of rainforest trees during tropical rainy seasons. Such a reduction in irradiance might have especially strong inhibiting effects on light-demanding lianas. Second, the observed changes might reflect forest recovery from past disturbances. This supports the alternative hypothesis that African tropical forest are recovering from past disturbances (Richards 1952, Whitmore & Burslem 1998), Recent studies showed such recovery for trees in tropical forest worldwide (Chave *et al.* 2008, Laurance *et al.* 2004). Forest recovery over time after disturbance is generally accompanied by shifts in species composition. Our forest stand clearly shows such changes in taxonomic composition, with more persistent liana taxa characteristic of undisturbed forest. For the Ituri Forest we believe the most likely cause of liana decrease is the recovery from past disturbances. This is also indicated by a general lack of large sized lianas (chapter 2) in the plots, generally considered being a good indicator of past disturbances in Ituri Forest. Either the global drivers are less important than previously thought for explaining changes in liana abundance, or local stand dynamics override the more global drivers of liana change. Whether or not our findings represent a general phenomenon needs to be studied in detail by extending the species level changes in liana abundance for a large number of sites across a wide array of local conditions.

Appendix 5.1. Species density ratio, bootstrap percentile, significance levels, vital rates, and functional attributes showing increasing or decreasing population change in Ituri old-growth mixed forest plots. Dispersal syndrome (Anemo-, Baro-, Zoochory). Life light requirement (LD = light demanding, ST = Shade tolerant). Climbing = climbing strategy (Ho = hook, Te = tendril, Tw = twiner, Ro = root). Leaf size (L = large, S = small). The list is alphabeticaly ordered by family and species scientific name. + indicates a significantly increasing species, – a significantly decreasing one. 0 indicates no significant change.

| Family | Species scientific name | Density ratio | Percentile 0.5 | Percentile 2.5 | Percentile 97.5 | Percentile 99.5 | Change $P < 0.05$ | Change $P < 0.01$ | Growth (mm/y) | Mortality (%/ y) | Recruitment (%/ y) | Dispersal syndrome | Light requirement | Climbing strategy | Leaf Size |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Anacardiaceae | Trichoscypha reygaertii | 0.77 | 0.44 | 0.50 | 1.10 | 1.17 | 0 | 0 | 0.56 | 2.49 | 0.08 | Zoo- | ST | Tw | L |
| Annonaceae | Friesoldielsa enghiana | 1.18 | 0.42 | 0.58 | 1.17 | 1.67 | 0 | 0 | 0.33 | 2.56 | 0.17 | Zoo- | LD | Tw | L |
|  | Monanthotaxis cauliflora | 1.12 | 0.43 | 0.48 | 1.40 | 1.60 | 0 | 0 | 0.33 | 3.42 | 0.05 | Zoo- | LD | Tw | L |
|  | Monanthotaxis ferruginea | 1.50 | 0.64 | 0.71 | 1.56 | 1.70 | 0 | 0 | 0.70 | 2.2 | 0.09 | Zoo- | LD | Tw | L |
|  | Monanthotaxis foliosa | 1.28 | 0.77 | 0.86 | 1.93 | 1.30 | 0 | 0 | 0.52 | 2.69 | 0.2 | Zoo- | LD | Tw | L |
|  | Monanthotaxis lucidula | 2.77 | 0.96 | 1.08 | 1.33 | 1.80 | + | 0 | 0.27 | 2.34 | 0.26 | Zoo- | LD | Tw | L |
|  | Monanthotaxis schweinfurthii | 0.64 | 0.00 | 0.17 | 1.17 | 1.40 | 0 | 0 | 0.37 | 3.85 | 0.06 | Zoo- | ST | Tw | L |
|  | Uvaria pulchra | 0.92 | 0.67 | 0.71 | 1.10 | 1.19 | 0 | 0 | 0.41 | 2.33 | 0.08 | Zoo- | LD | Tw | L |
| Apocynaceae | Alafia lucida | 0.90 | 0.42 | 0.50 | 1.80 | 5.00 | 0 | 0 | 1.04 | 3.85 | 0.17 | Anemo- | LD | Tw | L |
|  | Ancylobotrys scadens | 0.75 | 0.19 | 0.15 | 0.67 | 0.75 | - | - | 0.59 | 4.14 | 0 | Zoo- | LD | Te | L |
|  | CLitandra cymulosa | 0.81 | 0.61 | 0.65 | 0.99 | 1.03 | - | 0 | 0.75 | 2.86 | 0.07 | Zoo- | LD | Te | L |
|  | Landolphia forsterii | 1.25 | 0.82 | 0.93 | 1.33 | 3.15 | 0 | 0 | 1.11 | 1.44 | 0.14 | Zoo- | LD | Te | L |
|  | Landolphia incerta | 1.40 | 1.09 | 1.16 | 1.71 | 1.88 | + | + | 0.51 | 0.56 | 0.13 | Zoo- | LD | Te | S |

| | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Landolphia ligustrifolia | 0.70 | 0.50 | 0.50 | 1.50 | 0.00 | 0 | 0 | 0.70 | 3.08 | 0.06 | Zoo- | LD | Te | S |
| | Landolphia mannii | 1.00 | 0.60 | 0.67 | 1.00 | 1.00 | 0 | 0 | 0.78 | 0.64 | 0 | Zoo- | LD | Te | L |
| | Landolphia owariensis | 1.43 | 1.10 | 1.14 | 1.58 | 1.69 | + | + | 0.94 | 1.4 | 0.15 | Zoo- | LD | Te | S |
| | Landolphia sp | 0.87 | 0.17 | 0.17 | 0.78 | 0.84 | - | - | 1.03 | 4.31 | 0.05 | Zoo- | LD | Te | S |
| | Landolphia sp4 | 0.64 | 0.00 | 0.38 | 0.89 | 1.00 | - | 0 | 0.58 | 2.75 | 0 | Zoo- | LD | Te | L |
| Apocynaceae | Orthopichonia seretii | 0.43 | 0.41 | 0.47 | 0.82 | 0.87 | - | - | 0.64 | 3.15 | 0.03 | Zoo- | LD | Tw | S |
| | Tabernaemontana eglandulosa | 1.00 | 0.74 | 0.79 | 1.17 | 1.36 | 0 | 0 | 0.27 | 3 | 0.16 | Zoo- | LD | Tw | L |
| Arecaceae | Laccosperma secundiflorum | 0.52 | 0.11 | 0.18 | 0.85 | 0.93 | - | - | -0.03 | 5.06 | 0.12 | Zoo- | LD | Ho | L |
| Celastraceae | Bequaertia mucronata | 0.94 | 0.36 | 0.44 | 0.76 | 0.83 | - | - | 0.47 | 3.02 | 0 | Anemo- | LD | Tw | S |
| | Campylostemon bequaertii | 1.61 | 1.06 | 1.18 | 1.11 | 1.54 | + | + | 0.63 | 0.43 | 0.19 | Anemo- | LD | Tw | S |
| | Loeseneriella apiculata | 1.27 | 0.50 | 0.67 | 1.15 | 4.00 | 0 | 0 | 0.91 | 0.7 | 0.11 | Anemo- | LD | Tw | L |
| | Salacia cerasifera | 2.21 | 1.16 | 1.40 | 5.00 | 7.00 | + | + | 0.97 | 0.55 | 0.3 | Zoo- | LD | Tw | S |
| | Salacia elegans | 1.56 | 0.92 | 1.02 | 1.57 | 3.17 | + | 0 | 0.81 | 1.81 | 0.24 | Zoo- | ST | Tw | S |
| | Salacia kivuensis | 1.40 | 1.00 | 1.07 | 3.67 | 9.00 | + | 0 | 1.10 | 0.77 | 0.14 | Zoo- | LD | Tw | L |
| | Salacia laurentii | 1.22 | 1.04 | 1.07 | 1.56 | 1.73 | + | + | 0.57 | 1.35 | 0.13 | Zoo- | LD | Tw | L |
| | Salacia pyriformioides | 1.20 | 0.99 | 1.02 | 1.49 | 1.62 | + | 0 | 0.41 | 1.59 | 0.13 | Zoo- | ST | Tw | L |
| Combretaceae | Combretum cuspidatum | 1.04 | 0.70 | 0.79 | 1.51 | 1.81 | 0 | 0 | 0.90 | 2.68 | 0.15 | Anemo- | LD | Tw | L |
| | Combretum marginatum | 1.17 | 1.00 | 1.03 | 1.18 | 1.33 | + | 0 | 1.03 | 1.85 | 0.13 | Anemo- | LD | Tw | S |
| | Combretum mortehanii | 0.56 | 0.75 | 0.82 | 1.62 | 1.91 | 0 | 0 | 0.72 | 1.71 | 0.13 | Anemo- | LD | Tw | S |
| | Combretum multiflorum | 0.87 | 0.82 | 0.84 | 1.02 | 1.06 | 0 | 0 | 0.46 | 2.7 | 0.09 | Anemo- | LD | Tw | S |
| | Combretum racemosum | 0.75 | 0.60 | 0.65 | 0.96 | 1.09 | - | 0 | 0.27 | 4.22 | 0.15 | Anemo- | LD | Tw | L |
| Connaraceae | Agelaea paradoxa | 0.96 | 0.90 | 0.91 | 1.05 | 1.07 | 0 | 0 | 0.38 | 1.69 | 0.07 | Zoo- | LD | Tw | L |

| | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Connaraceae | Agelaea pentagyna | 0.83 | 0.76 | 0.78 | 0.89 | 0.91 | - | - | 0.51 | 2.15 | 0.04 | Zoo- | LD | Tw | L |
| | Agelaea rubiginosa | 0.85 | 0.78 | 0.79 | 0.94 | 0.99 | - | - | 0.60 | 2.29 | 0.05 | Zoo- | LD | Tw | L |
| | Cnestis urens | 0.59 | 0.77 | 0.80 | 0.95 | 0.97 | - | - | 0.29 | 1.97 | 0.04 | Zoo- | LD | Tw | S |
| | Connarus griffonianus | 1.06 | 0.62 | 0.74 | 1.50 | 1.67 | 0 | 0 | 0.19 | 1.44 | 0.07 | Zoo- | LD | Tw | L |
| | Manotes expensa | 1.10 | 0.86 | 0.91 | 1.30 | 1.41 | 0 | 0 | 0.48 | 0.96 | 0.07 | Zoo- | LD | Tw | L |
| | Rourea parviflora | 2.00 | 0.76 | 0.83 | 1.41 | 1.67 | 0 | 0 | 1.31 | 1.1 | 0.07 | Zoo- | LD | Tw | L |
| | Rourea thomsonii | 0.93 | 0.85 | 0.87 | 0.98 | 0.99 | - | - | 0.38 | 2.15 | 0.07 | Zoo- | LD | Tw | L |
| Dichapetalaceae | Dichapetalum afzelii | 1.00 | 0.84 | 0.86 | 1.11 | 1.19 | 0 | 0 | 0.46 | 1.58 | 0.08 | Zoo- | ST | Tw | S |
| | Dichapetalum fructuosum | 0.86 | 0.67 | 0.75 | 1.00 | 1.14 | 0 | 0 | 0.28 | 1.99 | 0.03 | Zoo- | ST | Tw | S |
| | Dichapetalum heudelotii | 0.95 | 0.84 | 0.87 | 1.05 | 1.08 | 0 | 0 | 0.24 | 1.92 | 0.05 | Zoo- | ST | Tw | L |
| | Dichapetalum librevillense | 1.10 | 0.97 | 1.04 | 1.39 | 1.48 | + | 0 | 0.42 | 0.68 | 0.08 | Zoo- | ST | Tw | L |
| | Dichapetalum mombuttense | 1.53 | 0.33 | 0.62 | 1.40 | 3.67 | 0 | 0 | 0.36 | 2.56 | 0.1 | Zoo- | ST | Tw | L |
| | Dichapetalum staudtii | 0.95 | 0.85 | 0.87 | 1.02 | 1.06 | 0 | 0 | 0.38 | 1.9 | 0.07 | Zoo- | ST | Tw | S |
| Dilleniaceae | Tetracera alnifolia | 1.57 | 0.50 | 0.62 | 1.19 | 1.42 | 0 | 0 | 0.34 | 2.56 | 0.09 | Zoo- | LD | Tw | L |
| Euphorbiaceae | Alchornea cordifolia | 0.13 | 0.08 | 0.09 | 1.00 | 1.50 | 0 | 0 | 1.29 | 6.23 | 0.1 | Zoo- | LD | Tw | L |
| | Macaranga angolensis | 1.25 | 0.60 | 0.60 | 1.67 | 0.00 | 0 | 0 | 0.95 | 2.96 | 0.07 | Zoo- | LD | Tw | L |
| | Manniophyton fulvum | 0.03 | 0.02 | 0.01 | 0.04 | 0.04 | - | - | 0.32 | 7.59 | 0.21 | Baro- | ST | Tw | L |
| | Plukkenettia conophorum | 0.55 | 0.11 | 0.15 | 0.80 | 0.92 | - | - | 1.11 | 5.59 | 0.15 | Baro- | LD | Tw | S |
| Fabaceae | Baphia spathacea | 0.60 | 0.31 | 0.40 | 0.68 | 0.71 | - | - | 0.40 | 3.04 | 0 | Baro- | LD | Tw | L |
| | Entada gigas | 1.10 | 0.33 | 0.33 | 1.50 | 1.57 | 0 | 0 | 3.51 | 4.62 | 0.38 | Baro- | LD | Te | S |
| | Leptoderris congolensis | 1.39 | 1.07 | 1.19 | 1.38 | 3.67 | + | + | 0.71 | 1.92 | 0.21 | Anemo- | LD | Tw | L |
| | Leptoderris ferrugineus | 0.91 | 0.80 | 0.84 | 1.15 | 1.57 | 0 | 0 | 0.41 | 1.99 | 0.05 | Anemo- | LD | Tw | L |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Fabaceae | Millettia barterii | 0.83 | 0.71 | 0.73 | 1.00 | 1.33 | 0 | 0 | 0.89 | 2.43 | 0.07 | Baro- | LD | Tw | L |
| | Millettia psilopetala | 0.80 | 0.73 | 0.75 | 0.87 | 0.90 | - | - | 0.26 | 1.95 | 0.02 | Baro- | ST | Tw | L |
| Hernandiaceae | Illigera pentaphylla | 0.80 | 0.00 | 0.11 | 0.88 | 1.12 | - | 0 | 1.81 | 5.38 | 0.05 | Anemo- | LD | Tw | L |
| Icacinaceae | Pyrenacantha klaineana | 0.97 | 0.66 | 0.71 | 1.19 | 1.39 | 0 | 0 | 0.55 | 2.83 | 0.14 | Zoo- | ST | Tw | L |
| Lamiaceae | Vitex thyrsiflora | 0.55 | 0.00 | 0.15 | 0.80 | 1.00 | - | 0 | 0.58 | 3.85 | 0 | Zoo- | LD | Tw | L |
| Linaceae | Hugonia platysepala | 0.70 | 0.49 | 0.56 | 0.93 | 1.02 | - | 0 | 0.44 | 3.5 | 0.07 | Zoo- | LD | Ho | S |
| Loganiaceae | Strychnos angolense | 0.75 | 0.57 | 0.61 | 1.04 | 1.14 | 0 | 0 | 0.45 | 2.82 | 0.06 | Zoo- | LD | Ho | S |
| | Strychnos longicaudata | 0.60 | 0.67 | 0.68 | 0.82 | 0.83 | - | - | 0.35 | 2.74 | 0.04 | Zoo- | LD | Ho | S |
| | Strychnos phaeotricha | 1.31 | 0.59 | 0.64 | 1.11 | 1.17 | 0 | 0 | 0.20 | 1.78 | 0.02 | Zoo- | LD | Ho | S |
| | Strychnos urceolata | 1.16 | 0.91 | 0.97 | 1.41 | 1.53 | 0 | 0 | 0.47 | 0.48 | 0.06 | Zoo- | LD | Ho | S |
| Malvaceae | Ancistrocarpus bequaertii | 0.78 | 0.64 | 0.68 | 0.92 | 1.00 | - | 0 | 0.33 | 2.18 | 0.02 | Zoo- | LD | Tw | L |
| | Grewia seretii | 0.86 | 0.75 | 0.78 | 1.08 | 1.15 | 0 | 0 | 0.57 | 2.22 | 0.07 | Zoo- | LD | Tw | L |
| Passifloraceae | Adenia cinanchyfolia | 0.24 | 0.00 | 0.00 | 1.00 | 1.52 | 0 | 0 | 0.94 | 6.33 | 0.09 | Zoo- | LD | Te | L |
| Piperaceae | Piper guineensis | 0.09 | 0.00 | 0.00 | 0.33 | 0.55 | - | - | 0.18 | 7.34 | 0.23 | Zoo- | ST | Ro | L |
| Rhamnaceae | Ventilago diffusa | 1.60 | 0.83 | 0.89 | 1.09 | 1.50 | 0 | 0 | 1.06 | 2.31 | 0.18 | Zoo- | LD | Tw | L |
| Rubiaceae | Keetia molundensis | 0.40 | 0.06 | 0.12 | 1.33 | 1.00 | 0 | 0 | 0.82 | 5.13 | 0.06 | Zoo- | LD | Tw | L |
| | Sherbournia batesii | 0.36 | 0.00 | 0.00 | 0.89 | 1.10 | - | 0 | 0.18 | 2.8 | 0.3 | Zoo- | LD | Tw | S |
| | Uncaria africana | 0.52 | 0.13 | 0.30 | 0.77 | 0.92 | - | - | 1.16 | 4.74 | 0.08 | Anemo- | LD | Ho | S |
| Urticaceae | Urera camerooniana | 0.75 | 0.47 | 0.52 | 1.07 | 1.19 | 0 | 0 | 1.35 | 3.89 | 0.13 | Zoo- | LD | Ro | L |
| | Urera trinervis | 2.73 | 0.46 | 0.74 | 16.00 | 43.00 | 0 | 0 | 1.48 | 6.41 | 1.02 | Zoo- | LD | Ro | L |
| Vitaceae | Cissus dinkglagei | 1.34 | 0.87 | 0.97 | 1.00 | 1.16 | 0 | 0 | 1.10 | 2.1 | 0.22 | Zoo- | LD | Te | L |
| | Cissus producta | 0.48 | 0.12 | 0.18 | 0.71 | 0.80 | - | - | 1.00 | 4.43 | 0.03 | Zoo- | LD | Te | L |

