

LIANAS AND LOGGING IN WEST AFRICA

Parren, M.P.E.
Lianas and logging in West Africa

PhD thesis, Wageningen University, Wageningen, The Netherlands
with summaries in English, Dutch and French.

Keywords: West Africa, silvicultural treatments, logging damage, lianas, climber cutting, lowland rain forest

ISSN 1566-6484
ISBN 90-90-5808-871-5 (thesis version)
90-5113-066-X (Tropenbos edition)

© 2003 Tropenbos International

The opinions expressed in this publication are those of the author(s) and do not necessarily reflect the views of Tropenbos International

This study was carried out at the Forest Ecology and Forest Management group (P.O.Box 342, 6700 AH Wageningen), Department of Environmental Sciences, Wageningen University, the Netherlands in collaboration with the Ministry of Environment and Forests of the Republic of Cameroon and Tropenbos International.

No part of this publication, apart from bibliographic data and brief quotations in critical reviews, may be reproduced, re-recorded or published in any form including print photocopy, microfilm, electromagnetic record without the prior written permission.

Cover design Duotone, Wageningen University, the Netherlands
Cover photo Woodcutter (1912-13), Kazimir Malevich, collection Stedelijk Museum Amsterdam
Printed by Ponsen en Looijen, Wageningen, the Netherlands

LIANAS AND LOGGING IN WEST AFRICA

Marc P.E. Parren

PROEFSCHRIFT
ter verkrijging van de graad van doctor
op gezag van de Rector Magnificus
van Wageningen Universiteit
Prof. dr. ir. L. Speelman,
in het openbaar te verdedigen
op woensdag 8 oktober 2003
des namiddags om 13.30 uur in de Aula

Promotor: **Prof. dr. F.J.J.M. Bongers**
persoonlijk hoogleraar
bij de leerstoelgroep bosecologie en bosbeheer

Prof.dr.ir. G.M.J. Mohren
hoogleraar in de bosecologie en bosbeheer

Samenstelling promotiecommissie:

Dr. G. Caballé (Université de Montpellier II)
Prof. dr. F.E. Putz (University of Florida)
Prof. dr. H. Schanz (Wageningen Universiteit)
Prof.dr.ir. M. Sosef (Wageningen Universiteit)
Dr. R.J. Zagt (Tropenbos International, Wageningen)

LIANAS AND LOGGING IN WEST AFRICA

Marc P.E. Parren

Tropenbos International
Wageningen, the Netherlands
2003

TROPENBOS-CAMEROON SERIES 6

The Tropenbos-Cameroon Series publishes results of research projects carried in the framework of the Tropenbos-Cameroon Programme (TCP). The TCP operated within the framework of the programme of Tropenbos International. The multidisciplinary Tropenbos-Cameroon programme contributes to the conservation and wise utilisation of forest resources in Cameroon by conducting strategic and applied research and building capacity in Cameroon in the field of forest-related sciences.



WAGENINGEN UNIVERSITEIT
University for Life Sciences



PREFACE

Referring to lianas does ones mind wander to Olympic champion Johnny Weissmuller who became the magic 'Tarzan', a forest-dwelling white man who glided between tree canopies by means of these large climbing plants in the African forest. Tarzan's pristine tropical moist forests where you could have regular encounters with elephants, gorillas and crocodiles are nowadays hard to find. Major changes have taken place since the 'white man' penetrated deep into these 'jungles' and started to exploit them. In 1982, when I first set foot on the African continent, unexploited West African forest hardly existed anymore. In those days I ended up in the aftermaths of Ft. Lt. J.J. Rawlings, also referred to as Junior Jesus at the time, coupe d'état. These were the revolution days and the Cold War still raged on, so I witnessed the attack of the American Embassy in Accra and ended up with Khadaffy's Green Booklet at hand. Most of my stay was spent in the little town of Larteh in the Akwapim Ridge close to Accra trying to arrange a visa extension. However, since I was a 'white man' from the so-called capitalist West, officials had become revolutionaries and were not willing to help. Still my afternoons were spent on a veranda in Larteh with a magnificent view over the Accra plains and monkeys jumping between the tree crowns of big Kapok (*Ceiba pentandra*) trees.

Two years later I returned to Ghana and found that the country had burnt severely the previous year and no longer could monkeys be sighted from my veranda. The landscape had drastically changed since many forest fragments and individual trees had burnt and disappeared. At the time the event was described as an extreme dry year and combined with farm burning, which got out of control, it changed the landscape. Nowadays, we know that the extreme drought in West Africa was not just a local event but a global effect related to the El Niño event in the Pacific Ocean. Deforestation attracted my attention and how to halt this process somehow. This made me to decide to study forestry. During my studies and later on I returned on a regular base to West Africa and was able to visit many forest reserves often just a couple of thousand ha in size. The management issues of these reserves related to natural dynamics, (non-) timber exploitation and the manipulation of these forests by applying silvicultural treatments intrigued me. What also fascinated is the fact that the more or less same types of forests were managed in completely different ways in the respective countries in the region. This lead to a study culminating in a book jointly written with my first maître and colleague Reitze de Graaf on forest management in Ghana, Côte d'Ivoire and Liberia. This study was my first project in which I collaborated with Tropenbos International and the support of Erik Lammerts van Bueren and Mrs Wanda Tammens-de Rooij are still very much appreciated. Around that time, I got a chance by the Department of Forestry of Wageningen University to shift my working field beyond the Dahomey Gap and to study the ecological effects of logging in Cameroon. Cameroon is at the crossroad of West and Central Africa since to the British it forms part of West Africa while the French consider it to form part of Central Africa. This gave me the opportunity to work in the relatively untouched forests of the Congo Basin and study this 'jungle'. Studying the role of lianas seemed to be logic to me since the African forests were considered to be rich in lianas, loggers often find lianas a hindrance in their operations and large-scale liana cutting had taken place in the past in West Africa but mostly halted for no obvious reasons since no proper evaluation had

been made. At the same time the FAO and the French standard work for Africa 'Memento du forestier' in their harvesting code still recommended liana cutting.

The almost three years I lived in Cameroon proved to be very challenging. I formed part of a multi-disciplinary research team of the Tropenbos-Cameroon Programme that investigated an integrated approach, in which basic assumptions concerning social and technical forestry conditions for sustainable forest management were to be combined with qualitative understandings of actual forest use and the applicable regulations. Interactions with all the disciplines present proved not to be as easy as it looks on paper and can be very demanding. The actual research zone was formed by the concession of the Dutch timber trading company G. Wijma & Zonen some 100 km east of Kribi where the project office was based. The actual zone of my studies had never been logged before and as such represented something of Tarzan's jungle described before. However, most distressful all the big mammals had already ended up as bushmeat on someone's table. I teamed up with the late Roger Bibani Mbarga and together we established a great number of permanent sample plots 9-ha in size and inventoried them for lianas and trees. Pre-harvest silvicultural treatments were to be applied by me, in this case liana cutting, while Bibani applied post-harvest silvicultural treatments in the form of liberation thinning. I remember well the first plots we established were over one hour's foot march from the nearest logging truck road while later on the forest operations team of Wijma were approaching us closer and closer every month. The noise of the machines increased while those of animals halted all together.

As for the Tropenbos-Cameroon Programme team over the years I like to thank the management team Wim van Driel, Oscar Eyog Matig, Bernard Foahom, John Hendrison, Wyb Jonkers, Jean-Paul Tsimi Mendouga, Pieter Schmidt for their support. The regular team meetings and especially the Friday after work ones on Kribi's beach front led to many exchanges of ideas and collaboration with colleagues such as those in forestry: Charles Bongjoh, Roger Bibani Mbarga, Richard Eba'a Atyi, Gart van Leersum, Flavien Ngibaot, Nsangou Mama and Nerée Onguene Awana; in socio-economics: Jolanda van den Berg, Karen Biesbrouck, Han van Dijk, Nicole Marie Guedje, Guillaume Lescuyer, François Nkoumbele and François Tiayon; and in land use planning: Barend van Gernerden, Gerard Hazeu, Laurent Nounamo, Jean-Claude Ntonga, Maarten Waterloo and Martin Yemefack. I have especially fond memories of my stay in the Ebom village, closest to my research plots. Many a Bulu villager has been working in these plots in collaboration with me and I can only mention a few of them whom I am very indebted: Joseph Anjo, Joseph Entoundi, Benjamin and Marcel Mva, Paul Nkolo and Alain Paul Nkomo. Without the assistance of Scott Okie and Maurice Elad Epah to guide the working teams, and Maurice who identified the plants in the forest, the work would never have come to an end. I also like to express my gratitude for the fine collaboration in the forest with the late Roger Bibani Mbarga, his assistant Jean Essama Etoundi and our own RIL-expert Gart van Leersum. Many students collaborated in the setting up of the permanent sample plots and did some detail studies for which collaboration I am most indebted, in order of appearance they were: Taco Bosdijk, Onno Heerma van Voss, Michiel van Breugel, Tieme Wanders, Jan Janssen, Suly Mutsaers, Joris Voeten and Tom Van Loon. They enjoyed the same hospitality in the Bulu village and witnessed the logistic circus of a project such as the Tropenbos-Cameroon Programme operating on distance over an area of 2,000 km².

This brings me to thank Wijma-Douala SARL for enabling me to work in their concession and to provide assistance with the exploitation aspects and especially their director Yves Mâry.

When back in the office the office assistants Aristide Diady, Hannah Enjema Mokome and Angèle Mbamba took good care of us. Some precarious and often also funny situations were encountered en route with the unforgettable drivers Jean Djon Djon, Gervais Meyo and Jean Owona. Joseph Mbamba was our good old botanist and 'maître de herbier' who enabled the despatch of botanical specimens to be identified by Jan Just Bos, Frans Breteler, Carel Jongkind, Anton Leeuwenberg, Jan Wieringa and J. de Wilde at the National Herbarium Netherlands, Wageningen University branch (Herbarium Vadense). I am especially indebted to Frans Breteler who spent many hours with these imperfect specimens, since mostly lacking flowers and fruits, and enlightening me in the taxonomic world. Back in the Netherlands I also have fond memories of Frans Bongers tropo-team with whom we had some most stimulating U.K. roadshows: Patrick Jansen, Peter van der Meer, Lourens Poorter, Renaat Van Rompaey, Toon Rijkers and Frank Sterck. At the Department of Forestry of the Wageningen University I like to thank the following professors: Roelof Oldeman, for driving me in the arms of the forest elephant, Marius Wessel, for being around when the ship was just floating, Frits Mohren, to help with the finishing touch and last but not least Frans Bongers, for being a most stimulating support in good and bad days. Kathinka Huisman, Joke Jansen and Ruud Plas proved invaluable in the background for giving the support and services that made this project possible.

Persons and organizations consulted in the course of this project are too numerous to mention individually by name. Still I like to recall the names of some organizations visited and persons met during my stays abroad. As for my experiences in Ghana over the years I like to acknowledge the Forestry Commission and in particular the late Chief Conservator of Forests, John François, besides him also Victor Agyeman, Jan Decher, William Hawthorne and Kwesi Orgle. Abidjan, the capital of the Côte d'Ivoire, formed something of a sally port for many visits in the region. I like to acknowledge the forest service SODEFOR and Vincent Beligné, Léonie Bonnénin, François Kouamé, Hans Jörg Wöll and Dr Ekki Waitkuwait. Liberia was finally visited in the new millennium and Florence Blyden, Alex Peal, Jamison Suter, Anyaa Vohiri and Zwuen made this an unforgettable experience. In Equatorial Guinea, Helen and Frank Stenmanns were some excellent hosts and gave insight in this hardly known country. Apart from the Tropenbos project I had regular contacts in Cameroon with MINEF, ONADEF and the University of Dschang, at CIRAD-Forêt's API-Dimako project Eric Forni proved to be most helpful, like Terry Sunderland and Mr. Ndam at the Limbe Botanic Gardens. The Earthwatch Expedition to Mt. Kupé with Martin Cheek was also one not easily to be forgotten.

Over the years I encountered a group of fellow liana aficionados at meetings in Aarhus, Mexico City and Panama City among which were Robin Burnham, Guy Caballé, Sandra Dewalt, Mirjam Kuzee, Jacob Nabe-Nielsen, Diego Pérez-Salicrup, Jack Putz and Stefan Schnitzer, which proved to be most stimulating colleagues. Stimulating over the years were also my regular encounters over the globe with Jacqueline de Graaf, Margreet Hofstede, Arthur van Leeuwen, Robbert Wijers, Peter Grave and Odile Smeets. The latter too made even sure that I was not making a

financial mess out of my regular visits abroad and kept a closed watch on the bureaucratic flow of paper trying to trace my whereabouts.

The last couple of years I have been a tropical forestry lecturer at the University of Professional Education Larenstein in the Netherlands. I hope I have not been too much of a burden for my colleagues over there with my focus on completing this dissertation. I appreciate the patience shown by Arjen Hettema and Hans van Rooijen to get this project to a good end. I like to thank David Dunn for correcting my Denglish, and Peguy Tchoutou for the translation of the French text.

Finally, writing a dissertation is a long-winded project. Brakes were the births of my daughters Dominique and Kim. Thanks to their turbulent presence it proved not to be hard to put into perspective my scientific research. Therefore I dedicate this dissertation to them and their unsurpassed mother.

Marc Parren
Wageningen 31 August 2003

CONTENTS

- Chapter 1. General introduction
- Chapter 2. Latest trends in West African natural forest management aimed at timber production
pp. 2-16 in A.H.W. Seydack, W.J. Vermeulen and C. Vermeulen (eds.), *Towards sustainable management based on scientific understanding of forests and woodlands*. Proceedings of the Natural Forests and Woodlands Symposium II (1999, Knysna). Knysna, South Africa, Department of Water Affairs and Forestry (2000)
- Chapter 3. On censusing lianas : A review of the common methodologies
with F. Bongers, G. Caballé, J. Nabe-Nielsen and S.A. Schnitzer
submitted
- Chapter 4. Logging and lianas in West Africa
with F. Doumbia
submitted
- Chapter 5. Abundance and distribution of lianas in a lowland tropical rain forest in southern Cameroon
with F. Bongers
- Chapter 6. Does climber cutting reduce felling damage in southern Cameroon?
with F. Bongers
Forest Ecology and Management 141: 175-188 (2001)
- Chapter 7. Recruitment of lianas into logging gaps and the effects of pre-harvest climber cutting in a lowland forest in Cameroon
with S.E. Schnitzer and F. Bongers
Forest Ecology and Management accepted for publication
- Chapter 8. Synthesis
Summary

1. GENERAL INTRODUCTION

The main objective of this thesis is to analyse the role of lianas in the tropical moist forest ecosystem in relation to logging activities. One important aspect is to assess the influence of physical damage on the remaining vegetation in a logging gap and the response of the vegetation to changed conditions. Logging in African tropical moist forests was concentrated in West Africa until the 1970s, after which it shifted to Central Africa. The increased logging of natural forests has broadened the interest of those involved and stimulated the setting up of sustainable management systems throughout the tropics. A prime aspect of these systems is sustainable timber production. This should ensure that an equal yield can be harvested after 20-40 years in a projected felling series within the same concession and at reduced damage levels to the residual stand. The framework for this study is thus forest management based on sound ecological knowledge and ultimately the manipulation of the forests by silvicultural interventions.

The forest composition and its condition determine what forest use is possible without disrupting the functioning of the natural forest ecosystem. In unlogged forests, larger diameter lianas are a common phenomenon and are known to connect several tree canopies. Most large lianas link several tree canopies and when a large tree falls, these lianas may enlarge gaps, as they may tear down or damage several other trees. Lianas flourish after the canopy is opened since they often have a heliotropic character. When the canopy of the forest opens, the seedlings and shrubs of lianascent species rapidly produce long shoots and become lianas. The regular occurrence of treefall gaps in a forest will maintain the succession of lianas and trees.

However, disturbance levels due to logging are often more intensive and frequent than the dynamics in an unlogged forest. Logging operations, often followed by conversion to other land uses, can lead to forest fragmentation at the landscape level. The logging gaps themselves will also lead to more edge effects. Lianas are likely to respond quickly to these changes by forming many new apexes — they proliferate and in this way benefit more than trees from these environmental changes. In many moist forests, mats of lianas are a very serious impediment to recovery after intensive logging. The natural regeneration of tree species can be hampered for years if not decades by a blanket of lianas. This phenomenon is described by several forest researchers in African moist forests and seems to play an essential role in the succession process (Fickinger 1992, Bertault 1986, Osafo 1970, Dawkins 1960, Foggie 1960). One of the control options is to apply liana cutting before harvesting to reduce the damage at the felling site and as a measure to control the proliferation of lianas in the felling gap.

1.1. THE IMPORTANCE OF LIANAS

The term ‘liana’ is used here for woody, climbing (or scrambling) plants. African moist forests are relatively species-poor when compared with Neotropical and Australasian moist forests. Liana density, however, is greater in these forests compared to other continents (Reitsma 1988, Gentry 1991a). A special group of

lianas are the climbing palms (Palmae). They are also referred to as rattans, and with their proclivity for colonising recently disturbed forests, rattans are widespread and are quite common in Asian (Appanah *et al.* 1993, Siebert 1993) and African forests (Sunderland 1999), although relatively rare in Neotropical (Siebert 2000) forests.

The role of lianas in tropical forests is important, and threefold. First, they contribute to canopy closure after treefall, thereby stabilising the microclimate underneath (Schnitzer and Bongers 2002). Second, lianas have a kind of antagonistic relationship with their hosts. Since lianas need support to reach the canopy they can save on the heavy investments made by woody plants for the production and maintenance of supporting tissue (Ewers and Fisher 1991, Caballé 1993). Instead, they can invest more resources in growth, leaf production and sexual reproduction. However, at the same time, lianas negatively influence growth, leaf production and sexual reproduction of the support agent: liana-laden trees have been seen to show smaller diameter increments (Lowe and Walker 1977, Putz 1984b, Putz *et al.* 1984, Whigham 1984, Finegan *et al.* 1999, Pérez-Salicrup and Barker 2000), slower height growth (Pérez-Salicrup 2001), reduced fruit production (Stevens 1987), and higher mortality rates (Putz 1984a). Third, they tie the tree crowns together, giving the canopy more coherence. Liana-laden trees are quite common as over 50% of all large trees (> 10 cm dbh) typically bear at least one liana in both Neotropical and Southeast Asian forests (Putz 1983, Putz and Chai 1987, Campbell and Newbery 1993, Pérez-Salicrup *et al.* 2001b). To give an idea of the potential expansion by lianas, Caballé (1980b) showed the example of an *Entada gigas* liana individual of over 30cm dbh that used 13 canopy trees to reach gaps covering a distance of several hundred metres. Several of the larger diameter liana species have the potential to twine multiple tree crowns at the forest canopy, thus attaining great lengths. It is even more striking to see their role in relation to trees when one considers their contribution to the total aboveground biomass. In most tropical moist forests, lianas form a minor proportion of less than 5% of the total aboveground biomass. This is the case for most of the Amazon Basin (Shanmughavel *et al.* 2001, Nascimento and Laurance 2002). Sometimes, however, liana omnipresence results in so-called liana forests in the Amazon and ultimately can result in lower statured forest where lianas contribute up to 12% of the total aboveground biomass (Gerwing and Lopes Farias 2000, Troy *et al.* 1997). Liana forests may also occur in dry areas where drought adaptations of lianas may give them a competitive advantage (Killeen *et al.* 1998).

Liana abundance seems first to be determined by disturbance regimes and whether the forest is continuous or fragmented. Disturbance regimes in the pantropics can have natural causes such as windfall, lightning, floods or landslides; or can be human induced for example by farming and logging, which open the forest canopy and eventually lead to forest fragmentation. In Queensland, Australia and Central Amazonia many more small lianas and relative fewer large lianas (including climbing rattans) were present at fragment edges and interiors than in continuous forest interiors (Laurance 1997, Laurance *et al.* 2001). Edges of forest fragments in the Atlantic moist forests of Brazil were notable for having a particularly high frequency of liana tangles and could be effectively controlled by liana cutting (Oliveira-Filho *et al.* 1997, Viana *et al.* 1997). So a marked proliferation of lianas exists (including climbing rattans), trends that typify chronically disturbed tropical forests. Mortality rates of large trees (> 60 cm dbh) is also much higher at edges (Laurance *et al.* 2000), since there are more

lianas at edges, and large trees tend to be particularly susceptible to liana infestation. Most remaining West African forests are fragmented and of a rather small size. These forests have repeatedly been selectively logged over short timespans and have often been partly burnt by fires set by farmers either outside or even inside reserves. So lianas will become more prominent in these fragmented forests (see also Carrière *et al.* 2002). An additional characteristic of lianas is that next to genets they also produce ramets and show prodigious resprouting capacities. This means that as a lifeform they are more flexible than trees to disturbance, and possess the potential to increase their dominance.

The importance of lianas for fauna is little known. However, lianas can bear fruit in lean tree-fruiting periods and form an essential diet of many animals during such periods (Putz and Windsor 1987, Heideman 1989, Ibarra-Manríquez *et al.* 1991, Opler *et al.* 1991, Hecketsweiler 1992, Morellato and Leitao-Filho 1996). Even though they do not form the bulk of the aboveground biomass, lianas provide suspended connectivity that is important to many small arboreal animals. Lianas provide pathways between individual tree crowns for various primates and rodents (Charles-Dominique *et al.* 1981, Schwarzkopf and Rylands 1989, Mamede-Costa and Gobbi 1998) and certain species of small primates show distinct habitat preferences for liana forest patches (Bobadilla and Ferrari 2000).

1.2. EFFECTS OF LOGGING AND THE NEED FOR SILVICULTURAL TREATMENTS

Sustainable timber production typically combines harvesting guidelines designed to increase the growth of marketable timber with efforts to lower the damage to commercial trees. Direct effects of logging are the opening of the forest by constructing a road and skid-trail network, loading bays and the removal of harvestable trees. In this way biomass is destroyed in the stand, while the chablis formed by the felling of trees causes physical damage to the remaining vegetation. This often goes hand in hand with liana proliferation. Degradation of the stand is often increased by repeatedly re-entering compartments at short time intervals. At present, most logging in the tropics (apart from plantations) can be considered to be unsustainable.

Silviculture plays a central role in sustainable timber production. Most initiatives employ polycyclic felling systems, such as the Celos system developed in Suriname (Boxman *et al.* 1985) and lately applied on a commercial scale in Brazil. These systems do not only assure that potential crop trees are saved and will form part of the next harvest within 25-40 years (felling cycles) but often the productivity is increased by removing or poisoning non-commercial trees. Regeneration of tree species is encouraged by some combination of careful logging and transport, cutting lianas that link tree canopies prior to harvest, leaving seed trees, and sometimes scarification of the top soil to overcome soil compaction. Other sustainable timber production systems include the Malaysian Uniform System (MUS) and the related Tropical Shelterwood System (TSS), practised in West Africa. These are both monocyclic systems in which all marketable trees are harvested in a single harvest. Large, non-commercial stems are removed immediately following harvest and additional silvicultural treatments are repeated at regular intervals over the course of a 60-100 year rotation period (equalling one felling cycle). While, in theory, all of

these silvicultural systems can ensure sustainable harvests, for a variety of reasons, they have only rarely been put into practice.

Most silvicultural systems are found to be too costly and insufficiently compensated by higher growth (i.e. harvestable volumes) and/or increased desired regeneration. This has given rise to more recent attempts at controlled logging, also referred to as reduced-impact logging (RIL). Such efforts focus more on reducing the physical impact of logging than on providing sustainable timber yields of desired species. Reduced-impact logging techniques may include careful planning of skid trails to reduce the distance travelled; minimising loss of forest cover, soil erosion and soil compaction; and practising directional felling of harvested trees to minimise damage to the surrounding forest. Liana cutting often forms part of RIL prescriptions, since lianas are often regarded as a hindrance to forest operations and are believed to lead to increased damage levels. The negative effect of liana abundance and liana strength has received considerable attention in relation to damage reduction during RIL operations (Appanah and Putz 1984, Pinard and Putz 1994, Putz 1995, Cedergren 1996, Ek 1997).

Kasran (1989) and Jonkers and Schmidt (1984) showed that the uncontrolled harvesting (conventional logging) of Dipterocarp forests in Southeast Asia of volumes up to 40-100 m³ ha⁻¹ has led to serious erosion, water pollution and drastic changes in species composition and forest structure. In Brazil and the Guyana Shield, conventional logging intensity varied between 6 to 20 trees per ha of volumes up to 30-60 m³ ha⁻¹. However, controlled logging of up to 5 trees per ha or volumes 6-40 m³ ha⁻¹ was found to lead to reduced damage to trees in the residual stand and reduced surface disturbance by heavy machinery (Hendrison 1990, Barreto *et al.* 1998, Van der Hout and Van Leersum 1998). The critical values in the Cameroonian context are still not well known. Recent experiences with RIL, and comparisons between the different continents, including experiences from Cameroon, show that they lead to reductions in damage to vegetation and soil, higher recovery of usable timber, with only minimal cost increase (Holmes *et al.* 2002, Jonkers 2002). However, without the silvicultural interventions needed to ensure sustained yields, reduced-impact logging is not likely to be sustainable, and will therefore not differ greatly from conventional timber harvesting in the long term.

Controlled logging, especially at removal intensities of less than 50 m³ per ha, has a minimal effect on the canopy characteristics (structure, crown and leaf cover, aerodynamic roughness). Consequently, the immediate changes in microclimate and medium-term effects on the hydrological regime are relatively small, and are restricted to a small part of the area (Brünig and Poker 1991). Smaller and less frequent canopy disturbance might also result in fewer problems with lianas. However, logging and the possible prescription of liana cutting might not only lead to fewer lianas in tree crowns but might also seriously affect arboreal animals. Faunal elements play an important role in the regeneration process and their behaviour will be seriously disturbed by logging activities (Jansen and Zuidema 2001). The dispersal of the large and heavy seeds of certain tree species might be seriously hampered since the dispersers might leave the logging area for a long period of time. This process is either due to the noise of the operations (Van den Berg and Biesbrouck 2000) or to the change in structure of the forest (leading to food scarcity) so the dispersers no longer find suitable habitats (see

Johns 1988, 1992, Skorupa 1986). What is most important in this respect is that liana and tree phenology are not synchronised. Lianas can bear fruit in lean tree-fruiting periods and form an essential diet of many animals to get through such periods. The effects of liana cutting on arboreal animals in this respect would appear to be obvious but have never been researched. In general, large-bodied frugivores are the most susceptible to habitat disturbance (Johns and Skorupa 1987, Struhsaker 1997, White and Tutin 2001), although the timespan to repopulate can be quite different amongst different primate species in the same area (Grieser Johns and Grieser Johns 1995). Logging followed by increased hunting activities is also a well-known negative phenomenon (Bennett and Robinson 2000) that will influence tree recruitment (Guariguata and Pinard 1998). It can eventually even lead to diminished seed dispersal rates that will negatively affect the regeneration of commercial species and thus threaten sustainable timber production (Guariguata *et al.* 2000).

A shift in faunal and flora elements towards species that prefer more open conditions can be anticipated with the repeated disturbances of logging operations (Okuda *et al.* 2003). Since many liana species prefer more open conditions, many heliotropic species might benefit and increase in numbers, whereas shade tolerant liana species might reduce in numbers. A shift from rare to more common species in mature forest can be expected. However, the actual loss of tree and liana species after large scale logging interventions will be hard to prove (Plumptre 1996, Cannon *et al.* 1998, Parrotta *et al.* 2002). Most interestingly in Amazonian forests, controlled logging, especially at removal intensities of less than 50 m³ per ha, does not seem to cause reductions in flower and fruit production of understory plants and as a result hardly affects resources for animals at those levels (Costa and Magnusson 2003). In general, Bawa and Seidler (1998) concluded that “logging at any level appears to have simplifying and homogenising effects on tropical diversity when examined at community or regional scales.” However, the question remains whether controlled logging can avoid these negative effects in the long term.

1.3. OBJECTIVES

As lianas are mostly seen as a nuisance by foresters, the cutting of liana stems has been an important operation in forest management practices. Pre-logging liana cutting has been applied over several 100,000 ha in both Ghana and Nigeria and sometimes even included poisoning of all lianas (Parren and de Graaf 1995). This operation aims to reduce logging damage, to improve felling precision, to enhance the development of the growing stock and to reduce the regrowth capacity of lianas. Studies that evaluate the effectiveness of pre-logging liana cutting are scarce however. Studies in Southeast Asia and the Amazon Basin have shown positive effects of liana cutting in reducing logging damage to residual trees (Appanah and Putz 1984, Vidal *et al.* 1997, Pereira Jr. *et al.* 2002). The African forest is known for its high liana abundance, and liana cutting was prescribed over vast areas. Proper evaluation, however, was never carried out. Therefore, an experiment was set up in southern Cameroon to test the effectiveness of liana cutting as a pre-logging silvicultural treatment. The project formed part of a much larger programme that aimed to increase productivity of the stand by applying post-logging silvicultural treatments to favour desired species. The post-logging treatments consist mainly of the

elimination of non-commercial trees in order to stimulate the growth of promising commercial trees.

- In this study the following questions were asked:
- How to inventory lianas?
- How abundant are lianas in the forest studied?
- What spatial distribution patterns do liana species have?
- To what extent does liana cutting result in the death of the lianas and what is their resprouting capacity?
- What is the effect of pre-felling liana cutting on the felling gap sizes, on the number of dead or damaged trees, and on the felling direction?
- What type of forest management strategies are required in timber production areas to reach sustainability?

1.4. THE FOREST SECTOR IN CAMEROON

In the tropics, commercial logging on a significant scale dates back to the end of the nineteenth century. Since then, deforestation of unprotected forests in densely populated West African countries (Nigeria, Ghana and the Côte d'Ivoire) has been almost complete. The permanent forest estate (both timber production reserves and conservation areas) is the last stronghold of forests in these countries. The actual allowable annual yield in each of these countries equals approximately 1 million m³; a sharp drop compared to previous figures of up to 6 million m³ (Martin 1989, Parren and de Graaf 1995). When in the early 1990s the timber crises first appeared in these countries, an upsurge of logging activities could be seen in the Congo Basin, and Cameroon more specifically. By the end of the 1980s Cameroon, located transitionally between west and central Africa, was still covered by about 17 million ha of tropical moist forest or about 70% of the original moist forest zone. The country aimed to become the principal timber exporting country of Africa, a target it reached in 1999. The production level in the late 1990s reached c. 3 million m³, of which two thirds were exported as roundwood and over half to the Asian markets (Eba'a Atyi 2000), while a projected annual yield has been set of 5 million m³ by the year 2010

The underlying causes are the following. Since the start of the economic crisis (1986-87) in Cameroon, some 67% of all accredited enterprises over a 10 year period were start-ups, a fact which accounts for the unexpected investments during this period (Eba'a Atyi 1998). This could have been caused by (1) the timber crisis in countries like Ghana and Côte d'Ivoire, which supplied the same species; (2) the vast concessions (Cameroon, max. 200,000 ha) of unlogged forests still accessible in the Congo Basin; (3) the devaluation of the CFA Franc in 1994; (4) the increasing demand for African timber in Asia at the time; and (5) Cameroon's national policy to become the principal timber exporter of Africa. Conversion of c. 0.5 million ha of moist forests to smallholder coffee and cocoa plantations from the 1950s to the 1970s resulted in relatively equitable economic growth, averaging 3 to 4% per annum. In more recent years, timber exploitation has overtaken coffee and cocoa production as the most important economic activity in the moist forests. Cameroon is now the leading African exporter of tropical timbers, with over \$270 million in annual export sales. As a result deforestation increased from 100,000 to 200,000 ha per annum (Cleuren 2001).

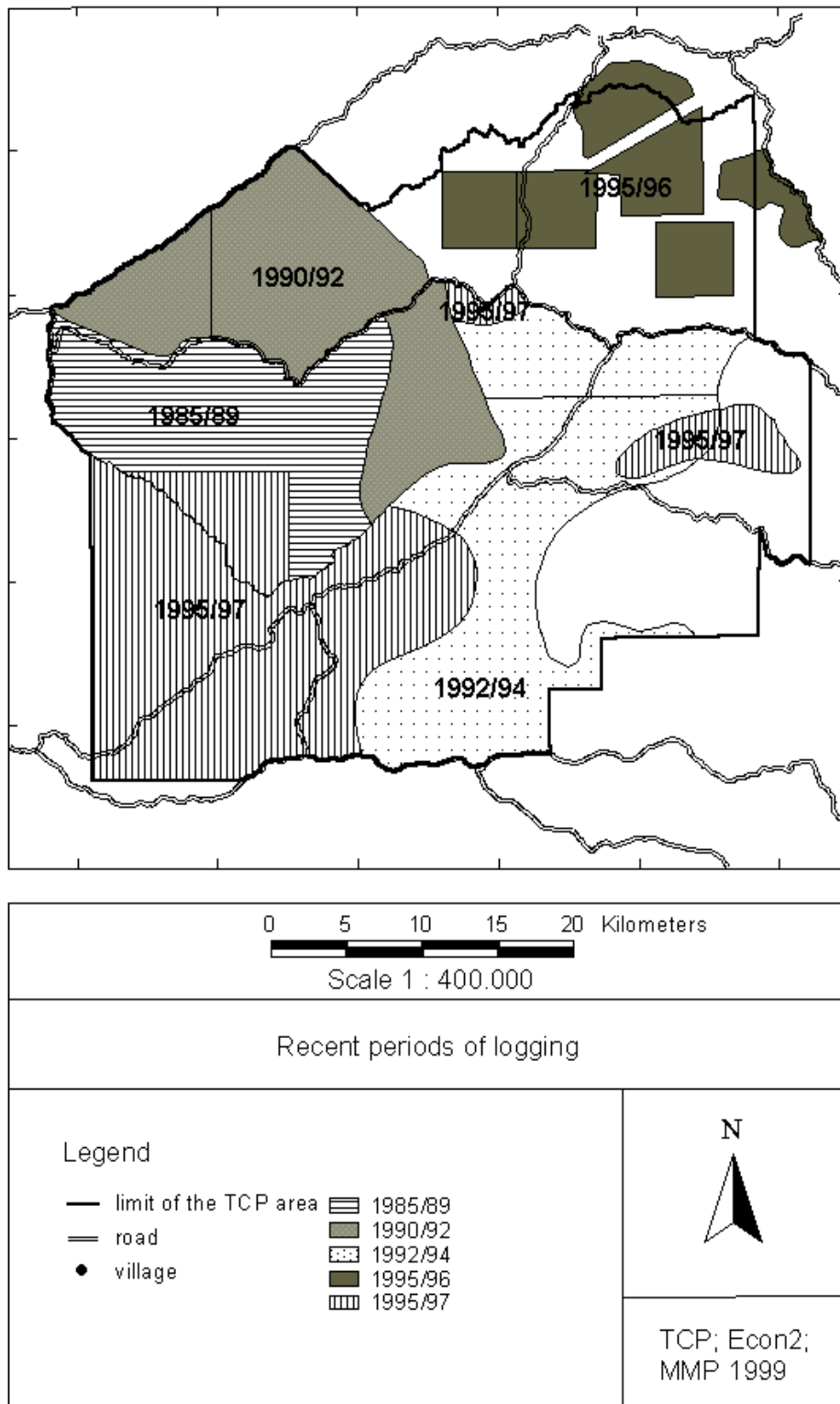


Figure 1.1. Wijma en Zonen B.V. (GWZ) concession map indicating the localities of harvesting during different periods. The Ebom experimental area is located in the north-east corner and logged between 1995/96.

By and large a poor nation, Cameroon has little choice but to develop its forest resources. From the standpoint of government policy, the critical question is whether Cameroon's moist forests will be turned into sustainable agricultural and forestry production systems or 'mined' into a state of degraded vegetation. During the 1990s a national land use planning exercise aimed to reserve 30% of the national territory as permanent forest estate of which some 9 million ha of moist forest (Côté 1993). This is possible since the government abolished customary land tenure in 1974 and nationalised all land held under such tenure (Cleuren 2001). In total 7.2 million ha are designated timber production areas and 5 million of these are handed out as concessions, as was the case in 2001.

1.5. STUDY SITE

Most of the field work for this study was carried out in the Bipindi–Akom II–Lolodorf region, south Cameroon (3° North, 10° East) 100 km east of Kribi. This region forms part of the 2,000 km² forest logging concession of the Dutch-owned timber company, Houthandel Gebroeders Wijma en Zonen B.V. (GWZ) (Fig. 1.1). The concessionaire, Wijma, has a long history in construction in the Netherlands (harbours, dams, bridges, and railway sleepers). The company is primarily interested in logging high-density wood species, leaving aside the species used in the production of veneer and plywood. As a result, the forest is not harvested to its full potential. For example, one can find remarkable seven tall emergent trees per ha with trunk diameters of 1 to 2.5 meters. Only a few of these giants belong to marketable species. The most important commercial species is Azobé (*Lophira alata*), characteristic of low altitude evergreen forest. It is this species that the logging company is particularly interested in, and it makes up around 60% of the extracted volume. This type of logging can be characterised as being relatively selective and light (10 m³ ha⁻¹ or 0.7 trees ha⁻¹) compared with forest concessions of the Neotropics and Southeast Asia (see Parren and de Graaf 1995, Jonkers and Van Leersum 2000). The felling and skidding operations cause small direct loss of forest cover (av. 5%) with higher local disturbance rates where species such as Azobé are found in clumps. As a result, substantial parts of the forest are not affected by logging.

The actual experimental area encompassed c. 500 ha within a block of a concession of 90,000 ha that was put into production in 1988 and returned to the Government in July 1998. Productivity in this concession was very low in its final stage of exploitation and thus the company was given several 'ventes de coupe' adjacent to the concessions to make up for this low productivity (J. Mary pers. comm.). It is in these areas of 2500 ha each, that the present study was conducted (see north-east corner Fig. 1), near the village Ebom (3°02' N, 10°52' E). The 500 ha study area was located within a relatively flat, homogeneous area of the forest, although the topography of the entire forest ranges from undulating to rolling with some relatively small, isolated hills (350-500 m a.s.l.). A total of 33 1-ha plots were established, dispersed over the 500 ha study area (Fig. 1.2). The parent material consists of Precambrian metamorphic rocks and old volcanic intrusions (Franqueville 1973). The Ebom soils are deep to very deep, well drained and are characterised by their clayey subsoils with less clayey topsoils, and are classified as Acrid-xanthic Ferrosols (Van Gemerden and Hazeu 1999). The mean annual rainfall

in this area is 2000 mm with two distinct dry seasons, from May until August and December until March (Waterloo *et al.* 1997). Relative humidity is generally above 80%. Average monthly temperatures vary between 22.9 and 27.5° C (Olivry 1986).

The forest is evergreen of the Atlantic Biafrian type (Letouzey 1968), with a 25-40 m closed canopy and emergent trees surpassing 60 m in height (Parren and Bongers 2001) with a total aboveground biomass of 581 tons ha⁻¹ (Ibrahima *et al.* 2002). The Bipindi–Akom II–Lolodorf region is rich in plant species, with 1264 species recorded so far. About one tenth are endemic to the Lower Guinea forest region (Nigeria – Gabon) of which 51 species are restricted to the moist forests of Cameroon (B.S. van Gemerden, pers. comm.). Looking only at the tree species richness of 19 1-ha unlogged forest of the Ebom forest, some 416 different species from 54 families and 238 genera were recorded of trees larger than 10 cm dbh. Families present in every plot were Anacardiaceae, Annonaceae, Burseraceae, Ebenaceae, Euphorbiaceae, Flacourtiaceae, Guttiferae, Irvingiaceae, Meliaceae, Moraceae, Myristicaceae, Olaceae, Rubiaceae, Sapindaceae, Sterculaceae and Tiliaceae, and the sub-families Caesalpinoideae, Papilionoideae and Mimiosoideae. Species rich families were Euphorbiaceae, Annonaceae and Caesalpinoideae. The total number of species in the area is estimated to be c. 550 tree species. The diversity indices for Fisher's α was 88.86 and for Shannon-Wiener 4.86. On a pantropical scale these are relatively high values, especially for Africa.

The number of tree species per ha ranged from 104-148. The most abundant species are *Coelocaryon preussii*, *Pycnanthus angolensis*, *Plagiostyles africana*, *Treculia obovoidea*, *Staudtia kamerunensis*, *Lophira alata*, *Cola lepidota* and *Coula edulis*. They all produce valuable timber, except for *Plagiostyles africana* and *Cola lepidota*. These trees however have other important functions for the local people. Therefore, this forest contains very valuable trees, which are available in great numbers. The forest is very homogeneous, as the following results clearly show. The diversity values of each plot are very much the same (mean: 6.07, sd: 0.14) and the evenness indices look even more similar (mean: 0.87, sd: 0.01). Some 260 species or 62.2 % of the total amount of species are represented with fewer than 10 individuals. No relation could be found between the diversity and density. The dominance-diversity curve that has been constructed showed the typical slightly S-shaped curve of a species rich lowland moist forest.

The majority of the most abundant upper canopy species *Coelocaryon preussii*, *Pycnanthus angolensis*, *Treculia obovoidea*, *Staudtia kamerunensis*, *Lophira alata* and *Coula edulis* are light demanding species in their recruitment phase (Van Gemerden *et al.* in press). *Lophira alata* prefers logging gaps (over 0.03 ha in size) while *Coelocaryon preussii*, *Pycnanthus angolensis* and to a lesser extent *Staudtia kamerunensis* have a preference for regenerating in shifting cultivation fields (over 0.1 ha in size). A majority of the 19 1-ha plots appears to have been disturbed in the past, most likely by shifting cultivation since the vegetation records were of unlogged forest.

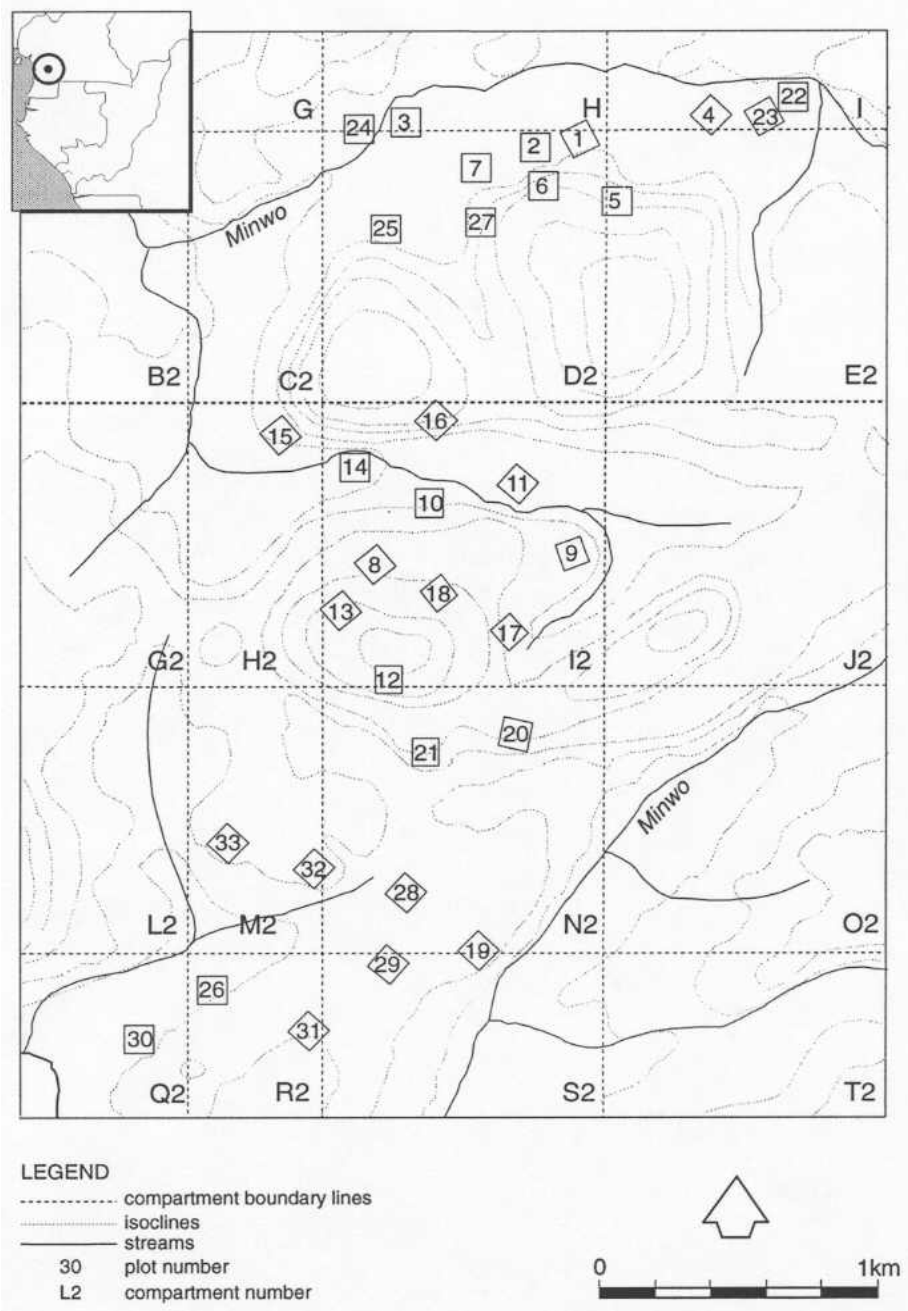


Figure 1.2. Map of the Ebom study area with the 33 1-ha plots in the Minwo catchment area. The compartments shown belong to coupe 1223 (G, H, I), coupe 1222 (D2, E2, I2, J2, N2, O2, S2, T2) and coupe 1222 bis (B2, C2, G2, H2, L2, M2, Q2, R2). A normal coupe encompasses a surface of 2500 ha sub-divided into 25 compartments of 100 ha each, numbered from A to Y. However, during prospecting and coupe layout a mistake was made leaving a zone untouched between coupes which was later divided and renumbered (1222 bis).