# *Chapter 6*

## *General Discussion*

Lianas, woody vines, are a characteristic component of tropical forests (Richards 1952). However, they are most diverse in tropical forests near the equator (Gentry 1991, Schnitzer and Bongers 2002). Schnitzer & Bongers (2002) reviewed their role in tropical forest functioning, while Schnitzer & Carson (2001, 2008, 2010) addressed mechanisms by which lianas influence tropical forest diversity and regeneration. Lianas are favoured by forest disturbances, thus also human-induced disturbances, and increases in atmospheric $CO_2$ concentrations are likely to promote liana abundance (Laurence *et al.* 2001). These environmental modifications are reported to be responsible for the observed increase in the abundance, growth rates, leaf productivity and tree crown infestations of lianas in tropical forests (Phillips *et al.* 2002, Wright *et al.* 2004, Ingwell *et al.* 2010, Schnitzer & Carson 2010). However, although this reported increase is reasonably well investigated in Neotropical forests, the question remains whether or not this is a worldwide trend. Long-term data from Paleotropical forests are extremely scarce. Apart from the general trend in liana abundance, species specific demographic changes of lianas remain largely unexplored, worldwide. This thesis describes the liana community and analyses its dynamics in the Ituri Forest Dynamics Plots, a Congo Basin forest in northeastern DR Congo. All lianas in this plot are being meticulously recorded over a period of 13 years now, the longest record available on liana dynamics in the tropics.

### ANSWERING THE RESEARCH QUESTIONS

#### *(1) What is the overall diversity and structure of the liana assemblage in the mixed rain forest of Ituri?*

Hart *et al.* (1998) demonstrated that the contemporary forest has been a Pleistocene forest refuge (Maley 1996, Sosef 1996), but that its composition and structure changed considerably over the past 4000 years. Tracks of past forest disturbance can still be observed today. The Ituri Forest survived the last maximum glaciations, but important windstorm disturbances that took place in the recent past strongly influenced the present forest structure and composition. Richards (1952) stated that Africa is typical for its high liana density, but this is not supported by quantitative reviews (Parren 2003, DeWalt *et al.* 2010). For the Ituri Forest, liana abundance, species richness and diversity was high compared to other African forests, and more or less similar to that observed in the Neotropics. In contrast to the general assumption that lianas are only rich and abundant in degraded habitats, our study revealed that old-growth forests also show high diversity and abundance of lianas.

Its high liana density may be related to the fact that the forest is quite seasonal, with 4-5 dry months per year. Recently, DeWalt *et al.* (2010) analyzed pan-tropical patterns of lianas abundance and basal area, and found that liana density and basal area increase with increasing rainfall seasonality and decreasing rainfall (cf. Toledo 2010). Thus, this extensive review supported the hypothesis of Gentry (1991) and Schnitzer (2005) stating that lianas are most abundant and have higher basal area in drier tropical forests (i.e., < 2000 mm $y^{-1}$) with greater seasonality of rainfall.

In the Ituri forest, twiners, zoochorous, light-demanding and meso- or microphyllous species dominate. Flower types were equally distributed among conspicuous and inconspicuous classes. In general, our results are consistent with other studies which reported also comparable dominance of these functional traits for tropical forest lianas worldwide (Addo-Fordjour *et al.* 2008, Cai *et al.* 2009, Gentry 1991, Hegarty & Caballé 1991, Putz 1984, Senbeta *et al*. 2005). In this forest, lianas are widely distributed, although their abundance varied with canopy openness, habitat moisture, and elevation.

The Ituri Forest liana community composition is a reflection of both the regional species pool (the flora of African tropical forests) and past local dynamics. In Chapter 2, I acknowledged that, in terms of structure and taxonomic composition, the liana community in the Ituri forest is typical for Guineo-Congolian old-growth forest, with prominent liana taxa belonging to the Dichapetalaceae, Connaraceae, Fabaceae, Apocynaceae and Loganiaceae. This suggests that West and Central African lowland forests are similar in the taxonomic composition of their liana communities. However, the Ituri Forest also differs from other Guineo-Congolian forests because it has a high liana abundance, basal area, and species richness in the small diameter size classes; which might indicate a population emerging from recent disturbances. Furthermore, this chapter showed that the liana community was oligarchic (i.e. dominated by a few species only). The extreme dominance of one single liana species (*Manniophyton fulvum*) renders it unique compared to other forests worldwide.

### *(2) What are the dynamics in the liana assemblage of this forest?*

Our general knowledge of the ecology of lianas, their dynamics and their role in forest dynamics lags far behind that of trees (Schnitzer and Bongers 2002). Such knowledge is a necessary prerequisite for developing a better understanding of the distribution and ecology of lianas in all types of terrestrial ecosystems. Chapter 3 shows that the overall liana population in our old-growth Ituri forest has decreased dramatically over the past 13 years. Despite this decrease in liana abundance the species richness increased slightly during the same period. The general decrease in liana abundance that I found is one of the first studies documenting a decrease- rather than the widely documented increase of lianas over the last decades. The only other study showing a decrease in liana abundance was in Gabon (Caballé & Martin 2001), observed over the period of 13 years. Likely, this is due to the undergoing recovery from past disturbances in many African forests (Richards 1952, Chave *et al.* 2008) rather than the atmospheric $CO_2$ increase as has been suggested for the Neotropics.

This study is also the first one to document that stand-level liana dynamics are completely driven by one species only (*Manniophyton fulvum). Manniophyton* represents 24% of the liana stems in the Ituri forests, and declined from 3299 stems in the first census period, to 94 stems in the last census. Such a massive die-off is not likely due to global change phenomena, such as rising $CO_2$ levels or enhanced nitrogen deposition. Instead, it is more likely to be caused by large scale pathogen infection, although it could also be the result of species-specific responses to drought or past disturbance events. Clearly, much more in-depth studies of the autoecology of *Manniophytion* are needed to unravel the cause of its dramatic decline. In the Neotropics, *Machaerium cuspidatum* (Fabaceae) is the most abundant liana species in floodplain and *terra firme* habitats in Yasuni, (Burnham 2002), whereas *Adelobotrys adscendens* (Melastomataceae) and *Cydista aequinoctialis* (Bignoniaceae) are also the most abundant in other sites (Romero-Saltos 1999) in Ecuador. DeWalt *et al.* (2000) found *Maripa panamensis* (Convolvulaceae) as the most abundant species in Panama. Pérez-Salicrup *et al.* (2001) recorded *Tynanthus schumannianus* (Bignoniaceae) as the most abundant liana in eastern Bolivia. Surprisingly, none of these species come close to the Ituri *Manniophyton fulvum* (Euphorbiaceae) abundance.

I also found that changes in liana dynamics and composition differed dramatically between the first and the second census interval, despite the fact that these census intervals spanned a relatively long time period (6-7 years), in which year-to-year fluctuations are expected to average out. Thus, it strongly depends on the time window considered what results will be found. This strongly suggests that long-term studies are really needed in order to distinguish between short-term fluctuations and long-term trends. As for trees, underlying dynamics of lianas would need such long-term approach if one is interested in documenting and obtaining reliable patterns in forest dynamics (Phillips *et al.* 2002).

This study illustrates four main patterns: (1) the long-term trends show that overall liana density, basal area and biomass decreased, (2) the liana population shows very little recruitment over time; small lianas die or recruit into larger size classes and are not being replaced; (3) growth of individual lianas is not large enough to compensate the basal area and with that also biomass for losses in abundance, and (4) species richness and diversity remained rather constant over time, despite the continuous decrease of liana abundance. The community composition as a whole changed in a non-directional manner, in which the ten most abundant species remained rather constant over the 13 year period, and did not change markedly in abundances (rank and absolute abundance) in response to the *Manniophyton* collapse.

### *(3) How do liana species vary in their demographic vital rates and how are these rates related to the liana species' abundance and their functional traits?*

Our study is one of the first addressing demographic vital rates for a large number of liana species. The majority of species showed low to medium growth and recruitment. Most of the species had low recruitment (<2%/y) and growth (<1%/y), while mortality showed a peak between 2 and 3%/y. Species had a variation in recruitment rate up to 10.9% $y^{-1}$, mortality rates of 8% $y^{-1}$, with growth rates of 3.5 mm $y^{-1}$ at the upper end. Comparing to lianas, Ituri forest trees had similar mortality rates of up to 10% $y^{-1}$ (Condit *et al.* 2006). At a deterministic equilibrium, an indefinite number of species can coexist if species differ from all others along a continuum from short lifespan with high growth to long lifespan with low growth (Pacala & Rees 1998, Bonsall *et al.* 2004). As many species show a similar demography, this suggests that these species converged in their strategy, as Hubbell (2005) pointed out. Alternatively, it might also imply that these vital rates are not so important for coexistence.