This confirms Letouzey's (1968, p. 153) observation that an omnipresence of *Pycnanthus angolensis* and *Lophira alata* indicates that we are dealing with a degraded form of the Atlantic Biafrican type of forest. African forests have high diversity and some of them may be cultural artefacts created by Bantu migration over previous centuries (Laburthe-Tolra 1981, Schwartz 1992, Oslisly 2001). Present-day biodiversity may exist in West- and Central Africa not in spite of human habitation, but because of it (White and Oates 1999, Mbida Mindzie *et al.* 2001, De Kam *et al.* 2002).

1.6. OUTLINE OF THESIS

From the above it appears that lianas play an important role in African forests. In this thesis, we investigate the ecological functioning of lianas and consider how human interventions can produce more appropriate management systems, which will in turn lead to more sustainable timber production. For this a pre-logging silvicultural treatment was applied, i.e. liana cutting. The research was set up in close collaboration with the work conducted by the Cameroonian researcher R. Bibani. In his study, the effects of post-logging silvicultural treatments were investigated in 9-ha plots of which the central 1-ha plot formed the measurement unit for trees and lianas of the present study.

Chapter 2 gives an overview of the forest management options chosen from Liberia to Cameroon. This provides a historical overview of sustainable forest management in the region. We deal with the same forest physiognomies in which different management options are tried out over time, determined by the differences in colonial backgrounds. Chapter 3 provides an overview of the methodological problems related to lianas, based on experiences of researchers from around the globe. Since lianas rely on support during the expanding phases of their lifespan and do not behave in the same way as trees, measuring them can be problematic. This often means that lianas are left out of inventories. In Chapter 4, West African liana-tree interaction experiences are presented. Several experimental studies will be discussed in mostly highly disturbed forests which have witnessed repeated logging (creaming), often followed by fire. This will then allow us to look in Chapter 5 at liana abundance and distribution in an unlogged forest in southern Cameroon. How abundant are lianas in these forests? Do these lianas have a clumped distribution or not? It was also of interest to see whether lianas are more abundant in these forests than elsewhere in the tropics. Chapter 6 analyses the effects of liana cutting on damage levels at the felling site and the impact of such a silvicultural treatment on the liana population. Tree selection for felling targeted the concessionaire's most demanded timber species *Azobe*, *Lophira alata*, and tried to avoid multiple treefall gaps. Damage levels were expressed at crown and stem level of surrounding trees as well as in the sizes of the created felling gaps. In Chapter 7, regeneration studies were then made in these felling gaps to investigate the interactions of tree seedlings and lianas and to discover the extent to which resprouting played a role in the building phase. The development of tree seedlings is often impeded by liana tangles. This type of interaction was studied in felling gaps with and without pre-felling liana cutting and in a chronosequence of felling gaps created some six years earlier. Finally, in Chapter 8, the main goals and results of this thesis are evaluated on the basis of how they compare to results obtained by others.

2. LATEST TRENDS IN WEST AFRICAN NATURAL FOREST MANAGEMENT AIMED AT TIMBER PRODUCTION

2.1. INTRODUCTION

In West Africa commercial exports of timber started in the late 19th Century, focusing mainly on African mahogany (*Khaya* and *Entandrophragma spp.*). At that time, the Governor of the Colony of Lagos warned already for the depletion of the commercial stock of the forests from Sierra Leone to Nigeria (Moloney 1887). Intensive exploitation and rapid deforestation might partly explain why silvicultural experiments started quite early in the region. This paper will focus on projects and experiments of natural forest management aiming at nurturing the natural regeneration and to increase stand productivity by applying silvicultural treatments. Most silvicultural systems with natural regeneration are still experimental and are monitored or executed since the 1970s. This paper will discuss them and place them at the background of earlier experiments.

The actual state of the forests and the production potential of the countries under discussion can possibly in general terms best be described as follows. The forests of Côte d'Ivoire and Nigeria are presently seriously degraded, Ghana has a small permanent forest estate in fairly good condition, in Liberia some large stretches of fine forest are left, while the moist forest zone of Cameroon is still largely covered by unlogged forest but these forests are rapidly opened up.

2.2. EARLY SILVICULTURAL SYSTEMS

Most early silvicultural systems aimed at the transformation or conversion to uniform high forest. In Côte d'Ivoire the earliest natural regeneration experiments date back to the early 1920s but they were abandoned soon since seedlings of the commercial species were found to disappear after one year, even after opening the canopy (Chevalier and Normand 1946, Schnell 1950). During the late 1920s and 1930s foresters in Nigeria tried several refinement and liberation operations to assist the natural regeneration. The Uniform System laid down at Sapobe by Kennedy (1935) consisted already many aspects of the later introduced Tropical Shelterwood System (Kio *et al.* 1986). Experiments based on the Malayan Regeneration Improving Felling System were initiated in Nigeria. This modified system was later named the Tropical Shelterwood System (TSS). In Nigeria the TSS has been applied over 200,000 ha between 1944 and 1966 (Lowe 1978, Schmidt 1987), while in Ghana the TSS was applied over 4,800 ha between 1947 and 1969 (Osafu 1969, F.P.R.I. 1970, Ghartey 1990). In Nigeria both Kio (1978) and Lowe (1978) found that the goals of TSS were generally achieved, although Lowe considered the stocking of immature commercial species after treatment still inadequate. On the other hand in Ghana, Mooney (1963) expressed that TSS was successful to favour the favoured shade-tolerant commercial species up to the stage where the overwood (or shelter) had to be removed. Growth responses to treatments lasted only some 10 to 15 years before they faded out. The TSS with its basal area reductions of up to

85% recovered to a normal forest structure in 2 to 3 decades with four times as high commercial volumes of class I species (i.e. *Tieghemella heckelii* and *Khaya* species) compared to a forest managed under the usual selection logging operations (Alder 1993). For a brief period during the late 1940s a variant of the TSS the Post-Exploitation System (PES) was tried in Ghana. Regeneration assessment showed that the regeneration mainly consisted of class II species (i.e. *Lophira alata* and *Guarea* species) and accordingly the PES was abandoned and TSS adopted because it gave more promising results (Stevenson 1952, Osafo 1968).

At the same time Côte d'Ivoire opted for experiments with natural regeneration in forest reserves well stocked with *Heritiera utilis* and *Turraeanthus africanus* (d'Aviau de Piolant 1952). These experiments, later named Amélioration des Peuplements Naturels (APN) were inspired by the first published results of the TSS applied in Nigeria and Ghana (Catinot 1965, Gutzwiller 1956, Foggie 1960). APN was applied in Forêt Classée (FC) Téké (about 5,000 ha), in FC l'Eyania (22,700 ha) and in FC Yapo (5,000 ha), but the actual surface treated cannot be traced with certainty (G.L. Aïdara pers. comm.). The treated forest resembled an almost pure stand of commercial species resulting from silvicultural interventions that took place some 30 years ago.

In Ghana experiments were done with TSS and with a selection system which could promote natural regeneration. The selection system, mainly a 'girth-limit' system aimed at reaching sustained yield, was applied on a large scale. This so-called (Ghana) Selection System started in 1956 and lasted until 1971 when 30,000 to 38,500 ha were treated annually. It involved the stock mapping of all economic trees over 67 cm drh, the improvement thinning of the immature stock and selective felling on a 15 year cycle (Catinot 1965). This cycle was later extended to 25 years (Baidoe 1970), with the aim to provide a predictable yield. The mean annual diameter increment in the 48-86 cm drh class was less than 0.6 cm, which was regarded as being poor (F.P.R.I. 1968, Osafo 1970). However, this verdict is unfair when this increment rate is compared with increment rates in other African lowland tropical forests. In more recent Liberian research the highest mean annual increment rate after treatment was about 0.6 cm (Poker 1989). Annual increment rates for 6 commercial species of trees over 60 cm drh in undisturbed Taï National Park averaged between 0.3 and 0.7 cm depending on the species (Kuppen *et al.* 1992). However in Malaysia increment rates of over 1.0 cm (Whitmore 1984) in natural or semi-natural *Shorea* forest are common and it could be that this comparison has been the cause of the negative appraisal.

According to Karani (1970) the Ghanaian foresters considered their (Ghana) Selection System with just thinning as treatment to be highly successful. The required regeneration was obtained by the (Ghana) Selection System, but because of the lack of sufficient sample plots this success could not be demonstrated. In Nigeria the TSS was evaluated more positively than in Ghana, although it had certain drawbacks as for high labour costs, not being species specific and the poisoning of species that later became class I and II species. It is of interest to note that Lowe (1978) and Kio *et al.* (1993) state that the TSS was not abandoned for silvicultural reasons, but because of pressure for other forms of land use than forests. The question remains whether they had an alternative silvicultural system with natural

regeneration at the time. An option which Ghana had in the form of the (Ghana) Selection System and subsequently opted for.

2.3. DEVELOPMENTS OVER THE LAST TWO DECADES

New ideas and concepts have entered in forest ecology since the 1960s such as gap dynamics and the essential role of fauna in the forest for pollination and seed dispersal. What do these imply for silviculture? In various pilot projects known from Liberia and Côte d'Ivoire the old question of regeneration of commercial species and sustained timber yield is tried to solve by focusing on the commercial timber species. These species with their large individuals are indeed important for the forest dynamics and functioning, but are not the sole forest components involved in the maintenance of the forest. Forest management and silvicultural experiments in West Africa in the past was merely concentrating on timber production of just a few species. The prime need was -and often still is- to demonstrate to central government the possibilities of and also the attraction of forest management by concentrating on the proven money-maker: timber. Most other functions and forest products can be combined with such silvicultural regimes that promote growth and the regeneration of the large trees and, indeed, will be combined as soon as forest management is established with the cooperation of local authorities. This will be better for the viability of forest management, provide additional income and other stimuli for forest conservation for those living close to the forest as will be demonstrated next.

2.3.1 Focus on sustainable timber production during the 1970s

Most of the new developments during this period took place in Liberia and Côte d'Ivoire. The initiatives were focused on the sustainable exploitation of the commercial stock. At the same time Ghana stucked to its selective logging as described above based on stock maps but halted all silvicultural interventions. The same more or less applied for Nigeria with a shift in attention towards artificial regeneration as can be seen in Cameroon where all silvicultural efforts were concentrated on plantation forestry and only the primitive diameter instrument was applied to regulate the yield.

Silvicultural potential of logged-over forests: Liberian experiences

Sustainable forest management became an issue in Liberia some years after a national forest inventory took place in the 1960s. The Liberian forest service introduced a system which they named the Liberian Selective Logging System. This is not a silvicultural selection system focussing its attention on the selection of trees to be preserved as was seen in Ghana. It was selective exploitation without silvicultural treatments, but claimed to ensure a good and sufficient natural regeneration of the stand by the forest service. This can be best considered to be a doubtful statement. In the mid-1970s with aid of German foresters some silvicultural experiments were started which would last until the outbreak of the civil war in 1990.

Starting in 1978 several pilot projects were established to determine the silvicultural potential of logged-over forests. The forest structure, the effects of treatments and the increment rates were monitored and analyzed. Their results, combined with those

of diagnostic sampling, should culminate in the introduction of Forest Management Units in concession areas. Most of the silvicultural treatments concentrated on liberation of Potential Crop Trees (PCT) from competition by increasing exposure to light. Liberation took place if the share of PCTs in the 10(20) - 40(60) cm drh class was above 20 trees per ha otherwise refinement, a mere non-selective surface wide intervention, would take place (Wöll 1981, 1986, Poker 1989, Weingart 1990). After analyzing the data of the four forest blocks where such silvicultural treatments were applied the stock of PCTs proved to be insufficient in most cases (Parren & de Graaf 1995). For the Cavalla experiment H.J. Wöll (pers. comm.) found an almost twice as high productivity of the treated stand with annual diameter increments of 0.5 cm compared to a control with annual diameter increments of 0.3 cm. Poker (1989) showed similar increment rates for the Grebo experiment. These figures confirm the misinterpretation of the increment data for the (Ghana) Selection System a decade earlier as being too low to warrant the interventions as being successful.

The Liberian experiments focused mainly on sustainable timber production and hardly took other functions of the forest into consideration. This is probably caused by Liberia's low population densities and the underdeveloped forest sector.

Côte d'Ivoire and the need for rehabilitation after serious deforestation

The alarming deforestation rates in the 1960s (Lanly 1969) and early 1970s, in combination with the inadequate reforestation efforts made that something had to be done at short notice. The necessity of managing the permanent forest estate adequately in future made the authorities realize that it was vital to understand the dynamics of the natural forest. The outcome was the establishment of three experimental sites where forest dynamics were to be followed after silvicultural treatments. Previously, a large number of experimental and trial plots had been set up in the Côte d'Ivoire, but these were, as Maître underlined in 1991, almost invariably too small in area and had no links between them in the absence of a basic methodology and agreed research design. Consequently there were few practical possibilities for either the interpretation of or a comparison of the data collected.

The Irobo-Mopri-la Téné experiments. The failure of the earlier APN system was attributed to inadequate intervention in the canopy (Bertault 1986). The new interventions proposed were, therefore, far more radical than those of the APN. The principal aim was to stimulate the growth of desired tree species by relatively simple, low-cost treatments that could be undertaken on a large scale. No particular treatment was envisaged for improving seedling regeneration, as regrowth at ground level was known to be difficult to manipulate and control. Favourable or unfavourable regeneration growth was thought to be determined by the intensity and type of silvicultural treatment at a higher level in the vertical strata. In 1976 the Centre Technique Forestier Tropical (at present CIRAD-Forêt (Centre de coopération Internationale en Recherche Agronomique pour le Développement)) established twentyfive 16 ha plots in evergreen (Irobo), moist semi-deciduous (Mopri) and transitional forest (la Téné).

The overall design and the initial results of these trials were presented by Mielot and Bertault (1980), Maître and Hermeline (1985), Bertault (1986), Maître (1986a, 1986b, 1991) and Aïdara (1992). Silvicultural treatment on the three sites was

confined to refining (poison girdling of undesired trees and some additional climber cutting). Three refinement intensities were chosen aiming at a basal area reduction of either 20%, 30% or 40%. Initial refinement operations did not lead to the foreseen basal area reductions, and an after-treatment was given in 1979 to reach the goal set (Mielot and Bertault 1980). The trees death occurred within 6 months to two years after poison girdling.

It proved to be difficult to distinguish and group the resulting basal area reductions. For further analysis the plots were therefore pooled into groups with a similar remaining basal area. This makes indeed more sense, as the main concern of a forester is the condition of the remaining stand and not what has been removed.

Maître (1986a) presented some of the most striking results. Opening of the canopy had most effect on the growth of small and medium-sized trees. All commercial species responded favourably to the treatments. Volume increments (Maître and Hermeline 1985) for stems of commercial species over 10 cm drh were:

- 0.7 - 1.8 m³ha⁻¹yr⁻¹ for control plots
- 2.9 - 3.6 m³ha⁻¹yr⁻¹ for plots with moderate refinement
- 2.2 - 2.9 m³ha⁻¹yr⁻¹ for plots with heavy refinement

From these data it becomes clear that the moderate refinement regimes led to the most favourable volume increments. Where moderate and heavy refinements led to similar recruitment and growth rates, the latter led to substantial increases in mortality rates. The cause of the heavy mortality on heavily refined plots is not given by Maître, but could well lie in the considerable change in the microclimate after extensive opening of the canopy. Another reason for an increased mortality could be an increased liana infestation. A study in Mopri, 14 years after treatment showed that heavy refined plots had on average 1.5 times as many lianas compared to untreated plots (Dombia 1993).

From all observations it is clear that silvicultural treatments are beneficial to improve timber production. This is demonstrated by Table 2.1 which shows us that the mean annual diameter increment for desired tree species increases between 1.4 and 2.0 times compared to control after intervention at four sites in Côte d'Ivoire and Liberia discussed above.

Table 2.1. Mean annual diameter increment at several West African sites for desired tree species ≥ 10 cm drh after silvicultural intervention. Intervention period for Irobo 10 years (Brevet 1994a), Mopri 10 years (Brevet 1994b), Cavalla 4 years (Wöll pers. comm.), Gola & Kpelle 2 years (Weingart 1990).

	Côte d'Ivoire		Liberia	
	Irobo	Mopri	Cavalla	Gola & Kpelle
control	0.31	0.27	0.34	0.50
moderate refining	0.51	0.42	0.54	0.70
heavy refining	0.60	0.48		

Fourteen years after intervention the natural regeneration in the 2-10 cm diameter class per ha was similar for all three treatments; with on average 500 individuals of desired tree species and 2800 individuals of undesired tree species (Doumbia 1993). It is remarkable to see that the representation of the most desired commercial species (P1-class species), is twice as high in the heavy refined plots, an average 300 individuals ha⁻¹ compared to 150 individuals in control. While the moderate refinement showed 200 individuals ha⁻¹. Liana abundance increased progressively from 500 individuals ha⁻¹ in control plots, to 690 individuals ha⁻¹ in moderately refined plots reaching 780 individuals ha⁻¹ in heavy refined plots. This shows that the heavy refinement has the potential to stimulate regeneration, but the question remains at the costs of how many interventions? Progressive opening of the forest will increase liana numbers accordingly. These lianas might have to be kept in check as they can hamper the development of the tree regeneration.

The refinement treatments used covered only a small range; from 20% to 40% so refinement regimes were quite narrow. The conclusion of Maître (1986a) that hardly any difference exists between the heavy and moderate refinement regimes is therefore not surprising. The moderately refinement treatment is most promising since stand productivity is doubled compared to untreated stands. Durrieu de Madron *et al.* (1998a,b) recommend to fell 2 to 3 trees per ha in future instead of the practise of 1 tree per ha now, to mimic the moderate refinement somehow. This recommendation is also made for the semi-deciduous forests in Cameroon and the Central African Republic (Durrieu de Madron and Forni 1997, Favrichon 1997). Future efforts should be guidelines for refinement should be formulated in terms of remaining basal areas instead of basal area reductions. In this respect it is surprising to see that Durrieu de Madron *et al.* (1998a,b) still suggest to utilise maximum basal area reductions.

The Yapo experiment. The promising results of the three pilot projects led the Caisse Centrale de Coopération Economique (France) to finance a project in the evergreen Yapo forest reserve starting in 1983. The forest area at Yapo was subdivided into compartments (Unités Primaires) of 250 ha. The experimental site consisted of twenty-seven compartments (UP1 to UP27) with a total surface of about 7,000 ha. Between 1984-87 the compartments were inventoried and grouped according to site conditions. The compartments were exploited followed by a refinement consisting of climber cutting and poison girdling since an uniform basal area reduction of 30% was desired.

To give an idea of the net gains by the treatments, a comparison is made between Yapo and the previous experiments (Table 2.2). It is striking to see that the refined stands in Yapo have similar increment rates as the the control stands, while Irobo and Mopri show a clear benefit from the interventions. In Yapo the stimulating growth effect of the refinement was counteracted by extraordinary high mortality rates. It has been suggested that these high mortality rates are caused by the exceptional high number of lianas (Brevet *et al.* 1993). Liana density averaged 900 lianas ha⁻¹ for Yapo compared to 300 lianas ha⁻¹ for Irobo, whereas both forests belong to the same forest type. The Yapo forest has heavily been logged this in contrary to the Irobo forest which is more or less primary, since selective logging took place only at the beginning of the century.

Table 2.2. Mean annual increment as for the basal area and volume of desired trees ≥ 10 cm drh. Intervention period for Yapo 6 years (Brevet and Diahuissie 1994), Irobo 10 years (Brevet & Diahuissie 1994), Mopri 12 years (Doumbia 1993).

		Gc	Vc
Yapo	control	0.13	1.58
	refinement	0.11	1.52
Irobo	control	0.12	2.35
	moderate refining	0.23	3.39
	heavy refining	0.28	3.52
Mopri	control	0.10	2.75
	moderate refining	0.25	4.16
	heavy refining	0.24	3.91

G = basal area ($\text{m}^2\text{ha}^{-1}\text{yr}^{-1}$); V = volume ($\text{m}^3\text{ha}^{-1}\text{yr}^{-1}$); c = commercials

The stock of commercial species in Yapo (Table 2.3) leaves doubts whether sustained yield can be guaranteed. If we take an annual diameter increment of 0.5 cm in Irobo (Table 2.1) to be representative for the Yapo situation, then it would take a tree 40 years to pass through the 40 - 60 cm drh class. For a yield of 20 m^3 some 5 exploitable stems would be required and mortality should be nil. However at the end of the 1980s the commercial stock of trees ≥ 60 cm drh averaged only 1.5 stems per ha at a volume of just 9 m^3ha^{-1} (Mengin-Lecreulx 1990). After treatment recruitment of desired tree species (≥ 10 cm drh) was 0.06 stems $\text{ha}^{-1}\text{yr}^{-1}$ while the mortality rate was 0.03 stems $\text{ha}^{-1}\text{yr}^{-1}$ which implies a net ingrowth of just 0.03 stems $\text{ha}^{-1}\text{yr}^{-1}$ (Brevet and Diahuissie 1994). From the foregoing and the figures of Table 2.3 it is evident that for several decades exploitation should be halted. The volumes presented shows us that the forest is still in a building phase. It will be essential to have a more stable forest composition also in the higher diameter classes.

Table 2.3. FC Yapo: standing volume (m^3ha^{-1}), development of volume determined by increment, ingrowth, mortality and net increment ($\text{m}^3\text{ha}^{-1}\text{yr}^{-1}$) of trees ≥ 10 cm drh of commercial tree species in 4 treated and 3 control plots. Modified from Cabrera Gaillard (1988).

	volume	increment	ingrowth	mortality	net increment
treated	131.9	2.0	0.1	1.6	0.5
control	132.1	2.1	0.2	0.6	1.7

It was found that the compartments 4, 8, 22, 27 of group 1 were well stocked and exploitation took place in 1989-90. The standing stems were sold at the highest bid. Next to timber sales, substantial financial returns came from the sale of firewood, from sale of small and medium-sized trees of *Funtumia africana* and *Discoglypremna caloneura* for match sticks and of *Garcinia kola* wood for native toothpicks. Stems of *Funtumia africana* and *Discoglypremna caloneura* were exploited with a lower felling limit of 35 cm drh. This proved to be unsustainable and exploitation was therefore halted in the course of 1990. The 1989 production amounted to some 1000 individuals or 900 m^3 and gave a return of 20 US\$ per m^3 . Optimistic ideas about future successes with this type of management should recognise that such a system of selling timber on stump, to be harvested by the buyer, requires sound control of the logging operations by the forest service. This

proved to be difficult in the Yapo project. During operations a number of valuable *Khaya* mother trees were taken by the logger without permit. Control has its price and, what is more, needs preparation to provide the trained personnel needed.

2.3.2 Sustainable forest management initiatives since the 1980s

In the 1980s the FAO launched the so-called Tropical Forestry Action Plans for most tropical countries in the world. At the UNCED environmental conference organised by the United Nations in 1982 biodiversity and forests stood high on the agenda. This period saw much more attention to other functions of the forest next to the sustainable exploitation of the timber resource. This implies not only focussing on the commercial stock but also taking into account non-timber forest products, as well as ecological and biodiversity aspects which can be seen in Ghana and Côte d'Ivoire. Cameroon in the meantime set its goal to become the principle timber exporter of the continent and started the planning of a permanent forest estate. Collaborative forest management became a key element in guarantying appropriate management of the forest resource as is seen in most countries discussed here. Unfortunately in Liberia the civil war raged at the end of 1989 which lasted till the late 1990s and all activities came to an halt.

A reshuffle of the forest sector in Ghana

From 1985 to 1993 a national forest inventory of the moist forest zone has been carried out in Ghana by the Forestry Department with assistance from the British Overseas Development Administration (present Department for International Development (DFID)). The inventory covered all forest reserves within the moist forest zone. In combination with a network of 500-1000 permanent sample plots this should lay the foundation for sound and sustainable forest management. The recording of the results in these plots will take place every five years and the first results are already present.

Gross standing volume of well formed trees ≥ 30 cm drh is estimated at 188 million m^3 , of which 101 million m^3 in trees over 70 cm drh. Some 98% of the total volume of trees that attain sizes over 70 cm drh belong to the traditional marketable class 1 species. Silvicultural efforts should be concentrated on the class 1 species which have a proven market (Ghartey 1989). To regulate the yield a modification was needed to the silvicultural systems that had been tried and developed in Ghana (Nolan 1989). The annual allowable yield should be approximately 1.2 million m^3 since the production area totals 1.16 million ha, and $1 m^3 ha^{-1} yr^{-1}$ could be felled on a sustained base. Given a total standing volume of 101 million m^3 of class 1 and 2 species over 70 cm drh and an annual allowable yield of 1.2 million m^3 , the felling cycle should be approximately 80 years (Alder 1989) Given the fact that the condition of many production forests is poor or confined to slopes with an incline of over 30%, an annual allowable yield of 200,000 to 300,000 m^3 might be nearer to reality (W.D. Hawthorne pers. comm.).

Officially recorded annual levels of harvest rose from just above 1 million m^3 in the late 1980s (Nolan 1989) to unsustainable levels of just below 2 million m^3 in 1994 and dropped again to 1.3 million m^3 in 1995 (Henderson-Howat *et al.* 1995, Aferdi Dadebo and Shinohara 1999). The figure of 2 million m^3 equals the potential

sawmill capacity at the time. A major problem is that most of the production comes from the most valuable and traditional heavily exploited species. In addition the domestic timber demand already is in the order of 0.7 million m³ per year. Obligatory exploitation of all trees of the allowed yield of a wide range of species should be enforced to reduce the pressure on the limited number of preferred species. A similar prescription exists in Liberia since 1976 where the forest service has listed obligatory and future obligatory species for exploitation by concessionaires. A drastic reduction of logging activities would be needed and as such a reduction in sawmill capacity too. This is difficult to realise, since many interests are at stake and so far the political will lacks to take such drastic steps. Another problem is that financial returns of the forest sector are not sufficiently redirected to this sector for a financially sound implementation and execution of the forest policy. Forestry revenues are merely seen as an easy way to obtain foreign exchange earnings to benefit the national treasury.

A set of measures have been introduced to avert the overexploitation of the forests. A ban on the export of logs of a total of eighteen species came into force in 1988 but will be abolished in 1999. This has to do with price mechanisms and to reduce waste of these species at inefficient sawmills. As from late 1989, higher minimum diameter limits were imposed and a special felling permit was required for a number of species. In the first half of 1990 the allowable annual yield was reduced by 30%, which mainly affected the high diameter classes and the felling cycle was set at 40 years instead of 15 years. In future the permanent sample plots will be a good instrument to help assess more appropriate felling cycles for each forest.

The forest reserves have been grouped into Forest Management Units (FMU) with an area of approximately 500 km² each. Each FMU belongs to one forest district and forest type and forms the basic unit in which sustained yield management can be practised according to prescribed working plans (Nolan and Gartey 1992). Currently the number of stems to be harvested per coupe area contain about 60% of all stems above the minimum felling limits by assuming a 20% mortality rate during the felling cycle, and 40% retention of trees above the felling limit. Maginnis (1994) suggested that the annual yield should be calculated based on the extent of the concession area and its current stocking, minimum diameter limits, and the understorey condition of each compartment. A chance to test the (Ghana) Selection System more profoundly has been missed since silvicultural experiments form no part of this phase of setting new yield regulations to the forest management. Felling cycles and rotation periods might have been shorter when silvicultural treatments were included.

Because of the reorganisation of the forest sector no new concession grants were handed out until 1991 when the Concessions Unit was created within the Forestry Department. This situation has existed since 1988 when the National Investigation Committee (a kind of internal security organisation) started an investigation on malversations in the forest sector over the last decade. The Forestry Department wants to match the sawmill capacity with the calculated annual allowable yield of 1.2 million m³yr⁻¹. At present there exists a situation of sawmill overcapacity. Added-value processing will be promoted in order to create more jobs and higher revenues for the state. Accordingly, concession rights will be withdrawn from all

persons who possess a felling license but who do not possess processing facilities. Finally a reallocation of concession areas, totalling 1.16 million ha of production forests has been envisaged. Based on a 40 years felling cycle, the annual coupe area per FMU will cover a surface of 1,250 ha (or 2.5% of FMU). While concession areas between a minimum of 8,000 ha (16% of FMU) and a maximum of 12,000 ha (25% of FMU) are granted to qualified concession holders (Aferdi Dadebo and Shinohara 1999).

In 1994 a new Forest and Wildlife Policy came into being. The same minimum diameter limits apply for trees inside the reserves, as for forests outside the forest reserves. Special permits are required to fell undersized trees outside forest reserves. Since 1995 these forests outside the forest reserves fall under the jurisdiction of the Forestry Department. This attempt to apply the concept of sustainable management for unreserved forests is unique in the tropics. This is an important step as over 50% of the national timber output originated from 'unreserved forest' or farmland (Sargent *et al.* 1994). This period also saw a shift from a top-down approach in forest management, dictated by the forest service, towards collaborative forest management where benefits and responsibilities are shared with the population living around the forest reserves (Kotey *et al.* 1998).

Biodiversity and conservation. After World War II most of the permanent forest estate was designated as areas for timber production. Some parts of the forest reserves, however, were set aside for protection under a 'protection working cycle'. In practice, this meant that either no management plan existed or that the plan was so vague that logging could continue. At the end most of these protection forests were located at inaccessible areas, often steep terrain and it proved necessary to redefine the protection forests. Next the steps taken will be described in brief.

The condition of the forest reserves was evaluated based on the degree of canopy disturbance. Slightly more than half of the reserved forests proved to be in reasonable condition. Forests in bad condition were mainly confined to the drier areas (Hawthorne 1996). This is not without reason, since it is the semi-deciduous forest which shows the highest share of commercial species and which has accordingly suffered excessively from both logging and the following fires (see also Hawthorne 1993, 1994). Hawthorne (1996, Hawthorne *et al.* 1998) recommends a multi-scale approach to the protection of forests. Protection at a large-scale (e.g. several 1000 ha) would be required for large protected areas like national parks or 'hill sanctuaries' in hotspots of biodiversity and fragile areas. Medium-scale (e.g. several 100 ha) protection to establish long-term buffers, to supply adjacent logged forests of adequate regeneration and provide good niches for flora and fauna elements, amongst other functions. These areas are selected as genetic stock reserves, to assure minimum viable populations of flora and fauna elements which then will determine the needed reserve area (see also Shafer 1990). Fine-scale (e.g. <100 ha) small forest patches (e.g. sacred groves), pockets or individuals of rare tree species and restricted forest use for certain areas and/or species (including non-timber forest products) are designated to be protected under this type of protection. Forests which require special attention are those with a high biodiversity and rare species, mainly confined to the perhumid forests both lowland and upland and some outliers of dry semi-deciduous forests. It should be noted that such characterisation

is very local as perhumid forest is common in such countries as Liberia and Cameroon. So each region or country has to adopt its own criteria placed in a wider regional context. Hawthorne has worked out a plant species classification according to scale of endemism to enable the selection of the above mentioned protection areas (Hawthorne 1995). It would be of interest to match in future the botanical classification with a similar one for fauna elements to fine tune or even enforce the conservation effort.

These are some of the measures which have been taken and will be taken in Ghana in the course of the coming years. They aim at obtaining a sound forest sector with the main goal of working on a sustained base. At present the silvicultural system with natural regeneration has many characteristics of the pre-1970 selection system. This will have to be brought to a state-of-the-art level by additional ecological research in the coming years such as on phenology, species autoecology, interactions between trees and lianas. Some post-logging treatments as liberation of potential crop trees might be reconsidered as well.

Case study of forest reserve management: the example of FC Bossematié, Côte d'Ivoire

In Côte d'Ivoire several reserves were designated to be rehabilitated in cooperation with the private sector and international institutions. Two demonstration projects were selected for rehabilitation at an intensive level: the FC Haut-Sassandra in west Côte d'Ivoire and the FC Bossematié in east Côte d'Ivoire. The latter forms part of a German-sponsored research and management project to rehabilitate 7 forest reserves within the jurisdiction of the Abengourou district forest office and will be discussed here. FC Bossematié forms the demonstration project and lessons learnt and principles derived will be applied in the other six reserves in east Côte d'Ivoire at a less intensive scale. The rehabilitation project is underway since 1990.

Today, forest covers only 5 to 10% of the total surface in Abengourou district. Closed forests are still present in the forest reserves, but these are strongly overexploited and degraded. It has been estimated that 50% of all forest reserve areas are illegally occupied by farmers, growing food and cash crops such as cocoa and coffee (Wöll 1992).

The semi-deciduous forest of FC Bossematié encompasses 22,400 ha. Like most other forest reserves in the region, it has been selectively logged 5 to 6 times, between the early 1960s and 1990. Exploitation has been halted when SPOT images confirmed that the vegetation in FC Bossematié was overexploited and partly ruined. To check the SPOT images detailed inventories on 2 plots of 50 ha each were conducted at the northern section. These studies revealed that the Bossematié forest had an abundant regeneration of commercial species. This enables the implementation of silviculture with natural regeneration. The work conducted in Bossematié relies considerably on the German experiences gained in Liberia during the late 1970s and 1980s (Weingart 1990, Wöll 1981, 1986). The essential difference with the Liberian experience is that in the Bossematié project recent ecological knowledge has been incorporated in the management plan. Complete harmony between ecology and economy is considered utopian, and therefore workable compromises between the two are sought for. Key words of this forestry

project are silviculture, ecology and conservation. This entails a break with the past forest policies that concentrated on timber production. More recently co-management became a key issue too as it was realised that without local participation no sustainable forest management could be reached.

A management plan has been worked out by zoning the reserve area according to stock and ecological information, the latter mainly based on fauna distribution (Bledoumou *et al.* 1994). The first assessment was based on a 10% forest inventory. Accordingly some 14,200 ha (64% of the area) were designated for silviculture with natural regeneration since adequate stocks of regeneration were encountered. The remaining area had an inadequate stock, like abandoned farmland, and were designated for enrichment planting. The original 200 farmers were ordered to abandon their mostly extended farm (which they do not entirely depend on). Such reclaiming of (un)authorized enclaves is also seen as a political signal.

It is important that people value the forest, by offering them a stake in the management and usufruct rights. The preservation of the forest reserve depends largely on the participation of the local population. An ethnobotanical survey is conducted to find out local priorities in the use of non-timber forest products. In future the controlled harvest of these products within the reserve will be allowed and the cultivation of certain products outside the reserve will be propagated. A good example is the giant snail (*Achatina spp.*) which was over-exploited and became extinct, they were re-introduced and gathering rights given exclusively to the local population. When outsiders came to collect them without authorisation the local population warned the forest service and accordingly they were arrested (W.E. Waitkuwait pers. comm.). This shows that collaborative forest management does work.

Integration of faunastic knowledge. Ecological research focuses on distribution and abundance of faunal key species within the reserve to determine areas with highest conservation priority (Sivha *et al.* 1993). In Ghana a similar process is underway, but here instead of fauna elements floristic components are studied to determine conservation areas (Hawthorne 1996, Hawthorne *et al.* 1998). The fauna of FC Bossematié is impoverished since an extensive closed canopy structure with emergents and upper-canopy trees is no longer available. Guenon monkeys and bird species with preference for closed canopy conditions are missing (McGraw 1998). Poaching has brought some species to the brink of extinction in FC Bossematié and only strict control has prevented this. Fauna elements are important in the regeneration process and animals may even be key species as far as seed dispersal and predation is concerned. Some 70 to 95% of all tree species are thought to be animal dispersed. To assess this link, footprints around natural waterholes were monitored. Dung piles of forest elephants and chimpanzees were analyzed for seeds and germination trials done. Observation of waterholes at intervals of 500 m and 2 km from the reserve boundary, as well as at the centre of the reserve, take place to find out the frequency of animal visits (Waitkuwait 1992). Three biological reserves were selected within the forest reserve to conserve the tree genetic stock and as resting-places for animals. FC Bossematié's biological reserves measure at least 2,000 ha, with all catena positions and vertical strata present.

Restoration of the timber stock. Silvicultural treatments are confined to liberation thinning, since an adequate stock was found. Wöll (1991, 1992) assessed that the minimum number of potential crop trees (PCT) should be 60-70 trees per ha in the 5 - 40 cm drh class. Assuming a mortality rate of 1%, it is expected that 30 of these PCT will die in 50-60 years. A felling cycle of approximately 25 years is envisaged in which 5 trees can be felled. Species like *Parinari excelsa*, which are important fruiting trees for animals, can be spared when looking at the liberation of PCT. A mild liberation operation was applied killing on an average 1.5 m²ha⁻¹ or approximately 10% of the total basal area. The removed species consisted mainly of the pioneer species *Musanga cecropioides* and this operation was combined with selective climber cutting around the released PCT. When assessing the crown positions it was surprising to find out that only one fifth of the PCT in this overexploited forest were not suppressed and could be classified as fully exposed (cf. Dawkins 1958). While even of these PCTs some two-third were infested by lianas. In the Ghanaian Tropical Shelterwood System such liana tangles were also encountered in drastically opened up forest. Enrichment planting took place in impoverished areas (poor stock of PCT and/or former farmland) especially at the farm-infested boundary sites of the reserve.

A management plan as made for FC Bossematié seems to be best suited for rehabilitation of seriously degraded forest reserves, like many forests of Côte d'Ivoire. The concept of biological reserves within forest reserves is not new, but should be incorporated in all management plans to ensure ecological niches for flora and fauna elements. Monitoring along transects, to assess whether the abundance of flora and fauna populations are declining or expanding, are to be incorporated (Voegelzang 1998). A restoration of biomass and crown cover will be essential for the functioning of all Ivorian moist forest formations. The national production targets should be harmonized with local forest management, and set at a minimum, not a maximum like actually is done. A ban on logging like in FC Bossematié probably is a necessity to restore the forest ecosystem, and a conservative production target for the next felling cycle may be the best option. Continued annual creaming of 5,000 ha (2 compartments) of seriously degraded forest like envisaged in SODEFOR's other pilot project in FC Haut-Sassandra overreaches the sustainable carrying capacity of the ecosystems.

Low impact logging for bufferzone management: the Tai case study

West Africa shows a remarkably low number of conservation areas in the moist forest zone, at the moment numbering less than 20 gazetted parks and reserves. In regions with increasing population densities where these conservation areas are confined, some kind of utilisation should be allowed for household consumption and to vest an interest in these conservation areas with the local population. This probably can be best realised in bufferzones surrounding a core area of high diversity to be preserved. The question remains how to exploit such bufferzones? Exploitation should aim at matching as closely as possible the ecological processes. Next to exploitation of non-timber forest products one might even opt for high quality timber extraction.

The time of harvesting should be determined by the physiognomic characteristics of individual trees. Restricting harvesting to trees already senescent, as can be

determined from crown aspects, e.g. as seen in aerial photographs, would be highly conform the natural tree dynamics (Vooren and Offermans 1985, Vooren 1992, Vooren 1999). The advantage is that these trees, although senescent, retain for a long period their function as seed trees. These principles are confirmed by ecological research in pristine parts of Taï forest, Côte d'Ivoire, where a remarkable low dynamism in gap formation was found, nearly twice as low as reported for South American and Central African moist forest (Jans *et al.* 1993). This results in a long forest turnover time, and a dominance of shade-tolerant canopy species. It implies that an extended number of commercial species should be felled to avoid some of the regeneration problems in future. A prescribed yield to be felled obligatory as applied in Liberia, will prevent the prevailing creaming of the forest. This probably will permit only low volumes to be taken annually over large areas.

Such a system, though possibly suffering a financial drawback, because of the large standing stock of timber, might produce better than systems concentrating on the juvenile stages, as these last ones have to bear long investing periods to reach mature timber stages. In such a system there is no scope for the well-represented large *Meliaceae* since regeneration is scarce in this pristine forest (De Klerk 1991, Poorter *et al.* 1996), whereas in Bossematié, a heavily destroyed semi-deciduous forest, these *Meliaceae* regenerate well at least when seed bearers are present (H.J. Wöll pers. comm.). Moreover this approach will not improve circumstances for the light demanding juvenile stages of many commercial species. In Taï it was found that most timber increment is on the largest trees, a good reason to conserve these in a selection felling system (Kuppen *et al.* 1992). However trees might start to show heartrot when they reach very large dimensions so the optimum time to harvest should be investigated for each exploited species. It would however cause least disturbance of the natural dynamics in Taï forest, and might be fit for bufferzone management around genetic conservation forest areas.

Recent developments in Nigeria and Cameroon

Nigeria's depleted forests. The output of the present permanent forest estate of Nigeria covers only one third of the local wood consumption. At present less than 10% compared to the originally targeted 25% of the total land area form part of the permanent forest estate. With the oil boom in the 1970s came the 1978 Land Use Decree which could overrule communal rights on forest land and award land titles to individuals. This made the permanent forest estate to dwindle down to the present low figure. Non-reserved forests outside the permanent forest estate are almost none existing and massive exploitation, both legally and illegally, within the forest reserves is by far unsustainable. The forest reserves will have to be rehabilitated in a way similar to the Bossematié project in Côte d'Ivoire. Still there is hope as a network of permanent sample plots established between 1984-88 showed that the production potential of logged over forests was still substantial. All trees over 5 cm dbh were measured (in 1-ha plots) and it was predicted that selective exploitation at felling cycles of 25 years would give yields of up to 50 m³yr⁻¹ of round wood (Kio *et al.* 1993).

Most efforts since the 1970s were directed towards the establishment of tree plantations to meet the domestic timber demand. In the mid-1970s planting covered an area of 20,000 ha per year and came down to annual planting of less than 5,000

ha in the 1990s. In the 1980s forest exploitation was virtually unregulated and endangered the resource base (Kio *et al.* 1993). The question remains whether the country can afford to halt the exploitation of already overexploited forest reserves. A complicating factor is that the forest service is highly decentralised as in each state they act more or less independently with just federal interference for forest research and education. At present the only forests in a reasonable condition are those in Cross River State at the border with Cameroon. New initiatives are taken to implement a forest inventory (Dunn *et al.* 1994) and to link the management plans with those of Korup National Park across the border in Cameroon. It is hoped that in this new phase with the involvement of DFID some of the aspects of their experiences in Ghana for the past decade will be integrated.

A dangerous side effect of an integrated approach to forest restoration was noticed by Oates (1995). Since 1990 the managers of the Okomu forest reserve in south-west Nigeria try to integrate conservation and agriculture by assisting migrant farmers in the reserve. Instead of halting the human impact within the reserve the agricultural programme attracted new immigrants, which worsened the situation. The participation of the local population to preserve the forest has its limits and can be best focussed on involving them in protection work, tourism, sustained yield forestry, in research and the gathering and cultivation of non-timber forest products. A clear zonation of exclusive forest and farming areas as is seen in Bossematié, Côte d'Ivoire helps to prevent many of these problems. A good monitoring system to assess the condition of flora and fauna are also often lacking but are an essential tool to detect changes in time.

Cameroon to become the main timber exporter of Africa. In contrast with the other West African countries, Cameroon still has a large stretch of exploitable moist forest (ca. 17.5 million ha). After the export crises of 1986, Cameroon wants to become the number one timber exporter of Africa by the year 2000. Yet, it should avoid the mistakes made in the past in Côte d'Ivoire where high exploitation levels led to serious deforestation in this country. The Cameroonian forests which are rapidly exploited, resemble Aviau de Piolant's (1952) characterization 'vacantes et sans maître' since a permanent forest estate is almost none existing. So far only some 1.9 million ha of the remaining 22.5 million ha of moist forest (including degraded and swampy forests) have been set aside as forest reserve (Côté 1993), but the annual production of 2.8 million m³ (Eba'a Atyi 1998) originates almost entirely from unreserved forests (1995 figures).

A national forest inventory is in progress, conducted by the forest service with assistance from the Canadian International Development Agency (CENADEFOR 1988a, 1988b). This has been followed by land-use planning for the entire southern forest belt of Cameroon. An enlarged permanent forest estate will be delimited of which some 6 million ha are earmarked as production forests (Côté 1993). However, so far it has hardly come into effect as discussions and negotiations are still in progress. Since the beginning of the 1990s the forest legislation is under review which led to the introduction of a new forest law (Law 94-01 of 20/01/94). Ever since many amendments on the new forest law have been made to reduce its effectiveness. The new forest law requires all logging companies to submit management plans within three years after logging operations have begun. At

present the annual area opened for logging amounts 415,000 ha. So in only 15 years all foreseen reserved production forests might be logged (Eba'a Atyi 1998) with the risk of being deforested as is presently the case in many reserves in West Africa (Parren 1994, Fairhead and Leach 1998). The World Bank advocates a policy in which most of the management activities are executed by private organisations. This concerns not only the pre-exploitation inventories by specialised agencies, and the exploitation itself, but also the negotiations with the local population to set aside the permanent forest estate. The latter might certainly lead to unbalanced decision making as the commercial interests might prevail. In the World Bank policy the forest service would have a function of regulation and control. In a situation like the one in Cameroon, where at present the forest service is highly centralised and lacks the means to check operations in the forest, this might sound a favourable strategy. Yet, it might also leave open many options for manipulation and malversation. Such a development could make forest exploitation by far unsustainable, and has nothing to do with fair and collaborative forest management.

Cameroon has hardly a history in natural forest management, but since the 1990s some six pilot projects with a total surface of 940,000 ha are underway (Eba'a Atyi 1997). The forest development project Aménagement Pilote Intégré (API) in Damako, eastern Cameroon is in progress since 1992 with French assistance (Faure 1993). At the coastal forests of Cameroon near Kribi the Dutch Tropenbos-Cameroon Programme started a research project in 1994. The two projects have a lot in common since they both study the logging impact on the forest productivity and their effects on the livelihood of the local population. Besides both cooperate with a concessionaire. The API project is confined to moist semi-deciduous forest while the Tropenbos research site to evergreen forest. Participation of the local population c.q. Bantus and Pygmies is looked for with the difference that in the API project rural development is an applied aspect which is not included in the Tropenbos research project. Reduced impact logging and silvicultural treatments are tested and evaluated in the API area (Durrieu de Madron *et al.* 1998c) as well as in the Tropenbos area (Van der Hout and Van Leersum 1998, Van Leersum 1999, Parren and Bongers 2001). The first impressions are that reduced impact logging does not give significant differences in damage levels compared to conventional logging. This is probably caused by the large dimensions of the trees, often with diameters of over 100 cm, which are harvested in the African moist forests. Still general guidelines for sustainable management of the two forest formations could result from these two projects. This will help the Cameroonian forest service to develop specified guidelines and hopefully implement apt management tools.