In chapter 4, I investigated the general question: how do liana communities maintain themselves in old-growth forest? One general hypothesis is that rare species are favoured over common species in their recruitment (i.e. reproduction), growth, and/or survival (Connell 1978, Janzen 1970). This is a compensatory mechanism to keep the most abundant species in check, and is also referred to as negative density dependence (reviewed in Connell 1978, 1979, Carson & Schnitzer 2008). I found that species growth indeed declined with species abundance, while recruitment and mortality rates were not significantly related to abundance. I conclude that negative density-dependent mechanisms alone are insufficient to explain species relative abundance and coexistence in this forest.

I found that species growth was positively, albeit weakly, correlated to mortality and recruitment rate, which suggests a trade-off between fast growth and recruitment on the one hand versus high survival and long lifespan on the other hand. It seems suggestive that during their life trajectories lianas involve into *r*-*k* strategies as proposed by MacArthur & Wilson (1967) and expanded later by Pianka (1970), in which organisms or species with *k*-strategies have a long life expectancy and devote a small proportion of energy and other captured resources to reproduction. The *r*-strategie is a type made up of species with a short life expectancy and large reproductive effort. Species mortality rate was not related to recruitment rate, which implies that some species should be increasing in abundance, and others decreasing. The Ituri Forest liana community as a whole is highly dynamic, which is consistent with earlier studies in the Neotropics (Phillips *et al.* 2005, Wright *et al.* 2004, Ingwell *et al.* 2010). Unfortunately, species-specific demographic liana studies are hardly available for comparison. An example from an individual species might serve as a useful illustration, though. In his study of the Neotropical liana *Machaerium* demography, Nabe-Nielsen (2002, 2004) recorded a population growth rate of 1.03. The dynamics of the species was most influenced by survival of large plants, which is typical for slow-growing woody species, and canopy openness in which the population growth rate was lower in tall forest (height> 10 m) than in the population in general. These results indicate that the species is shade-tolerant but that it is sensitive to variation in gap dynamics. The dominance of the species and the increasing population size suggest that the forest has had a low disturbance rate for a long time. *Machaerium* is ecologically comparable to our dominant *Manniophyton*, but *Manniophyton* had a considerably lower growth rate of 0.32 mm $y^{-1}$ and a high population decrease. In contrast to mechanism, a shade-tolerant species, *Manniophyton* is a light demanding one.

### *(4) Do lianas change in abundance over the last 13 years?*

To answer this question, I evaluated liana dynamics at the community level (Chapter 3), species-level (Chapter 4) and changes in population density of individual species (Chapter 5). Overall, I detected pervasive changes in density of lianas at the community and species level. The liana community as a whole shows a dramatic decline in stem density and very limited recruitment. Despite of this, there are little changes in the rank abundance of the most abundant species. Taxonomically, a pervasive alteration is observed at the species level, where 50% of the examined species changed significantly, over a 13 years monitoring period.

Tropical forests reflect biogeographical patterns. First, the Neotropical forests obviously harbor more lianas than Paleotropical forests (Gentry 1991). Second, studies in the

Neotropics showed an increase in lianas abundance, productivity and infestation (Laurance *et al.* 2001, Phillips *et al.* 2002, Wright *et al.* 2004, Allen *et al.* 2007, Ingwell *et al.* 2010, Schnitzer & Carson 2010) and a persistent change of trees communities (Laurance *et al.* 2004) and increasing turnover (Phillips & Gentry 1984), which has been attributed to atmospheric $CO_2$ increase and anthropogenic land-uses. However, in a rainforest in Gabon (Caballé & Martin, 2001) and in our Ituri forest we observed a decrease of lianas and an increase of tree growth (Chave *et al.* 2008), probably as result of recovery from past disturbances. Yet we do believe that the African data, with evidence from two sites, are not sufficient enough to definitively claim that lianas are systematically decreasing in African forests. African samples are only from wet forest, and data are lacking from a drier subset of the rainfall spectrum. To compare differences in liana change between the Paleo- and Neotropics properly, more long term liana surveys need to be conducted in Africa covering the full range in climatic conditions.

### SUCCESSIONAL DEVELOPMENT OF THE ITURI LIANA COMMUNITY

The analyzed data suggest that Ituri Forest is in a old-growth stage, but most of the liana species composition and size distribution reflect forest successional change. However, some species occurring in old gap patches across the plots are typical of early successional forest. As trellises are of large size in late-successional forest, only the large lianas that have already reached the canopy have a high probability of surviving in a tall forest. Lianas can serve as indicators of forest disturbance history (Laurance *et al.* 2001, Zagt *et al.* 2003). *Manniophyton fulvum* is a short-lived, light demanding species that after establishment in high light can persist for a long time as a shade-tolerant liana. The dominance of the species in the first census, followed by its dramatic decline later on suggests that the forest is changing towards a later successional stage. Similarly, the lack of large lianas may be evidence for past disturbance and that the forest is slowing down. Many of the decreasing species tend to be pioneer lianas. Pioneer lianas are unable to regenerate in a dark late-successional forest.

### LIANA COMMUNITY AND GLOBAL CHANGE

Recent concerns over forest fragmentation, abandoned agricultural lands, repeated timber harvesting, and increasing levels of carbon dioxide in the atmosphere have stimulated research on the relative response of lianas to these changes. It is suggested that, lianas are able to respond more quickly and more intensely to forest openings (Schnitzer *et al.* 2000), disturbance (Schnitzer & Bongers 2005), and increased $CO_2$ (Schnitzer & Carson 2001, 2010; Londre & Schnitzer 2006). Recent studies documented a substantial increase in the density and relative dominance of lianas in western Amazonia, which has been attributed to climate change induced by the increase in atmospheric $CO_2$ concentrations, and land uses. I failed to find convincing evidence for this in the Ituri forest. The documented increase in $CO_2$ concentrations is not a possibility, as lianas should respond strongly to $CO_2$ fertilization over the historical range of concentrations with increased photosynthesis and growth. Instead, I observed a decrease of many liana species, of which many are gap specialists. The effect of lianas tree infestation appears to be negligible as in the studied plots; trees are gaining biomass (Lewis *et al.* 2009). However, a number of predictions (Malhi *et al.* 2008) and climate models suggest that conditions which may favor lianas, such as synergisms between climate change and logging, forest openings for roads construction, and effects of continuous decreases in areas will contribute to increasing liana densities and magnify the impact either to tree growth or to forest functioning. As to quote Schnitzer & Carson (2010), "Better understanding of these risks will require intensive field research to improve the liana-on-tree mortality functions and to begin including lianas within full tropical forest vegetation models and coupled carbon cycle/climate models".

## USEFUL LIANAS FROM ITURI FOREST

Lianas are an important group of non-timber forest products. Many liana species have a high value for people, especially for people living in rural areas. In the Ituri Forest, lianas are the forgotten non-timber forest product, although they economically contribute to local communities' revenue. Liana species constitute a very important group of non-timber forest products (Abbiw 1990, Malaisse 1997, Van Andel 2000, Tra Bi 1997, Van Valkenburg 1997). For example, during his constant search for plant products, the Belgium King Leopold II explored and used to harvest rubber from many *Landolphia* liana species before the rubber tree *Hevea* was cultivated. The *Strophanthus kombe*, known for its cardiovascular virtue is only found in the Ituri Forest, but the size of population is unknown and the species seems to be going extinct, and has neither been recorded in our inventory. Unfortunately, there is no evaluation of lianas as a non-forest timber resource in the Ituri region. A rough appraisal of our species indicates that lianas are used for edible fruits (*Landolphia spp*), artisanal work and construction of traditional houses (*Loesenerialla spp, Laccosperma secundiflorum, Pyrenacantha lebrunii*) as no construction is made without lianas; medicine (*Manniophyton*, *Strophantus kombe*), hygienic teeth brush, hunting traps and nets or poisons (*Manniophyton*, *Pyrenacantha*, *Strophanthus*). It is particularly clear that lianas are an important resource for local communities. For example, in remote areas without roads in Ituri Forest, local people have built impressive bridges made entirely of lianas. Such bridges are found in a number of big rivers in the Ituri region, for example in the Ngayo and Ebiena rivers. Some lianas are extremely important for the livelihood of Pygmies (like *Loeseneriella spp*, *Manniophyton*, *Landolphia spp*.). Other liana species serve as appreciated forage for Okapi diet, an endemic forest giraffe species of the DR Congo forest (e.g., *Alchornea cordiolia).*

A number of studies have advocated the reliance on forest products by indigenous people as a reason for rain forest conservation (Myers 1982, Wiersum 2000). Unfortunately, in some regions, including Ituri, the knowledge of useful plants is disappearing even more rapidly than the plants themselves. If no efforts are made to conserve and study both the biological and cultural diversity of knowledge, that potential resource of new medicines for human disease, food crops, and indigenous management systems will disappear together with the forest.

## TAXONOMICAL CONSIDERATIONS

Lianas are omitted from most forest studies because of difficulties with taxonomic identification, because it is difficult to distinguish liana ramets from genets, and a self-supporting liana individual from shrubs (Parren *et al.* 2005). Lianas are hard to identify because it is difficult to collect vegetative and/or generative herbarium material, as this is located at the top of the canopy which is difficult to access. Because taxonomic uncertainties make lianas difficult to identify in the field, many studies group lianas into morphospecies.