Certification and collaborative forest management the latest trend

Since the early 1990s, after awareness campaigns by environmental pressure groups, certified timber from sustainably managed forests is in a rising demand. This has led to the formulation of international criteria for sustainable forest management (CIFOR, ITTO, ATO, FSC) which should be adapted to become locally acceptable and measurable criteria. Certified timber is still not available from West Africa but this may change in the near future (Eba'a Atyi 1997). In West Africa, certification criteria have been tested in the Haut-Sassandra and Bossematié forests in Côte d'Ivoire (Prabhu and Lay-Cheng Tan 1995), in the Kribi forest area in Cameroon (Prabhu *et al.* 1998) and will be tested in Ghana (Technical Working Group 1999).

In Cameroon and Ghana national certification platforms already exist to promote sustainable forest management. These platforms encompass members of different stakeholders: government, logging companies and representatives of local communities, scientists and NGOs. The tasks of such a national platform will be to initiate and supervise the process of interactive participation.

The fashionable keyword to reach the set goals is collaborative forest management (Parren *et al.* 2001). Even in Ghana were the local population, since the forest reservation in the early decades of this century, has remained a stake in the management their participation dwindled after the Second World War. It was not until the mid 1990s when the new forest law came into force that the attention shifted again towards active local involvement in management issues (Kotey *et al.* 1998). Special collaborative forest management units have been set up in both Cameroon and Ghana. This should not evoke a change in attention from conditioning the forest environment to a mere rural population focus as is seen in nature conservation at the moment.

2.4. DISCUSSION AND CONCLUSIONS

West Africa with its close by European market has been the scene of one of the most rapid deforestation processes in the world which has gone almost unnoticed by the rest of the world. It is remarkable to see how much good work is undertaken in the region often based on experiences gained by past foresters. Since the beginning of this century several periods can be distinguished in which silvicultural experiments with natural regeneration were abandoned for some time and superseded by periods where research and wider application of research results concentrated on artificial regeneration.

From the foregoing it is also obvious that the West African forest sector is in motion and searching for options and solutions to reach the goal of sustainable forest management. The Tropical Forestry Action Plan of the 1980s has triggered or at least speeded up many of the initiatives presently seen in the region. A shift from forest management focussing entirely on the income generated by timber towards a more integrated approach, taking into account ecological and social limitations, can be seen all over the region. Probably one of the best-managed natural forests in the world are those in Ghana.

The privatisation process advocated by the World Bank in the entire region should not be followed to its extreme as Cameroon might be doing. Positive and effective activities executed by the forest service such as inventory work and logging control might be best allocated to remain tasks of this service. The restructuring of the forest sector in Ghana on a national level is one to be followed, while experiences gained in Bossematié, Côte d'Ivoire is state of the art how to manage individual, even degraded, forest reserves. Most important in this respect is the political will to have changes for the better assisted financially by the international community but to become self-supporting in future. Participation in the management on all levels is another requirement, being it the government or the local population. Restoration of the permanent forest estate is in progress in Côte d'Ivoire and Nigeria. The big challenge for the coming decades will be to integrate the lessons from the past in the

future forest management in Liberia and Cameroon since these two countries still contain some of the largest and finest stretches of forest in West Africa.

Acknowledgements

Over the years numerous persons and organizations have been consulted. Especially I like to thank my colleagues at the Silviculture and Forest Ecology Group in Wageningen, The Netherlands and at the Tropenbos-Cameroon Programme site in Kribi, Cameroon for discussions and encouragement. Valuable comments on the manuscript were provided by F. Bongers and L. Poorter. For financial support I like to thank the Tropenbos Foundation, Wageningen, The Netherlands. This paper is a contribution of the ECOSYN project funded by DG VIII of the EC grant # B7-5041/95.02/VIII.

3. ON CENSUSING LIANAS: A REVIEW OF THE COMMON METHODOLOGIES

3.1. INTRODUCTION

Lianas are an abundant and diverse group of plants whose importance in tropical forests is becoming increasingly recognized. Lianas commonly compose an average of 25% of the woody plant abundance and diversity in forests throughout the tropics (Gentry 1991b, Schnitzer and Bongers 2002), and can even attain much higher densities in some extraordinary forests (Pérez-Salicrup 2001, Parthasarathy *et al.* in press). Lianas are a detriment to tree establishment, regeneration, growth, and fecundity (Stevens 1987, Pérez-Salicrup 2001, Schnitzer *et al.* 2000, Grauel and Putz in press), probably via competition for both above- and below-ground resources (Schnitzer *et al.* in review). Lianas also negatively affect tree seedlings, saplings, and adults by physical suppression via adding a considerable amount of weight that the tree must then bear and also by shading the canopy of the tree (Neil 1984, Bertault *et al.* 1993, Schnitzer *et al.* 2000). Lianas have been reported to increase the area of gap formation by pulling down additional trees that are bound to the gap-making individual (Appanah and Putz 1984, Vidal *et al.* 1997, Pereira *et al.* 2002, but see Parren and Bongers 2001). Consequently, lianas may have an effect on the turnover rate of the forest and may play an important role in creating regeneration niches for pioneer tree species (Clark and Clark 1990, 1991). Furthermore, lianas can suppress gap-phase regeneration, keeping gaps in a low-canopy state of regeneration for many years (Schnitzer *et al.* 2000). Knowledge of liana behaviour and bio-mechanics can be used to reduce damage to neighbouring trees during selective logging in sustainable forest management systems as well as promote tree regeneration in gaps (Putz 1985, Suzuki 1989, Kennard 1998, Gallenmüller *et al.* 2001, Gerwing and Vidal 2002, Schnitzer *et al.* in press).

Although the negative impacts of lianas in tropical forests have been the focus of many studies, lianas can also contribute positively to forest complexity and functioning. Specifically, lianas add considerably to forest plant diversity and provide valuable habitat and connections among tree canopies that enable arboreal animals to traverse the treetops (Emmons and Gentry 1983, Schnitzer and Carson 2001). Additionally, lianas provide important food sources for animals (Hladik 1978, Gautier-Hion *et al.* 1981, Emmons and Gentry 1983), particularly because their fruiting and leafing phenologies often do not coincide with that of trees (Putz and Windsor 1987, Heideman 1989, Ibarra-Manríquez *et al.* 1991, Opler *et al.* 1991, Hecketsweiler 1992, Morellato and Leitao-Filho 1996, but see Hegarty 1990). Lianas are also widely used by humans for a variety of purposes, including as food, medicine, and for construction (Gentry 1989, Phillips 1991, Paz y Miño *et al.* 1995, Tra Bi 1997, De Jong *et al.* 2000).

The study of lianas, including their diversity, morphology, climbing mechanisms, aerial architecture, and species was at its peak during the second half of the 19th Century (Darwin 1867, De Vries 1880, Schenck 1892-1893). During much of the 20th century, however, lianas have been mostly ignored and they have been under-represented in most studies of forest dynamics. The omission of lianas in these

studies may be attributed to the difficulties in liana identification, determining liana ramets from genets, and the difficulty in including lianas in a study due to their erratic growth form. Furthermore, lianas were probably considered to be of nominal importance in the forest because of their relatively thin stems compared to the massive trunks of trees.

During the last two decades, however, the enthusiasm for liana research has been renewed, as the prevalence and importance of lianas in many aspects of forest dynamics is becoming understood (e.g., Putz and Mooney 1991, Schnitzer and Bongers 2002, Pérez-Salicrup *et al.* in press). Methodologically, however, the study of lianas is currently in disarray, as researchers are still trying to determine the most appropriate ways to census lianas. Indeed, the multitude of methods used by different researchers over the last two decades is a testament to this assertion. The stem measurement location, the decision to include or exclude ramets, the plot shape, and even the criteria of what constitutes a liana differ among studies and can have profound effects on the data collected (Schnitzer *et al.* unpublished manuscript). In this paper we compare and contrast the different methods that have been used for studying lianas and discuss the potential ramifications of these methods. We focus on problems confronted when including lianas in forest censuses. Protocols for measuring climbing palms were recently discussed by Stockdale and Wright (1996) and a quantitative comparison of the different methods of censusing lianas has been conducted by Schnitzer *et al.* (unpublished manuscript), so they will not be treated in detail here.

3.2. LIANA CENSUSES

Lianas are included in forest censuses for a number of reasons, including such basic information as the identity and relative abundance of species in the liana community, the long-term demography of the liana community, the role of lianas in forest regeneration and functioning, and the contribution of lianas to such large-scale forest processes as carbon sequestration and whole-forest transpiration. However, in order to address any of the above-mentioned issues, a number of questions must be resolved. (1) What is a liana and what taxa should not be considered lianas, (2) because lianas readily regenerate via vegetative propagation, what is the best way to distinguish ramets from genets (3) what are the most appropriate size and shape of study plots and how they should be deployed in the study area, and (4) how to measure lianas in the field, (5) how to measure liana-tree competition, and (6) how to measure liana growth and development.

The difficulties of liana taxonomy

It is often difficult to identify lianas because of the problems associated with locating and collecting leaves, which are typically located at the top of the canopy. Hecketsweiler (1992) and Putz (1984a) were two of the few to make direct observations and collections by climbing the supporting trees. Even more difficult is the task of locating and collecting liana flowers and fruits, which are not only found high in the canopy, but seem never to be present when needed. Furthermore, most floras and field guides use keys based on fertile material, while very few taxonomic keys are based on leaf or stem characters (but see Croat 1978, Gentry 1993, Hawthorne and Jongkind in press). Some phenological studies have been conducted

on liana leaf and flower production (see Putz and Windsor 1987, Ibarra-Manríquez *et al.* 1991, Ramírez 1993, Morellato and Leitao-Filho 1996), however, these studies exist for only a very few sites. In general, lianas are identified in the field via a combination of characteristics from the leaf, bark, stem shape and exudate (e.g., sap or resin), and smell (Gentry 1993). Lianas may also be identified using anatomical features of the wood and bark from stem cross sections (Caballé 1993, Gentry 1985), however, we do not recommend this technique as it will lead to the death of the individual, making long-term studies difficult.

In species-rich areas where little is known about the local taxonomy, liana identification may prove to be particularly difficult. In some cases, it may be difficult even to distinguish a ‘true’ liana, which is defined as a woody climbing plant, from a shrub, small tree, epiphyte, or secondary hemi-epiphyte, which starts its life as a liana and later becomes an epiphyte when its roots degenerate. Examples of this last group are found in the aroid genera *Philodendron* and *Monstera* and the Cyclanthaceae *Asplundia* (Blanc 2002). Moreover, in some cases, aerial adventitious roots can be formed again, and establish contact with the ground for a second time. Secondary hemi-epiphytes would then become primary hemi-epiphytes, a term used for plants which start their life as epiphytes but subsequently establish soil contact via hanging roots. Most liana inventories exclude hemi-epiphytes, considering them to be a distinctly different growth form (Putz and Chai 1987, Chalmers and Turner 1994, Nabe-Nielsen 2001, Pérez-Salicrup *et al.* 2001b, Burnham 2002, but see Putz 1983, Clark and Clark 1990, Ibarra-Manríquez and Martínez-Ramos 2002). However, in some families, such as the Marcgraviaceae, both hemi-epiphytes and lianas are present, making them difficult to classify. Accordingly, Burnham (2002) counted all of the individuals of this group for density measures, but excluded them from all species-level analyses because genera could not be reliably distinguished vegetatively. Including epiphytes and hemi-epiphytes may substantially inflate the number of lianas recorded at a site, particularly if it is a wet or aseasonal tropical forest. We recommend omitting epiphytes and hemi-epiphytes, which is consistent with the majority of liana studies.

When is a climbing plant a liana?

The term ‘liana’ is usually reserved for woody, climbing (or scrambling) plants, but there is no exact agreement about which species or genera to include or exclude. For example, the rattans, a group of climbing or scrambling palms that are common in Asia and Africa are excluded from some liana inventories (e.g. Babweteera *et al.* 2000, Burghouts *et al.* 1994, Caballé 1986, 1998, Campbell and Newbery 1993, Makana *et al.* 1998, Muthuramkumar and Parthasarathy 2000), but included in others (Putz and Chai 1987). Rattans may have been excluded from many censuses because they are extremely abundant, diverse, and taxonomically difficult. Furthermore, rattans often form such dense clusters of stems that it is difficult to determine what constitutes an individual (e.g., Troy *et al.* 1997). In the Neotropics, Putz (1984a) included the climbing palm, *Desmoncus isthmus*, but excluded all Araceae, while Paz y Miño *et al.* (1995) excluded the climbing palms, but included one genus of the family Araceae. Other researchers have excluded climbing palms and grasses but included other monocots such as members of the Smilacaceae (e.g., DeWalt *et al.* 2000, Schnitzer *et al.* 2000). In a study of Panamanian families with ‘real woody climbers’ Gentry (1985) excluded Araceae but included Urticaceae,

Cyclanthaceae and Palmae. In Ecuador, Burnham (2002) included ‘only climbing plants originally and permanently rooted in the ground and climbing with support from another plant, thus excluding all members of the Clusiaceae, Cyclanthaceae, and Araceae, families that include hemi-epiphytes. Of course, climbing monocotyledonous plants do not have true wood, and thus strictly speaking, are not woody, but many of them (e.g., palms and smilax) seem to grow and compete like ‘true’ lianas and thus are included in most liana censuses. We believe that this rationale is justified. What taxa should ultimately be included in liana censuses is not an easy question to address due to the philosophical differences of researchers in their interpretation of what constitutes a liana or climber. The extent that including and excluding certain taxonomic groups (e.g., climbing palms) can influence the abundance and thus perceived impact of lianas in forests is currently unknown. Nevertheless, we urge researchers to present explicitly the abundance of each of the species that are not considered ‘true’ lianas to facilitate comparisons among studies using slightly different methods.

Ramets vs. genets

Distinguishing liana ramets from genets is a contentious issue in liana ecology. Many liana species readily propagate vegetatively and these new stems may remain connected below-ground or become disconnected from the parent stem, making it difficult if not impossible to distinguish a liana genet from a ramet in the field. Lianas commonly split into several stems or stem parts as in the case of the papilionoid legume *Dalhousiea africana* in Central Africa (Caballé 1994) and stem parts might get rooted and disconnected. Inventories in which ‘true’ liana genets are distinguished and counted are scarce (but see e.g., Hladik and Blanc 1987, Gerwing 2001). The possible connections among individuals can sometimes be tracked and dug out, which has been done in a limited number of studies (Peñalosa 1984, Caballé 1994, Gerwing and Vidal 2002). The connections between liana ramets, however, often decay, making delimitation of genets impossible without expensive and time-consuming genetic analyses. Indeed, a number of studies now refer to seemingly independently rooted lianas as “individuals” (sensu Putz 1983) or “apparent genets” to avoid the confusion between true genets and ramets (DeWalt *et al.* 2000, Mascaro *et al.* in press, Schnitzer *et al.* unpublished manuscript). Nevertheless, vegetative propagation is a valid and successful form of reproduction and it is important to distinguish independent liana individuals (apparent genets) from non-independent ramets. In a study comparing liana census methods in French Guiana, Schnitzer *et al.* (unpublished manuscript) reported that liana abundance can be approximately 15% higher and basal area and estimated biomass can be up to 20% higher when non-independent ramets were included. Mascaro *et al.* (in press) asserted that liana ramets that are still attached to the main stem should be considered to be more analogous to the branches of a tree than that of independent individuals, while independently rooted stems, whether they arise from sexual or vegetative reproduction, should be considered to be genets or apparent genets.

The decision to include apparent genets or all liana ramets is dependent on the question being addressed. For questions involving the relative contribution of lianas to forest biomass or the impact of lianas on host trees, all liana ramets should be included in the study. In contrast, to determine the demography of the liana community, only apparent genets should be included. Optimally, any study on lianas

Table 3.1. Liana inventory studies with main characteristics, ordered by decreasing plot size.

Size	shape	liana size treshhold (cm) and measurement	References
30 ha (500 x 600 m)	rectangular	1 dbh but measured 1-1.3 m from their base and tagged	Muthuramkumar and Parthasarathy (2000)
4.375 ha (125 x 350 m)	rectangular	< 1.5 dbh or below the lowest branch whichever came first of climbing stems of both genets and ramets rooted in the plot, and ramets rooted outside the plot when they were part of a genet that fell inside the plot	Gerwing (in press)
1 ha (100 x 100 m)	square	10 dbh	Proctor <i>et al.</i> (1998)
1 ha (100 x 100 m)	square	< 2 dbh cutting through the imaginary surface at breast height	Parren & Bongers (2001)
1 ha	?	2dbh independently rooted	Appanah & Putz (1984)
1 ha	?	10 dbh	Gentry (1988)
1 ha	non-square	10 dbh	Hegarty (1988)
0.78 ha (24 x 36 m) 9 plots	rectangular	0.2 dbh and > 1.3 m tall, measured 1.3 m from base. Multiple stems were excluded	Mascaro <i>et al.</i> (in press)
0.5 ha (20 x 250 m)	rectangular	1 dbh liana individuals rooted in plot and checked for possible underground stem connections	Ibarra-Manriquez and Martínez-Ramos (2002)
0.5 ha (10 x 500 m)	rectangular	< 1 dbh	Gerwing (2002)
0.2 ha (2 x 1000 m)	rectangular	1 dbh liana individuals rooted in plot	Gerwing & Vidal (2002)
0.2 ha (20 x 100 m)	rectangular	< 1 dbh liana individuals rooted in plot avoiding double counting of shoots from a runner	Nabe-Nielsen (2001)
0.2 ha (five parallel 4 x 100 m transects within 1-ha)	rectangular	> 1 dbh at the thickest point for (independently) rooted lianas in or those from a rooted position growing outside into the transect < 2 m above the ground	Burnham (2002)
0.1 ha (ten almost parallel 2 x 50 m transects)	rectangular	2.5 dbh rooted in each transect	Gentry (1982, 1988), Gillespie <i>et al.</i> (2000)
0.1 ha (20 x 50 m)	rectangular	1 dbh lianas rooted in plot	Putz & Chai (1987)
0.1 ha (20 x 50 m)	rectangular	< 5 dbh and < 2 m tall, multiple stems were treated as separate individuals if the bifurcation was below dbh and as one if above dbh	Killeen <i>et al.</i> (1998)
0.1 ha (25 x 40 m)	rectangular	< 1 dbh free- standing lianas rooted in plot and climbing into a plot	Putz (1984a)
0.09 ha (30 x 30 m)	square	2 dbh avoiding double counting of individuals	Pérez-Salicrup <i>et al.</i> (2001)
0.08 ha (20 x 40 m)	rectangular	5 dbh	Caballé (1986a)
0.04 ha	Rectangular with contiguous nested	0.5 dbh or horizontal at the thickest point for (independently) rooted lianas in quadrat	DeWalt <i>et al.</i> (2000)

0.0314 ha (r = 10 m)	quadrats	2 dbh attached to trees recorded in plots	Cedergren (1996)
0.01 ha	circle forming a cylindrical volume from the ground to above the canopy	?, lianas rooted inside the plot climbing on trees in the plot and rooted outside the plot climbing on trees inside the plot	Putz (1984a)
0.01 ha in a grid system	circle	10 dbh, above major stem irregularities	Clark & Clark (2000)
0.01 ha (2 x 50 m)	rectangular	< 1 mm dbh perpendicular distance above the ground, not along the stem	Bullock (1990)
0.01 ha	?	> 2 m tall at 1.3 m above the level of the ultimate rooting point for (independently) rooted lianas in quadrat	Gerwing & Farias (2000)
0.00125 (1.25 x 10 m) 500 m apart in long transects	rectangular	> 10 cm tall	Rollet (1974)
0.0005 (1 x 5 m)	rectangular	1 dbh, including multiple stems of the individuals. Stems with a smaller diameter were included but assigned a diameter of 0.5 cm	Schnitzer <i>et al.</i> (2000)
0.0005 (1 x 5 m)	rectangular	1 – 4 cm dbh, excluding ramets	Schnitzer and Carson (2001)
0.0004 (2 x 2 m) 50 dispersed within 1-ha block	square	> 10 cm tall	Rollet (1974)
0.0001 (1 x 1 m) parallel continuous bands dispersed over gaps extending 10 m into the forest from the edge	square	> 1 m tall	Rollet (1983)

would include both apparent genets and ramets, with the two different types of stems clearly separated and treated in the appropriate manner depending on the question being addressed.

Sizes and shapes of study plots

Shape and surface area of study plots is an extremely important consideration because many tropical forests have a heterogeneous environment and the spatial distribution of lianas is also highly variable. We distinguish between rectangular, square, and circular plot types in inventories, of which the rectangular ones are the most common (Table 3.1). A characteristic of lianas that typically differs from trees is that lianas can root within the plot boundaries but enter the canopy outside of the plot or root far outside and grow into the plot. Whether such individuals are included in a census should be clearly indicated.

Transects are often used for estimating species richness, but their size and shape cause considerable variation in the estimate. Gentry (1982, 1991, Gentry and Dodson 1987) sampled 0.1 ha of forest composed of ten 2 x 50 m transects dispersed over an area and mostly roughly parallel to each other and separated by 20 m or more. This so-called ‘exploded quadrat method’ yields higher estimates of species richness than estimates from more conventional transects (Duivenvoorden 1994, DeWalt and Chave in review), possibly because Gentry’s ‘exploded quadrats’ may cover more than one habitat type and therefore measure a mixture of alpha and beta diversity (e.g., Colwell and Coddington 1994, but see DeWalt and Chave in review for an alternative explanation). In general, a long narrow transect gives a higher estimate of abundance and diversity than a square one of the same surface area (Condit *et al.* 1996, Schnitzer *et al.* unpublished manuscript). In the case of liana aggregation and when rare species are studied, transects may capture greater change in forest structure, even if the area is the same (cf., Troy *et al.* 1997). Burnham (2002) used parallel 4 x 100 m transects placed within square 1-ha plots, each transect separated by a minimum 16 m. Because large diameter lianas can travel a great distance, in some cases more than 0.5 km, with parts of the stem undulating from the ground to the canopy and back down again (Putz 1984a), transects should be located reasonably far apart and care must be taken not to count a liana stem more than once. Furthermore, as lianas, by their nature, do not typically grow straight up to the canopy, one individual can loop into a study site level several times, leading to overestimation of liana number, basal area, and biomass.

Measuring lianas in the field

The minimum size for inclusion in the census and the location on the stem to measure lianas are among the most variable components in contemporary liana studies (Table 3.1). The minimum height and diameter size limit for inclusion of lianas in a census will greatly affect estimates of abundance and diversity of the liana community (Schnitzer *et al.* unpublished manuscript). Minimum diameter limits of 0.2, 0.3, 0.5, 1, 2, 2.5, 5, and 10 cm have all been used in various field studies (Table 3.1). The lower cut-off size can also strongly influence family importance values obtained (Nabe-Nielsen 2000, Mascaro *et al.* in press) and diversity (Bongers *et al.* 1988). Many taxa of lianas are excluded from the inventories when the cut-off limit is too high. On the other hand, including small individuals or liana seedlings is extremely time consuming. In addition, it is often

difficult to identify a small liana to species or even to distinguish it from a tree because many lianas start their growth as free-standing individuals.

The location on the stem at which lianas are measured can also have profound and significant effects on their estimated abundance, basal area, and biomass (Schnitzer *et al.* unpublished manuscript). Measurement points range from 1.3 m above the ground (Figure 3.1: I), from the rooting point (Figure 3.1: II), 0.2 m above the ground, or at the thickest point on the stem, which is usually just above the ground. Gentry (1982), DeWalt *et al.* (2000), and Burnham (2002) measured lianas at the thickest point above the ground, excluding nodal swelling or damage, if growing horizontally above the ground or at 1.3 m above the ground if growing only vertically. In a large-scale liana inventory, Makana *et al.* (1998) marked liana individuals that had several rooted stems using a single tag (i.e. tag 73), but all leaf bearing stems (with leaves above 1.3 m) were mapped at their point of rooting and the diameter of these stems were measured at breast height. By mapping ramets, Makana's census was more thorough than nearly all other large-scale censuses, however, it would have also been instructive if all ramets would have been tagged as well (i.e. tags 73a, 73b, 73c etc.). Buttressed trees cause difficulty in dbh measurements, but for lianas a more apparent problem as their stems are often flat, lobed, split, irregular, or anomalous in some other way (Figure 3.2). In the case where a stem has a flattened shape, both minimum and maximum diameters of should be measured and the geometric mean should be used as an estimate of basal area (Schnitzer *et al.* unpublished manuscript). In the case where a liana is anomalous (flat, lobed, bulbous, curved or split) at its point of measurement, we recommend a measurement at the first regular part below the irregularity.

The 'height' of a liana can indicate either its length or the elevation it reaches vertically in the forest, measured from the ground level. Liana length can be measured as either the length of the longest shoot (main stem or axis) or as the total length of all stems. For among species comparisons, the first method is not recommended because it underestimates the overall size of a multi-stemmed liana compared to strongly monopodially growing individuals. Length measurement can be difficult and perhaps impossible when a liana is growing in a host tree with a dense crown or is horizontally entering the crowns of other trees. In addition, measuring the length of long lianas is extremely time consuming, especially if it has to be done repeatedly over time, and thus is of limited use for general forest inventories. Detailed monitoring of liana height growth, however, has been done in a few studies (e.g. Caballé 1980a, Peñalosa 1984, Nabe-Nielsen 2000, and Parren and Bongers 2001).

The height a liana can reach is influenced by its climbing mode and the successional status of the forest (DeWalt *et al.* 2000). Liana climbing mechanisms have been divided into passive or active ones (Hegarty and Caballé 1991). The climbing mechanisms of scramblers and lianas with thorns are passive, whereas root attachments, hooks or tendrils, and branch climbers and twiners are active mechanisms. Lianas with passive mechanisms usually do not climb high up into the forest canopy because they easily fall down, while 'active' lianas may reach higher up (Nabe-Nielsen 2001, Carsten *et al.* 2002).

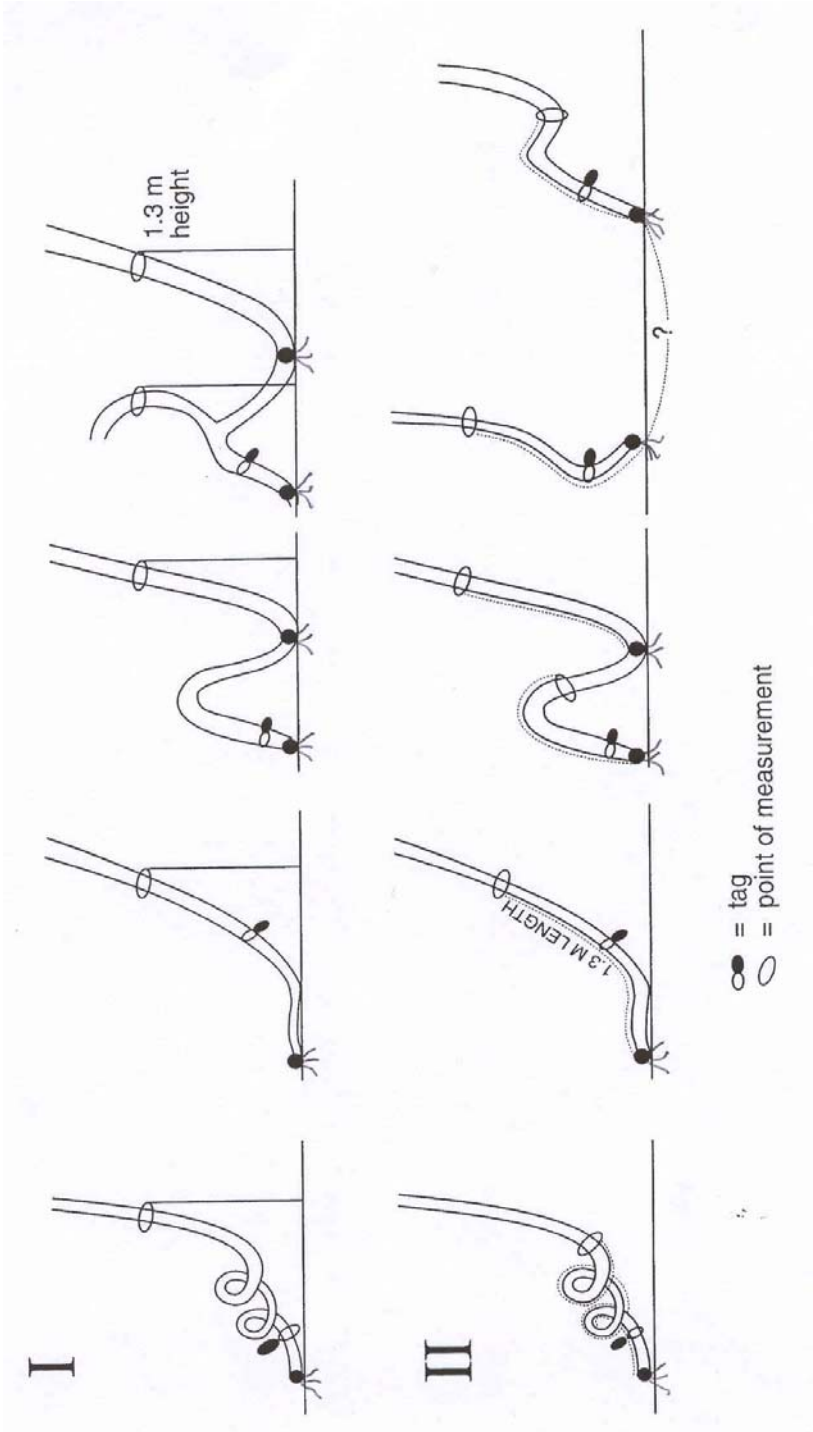


Figure 3.1. Diameter measurements at breast height (I) or at a distance of 130 cm from the root (II)

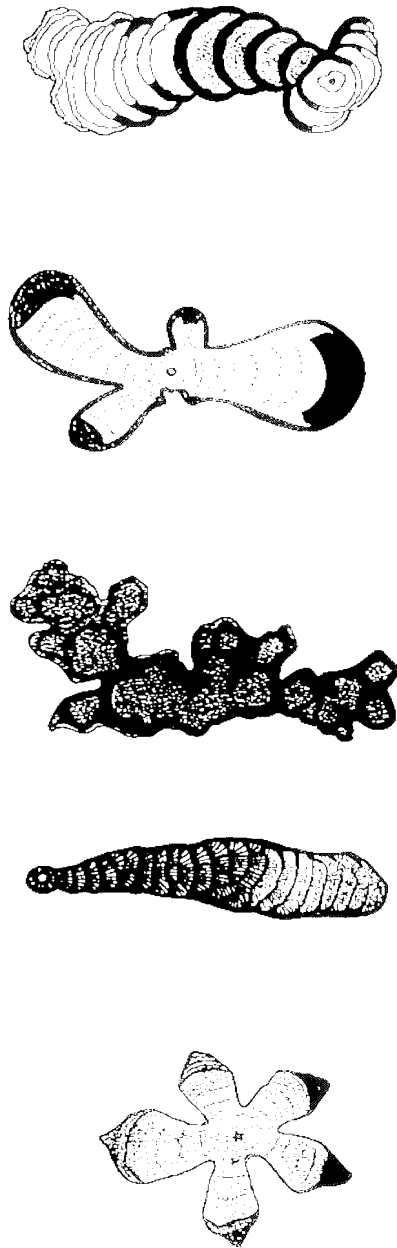


Figure 3.2. Diversity in forms of transverse sections of liana stems: xylem types. Some examples from left to right (a) *Santaloidella gilletii*, in rings, (b) *Coccoloba parimensis*, in lobes, (c) *Bauhinia* sp., in blocks, (d) *Curarea candicans* in rings and rays, (e) *Acacia kamerunensis* in a star (from Caballé, 1993).

Another way of measuring lianas is to calculate their basal area, biomass, or biomass production. Shanmughavel *et al.* (2001) weighed all lianas in their plots in southern China and found that they constituted 0.86% of total biomass. They also calculated regression models to relate liana diameter and length to biomass. Similarly, Pinar and Putz (1996) estimated liana biomass based on diameters in logged forest in Sabah, Malaysia, DeWalt *et al.* (2000) in secondary forests in Panama, Clark and Clark (2000) in Costa Rica, Laurance *et al.* (2001) in Brazil, and Schnitzer *et al.* (unpublished manuscript) in French Guiana. Most studies used the regression equation developed for Venezuelan liana species by Putz (1983). Only Gerwing and Farias (2000) and Gerwing and Vidal (2002) developed their own based on allometric relations for 17 of the most common liana species in their site in Brazil. DeWalt and Chave (in review), however, combined these two regression equations and formulated a new and probably more accurate equation, which was then used in subsequent studies (e.g., Schnitzer *et al.* unpublished manuscript).

Measuring liana-tree competition

Because lianas use other plants, usually trees, for support, the impact of lianas on trees is a widely studied area in liana ecology (Lowe and Walker 1977, Campbell and Newbery 1993, Dillenberg *et al.* 1993, Schnitzer *et al.* 2000, in press, in review, Pérez-Salicrup *et al.* 2001b, Grauel and Putz in press). Lianas appear to impact trees differentially, with some trees able to escape from heavy liana infestation while others cannot (Putz 1984a, Schnitzer *et al.* 2000, Schnitzer and Bongers 2002).

The infestation rate of lianas in trees may be related to successional stage of the forest, host tree growth rates, host tree stem flexibility, presence/absence of trunk spines, bark roughness and flakiness, tree architecture, whether or not trees have large leaves, and liana climbing strategies (Putz 1984b, Putz and Chai 1987, Kammesheidt 1999, DeWalt *et al.* 2000, Schnitzer *et al.* 2000, Pérez-Salicrup *et al.* 2001b, Carsten *et al.* 2002, but see Boom and Mori 1982). The trunk of a tree is not the sole access route for climbers to the canopy and it is important to distinguish between the tree or other lianas that made it possible for a liana to ascend to the canopy (primary host) and any additional trees that were invaded afterwards (secondary host).

When studying liana-tree interactions several questions may be important. For example, do lianas compete more above- or below-ground? How close must a liana be to a tree before there is a liana-tree interaction? Are lianas only on the bole competing with that tree or are only the lianas in the canopy competing with the tree? Liana-tree interactions can be also studied from the liana point of view. For instance, by following the growth of individual lianas rooted in a plot as they grow through the crowns of trees and are supported by their branches and boles (Putz and Chai 1987).

Aboveground competition between lianas and trees is the most obvious interaction to the human observer, and many studies have examined the above-ground effects of lianas on trees. Lianas can form mats on top of dead wood material and/or seedlings, especially in disturbed environments. An extreme case was observed on Mayotte Island in the Indian Ocean where the mimosoid legume *Leucaena chrysostachys* formed extensive mats on top of the vegetation and severely suppressed its development (G. Caballé pers. obs.). Schnitzer *et al.* (2000) reported that liana tangles in gaps can retard gap-phase regeneration for more than 13 years (see also Uhl *et al.* 1988, Tabanez and Viana 2000). Various indices have been used for estimating the above-ground effects of lianas on trees. A five-class liana occupancy index for trees was developed by Clark and Clark (1990) and consisted of the following: 0 = no lianas in tree, 1 = 1-25% of the canopy covered by lianas, 2 = 26 - 50% of the canopy covered by lianas, 3 = 51-75% of the canopy covered by lianas, and 4 = 76 - 100% of the canopy covered by lianas. The Clark and Clark index was further modified by Schnitzer *et al.* (in press) and even simplified into three liana cover classes by Gerwing (2002). Changes in liana cover can also be estimated using of hemispherical canopy photographs (see Pérez-Salicrup 2001) or radiation quantum sensors (Wirth *et al.* 2001). The contribution of liana versus tree leaf cover can be assessed when liana cutting is applied in silvicultural experiments, using hemispherical photographs or LiCor LAI 2000 measurements taken before and after treatment (Pérez-Salicrup 2001, Grauel and Putz in press). Liana cutting experiments allow us to test directly the effect of lianas on the growth and mortality of trees (see Stevens 1987, Barker and Pérez-Salicrup 2000, Pérez-Salicrup and Barker 2000, Pérez-Salicrup 2001), and on the liana populations themselves (Parren and Bongers 2001, Gerwing and Vidal 2002). Although above-ground competition between lianas and trees is known to be important, several studies now suggest that below-ground competition from lianas is extremely aggressive, possibly even more important than above-ground competition (Dillenberg *et al.* 1993, Pérez-Salicrup and Barker 2000, Schnitzer and Bongers 2002, Schnitzer *et al.* in review). Only detailed experiments

will tease-apart the relative contributions of above- and below-ground competition between lianas and trees.

3.3. GROWTH AND DEVELOPMENT OF LIANAS

The growth of lianas is typically expressed in terms of increased size (diameter, height, stem length, or number of ramets) or as a qualitative developmental change (ramification, new modular unit types). Lianas develop several secondary stems that, over time, may attain dominance and become the main stem. This development is hard to assess when many new stems are formed and others die back in the course of time. Several detailed studies at species level have been done on the height and diameter growth of lianas, e.g. for *Ipomoea phillomega* (Peñalosa 1983), for *Toxicodendron diversilobum* (Gartner 1991) and for *Machaerium cuspidatum* (Nabe-Nielsen 2002). These authors monitored all forms of growth of liana individuals for about one year. Gerwing (in press) monitored a large number of individuals in different size classes of six liana species over a three years period. Peñalosa (1983) mapped the stolon systems for *Ipomoea phillomega* by tagging all individual shoots and monitoring them at 2-10 day intervals. Long term studies of leaf production and leaf fall of lianas versus trees also offers insights into their relative productivity (Hladik 1974, Alvarez and Guevara 1985, Hegarty 1990, 1991, Burghouts *et al.* 1994, Wright *et al.* in review).

Mortality and turnover of liana stems is generally high. In a Gabonese forest, Hladik and Blanc (1987) and Caballé and Martin (2001) found high liana mortality (making no distinction between genets and ramets) compared to trees and shrubs. In Panama, Putz (1990) found similar mortality rates for ramets compared to large trees, but considerably lower ones for genets. Similar patterns were found in Amazonian forest by Gerwing (2001, in press), although the mean annual mortality rates for both ramets and genets were substantially higher than those found by Putz (1990). It is possible that lianas, including their ramets, are longer lived than are trees, but this has yet to be substantiated. For example, the recensus after 13 years in Gabon (Caballé and Martin 2001) was limited, because individuals were not marked during the first census, so demographic analyses were conducted at the plot level rather than the individual level.

The main causes of liana mortality are probably competition for resources with trees and other lianas, fungal and viral infections, and herbivory, but stem injury from twisting and girdling may also strongly limit development of lianas (Fisher and Ewers 1989, 1991). Catastrophic events, such as branch and treefalls, fires, or logging damage also increase mortality rates. However, in many cases, mortality is lower than expected due to stem toughness and the maintenance of functional xylem vessels (Putz and Holbrook 1991), rapid healing of injuries and prevention of total vascular disruption by the presence of non-lignified tissue and multiple cambia (Fisher and Ewers 1991), high resprouting capacities after damage (Appanah and Putz 1984, Vidal *et al.* 1997, Pinard *et al.* 1999, Pérez-Salicrup *et al.* 2001a, Parren and Bongers 2001, Schnitzer *et al.* in press), and vigorous growth rates.

Diameter growth rates assessments of individual liana stems are difficult to make, particularly over merely a few years (Putz 1990). Lianas show various types of

anatomical ontogeny that result from secondary growth processes (Caballé 1993). Determination of diameter growth rates is difficult because of irregularities in the liana stem (see above and Figure 1) and methods to measure precisely the surface of transverse sections of irregularly formed lianas in a non-destructive way are far from perfect. In some cases, it might be better to look at changes in liana abundance and basal area at the population level rather than at the individual level because these changes may be a more accurate estimate of liana growth than the incremental growth of individuals (Gerwing and Vidal 2002, Gerwing in press).

When monitoring individual lianas, marking a fixed point of measurement (Figure 3.2) is extremely helpful, since lianas can change position by falling partially from the canopy. Timing of measurements may also be important because of the strong effect of seasonal growth. Also, the interval between measurements is important since new shoot production, particularly after cutting or injury, can be very rapid. For example, in a study on the effects of liana cutting on resprouting capacity, Parren (unpub. data, Figure 3.3) observed that one month after a liana was cut new shoots grew as much as 6 m in length.

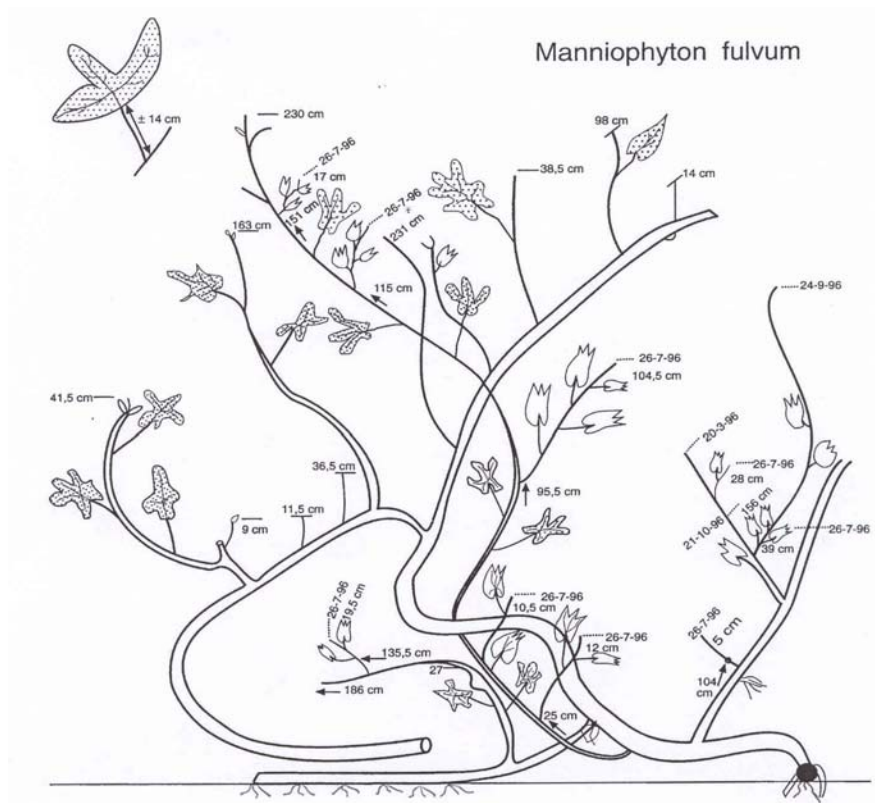


Figure 3.3. Monitoring of growth and development of an individual of *Manniophyton fulvum* (Euphorbiaceae) in Cameroon (M. Parren, unpub. data).

Castellanos *et al.* (1992) used imaginary cubes for three-dimensional mapping of lianas to determine differential space occupation by leaves and stems. Certain aspects of liana growth patterns are hard to describe in words because they show excessive branching, splitting that is unique to their growth form. Drawings and photographs may provide a better illustration of these patterns (Caballé 1977, 1980a,b, 1994). Ontogenetic development of lianas can be described in terms of branching patterns, flowering positions, phyllotaxy, and plagiotropy vs. orthotropy (Hallé and Oldeman 1970, Hallé *et al.* 1978). However, this is quite complicated because of the extremely high growth rates, as Cremers (1973, 1974) demonstrated for young lianas in West Africa and Coudurier (1992) for mature lianas in French Guiana. For architectural studies, several individuals of a species in different stages of development are studied, drawn and mapped. In some cases, individuals are cut into pieces and reconstructed afterwards (Coudurier 1992).

3.4. CONCLUSIONS

Lianas are a difficult group of plants to census and thus have been omitted from many forest studies. However, with the realization that lianas are an important component in tropical forests, liana censuses have increased considerably over the last couple of decades. Although we have not solved the problems of censusing lianas, we can offer some recommendations that may standardize some methodological aspects of liana censuses. In some cases, such as the minimum size cutoff or where exactly on the stem to measure diameter, we do not offer strict recommendations, because in these cases the answer is somewhat arbitrary and consistency is a more important consideration. To aid in comparing different studies, researchers should clearly describe the abundance and diversity of all lianas included in the study but that are not considered 'true' lianas. Hemi-epiphytes and epiphytes should not be included as lianas. Data on both apparent genets and ramets should be collected and presented as both: 1) apparent liana genets only and 2) all liana stems, including all genets. Collecting both sets of data will allow the data to be used for several questions and it will facilitate comparisons among studies.

The shape of the plot will, to some extent, influence the number, basal area and biomass of lianas present. Care should be taken to compare like-shaped plots among studies. Furthermore, plots should not be located too near each other because of the potential error of including a large liana stem in more than one plot. There are several locations on the stem that lianas are commonly measured and each may yield significantly different results. Consistency in stem location measurements is the most important consideration. Measure all climbers at a fixed distance from the rooting point. Clearly marking the point of measurements on liana stems will aid in relocating stems after slippage or falling from their support. Avoid anomalous and irregular parts of the stem. Different measurement locations will yield different results, so only similar measurement methods should be compared among studies. Indices of liana coverage on the canopy of trees appear to accurately estimate the amount of competition on trees. Liana growth can be considered by either the size increment of a given stem or by the change in the number of stems in the community. Each factor will reveal a slightly different insight into the demography of the liana individual, population, or community.