Western botanists have dedicated considerable effort in collecting in Central Africa and major regional flora of tropical Africa (e.g., Flore du Cameroun, Flore du Gabon, Flore d'Afrique Centrale [Congo-Rwanda-Burundi] and Flora of East and West Tropical Africa) are well advanced, and have been useful for plant identification as the majority of liana families are included. Throughout the course of our census in the Ituri plots, rules of data quality control were incorporated. One of the rules has been botanical collection consistency and efficiency. Botanical collection and identification were done by well-trained field botanists, who verified all lianas in the field sheets after each working day, and checked for their identification and if collections were made following the botanical collection protocol. About ten thousand collections were made, including all vegetative and climbing structures that could assist identification. The majority of collections are housed in the CEFRECOF herbarium at Epulu, with sets stored at the National Herbarium of the Netherlands (Wageningen branch), Meise (Brussels) and Missouri Botanical Garden

(USA). The Ituri first forest dwellers, the Mbuti (Pygmies), have extensive knowledge on the identification of plants and their use, and thanks to them most of our lianas were collected and identified. This collection was critical to the generation of reliable keys and field guides; they synthesized a substantial amount of the available vegetative information and created a more coherent taxonomy. The quality of the taxonomy of our data is good as collections were carefully made, and matched in the herbarium (Wag, Br, MBG) with well-identified material by expert taxonomist of most of the families. This study is one of the rare inventories where botanical identification has been excellent, as more than 95% of the stems were identified to species.

However, as i) lianas are more difficult to collect in flower or fruit, ii) are known vegetatively by fewer specialists, and iii) have been less collected and monitored activity over the last decade, I anticipate that training of field botanists is needed. Complete reporting of species identities, facilitated by exchange of specimens and photographs among experts will vastly improve this situation. Construction and usage of “Field Guides” (e.g., Hawthorne & Jongkind 2006) and web-based interactive vegetative keys to various areas of the tropics are starting points for this venture of liana biodiversity across the tropics. Greater collection of plant material in the established large permanent plots enhances the potential quantification of the variation in vegetative characters within and among woody plant taxa and provides didactic material for plant identification training. If not, species- or even genus-level identification of woody plants based on vegetative characters will only be feasible in those areas for which the flora has been well described and for plant groups in which the taxonomy is clear and workable.

## RECOMMENDATIONS FOR FURTHER RESEARCH

Our understanding of lianas ecology is still incomplete. More supplementary studies are essential for understanding the observed patterns in this thesis. These should include:

- The factors driving seedling liana dynamics are yet unexplored in tropical forests worldwide. It is important to know how spatial and temporal variation in regeneration dynamics act to maintain diversity and shape species abundance and composition within and across plant communities. Such insight in seedling ecology may be used to understand how species can adapt to different environmental conditions and also for the restoration of degraded habitats or for forest management.

- Determining the causes of commonness and rarity at the local scale is essential for understanding how liana communities are structured and has important implications for biodiversity conservation.

- Investigation of liana-tree associations is needed as liana infestation negatively affects tree productivity, and as liana infestation of trees has been shown to increase. Fortunately, data are being collected and in the near future we will evaluate the ongoing trends.

- Special attention should focus on the canopy dynamics and patterns of treefalls and branchfalls creating gaps. This will gave insights into structural changes in the forest canopy over time, and how these affect the dynamics of tree seedlings and lianas.

- It is important to investigate the functional ecology of lianas. Understanding of hard functional traits and differential species ecophysiology will enhance our knowledge on how lianas may respond to increasing atmospheric $CO_2$ concentrations, N deposition, and water stress.

- The phylogenetic structure of the liana community assemblage. Phylogenetically, climbers are found in over 125 families of flowering plants (Gentry 1991). This phylogenetic breadth strongly suggests multiple origins of the climbing habit within angiosperms. As better phylogenetic hypotheses become available for many groups of lianas families, studies in lianas community ecology can be informed by knowledge of the evolutionary relationships among coexisting species. Three primary approaches to integrating phylogenetic information into studies of community organization are recommended: 1. examining the phylogenetic structure of community assemblages, 2. exploring the phylogenetic basis of community niche structure, and 3. adding a community context to studies of trait evolution and biogeography (Webb et al. 2002, Cadotte *et al.* 2010). Much of these have been investigated for trees and among them, Chazdon *et al.* (2002) provide an example for woody plant reproductive traits.

- Finally, I suggest that an ethnobotanical study needs to be done on forest lianas and their uses. This information should be distributed widely for conservation and sustainable use. Guidelines should be developed for the management of the economically important lianas, aimed at sustainable use of this valuable resource.

## CONCLUSIONS

The liana assemblage of the Ituri Forest reflects both contemporary and past dynamics. Historical dynamics are well known to have occurred in West and Central African forest (Maley 1996, Sosef 1996). The Ituri forest, for example, is known as a Pleistocene refugium and plots exhibited no evidence of recent major disturbances, although some occasional tracks of windstorms prior to the establishment of the plots were perceptible (Hart *et al.* 1996). These factors influence the contemporary vegetation in terms of species composition and vegetation structure. The liana assemblage of this Congo Basin forest generally concurs with those of lowland tropical forests elsewhere. In terms of structure and family composition, the liana community in IFDP is typical for a Guineo-Congolian old-growth forest. However, the Ituri Forest also differs from other Guineo-Congolian forests because it has high liana abundance, basal area, and species richness, and more stems in the small size classes. In addition, the extreme dominance of one single liana species (*Manniophyton fulvum*) is unique compared to other forests worldwide. The old-growth forest of Ituri shows a strong decrease of its liana population. This general decrease is in contrast with the widely documented general increase of lianas over the last decades. Our study is also the first to document that the dynamics of the overall liana stand is completely driven by the dynamics of one species only. More studies on liana communities in old-growth forests are needed to confirm whether or not such single dominant species driven community dynamics is a general phenomenon in tropical old-growth forests. Whether lianas were found to increase or decrease depended heavily on the time-window used. Therefore, I argue that many more long-term and large scale studies are needed to evaluate the direction of community changes and to predict the eventual consequences of global change.

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# *Samenvatting*

Deze studie analyseert de diversiteit, samenstelling en dynamiek van de lianengemeenschap van het Ituri regenbos in noord-oost DR Congo. Ik heb data gebruikt van twee 10-ha plots, onderdeel van de Ituri Forest Dynamic Plots, waarin alle lianen met diameter-op-borst-hoogte (dbh) $\geq$2 cm werden gemerkt, gekarteerd en geïdentificeerd in 1994, 2001 en 2007. Bovendien werden plot topografie en de structuur van het kronendak gemeten.

Hoofdstuk 2 analyseert de lianengemeenschap (in termen van soortenrijkdom, abundantie en diversiteit), karakteriseert hun functionele eigenschappen en bepaalt de effecten van bosstructuur, topografie en edafische variatie op de lianensamenstelling. In 20 ha werden 15008 individuele lianen aangetroffen, die 195 soorten, 83 geslachten en 34 plantenfamilies vertegenwoordigen. Per hectare was het soortenaantal gemiddeld 64, de bedekking was 0,71 $m^2$ en de Fisher alfa, Shannon en Simpson diversiteitindexen waren respectievelijk 17,9, 3,1 en 11,4. Er was oligarchische dominantie van 10 plantenfamilies die 69% van de totale soortenrijkdom, 92% van de lianenabundantie en 92% van de bedekking vertegenwoordigden. Eenenveertig soorten (21%) waren door slechts één individu vertegenwoordigd. De meeste lianen waren lichtminnend, klimmen via windingen, en hadden opvallende bloemen, bladen van gemiddelde grootte en zaadverspreiding via dieren. Lianenabundantie nam toe met de aanwezigheid van middelgrote en grote bomen, maar was, verrassend, onafhankelijk van de abundantie van kleine bomen. Openheid van het kronendak, bodemvochtigheid en grootte van de boom bleken de belangrijkste omgevingsfactoren die de abundantie en verbreiding van lianen bepalen.

In Hoofdstuk 3 onderzoek ik de veranderingen in structuurkenmerken, diversiteit, verjonging, sterfte en groei van de lianengemeenschap over dertien jaren (1994 – 2007). Lianendichtheid nam af van 750 (1994) via 547 (2001) tot 499 (2007) stammen $ha^{-1}$, gepaard gaand met afname in bedekking en bovengrondse biomassa. Ondanks afnemende stamdichtheden, bleef de soortenrijkdom constant. Snelheid van verjonging van lianen nam licht af van 8,6% per jaar in de eerste periode tot 6,6% in de tweede, maar deze afname was niet significant. Snelheid in lianensterfte nam in deze twee periodes significant af van 7,2% naar 4,4% per jaar. Diametertoename en overleving nam toe met stamdiameter. Verrassend genoeg toonde lianenabundantie in Ituri recente afname in plaats van toename, zoals gerapporteerd voor tropische en gematigde bossen in beide Amerika’s. Interessant genoeg werden veranderingen in algemene structuur en samenstelling van de lianengemeenschap

aangestuurd door slechts één soort: de dramatische ineenstorting van de superabundante *Manniophyton fulvum* tussen de eerste en tweede telling.