Acknowledgements

We are grateful to the European Science Foundation for financing a meeting in Aarhus, Denmark, where this paper was initiated. We gratefully acknowledge the support of the following organisations: M.P.E. Parren the Tropenbos Foundation, The Netherlands. F. Bongers and S. Schnitzer the EC DG-VIII funded ECOSYN project (grant B7-5041/95.02/VIII), G. Caballé the CNRS, France, J. Nabe-Nielsen the Centre for Tropical Biodiversity (Danish Natural Science Research Council grant 11-0390). We thank R.J. Burnham, A. Dalberg Poulsen, S. DeWalt, M. Kuzee, M.A. Pinard, F.E. Putz and S. Wijdeven for constructive comments on earlier drafts of the manuscript. This is publication n° 98-075 de l'Institut des Sciences de l'Évolution, UMR 5554 of CNRS.

4. LOGGING AND LIANAS IN WEST AFRICA

4.1. LOGGING IN WEST AFRICA

Commercial exploitation of timber species in West Africa dates back to the end of the 19th Century when at first British and later French companies began harvesting African mahogany (*Khaya* and *Entandrophragma spp.* of the Meliaceae). Even during most of the next century logging in West Africa could be characterised as being highly selective. A limited number of species with diameters mostly surpassing one meter were harvested at very low densities often not surpassing one tree per ha. This situation was predominant until the last quarter of the 20th Century. The repeated removal of the best individuals of a limited number of species at very short felling cycles has led to overexploitation of the forests. The increased exploitation of Côte d'Ivoire's forests were most astonishing, leaping from 0.4 million cubic meters annually in the 1950s to 5 million cubic meters annually in the 1970s (Arnaud and Sournia 1980), which slowed down to around 3 million cubic meters per annum since 1987. Much timber comes from already exploited 'residual' forest. And after this timber is exploited the clearing for agriculture usually takes place. Both Côte d'Ivoire and Ghana's remaining forests are now heavily fragmented by plantation agriculture, primarily cocoa, coffee, oil palm and rubber. The forest cover of Côte d'Ivoire declined in just a 35 years timespan from c. 8.8 million ha in 1955 to just 2.7 million ha in 1990 (Fairhead and Leach 1998). The remaining forests are confined to the permanent forest estate which forests are often in a bad condition. There is an urgent need to restore forest cover and biomass.

The late 1990s saw the arrival of Asian buyers and operators in West- and Central Africa. They started cutting a very wide range of species and at high intensities per ha. The timber market never before accepted many of these species. This move was made since the Philippines and Vietnam were already almost deforested, while at the same time Thailand, Malaysia and Indonesia became much stricter about log exports and logging at all. Nearby supplier nations in the south Pacific and Siberia were not able to satisfy South-east Asian, Chinese and Japanese demand; but the South-east Asian sawmill, pulp and plywood installed capacity had been quadrupled (Sizer and Plouvier 1999). Nowadays, most of the Asian companies in Africa operate like the former companies. They harvest trees at densities of about one tree per ha and exploit only a limited number of species. This was most likely caused by economic factors such as the unusual low diameters felled combined with the high transport costs to Asia (Debroux and Karsenty 1997). In spite of high transportation costs, African timber and especially secondary species have become more sought in Asia. This kind of pressure is driving companies like Oriental Timber Corporation and Shimmer International (the West/Central African subsidiary of Rimbunan Hijau) to get access to the timber resource cheaply (Van Breugel and Parren 1997, Anon. 2001). In a place like Liberia, they also operate in forested coastal zones where many large sized tree species tend to have properties (low grain density) that are not as highly sought after as from the drier and more seasonal zones. The timber species traditionally in demand were found only in low densities in these coastal forests making logging operations more expensive. That also explains that the West African forests in bad condition are mainly confined to the drier areas in the interior (Hawthorne 1996). This is not without reason, since it is the semi-deciduous forest

which shows the highest share of commercial species and which has accordingly suffered excessively from both logging and the following fires (see also Hawthorne 1993, 1994). Coastal areas which tend to have the highest rainfall and plant endemicity are normally dominated by species of only moderate commercial value, such as Caesalpinoideae species like *Tetraberlinia tubmaniana* in coastal Liberia. Deforestation of the Upper Guinean forest ecosystem has generally encroached from the driest zones to the most moist. Generally speaking economic pressures and depletion of commercially richer forests opened up areas that did not used to be desirable for commercial timber and agriculture.

4.2. LIANA CUTTING AS A SILVICULTURAL TOOL

Over the past millenium most African forests have been disturbed by shifting cultivation (Richards 1996, White and Oates 1999) and the last century by logging. The gaps created have accordingly been colonised by lianas. During treefall, caused by natural mortality or felling, lianas often mechanically damage their hosts (Putz *et al.* 1984). The canopy binding effect is shown when liana-laden trees are felled, since these trees damage nearly twice as many surrounding trees than liana-free trees of the same size (7.2 vs. 3.9; Appanah and Putz 1984). Next, in the optimal light conditions of the created gaps, lianas have an advantage over tree seedlings and saplings as lianas hardly have to invest in supporting tissue and so can outcompete the former (Pérez-Salicrup 2001). Not surprisingly, forest managers often see lianas as a nuisance and cutting of lianas prior to or after logging is often prescribed where silvicultural treatment is practised: surface-wide or selectively around the tree to be felled to reduce felling damage. When lianas are cut surface-wide, all stems are systematically cut twice, near the forest floor and at breast height. Alternatively, lianas are cut selectively, only in a imaginative circle surrounding the stem to be felled and sometimes around the so-called Potential Crop Trees, trees to be felled in the next felling cycle (see Fox 1968, Guignonis 1978, Appanah and Putz 1984, d'Oliveira and Braz 1995, Pinard *et al.* 1995, Pinard and Putz 1996, Dijkstra and Heinrich 1996, Mason 1996, SODEFOR 1996, Amaral *et al.* 1998, Barreto *et al.* 1998, Sist *et al.* 1998, Holmes *et al.* 2002, Jackson *et al.* 2002, Pereira Jr. *et al.* 2002). For Ghana, Foggie (1960) states that after 'the occasional storms [...] large breaks in the canopy occur' where seedlings and saplings of emergent tree species will show a growth respond and 'lianas also swarm in, annuals and perennials, and within a year or two it is a dense liana tangle impenetrable except to the elephant [...]'. He continues regarding forest management 'The initial stage is always an attack upon the lianas by severing them at ground level and as high as can be reached. This not only lightens the canopy but allows mother trees freer crowns, reduces later felling damage, and reduces regrowth.' This negative appreciation of the role of lianas made that foresters preferred to control liana proliferation so liana cutting was applied over hundred thousands of ha of West African forests since the 1950s.

4.3. LIANA ABUNDANCE AND TREE INFESTATION

Most forest inventories concentrate on the tree component, hardly assessing any other lifeforms. This explains the fact that only very few studies are available providing quantitative data on liana abundance of the moist forest zone in the region. For Côte d'Ivoire we can present two logged wet evergreen forest sites: Irobo and

Table 4.1. Tree infestation by lianas in tropical forests, with different threshold values, liana abundances and forest history.
 Dbh = diameter at breast height, gbh = girth at breast height.

country	locality	Forest type (rainfall)	Host size (threshold (cm))	Percentage infested trees (liana threshold (cm))	Liana density (ha)	Area (ha)	Forest history	Reference
Africa								
Côte d'Ivoire	Songan	Wet evergreen (1500 mm)	10 dbh	40	-	8	Repeated selective logging between c. 1940 and 1992	Brinkmann 2000
	Monogaga I	Wet evergreen	5 dbh	68.5 (130 cm tall)	2870	0.1	Unlogged forest	M. Kuzee pers. comm.
	Monogaga II	Wet evergreen	5 dbh	80.3 (130 cm tall)	3520	0.1	Unlogged forest	M. Kuzee pers. comm.
Benin	Lama	Moist semi-deciduous (1100 mm)	5 dbh	36	-	3.8	Unlogged forest although anthropogenic disturbance in the past	Schäfer 1997
Cameroon	Ebom	Moist evergreen (2000 mm)	10 dbh	34.4 (2 dbh)	408	33	Unlogged forest	Unpublished data M. Parren
Asia								
Malaysia (Borneo)	Danum	Wet evergreen (2700 mm)	30 gbh	57 (2 gbh)	882	8	Unlogged forest	Campbell & Newbery 1993
	Ulu Segama	Wet evergreen (2700 mm)	20 dbh	75 (2 dbh)	586	-	Logged 13-14 years ago, fire swept through 5 years later	Pinard & Putz 1994, 1996
	Sawai	Moist forest	10 dbh	44.1	-	1	Control plot, logged 6 years ago	Putz <i>et al.</i> 1984
	Similajau	Moist forest	10 dbh	53.8	-	1	Control plot, logged 6 years ago	Putz <i>et al.</i> 1984
	Niah	Moist forest	10 dbh	47	-	6	Control plot, logged 6 years ago	Putz <i>et al.</i> 1984
	Batu Belah	Moist forest	10 dbh	57.3	-	-	Control plot, logged 26 years ago	Putz <i>et al.</i> 1984
	Lambir	Wet evergreen (2950 mm)	10 dbh	52.3 (1 dbh)	554	0.5	Unlogged forest in valley	Putz & Chai 1987
	Lambir	Wet evergreen (2950 mm)	10 dbh	33.9 (1 dbh)	228	0.5	Unlogged forest on ridge	Putz & Chai 1987

India	Kolli Hills (Eastern Ghats)	Monsoon forest (1000 mm)	30 gbh	10 (5 gbh)	48	8	Undisturbed and disturbed high forest (with harvesting of lianas)	Chittibabu & Parthasarathy 2001
	Varagalaiair (Western Ghats)	Seasonal moist forest (1600 mm)	30 gbh	28 (1 dbh)	373	30		Muthuramkumar and Parthasarathy 2001
South America								
Bolivia	Las Trancas	Seasonal dry forest (1130 mm)	10 dbh	75 (200 cm tall)	3876	10	Unlogged forest, anthropogenic disturbance in the past shown by charcoal and potsherds Liana forest within logging concession Logged forest, anthropogenic disturbance in the past shown by potsherds Unlogged forest	Killeen <i>et al.</i> 1998 Carse <i>et al.</i> 2000
	Oquiriquia	Seasonal moist forest (1200-1700 mm)	10 dbh	86.3 (2 dbh)	2471	2.16		Pérez-Salicrup <i>et al.</i> 2001b
	La Chonta	Humid forest (1560 mm)	10 dbh	73 (2 dbh)	1652	-		Alvira Reyes 2002 M. Pena-Claros and T.S. Fredericksen pers. comm.
Ecuador	Yasuni	Aseasonal moist unflooded forest (2500 mm)	10 dbh	53	-	-	Unlogged forest	Balslev <i>et al.</i> 1987
		Aseasonal moist floodplain forest (2500 mm)	10 dbh	31	-	-		Balslev <i>et al.</i> 1987
Brazil	Una (Bahia)	Atlantic aseasonal forest (1200-1800 mm)	10 dbh	38	-	-	Unlogged forest Unlogged fragmented and continuous forest Selectively logged 8 years previous, 3-9 trees ha ⁻¹ harvested, liana-dominated residual forest Logged and burned forest	Boom & Mori 1982, Mori <i>et al.</i> 1983
	Manaus (Amazon)	Seasonal evergreen forest (1900-3500 mm)	10 dbh	50 (2 dbh)	355	2.88		Laurance <i>et al.</i> 2001
	Paragominas (Amazon)	Seasonal evergreen forest (1700 mm)	5 dbh	90	> 4000	0.96		Gerwing 2001
	Olho d'Agua (Amazon)	Moist evergreen forest (1500-1800 mm)	10 dbh	39.5-45.5	-	5		Cochrane & Schulze 1999
Venezuela	San Carlos de	Evergreen forest	10 dbh	42.1 (200 cm	-	0.2	Unlogged forest, with	Putz 1983

	Rio Negro Caparo	(3500 mm) Moist forest (1750 mm)	deciduous	10 dbh	tall) 46.2 (30 cm tall)	-	4.6	charcoal fragments Unlogged forest (35%) and logged forest (65%) plots	Kammesheidt 1999
Central America									
Panama	Barro Colorado Island	Seasonal deciduous forest (2800 mm)	semi-	10 dbh	32 (2.5 dbh) 17 (5 dbh)	-	c. 5	Human disturbed forest prior 1914 isolation	Knight 1975
Panama	Barro Colorado Island	Seasonal deciduous forest (2800 mm)	semi-	20 dbh	47 (1 dbh)	773	1	Human disturbed forest prior 1914 isolation	Putz 1984a
Costa Rica	La Selva	Wet forest (4000 mm)		10 dbh	46 (50 cm tall)	-	-	Unlogged forest	Clark & Clark 1990
Mexico	Los Tuxtlas	Evergreen forest (4725 mm)		10 dbh	63.3 (2 dbh)	-	-	Unlogged forest	W. de Meijere pers. comm.

Yapo. In the Irobo forest, Bertault (1986) found for lianas in the 2-10 cm class some 202 ± 45 individuals ha^{-1} in control plots, and some 174 ± 38 individuals ha^{-1} in silviculturally treated plots. For very large lianas > 10 cm drh¹ some 1.8 ± 1.5 individuals ha^{-1} in control plots and 0.4 ± 0.5 individuals ha^{-1} in treated plots were present. In the Yapo forest, M'Bla and Diahuissie (1993) found for lianas > 2 cm drh some 819 ± 355 individuals ha^{-1} in control plots, and some 965 ± 233 individuals ha^{-1} in silviculturally treated plots. This shows that there is a large variation in liana abundance in the same forest type with some four times as high liana densities in the Yapo forest compared to Irobo. This might be explained by the repeated logging in the Yapo forest compared to the Irobo forest that most likely saw only one exploitation passage. Assess to records on the exploitation history might possibly explain the proliferation of lianas in the Yapo forest compared to the Irobo forest. Similarly a logging damage study in Nkrabia forest, gives us an idea of the presence of large lianas in Ghana. In a plot of c. 6 ha, some 394 trees ≥ 30 cm drh carried 173 lianas ≥ 5 cm drh of which 33 lianas ≥ 10 cm drh. These large lianas belonged to a rather small group of only 15 genera (Nuys *et al.* 1992). So on average every second tree carried a large liana. However, most likely they were aggregated, as fewer trees would carry a heavy liana load. Unfortunately individual tree liana hindrance data were not recorded.

Looking at liana infestation of trees in 8 ha (4 paired 1-ha plots) of wet evergreen Songan forest in southeastern Côte d'Ivoire, Brinkmann (2000) showed a similar picture as was shown for Nkrabia forest in Ghana. The average number of trees ≥ 10 cm drh was 413 ± 56 ($N = 8$) and the basal area varied between $22.2 - 28 \text{ m}^2\text{ha}^{-1}$ ($N = 7$) for most of the forest except for one ha which was very well stocked with a basal area of $34.9 \text{ m}^2\text{ha}^{-1}$. Some 60% of all trees did not carry any lianas and only 15% were hindered by lianas in their development. What was most striking is that at one site less liana hindrance was noticed although that part of the forest was most degraded. A comparison of liana infestation in the tropics (Table 4.1) shows that on the African continent less trees are infested with up to 40% of the trees occupied by lianas. Only seasonal forests in the Indian subcontinent and floodplain forests in the Neotropics show similar low infestation levels. The proportion of infested trees in some South American forests are extremely high, as are the liana abundance, compared with the African and Asian forests.

Although less trees are infested on the African continent, liana loads are positively correlated with tree diameter in Cameroon (Fig. 4.1). Old grown trees carry most lianas. In La Selva, Costa Rica, Clark and Clark (1990) found similar relationships and concluded that most tree individuals in the subcanopy size class (10-30 cm drh), were free of lianas, while over 50% of the large trees (≥ 70 cm drh) were colonised.

¹ Diameter at reference height is normally the point of measurement at breast height but in case of anomalies just above the anomaly and for trees 30 cm above the anomaly.

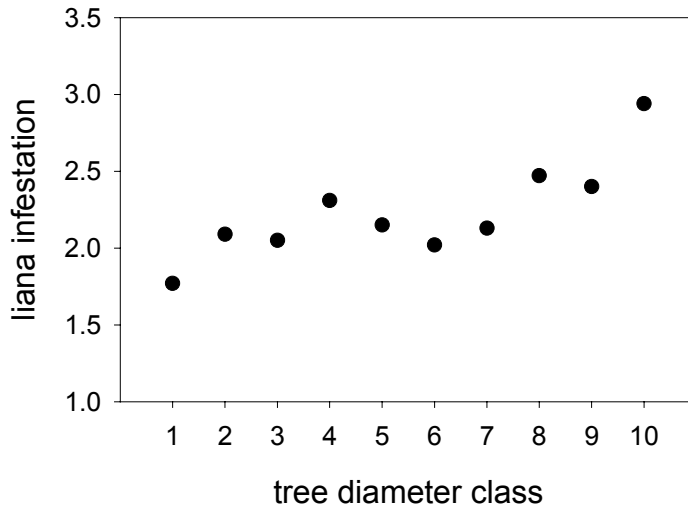


Figure 4.1. Average liana infestation of all trees over 10 cm diameter in 18 one-ha plots in southern Cameroon. Liana infestation classes are: 1= no lianas, 2= on stem only; 3= in crown, not connecting with other trees; 4=in crown, connecting with other trees; and 5=on stem and in crown, completely covered. Tree diameter classes: 1= 10-20cm dbh, 2=20-30cm dbh, etc. 10=over 100cm dbh.

4.4. SILVICULTURAL SYSTEMS WITH NATURAL REGENERATION AND LIANA CUTTING

With timber extraction by Europeans expanding rapidly since the late 19th Century an urgent need arose to regulate these indiscriminate activities. The colonial administration of both Ghana and the Côte d'Ivoire attempted to regulate forest exploitation by handing out concession rights and by implementing regulations to avoid the destruction of this renewable resource. Concession rights covering a lengthy timespan may be considered to stimulate responsible management aimed at sustained yields. Before forest management can be made to work, successful silvicultural systems have to be developed to form the core of such a management system. Silvicultural systems cannot be easily copied from existing systems in other regions but rather have to be built from examples, adapted and further developed to fit the regional ecological and socio-economic conditions. Concessionaires cannot usually be expected to be really interested in such research work, so the forest service has to struggle to find such systems for themselves. The options at hand are silviculture with natural regeneration for which the British colonial forest officers opted most or silviculture with artificial regeneration (plantation forestry) which was initially favoured by the French in Africa.

4.4.1 Amélioration des Peuplements Naturels (APN) [Natural forest stand improvement]

In Côte d'Ivoire experiments with natural regeneration on a larger scale had not begun before 1947, long after silviculture with artificial regeneration had started. This new approach was inspired by the finding that some logged over forest reserves were well stocked with medium-sized *Heritiera utilis* and *Turraeanthus africanus* individuals and had shown natural regeneration potential. It was thought to be a less expensive and easier alternative to artificial regeneration practices (d'Aviau de Piolant 1952). The APN system involved an inventory of the commercial stock, followed by liana cutting, the opening of the canopy and treatments to favour the desired species. By 1954 APN had been applied in 18 forest reserves while of 15,231 ha inventoried c. 75% were treated by liana cutting and surprisingly just 3,596 ha were refined afterwards (Bertault 1986). Refinement consisted of systematical opening of the canopy at two 6 month intervals. This opening is done by poison girdling of the seed bearers of non-commercial tree species oppressing the crowns of commercial tree species in the sub-canopy and the removal of large-crowned trees in all strata. It was not deemed necessary to open the canopy by treating each successive crown layer (Gutzwiller 1956). In 1960 many released trees were still overshadowed because of inadequate refining and the newly created more open environment was thought to favour liana growth. Accordingly the APN system was abandoned (Catnot 1965).

When implementing a silvicultural system with natural regeneration in FC Yapo, in the 1980s (see section below on the Yapo project), the forest service found evidence of application of APN over 442 ha in compartment 15 (SODEFOR 1986). The forest proved to be very rich in commercial species, mainly *Heritiera utilis*, of which over 20 trees per ha of over 50 cm drh were present. The overall stocking with commercial species of the APN treated forest proved to be significantly higher than the untreated natural forest. Lowe and Walker (1977) found in Idanre Forest Reserve, Nigeria, where the closely related Tropical Shelterwood System was applied in the mid-1950s, that only 11% of the *Khaya ivorensis* stems were infested by lianas some 20 years later, but as many as 44% of the *Sterculia rhinopetala* stems present. In these refined forests lianas thus still proliferated some 20 years after surface wide liana cutting was applied. This might be explained by the fact that *Sterculia rhinopetala* grew more slowly than *Khaya ivorensis*, and only the former showed a negative correlation between climber infestation and growth rate. So Catnot's (1965) observation that the refinement operations in the APN system created favourable conditions for liana proliferation could after all be correct.

4.4.2 The Irobo, Mopri and La Téné experiments

It was not until the mid 1970s that the country, confronted with the alarming deforestation figures and the inadequate reforestation efforts of the past decades, initiated three series of silvicultural pilot projects to study forest dynamics. The management principles aimed at inducing a more homogeneous structure to the stand by the manipulation of natural regeneration and were partly based on experiences gained with APN during the 1950s. According to Bertault (1986) the failure of APN was attributed to inadequate intervention in the canopy. The

intervention proposed was, therefore, far more radical than that of APN. The principal aim was to elucidate stand dynamics as affected by relatively simple, low-cost treatments -as opposed to those the APN system offered- that could be undertaken on a large scale.

The project covers 1,200 ha and comprises three separate sites each consisting of a block of 400 ha, subdivided into 25 plots, each of 16 ha. In each plot only the central 4 ha were monitored. The three sites are characteristic of the principal ecological zones of the moist forest: Irobo in wet evergreen forest, Mopri in the transitional zone of moist evergreen and moist semi-deciduous forest formations and La Téné in moist semi-deciduous forest. Silvicultural treatment on the three sites was confined to refining (poison girdling and liana cutting). Three intensities were chosen which resulted in an additional basal area reduction of either 20%, 30% or 40% after logging. Some 35 plots were refined, while 30 control plots remained untreated (10 on each research site) and 10 plots in La Téné were just logged-over. The 35 refined plots were afterwards regrouped in experimental plots with moderate refinement (less canopy opening and more basal area remaining) and plots with heavy refinement (higher canopy opening and lower basal area remaining) since the initial 20%, 30% or 40% basal area reductions were after all indifferent as all plots had previously been logged at different intensities and frequencies in time.

Table 4.2. Tree seedling versus liana ratio (I) and average number of lianas per ha (N) in the 2-10 cm drh class present at two sites in Côte d'Ivoire. The La Téné observations were made after the forest fires of 1983 (Bertault *et al.* 1999). Measurements were made 2 years ($I_2 = 1985$), 5 years ($I_5 = 1988$) and 10 years ($I_{10} = 1993$) after the passage of fires. Ten plots were monitored during 1985 and 1988 and only nine during 1993, just four plots were measured over the entire ten year period. In each plot an area of 0.4 ha was inventoried. Similar observations were made at Irobo eight years after the silvicultural experiments were first implemented in 1978. Some 40 plots (0.01 ha in size) each for treated and untreated areas were inventoried (Bertault 1986). While these plots were not touched by fire.