In Hoofdstuk 4 onderzoek ik de soortspecifieke dynamiek van de 79 meest algemene lianensoorten, die 13,156 van de stammen (97% van het totaal) in twee 10-ha plots vertegenwoordigen. Ik evalueer hun demografische prestatie en de relatie tussen hun vitale snelheden (groei, sterfte, verjonging) en de soortenabundantie en vier functionele eigenschappen (klimstrategie, verspreidingssyndroom, bladgrootte en lichtbehoefte) om de variatie tussen soorten te bepalen alsmede de belangrijkste karakteriserende strategieën. Soorten laten een grote variatie zien in verjongings snelheid (0,0-10.9% over 13 jaar), in sterfte (0,43-7,89% over 13 jaar), en in groeisnelheid (-0,03-3,51 mm $y^{-1}$). De meeste soorten hadden lage tot gemiddelde snelheden. Snelgroeiende soorten verjongen en sterven doorgaans ook snel, maar verjongings- en sterfte-snelheden waren niet direct gecorreleerd, suggererend dat de absolute abundantie van soorten verschuift over de periode van 13 jaar. Echter, met uitzondering van de ineenstortende *Manniophyton fulvum* populatie, soorten behielden hun dominantiepositie door de tijd. Groei per soort nam af met abundantie, maar verjongings- en sterftesnelheid waren niet gerelateerd aan abundantie. De demografische prestatie van lianensoorten varieert zwak met hun klimstrategie en verspreidingsmechanisme, maar was, verrassend genoeg, niet gerelateerd aan hun lichtbehoefte als plant. Een principale componentenanalyse (PCA) van lianenstrategieën in termen van functionele eigenschappen en van snelheden van verjonging, groei en sterfte liet zien dat deze vooral bepaald worden door lichtbehoefte en verspreidingssyndroom. Op basis van de PCA werden drie functionele groepen onderscheiden. Ik concludeer dat lianen soorten van primair bos een grote variatie in abundantie en van verjonging -, groei - en sterfte snelheden vertonen, en dat dichtheidsafhankelijke mechanismen onvoldoende zijn om de veranderingen in soortsabundantiepatronen gedurende de tijd te verklaren.

Men neemt aan dat lianen wereldwijd in dichtheid toenemen, maar er is beperkte kennis over de taxonomische patronen van deze verandering in lianenabundantie en de onderliggende snelheden van verjonging, groei en sterfte die veranderingen in lianendichtheid verklaren. In Hoofdstuk 5 worden de veranderingen in abundantie van 79 relatief algemene lianensoorten geëvalueerd. Het Ituri regenbos laat een alomvertegenwoordige verandering in de dichtheid van de lianenpopulatie gedurende het laatste decennium zien. 37 soorten veranderde significant in hun dichtheid: 12 (15% van het totaal) soorten namen toe, 25 soorten (32%) namen af, en 42 soorten (53%) bleven gelijk. Van de 48 genera nam 40% af en bleef 52% gelijk. Vijf van de 12 toenemende soorten behoren tot de Celastraceae, wat tevens de enige significant toenemende familie was.

Verrassend was dat geen van de vier functionele eigenschappen (lichtbehoefte als plant, klimmechanisme, verspreidingsmechanisme en bladgrootte) significant geassocieerd was met een verandering van populatiedichtheid per soort. Echter, veel afnemende soorten zijn geassocieerd met verstoorde habitats en zijn kort-levend. Veel toenemende soorten behoren tot het late successiestadium en zijn lang-levend. Toenemende soorten hebben een iets snellere verjonging, afnemende soorten een hogere sterfte. Deze studie suggereert dat veranderingen in de lianengemeenschap het gevolg is van bosherstel van vroegere verstoring. Toenemend atmosferisch $CO_2$-niveau was geen waarschijnlijke verklaring voor deze veranderingen: meer soorten namen af dan toe, en toenemende soorten hadden geen hogere groeisnelheden. In het Ituri regenbos overheerst de lokale dynamiek van opstanden de meer mondiale aansturing van veranderingen bij lianen.

**Trefwoorden**: Lianen, soortensamenstelling, gemeenschap, dynamiek, openheid kronendak, *Manniophyton fulvum*, functionele eigenschappen, populatiedichtheid, wereldwijde verandering.

# Résumé

Cette étude analyse la diversité, composition, et dynamique d'une communauté des lianas de la forêt dense humide de l'Ituri au Nord-Est de la République Démocratique du Congo. J'ai utilisé les données de deux parcelles de 10-ha des parcelles permanentes d'Etude de la Dynamique Forestière de la Forêt de l'Ituri, dans lesquelles toute tige de liane ≥ 2 cm de diamètre à hauteur de la poitrine (DPH) était marquée, cartographiée, mesurée et identifée en 1994, 2001 et 2007. En outre, la topographie des parcelles et la structure de la canopée était mesurée.

Chapitre 2 analyse la communauté des lianes (en termes de richesse spécifique, abundance et diversité), caractérise les traits fonctionnels des lianes et détermine les effects de la structure de la forêt, topographie et variation édaphique sur la composition spécifique des lianes. Dans 20 ha, on a quantifié 15008 individus de lianes, représentant 195 espèces, 83 genres et 34 familles. Le nombre moyen d'espèce par hectare était de 64, la surface terrière était de 0.71 $m^2$ et les indices de diversité de Fisher alpha, Shannon et Simpson étaient de 17.9, 3.1 et 11.4, respectivement. Il y avait une dominance oligarchique de 10 familles qui représentait 69% du total de la richesse spécifique, 92% de l'abondance et 92% de la surface terrière, pendant que les 10 dominantes espèces constituent 63% de l'abondance et 59% de surface terrière. Quarante et une espèces (21%) étaient représentées seulement par un individu. La plupart de lianes était des espèces de lumière, volubile, à fleurs apparantes, feuilles de taille moyenne et à dispersion des graines assurée par les animaux. L'abondance des lianes augmentait avec l'abondance des moyens et grands arbres mais, surprenant, elle était indépendante de l'abundance des petits arbres. L'ouverture de la canopée, humidité du sol, et la taille des arbres furent les plus important facteurs environementaux ayant influencé l'abundance et la distribution des lianes.

Au Chapitre 3 j'examine les changements des caractéristiques structurales, diversité, recrutement, mortalité et croissance de la communauté des lianes sur une période de treize ans (1994-2007). La densité des lianes a diminué de 750 (1994), puis 547 (2001) pour 499 (2007) tiges par hectare, avec une baisse concomittante dans la surface terrière et la biomasse en surface. En dépit de la faible densité des tiges la richesse spècifique est restée constante au cours du temps. Les taux de recrutement total ont légèrement diminué de 8.6% par an au cours de la première période à 6.6% dans la seconde, mais cette diminution n'était pas significative. Le taux de mortalité a significativement diminué de

7.2% à 4.4% par an au cours des deux intervalles de recensement. Le taux de croissance en diamètre et de survie a augmenté avec le diamètre des tiges. Surprenant, l'abondance des lianes en Ituri a montré une récente dimunition, plutôt qu'une récente augmentation, comme celà a été announcé pour les forêts tropicales et temperées en Amérique. Plus interressant, les changements de l'ensemble de la structure et composition de la communauté des lianes étaient principalement menée par une seule espèce : le considérable changement du superabondant *Manniophyton fulvum* entre le premier et le second recensement.

Au Chapitre 4 j'ai examiné la dynamique spécifique de 79 espèces des lianes les plus abondantes, représentant 13156 des tiges (97% du total) dans deux parcelles de 10-ha. J'ai évalué leur performance démographique et la relation des taux vitaux (croissance, mortalité, recruitement) pour l'abondance des epèces et quatre traits fonctionnels (stratégie de grimpage, syndrôme de dispersion, taille des feuilles et exigences de lumière) pour déterminer les variations générales et les importantes stratégies caractérisant les espèces entre elles. Les taux vitaux partagent une large variation interspécifique ; le taux de recrutement spécifique des espèces varie de 0.0-10.9%, mortalité de 0.43-7.8% au cours de 13 ans, et la croissance de -0.03-3.51 mm par an. La plupart d'espèces ont des taux faibles à modérés. Les espèces à croissance rapide ont aussi tendance de recruiter et mourir rapidement, mais les taux de recruitement et de mortalité n'étaient pas directement lié, suggérant que les espèces ont changé en abondance absolue au cours de cette période de 13 ans. Cependant, à l'exception du changement consiérable de la population de *Manniophyton fulvum,* les espèces ont maintenu leur rang de dominance au cours du temps. La croissance des espèces a diminué avec l'abondance, mais les taux de recrutement et de mortalité n'ont pas été liés à l'abondance. La performance démographique des espèces des lianes a faiblement varié avec leurs stratégies de grimpage et modes de dispersion mais était, en toute surprise, pas lié à leurs exigences de lumière au cours de leur vie. L'Analyse en Composantes Principales des stratégies des lianes en termes des traits fonctionnels et taux vitaux a montré que la demande en lumière, et le syndrôme de dispersion étaient des traits les plus déterminants. Trois associations fonctionnelles ont éte distinguées sur base du PCA. Je conclus que les espèces des lianes de la vieille forêt montre une grande variation dans l'abondance et les taux vitaux, et que les mécanismes de densité-dependance sont insuffisant pour expliquer les tendances d'abondance des espèces au cours du temps.

Il ya des prevenances que les lianes sont en train de mondialement augmenter en densité, mais nous avons des connaissances limitées à propos des tendances taxonomiques de changement en abundance, et les taux vitaux sous-jacents qui expliquent les

changements en densité des lianes. Au Chapitre 5 les changements en abundance de 79 espèces des lianes relativement abondantes sont évalués. La forêt de l'Ituri a montré un changement qui se répand partout dans la densité de population des lianes au cours de cette dernière décennie. 37 espèces on significativement changé dans leur abondance au cours du temps : 12 (15% du total) espèces ont augmenté, et 25 (32%) espèces diminué. 42 (53%) espèces n'ont pas changé. De 48 genres, 40% ont diminué et 52% restés inchangés. Cinq des 12 espèces en augmentation appartiennent au Celastraceae, laquelle était aussi la seule famille avec une significative augmentation. Il est surprenant qu'aucun des quatres traits fonctionnels (exigences de lumière au cours de vie, mécanisme de grimpage, mécanisme de dispersion, et taille des feuilles) n'être significativement associé au changement dans la densité de population des espèces. Cependant, nombre de ces espèces en diminution sont associées aux habitats perturbés et sont de courte-durée de vie. Beaucoups de ces espèces en augmentation sont de succession tardive et longue-durée de vie. Les espèces en augmentation ont un taux de recrutement légèrement élevé, les espèces en diminution une mortalité élevée. Cette étude suggère que les changements dans les communautés des lianes résultent du recouvrement de la forêt des perturbations antérieures. La montée du niveau de $CO_2$ atmosphérique n'était pas la probalbe explication pour le changement des lianes : plus d'espèces ont diminué qu'augmenté, et les espèces en augmentation n'ont pas été de taux de croissance élevée. Dans la forêt de l'Ituri la dynamique locale de la forêt a plus d'importance que les déterminants globaux de changement des lianes.

**Mots clés :** Assemblage des lianes, composition spécifique, communauté, dynamique, ouverture de la canopée, *Manniophyton fulvum*, traits fonctionnels, densité de population, changement total.

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While I sit here reflecting over the past four years I wonder if I would have had the courage to begin this journey if I had known at which cost it would take me. Although I knew where it would take me, it has been a journey filled with such extremes as I have learnt both about the wonders of humanity as well as its cruelty. This made me question how many other times I had to learn about life as an experience of obstacles. There is no word to describe what I faced in the course of my studies. It literally took months of day to day mental and psychological battles to overcome all the moral pains. Without the strong and loving support of my wife and our children; and family to conquer my psychological devastation, I know I would not have been able to complete this journey. This has shown me the true value of the family for which I eternally devote my life and will be grateful. ***Thanks and I love you all***. Mama Esse, as you are the "hero" of this journey I would like you to be with me on the defence.

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Félicien Bola, I am in lack of words for you, all that comes is *thank you*. Thank you so much for your 20 years of guidance. Dr. Jefferson Hall, you've been artisan of this journey, thanks for your support. To all the staff of CTFS, from Liz Losos to Stuart Davies, Rick Condit, Joe Wright, Suzanne Loo de Lao, Duncan Thomas, and all others unnamed here, including Sean Thomas, your support made me what to be today. To David Kenfack and your wife, I still miss you on the loop. A mes frères et sœurs Didier & Cecile Bolamba, Jacob Madidi & Nono Kibani, Félicien Bola & son épouse merci pour votre soutien combien inestimable à ma famille. Vous vous êtes depassés et substitués en mes devoirs pour voir réaliser mon object. You provided substantive help far beyond the financial. Que Dieu vous garde et vous pouvoit en abondance.

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***For all those who have shared our concern, the work goes on, the cause endures, the hope still lives and the dream shall never die***. This thesis is the end of a long journey, and yet I hope it is also another beginning.

# Short biography

Corneille (Ekokinya Ndomba) Ewango was born on 08 November 1963 in Bomongo (Equateur Province), Democratic Republic of Congo. He grew up in the forest region. Since he was fourteen old and after obtaining the diploma of Secondary School in Biology and Chemistry in 1985, he was involved in poaching activities that led him to discover the forest biodiversity and nurtured his passion to tropical botany. In 1987, he went to the University of Kisangani and started a higher education in biology in 1995 and obtained his "Licence" degree in Biological Sciences (Faculty of Sciences, Department of Ecology and Nature Conservation) with honours, with majors in Tropical Forest Ecology, Plant Taxonomy and Conservation. During his study, he took practical training and performed field research in the Réserve de Faune à Okapi, Ituri Forest. He contributed with his plant expertise to the establishment and botanical surveys of the Ituri 40-hectare plot, the first large African permanent forest dynamics study plot, in collaboration with Wildlife Conservation Society (WCS)'s Centre de Formation et de Recherche en Conservation Forestière (CEFRECOF)-Ituri Project and the Center for Tropical Forest Science (CTFS) of the Smithsonian Instutition.

After graduation in 1995, he was appointed as teaching Assistant at the Department of Ecology and Nature Conservation of the University of Kisangani. Shortly after he was employed by the Wildlife Conservation Society-DR Congo and CEFRECOF-Ituri Project. For about ten years, he has been involved in research on forest ecology, vegetation and ecosystem dynamics, plant taxonomy, conservation and human ecology in the Ituri Forest and central Congo Basin. His research interests focus on forest ecology, especially the monitoring and ecology of forest change (both natural and induced, climate change and carbon sequestration), natural resource uses in relation to forest management and the implications for conservation and management. In addition to taxonomic expertise on the flora of Tropical Africa, Corneille extended his research work to encompass the systematics of vascular plants (mainly Sapotaceae, Orchidaceae, and Pteridophytes), and the ecology of several groups of plants, mainly those growing in epiphytic environments and lianas. He coordinated the WCS-CEFRECOF Botanical program, the permanent dynamics plots, and developed a herbarium for the study of the regional flora that became a reference for the study of plant diversity and conservation of the Ituri Forest and DR Congo forest national parks and other areas of biodiversity importance. During his career, he has assembled botanical collections totalling about 3000 numbers and contributed to the description of some species new to science.

In 2003, after the deadly armed conflict that devastated DR Congo, he went to the University of Missouri, Saint Louis (USA), and in 2006 obtained an MSc in Ecology, Evolution and Systematics with a Graduate certificate in Tropical biology, Forest resources, and Plant conservation. In 2005, in recognition of his work and effort to protect the Reserve de Faune à Okapi (RFO) during the armed conflict, he received the prestigious "Goldman Environmental Prize" also known as the Nobel Prize for Environment (***www.*****goldmanprize.org**). He was then honored by the University of Missouri and became the first student to receive the "Chancellor of University of Missouri, St. Louis, Medal of Merit and Excellence". In 2006, Corneille received the National Geographic Society (NGS) Emerging Explorers Award for Africa and joined the society's explorers community (**www.ngs.org**). After graduation in 2006, he returned to his Ituri project as Director of the WCS-CEFRECOF/ RFO Project.

In 2007 he started his studies for a Ph.D degree at Wageningen University with Biosystematics Group and Forest Ecology and Forest Management Group. During the course of the PhD, he remained active in the WCS-DR Congo Program as senior staff (Team) and leader of research activities in Forest Ecology, Biodiversity and Climate Change. After completing his PhD in 2010, he will return to DR Congo well equipped to continue his work on the Congo basin forests. He aims to increase scientific understanding of forest ecosystems, to guide sustainable forest management and natural-resource policy, to monitor the impacts of climate change, and to build capacity in forest science. All for the long-term conservation of the tropical Congo Basin forests.

Corneille Ewango is married and a father of five children.

# *List of Publications*

DeWalt SJ, Schnitzer, SA, Chave J, Bongers F, Burnham R.J., Cai Z-Q, Chuyong G, Clark DB, **Ewango C.E.N**, Gerwing J.J, Gortaire E, Hart T, Ibarra-Manríquez G, Ickes K, Kenfack D, Macia MJ, Makana J-R, Martinez-Ramos M, Mascaro J, Sainge M, Muller-Landau HC, Parren MPE, Parthasarathy N, Pérez-Salicrup DR, Putz FE, Romero-Saltos H, and Thomas D. 2010. Annual Rainfall and Seasonality Predict Pan-tropical Patterns of Liana Density and Basal Area. Biotropica 42: 309-317.

Lewis, S.L., Lopez-Gonzalez, G., Sonké, B., Affum-Baffoe, K., Baker, T.R., Ojo, L.O., Phillips, O.L., Reitsma, J.M., White, L., Comiskey, J.A., Djuikouo, M-N., **Ewango, C.E.N.**, Feldpausch, T.R., Hamilton, A.C., Gloor, M., Hart, T., Hladick, A., Lloyd, J., Lovett, J.C., Makna, J-R., Malhi, Y., Mbago, F.M., Ndangalasi, H.J., Peacock, J., Peh, K.S-H., Sheil, D., Sunderland, T., Swaine, M.D., Taplin, J., Taylor, D., Thomas, S.C., Votere, R. & Wöll, H. 2009. Increasing carbon storage in intact African tropical forests. Nature 457: 1003-1007.

Chave, J, R. Condit, H.C. Muller-Landau, S.C. Thomas, P.S. Ashton, S. Bunyavejchewin, L.L. Co, H.S. Dattaraja, S.J. Davies, S. Esufali, **C.E.N. Ewango**, K.J. Feeley, R.B. Foster, N. Guanatilleke, S. Guanatilleke, P. Hall, T.B. Hart, C. Hernandez, S.P. Hubbell, A. Itoh, S. Kiratiprayoon, J.V. LaFrankie, S. Loo de Lao, J-R. Makana, Md. N. Supardi Noor, A.R. Kassim, C. Samper, R. Sukumar, H. S. Suresh, S. Tan, J. Thompson, M. D. C. Tongco, R. Valencia, M. Vallejo, G. Villa, T. Yamakura, J.K. Zimmerman & E.C. Losos. 2008. Assessing evidence for a pervasive alteration in tropical tree communities. PLoS Biology 6: 455-562.

Plumptre, A. J.; Davenport, T.; Behangana, M.; Kityo, Eilu, G.; Ssegawa, R. P.; **Ewango, C.E.N.;** Mierte, D.; Kahindo, C. 2007. The Biodiversity of the Albertine Rift. Biological Conservation 134: 178 –194.

**Ewango, C.E.N.** 2006. Sapotaceae. In: Akoegninou, A.; Burg, W.J. van der; Maesen, L.J.G van der (Eds.) Flore Analytique du Benin: 926-931, Cotonou/Wageningen: Backhuys Publishers, The Netherlands.

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Gerwing J.J, Schnitzer S.A., Burnham R.J., Bongers F., Chave J., DeWalt S.J., **Ewango C.E.N.**, Foster R., Kenfack D., Martinez-Ramos M., Parren M., Parthasarathy N.,

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Poulsen, A.D., Hafashimana, D., Eilu, G., Liengola, I.B., **Ewango, C.E.N.** & Hart, T.B. 2005. Composition and species richness of forest plants along the Albertine Rift, Africa. Biol. Skr. 55: 129-143.

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Kenfack, D., **Ewango, C. E. N.**, and Thomas, D. W. 2005. *Manilkara lososiana* Kenfack & Ewango (Sapotaceae), a new species of Sapotaceae from Cameroon. Kew Bulletin 59: 609-612.

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Makana, J-R, T.B. Hart, I. Liengola, **C. Ewango**. 2004. The Ituri Forest Dynamics Plots. In E.C. Losos and E.G. Leigh, Jr. (eds.) Forest Diversity Dynamism: Findings from a Network of Large-scale Tropical Forest Plots, pp. 492-505. The University of Chicago Press, Chicago.

Ashton, M. S., Brokaw, N. V. L., Bunyavejchwin, R., Chuyong, G. B., Co, L., Dattaraja, H. S., Davies, S. J., Esufali, S., **Ewango, C. E. N.**, Foster, R. B., Gunatilleke, N., Gunatilleke, S., Hart, T. H., Hernandez, C., Hubbell, S. P., Itoh, A., John, R., Kanzaki, M., Kenfack, D., S., K., LaFrankie, J. V., Lee, H.-S., Liengola, I., Makana, J.-R., Manokaran, N., Navarette Hernandez, M., Ohkugo, T., Perez, R., Pongpattananurak, N., Samper, C., Sri-ngernyuang, K., Sukumar, R., Fun, I.-F., Sureh, H. S., Tan, S., Thomas, D. W., Thompson, J. D., Vallejo, M. I., Villa Munoz, G., Valencia, R., Yamakura, T., and Zimmerman, J. K. 2004. Floristics and vegetation of the Forest Dynamics Plots. Pages 90-102 in E. C. Losos and J. Leigh, Egbert Giles, eds. Tropical forest diversity and dynamism: Findings from a large-scale plot network. University of Chicago Press, Chicago.

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Losos E.C. & CTFS Working Group. 2004. The structure of tropical forests. *In* Losos E.C. and Leigh, E.G. Jr. eds. Forest Diversity and Dynamism: Findings from a Large-Scale Plot Network. Pp. 69-78. University of Chicago Press, Chicago.

**Ewango, C.E.N.** 2001. Flore et Végétation de la Forêt naturelle de Nyungwe, Rwanda [Flora and Vegetation of the Natural Forest of Nyungwe, Rwanda]. Syst. Geogr. Pl. 71 (2) [Special Issue]: 1009-1015, in E. Robbrecht, J. Degreef and I. Friis (Eds). Plant systematics and phytogeography for the understanding of African biodiversity : proceedings of the XVIth AETFAT Congress, held at the National Botanic Garden, Belgium, August 28 - September 2, 2000.

**Ewango, C.E.N**. & Breteler, F.J. 2001. Présence du genre Pradosia (Sapotaceae) en Afrique description d'une nouvelle espèce, *P. spinosa*. Adansonia, Sér. 3. 23: 147-150.

Mercador, J., Runge, F., Vrydaghs L., Doutrelpont, H., **Ewango, C.E.N** and Juan-Tressears, J. 2000. Phytoliths from Archeological Sites in the Tropical Forest of Ituri, Democratic Republic of Congo. Quarternary Research 54: 102-112.

Poulsen, A.D., Lock, J.M, Liengola, I.B.and **Ewango, C.E.N.** 1999. A new forest species of Siphonochilus (Zingiberaceae) from Central Africa. Kew Bulletin 54: 203-207

## WORKING PAPERS

Plumptre, A.J., Masozera, M., Fashing, P.J., McNeilage, A, **Ewango, C**., Kaplin, B.A., and Liengola, I. .2002. Biodiversity Surveys of the Nyungwe Forest Reserve in SW Rwanda. WCS Working Paper No.19: 1-93. http://wcs.org/media/general/workingpaper19.pdf

Plumptre, A.J., Behangana, M., **Ewango, C. E.N.**, Davenport, T., Kahindo, C., Kityo, R. Ssegawa, P., Eilu, G., Nkuutu, D. and Owiunji, I. 2003. The Biodiversity of the Albertine Rift. Albertine Rift Technical Reports No. 3.

# *Education Certificate*

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

**Review of Literature (5.6 ECTS)**

- Diversity and species richness of liana in tropical old-growth forest; presented on the PhD discussion group on Forest ecology and Conservation (2007)

**Writing of Project proposal (4.5 ECTS)**

- Lianas Diversity, Distribution Patterns and Functional Ecology in a Central African Rain Forest, Ituri, North-eastern Democratic Republic of Congo (2007)

**Post-Graduate Courses (8.1 ECTS)**

- Multivariate Analysis; PE&RC (2007)
- Advanced Statistics; PE&RC (2007)
- Survival Analysis; PE&RC (2009)
- Geographic Information System; PE&RC (2009)
- What’s up in Tropical Forest Community Ecology?; PE&RC (2009)

**Deficiency, Refresh, Brush-up courses (3.0 ECTS)**

- Ecological Methods I (2007)
- Forest Ecology & Forest Management (2009)
- Ecological Methods II (2009)

**Competence Strengthening/ Skills Courses (1.8 ECTS)**

- Information Literacy for PhD + EndNote Introduction; WUR Library (2007)
- Techniques for Writing and Presenting a Scientific Paper; WUR Graduate Schools / CENTA (2007)

**PE&RC Annual Meetings, Seminars and the PE&RC Weekend (1.5 ECTS)**

- Research School Biodiversity and Biosystematics Group introduction day (2007)
- PE&RC Introduction weekend (2009)
- Annual PhD day Research School Biodiversity Symposium; Presentation (2010)

**Discussion Groups/ Local Seminars and Other Scientific Meetings (7.3 ECTS)**

- Current issues in Forest Management & Conservation; home institute Wildlife Conservation Society-CEFRECOF/ DR Congo (2007-2008)
- Wageningen Evolution and Ecology Seminars: Current issues in Biosystematics, PE&RC discussion group (2007-2010)
- Monthly chair group presentations: Biosystematics group (2007-2010)
- Weekly chair group presentations: Forest Ecology and Forest Management group (2007-2010)
- Ecological Theory and Application: Forest Ecology & Conservation, PE&RC discussion group (2008-2010)
- IUCN Netherlands Working Group Ecology and Development: Nature for Peace: The role of Conservation and natural resources management in conflict and peacebuilding Seminar, The Hague, the Netherlands; oral presentation (2009)

**International Symposia, Workshops and Conferences (9.9 ECTS)**

- TEDGlobal Conference: Africa – The Next Chapter, Arusha/ Tanzania; oral presentation (2007)
- Sustainable forest management in the tropics: Are we on the right track? (2007)
- NERN Annual meeting; Lunteren, the Netherlands (2008)
- Annual meeting of the Association of Tropical Biology and Conservation (ATBC) in Marburg, Germany; oral presentation (2009)
- Tropical forests and climate change: Are we on the right track ... beyond Copenhagen? (2009)
- Earth Day's 2010 International Year of Biodiversity- Rotterdam School of Management, Erasmus University; oral presentation (2010)

**Lecturing / Supervision of practical's / tutorials (3.2 ECTS)**

- Sustainability and Natural Resources Management: Companies in Ecologies-Learning from an environmental leader; Master class on sustainability; Rotterdam School of Management, Erasmus University (2009)
- Sustainability Management and Climate change: Conflicts, Resources management and conservation. Master's class on sustainability. Rotterdam School of Management, Erasmus University (2010)
- Forest inventories: field botany for identification of tree, lianas and carbon estimation in the tropical forest. Wildlife Conservation Society-CEFRECOF, Epulu. DR Congo (2010)