	La Téné			Irobo				
	I_2	I_5	I_{10}	N_2	N_5	N_{10}	I_8	N_8
Control	8	8.1	4.1	65.7 ± 29.2	65.2 ± 15.6	313	5.3	202 ± 44.5
Logged-over	11.4	8.5	4.6	58.2 ± 9.6	60.7 ± 54.8	205		
Refinement	17.8	18.7	4.5	48.5 ± 7.8	39 ± 14.1	345	7.2	174 ± 38.2

The opening of the canopy had most effect on small and medium-sized trees, which compete fiercely for light. Remarkably little information was given about the lianas presence. Regeneration counts for the 2-10 cm drh class in the Irobo forest some eight years after treatment showed that in comparison with the control plots ($N = 202$), refinement ($N = 174$) had hardly any effect on liana abundance (Table 4.2) and scarcely modified the floristic composition of the understorey. The high tree seedling versus liana ratio eight years after treatment of over five times as many tree seedlings compared to lianas indicates an extreme low liana presence. However, there was a dominance of a rather small group of liana species and genera (Table 4.3). An additional observation made was that hardly any trees ≥ 10 cm drh were used as trellisses in both the control and treated plots eight years after silvicultural intervention (Bertault 1986). This probably is due to systematic liana cutting at the moment of intervention. According to Bertault (1986) it was also striking that most

lianas had a shade-tolerant character (Table 4.3). When the canopy of the forest opens small shade-tolerant shrubs, such as several common Connaraceae species and other lianescent species, rapidly produce long shoots and appear to be lianas (Jongkind and Lemmens 1989). These shrubs would not be removed in silvicultural operations since they show their lianescent properties only after canopy opening and could account for their dominance. It is a general belief that light-demanding lianas will dominate and smother natural regeneration after opening the canopy of tropical moist forest (Schnitzer *et al.* 2000). However, whether shade-tolerant or light demanding liana species will dominate will depend on the gapsizes created and the frequency of such disturbance events.

Table 4.3. Floristic liana regeneration (2-10 cm drh class) inventories at : La Téné forest (total area 4 ha), 2 years after burning in 1985 (Bertault *et al.* 1999), and unburned Irobo forest (total area 0.8 ha), 8 years after silvicultural experiments were first implemented in 1978 (Bertault 1986).

		La Téné	Irobo
Family	Species		
Annonaceae	<i>Artabotrys jollyanus</i>		x
Apocynaceae	<i>Aphanastylis leptantha</i>		x
	<i>Motandra guineensis</i>	x	x
	<i>Strophanthus hispidus</i>	x	x
Asclepiadaceae	<i>Parquetina nigrescens</i>	x	
Caesalpiniaceae	<i>Caesalpinia benthamiana</i>	x	
	<i>Griffonia simplicifolia</i>	x	x
	<i>Mezoneuron benthamianus</i>		x
Combretaceae	<i>Combretum hirsutum</i>	x	x
	<i>Combretum racemosum</i>		x
	<i>Combretum spp.</i>	x	
Conneraceae	<i>Agelaea obliqua</i>		x
Convolvulaceae	<i>Neuropeltis spp.</i>		x
Dichapetalaceae	<i>Dichapetalum martinai</i>		x
Dilleniaceae	<i>Tetracera potetoria</i>		x
Dioscoreaceae	<i>Dioscorea spp.</i>	x	x
Euphorbiaceae	<i>Manniophyton fulvum</i>	x	
Flacourtiaceae	<i>Dasylepis assyiensis</i>		x
Icacinaceae	<i>Icacina manii</i>		x
	<i>Raphiastylis cordifolia</i>		x
Linaceae	<i>Hugonia afzelii</i>	x	x
Loganiaceae	<i>Strychnos dinklagei</i>		x
Menispermaceae	<i>Tiliacora dinklagei</i>	x	
Papilionoidea	<i>Ostryoderris leucobotrya</i>		x
Passifloraceae	<i>Adenia lobata</i>	x	
Rubiaceae	<i>Morinda longiflora</i>		x
	<i>Mussaenda elegans</i>		x
	<i>Sabicea ferruginea</i>		x
Vitaceae	<i>Ampelocissus spp</i>	x	
	<i>Cissus spp.</i>	x	x

Soon after the experiments started, the year 1983 witnessed the second largest El Nino event of the 20th Century and this caused in West Africa heavy droughts and fires that got out of control (Holmgren *et al.* 2001). As a consequence the La Téné experiment close to the forest-savanna boundary was almost entirely affected by fire that year. The devastating fires of 1983 had their own effects on the liana populations. The effects of these fires on the regeneration were assessed in strips of 200 x 5 m (0.1 ha) in the La Téné forest. The fires had initially negatively effected

the total number of lianas in the 2-10 cm drh class as they dropped to well below 100 stems per ha but restored after ten years to original numbers of over 200 stems per ha (see Table 4.2). The numbers of poles and saplings of commercial tree species was gradually seen restoring to a normal situation of 400-600 per ha (Bertault *et al.* 1999). In 1985 we can see an extremely high tree seedling versus liana ratio (I_2) of almost 18 in the refined plots which is twice as high as in the control plots. Initial liana cutting might already have eliminated quite a proportion of the liana population present then aggravated by the El Nino event resulting in even higher mortality rates. Similarly experiences are seen in Brazil where lianas ≥ 2 cm drh in logged and heavily burned forest stands were almost wiped out, while smaller ones more than compensated for these losses in terms of total liana density (Gerwing 2002). The same phenomenon might have been the case in La Téné although we lack information on lianas < 2 cm drh. Ten years after burning a steep increase in liana numbers was found showing a good restoration (cq. recruitment) potential of lianas on the long run. So forest fires seem to have a short term negative effect on the abundance of lianas ≥ 2 cm drh, but lianas seem to have sufficient plasticity to restore within ten years. The inventories also showed that in comparison with the control plots, the exploitation regime and the silvicultural intervention had scarcely modified the floristic composition of the understorey as most species were still present. However, two years after burning Bertault *et al.* (1999) found that the vegetation was dominated by a rather small group of liana species and genera (Table 4.3).

Most interestingly the La Téné fire experiences in Côte d'Ivoire encouraged controlled burning experiments in Tain Tributaries Block II forest in Ghana. A degraded forest was enumerated (plants > 2 m tall) in which a part remained unburnt and the other part was burnt. The mortality rates over a 1.5 years timespan for climbers in the burnt part was a staggering 65% opposed to only 9% in the unburnt part, while for trees these figures stayed well below 20% under both conditions. It was noticed that increasing bark thickness for larger trees made them less vulnerable to fire (Swaine *et al.* 1997). There exists a risk that as for liana species composition with reoccurring fire events and repeated liana cutting we might end up with a liana cutting and fire resistant group of lianas while species vulnerable to fire and liana cutting might diminish to extremely low numbers. Liana mortality rates are high after events such as liana cutting and fire and the survivors resprout vigorously as was noticed in Cameroon and the Amazon (Pinard *et al.* 1999, Gerwing 2001, Parren and Bongers 2001) in which some liana genera showed considerably better survival rates than others (Parren and Bongers 2001).

Of interest to know are the long lasting effects of liana cutting which formed part of the refinement operations. 15 years after application of liana cutting only the drier La Téné forest shows considerable lower liana numbers after treatment (Fig. 4.2). The wetter Irobo forest and the transitional Mopri forest showed even higher liana numbers after liana cutting. Looking more in detail on the intensity of interventions the disastrous effect of a drastic canopy opening becomes apparent. During various visits to Mopri forest reserve by the first author, in 1987 and early 1992, it was striking to see that the heavily refined compartments showed a very open upper-

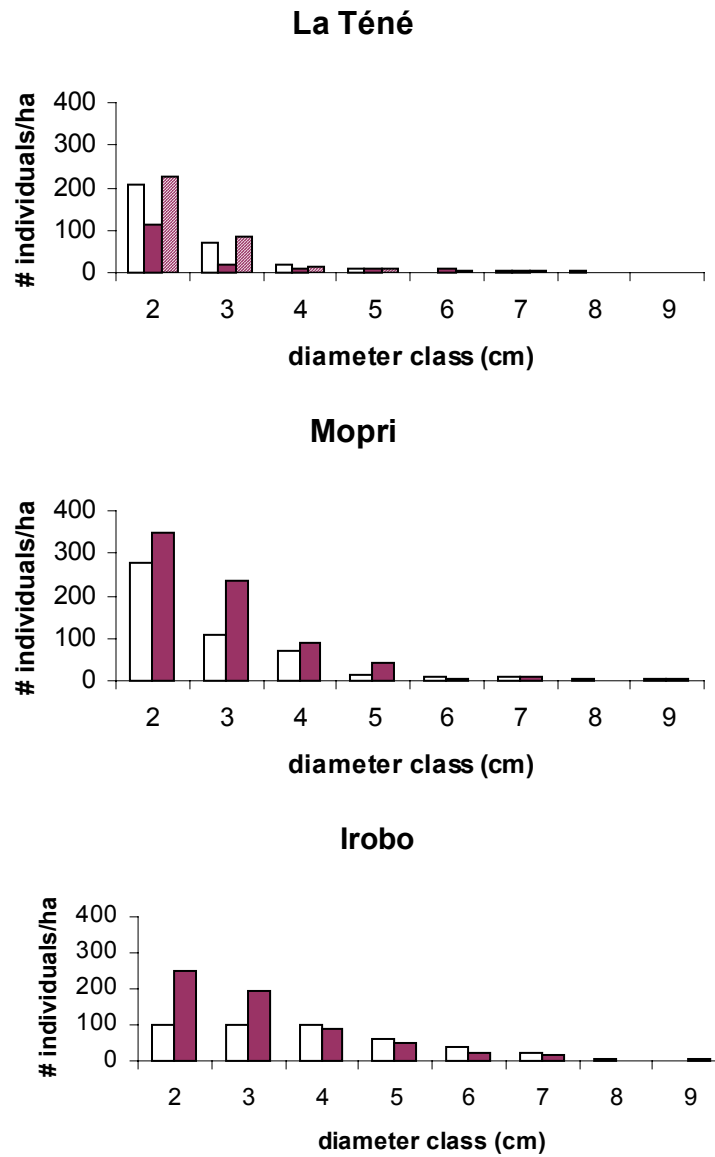


Figure 4.2. Liana diameter distribution (diameter class 2-9 cm) in 1993 at la Téné, Mopri and Irobo in Côte d'Ivoire. Control plots (white bar) and logged-over plots (striped bar) were not subjected to liana cutting while in refined plots (black bar) liana cutting was applied in 1978.

storey and hardly any tree regeneration. Few trees in the 10-20 cm drh class were present and a blanket of herbs (e.g. Marantaceae) and lianas covered large areas and appeared to be hard for tree seedlings to escape. The same phenomenon was observed by Brncic (2003) in the Central African Republic and in Gabon by White (2001) where some 17% of all trees smaller than 10 m in height were covered in dense climber towers, often killing the host tree. The stand density of 12.4 m²ha⁻¹ after the heavy refinement - a more than 50% reduction of basal area as compared

with stand data from unlogged nearby Divo botanical reserve- seems to be too low for the tree strata to fully dominate the ecosystem. The open structure in the Mopri plots, with the return to a normal closed forest structure obviously blocked by some internal cause, may be seen as a warning against heavy refining in this type of forest. So not surprisingly the moderate refinement showed the best response of commercial species. Logged-over plots showed better growth performance than control plots, but less good than the one provoked by the moderate refinement (Maître 1986a). So high liana densities in the refined Mopri and Irobo forest might indicate seriously disturbed forest. Repeated timber exploitation at short intervals with additional refinements could have lead to basal areas dropping below $15 \text{ m}^2\text{ha}^{-1}$ and cause liana mats and tangles to dominate the tree strata. These forests have been repeatedly logged over short timespans showing a very broken canopy cover of low stature and with abundant *Chomolaena odorata* present. This phenomenon was also found in Ghana and Borneo since the combined effect of logging and fire greatly enhanced invasive grasses, Marantaceae and Zingiberaceae forbes as well as liana proliferation (Hawthorne 1994, Swaine 1992, Woods 1989).

4.4.3 The Yapo project

The silvicultural interventions of the three pilot projects were evaluated to be beneficial: timber productivity of logged-over forests was increased. This prompted the European Union to fund a project in 1983 to upscale the trials to encompass a block of 7,000 ha in the evergreen Yapo forest reserve. Similar ecological and environmental conditions as in Irobo are found here. The last exploitation was in 1982, before treatments commenced (Cabrera Gaillard 1988). In total 27 compartments each 250 ha in size were installed. Silvicultural treatments consisted of poison girdling as practised in the earlier experiments, to reach a uniform basal area reduction of 30% by felling and refinement, the uniform killing of all trees of non-commercial species $\geq 30 \text{ cm drh}$. However, this time liana cutting did not form part of standard procedures (M'Bla and Diahuissie 1993). Sixteen 4-ha permanent sample plots (PSP) were selected for a detailed study with 4 untreated control plots and 12 treated plots in which all trees $\geq 10 \text{ cm drh}$ were measured. Most interesting a liana cutting experiment was set up in 8 out of 16 PSP in 1992. Each 4-ha plot was likewise split up in a northern half in which all lianas were cut during January 1993 and a southern half with no climber cutting. At the centre of each 1-ha subplot regeneration of trees and lianas in the diameter class between 2 and 10 cm drh was measured in a plot measuring 5 x 20 m. These regeneration plots were measured in 1992 (pre-liana cutting), 1995 and 1997 (post-liana cutting).

The liana cutting operation had a major impact on liana populations since the average number of individuals per ha was reduced by more than half as liana numbers dwindled down from c. 450 lianas to around 200 lianas per ha (Fig. 4.3a-c). This trend is confirmed by a remeasurement of an entire 4-ha PSP executed by us in 2001 where liana density in the untreated southern half averaged c. 400 lianas per ha while in the treated northern half the density averaged only c. 175 lianas per ha (Fig. 4.3d). Looking at the impact of liana cutting on the size distribution of lianas present, major changes were noticed for lianas $\geq 3 \text{ cm drh}$ as they are almost absent 2 years after climber cutting (4.3b) and only a gradual ingrowth in the 3 cm diameter

class can be seen 2 years later (4.3c). Not surprisingly large lianas (≥ 5 cm drh) were mainly confined to the untreated half of the plots.

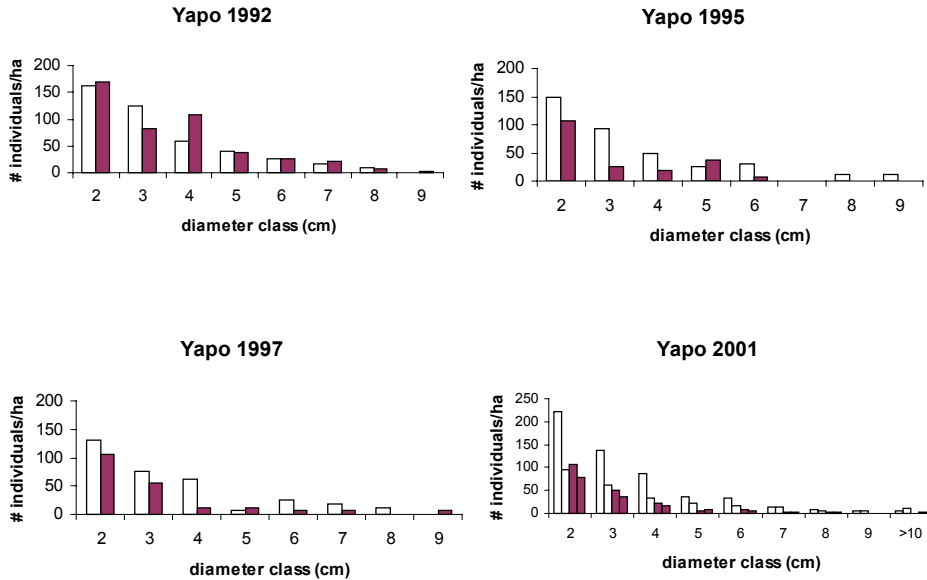


Figure 4.3. Development of lianas (diameter class 2-9 cm) in eight 4-ha PSP (a-c). Liana cutting was only applied in 1993 in the northern half of a 4-ha PSP. In each PSP two 0.01 ha (5 x 20 m) plots were installed in the part with liana cutting and two in the half without liana cutting. Measurements were taken in 1992 (a), 1995 (b), 1997 (c), and in 2001 (d). The 2001 (d) liana (≥ 2 cm dbh) inventory was not limited to the four 0.04 ha plots but encompassed the entire 4-ha of PSP 1. Control (white bar) subplots no liana cutting took place and treated (black bar) subplots were subjected to liana cutting. For (a) – (c) total number of lianas encountered in control and treated subplots for the eight PSPs (0.16 ha) were extrapolated to density per ha, for (d) the individual 1-ha subplots are presented.

4.4.4 Evaluation of the silvicultural experiments

Silvicultural interferences such as refinement and liberation thinning seem to improve the stocking with commercial timber species and provide higher increment rates (Parren and de Graaf 1995). Liana cutting often formed part of these silvicultural interventions. It was believed that these interventions would reduce liana numbers in the forest and such liana control would speed up the regeneration and crown development of commercial tree species. Although initially liana numbers drop drastically it looks, even after fire swept through some of these forests, that the plasticity exists to restore to almost initial densities within 10 years for most deciduous forests. However, it looks like a shift in species composition can be seen in favour of species that benefit by disturbance regimes. So total numbers might be equal but liana diversity might be reduced. Most unfortunate the studies available do not allow for proper conclusions since the timespan and space was too limited. On the other hand drastic openings by basal area reductions to less than 50% of the unlogged original remaining might lead to the forest ecosystem getting out of balance. Here it could be seen that lianas and other herbaceous species proliferate

and obstruct the succession for decades such as is seen in the semi-deciduous Mopri forest. This can lead to forest types often associated with recurring fires which are typically named Marantaceae forest and already occupy c. 30% of the Ghanaian moist forest formations (Swaine 1992, Hawthorne 1994). In wet evergreen forest such as the Yapo forest liana densities seem not to restore to original numbers after a decade in contrast to the similarly evergreen Irobo forest. So this leaves still many question marks and points to the need to compare similar types of forests and monitoring over longer time periods.

4.5. FOREST RESTORATION BASED ON A 'MODEL' FOREST

To reverse the deforestation trend at the end of the 20th Century (Fairhead and Leach 1998) several reserves were designated to be rehabilitated in co-operation with the private sector and international institutions. In the early 1990s two demonstration 'model' forest projects were selected in the moist semi-deciduous forest zone for rehabilitation at an intensive level: the FC Haut Sassandra in west Côte d'Ivoire and the FC Bossematié in east Côte d'Ivoire.

The Bossematié project Like most other forest reserves in the region, the FC Bossematié encompassing 22,400 ha has been selectively logged 5 to 6 times from the early 1960s until 1988. The forest was overexploited and, in part, seriously damaged with low canopy cover showing liana tangles (Lennertz 1993). However, the Bossematié forest had an abundance of regeneration of commercial species. The stocking of PCTs were found to be adequate too, implying that over 30 individuals per ha of the most wanted commercial species in the 20-50 cm diameter class were present. Some 90% of the Potential Crop Trees (PCT) were either suppressed by surrounding trees or had been infested by lianas. The latter is not so surprising, since a liana tangle was also encountered in the Ghanaian Tropical Shelterwood System, characterised as being drastically opened forest.

Since the stocking of PCTs was found to be adequate treatments were confined to liberation thinning. Since 1991 a mild liberation operation, killing on an average 1.5 m²ha⁻¹ or approximately 10% of the total basal area, and mainly of the pioneer species *Musanga cecropioides* combined with liana cutting, was applied over one fifth of the reserve. The first results showed a twice as high growth rate for liberated PCTs compared with unreleased ones, 0.7-1.1 versus 0.5-0.7 cm/yr with most favourable results for individuals in the 20-30 cm drh class (Fickinger 1995). This shows that these simple interventions are promising. Other forest parts had sufficient regeneration in the 5-20 cm diameter class ($N > 125 \text{ ha}^{-1}$) but insufficient PCTs and it was decided to wait with interventions while enrichment planting was executed at impoverished areas (areas with a poor stock of PCT and/or former farmland) especially at the farm-infested boundary sites of the reserve.

Next to the rehabilitation of a closed canopy cover, total biomass and increased commercial stock in these overexploited forests it was found that hunting activities for so-called 'bushmeat' had brought several mammal species important as seed dispersal agents to the brink of extinction. Corrective measures were taken to halt these indiscriminate hunting practices while at the same time measures were taken to

National standards The Mopri, Irobo, Téné, Yapo and Bossematié experiences evolved in the formulation of procedures for liberation thinning to be applied at a national level (Fickinger 1995, SODEFOR 1996).

The three main activities are as follows:

- ◆ line cutting at 50 m intervals for better orientation,
- ◆ selection of PCTs to be freed of lianas and marked with a cross by paint and
- ◆ finally the removal of around 2 to 3 competitors of these PCTs.

Competitors of PCTs smaller than 40 cm drh are just bark ringed, while large trees over 40 cm drh and those with buttresses are just partly ringed with additionally a few millilitre of arboricides applied. Within a 50 m band two tree spotters mark PCTs and trees to be removed and cut lianas attached to the PCTs (Fig. 4.4). Two forest workers who execute the girdling closely follow this team. However, arboricides are not applied during the rainy season.

Ecological restrictions in relation to PCT selection apply for 48 tree species who are not to be removed in any liberation thinning operation:

- ◆ 24 fauna species either important as food source, like *Tieghemella heckelii*, or fauna dependent for their dispersal, like *Balanites wilsoniana*;
- ◆ 10 endangered species caused by over-exploitation and forest fragmentation;
- ◆ 12 recently discovered species for Côte d'Ivoire and as such believed to be rare;
- ◆ 12 species who seem not to respond favourable on liberation thinning and are neither to be selected as PCTs.

Finally there is a difference in commercial stocking between evergreen and semi-deciduous forest. Since the former is poorer, at least 40 commercial trees per ha of the 5-40 cm drh class have to be present, while the drier forest should hold at least 60 commercial trees per ha of this diameter class.



Figure 4.4. Marking of potential crop trees and liana cutting forming part of a liberation thinning operation in Côte d'Ivoire. Girdling of the following trees (1) all trees towering over the PCT, (2) all trees restricting crown development of the PCT at lateral position, (3) all trees that scratch the stem of the PCT and cause bark damage and (4) liana cutting.

protect several tree species important as a food source or species which for their dispersal were highly dependent on certain fauna elements (see Box).

The Haut Sassandra project To study the logging impact on the natural regeneration three transects 3 km long and 50 m broad oriented east-west were established. Each three km transect was sub-divided in 1 km stretches of which the 2 km to the west were logged while the remaining 1 km stretch to the east remained unlogged. Liana abundance did not differ much after logging. The logged part showed on average 198 lianas per ha versus 167 lianas per ha for the other part, while at both sides of the transects around 2000 trees per ha were counted. However, the diameter distribution revealed differences (Fig. 4.5). Contrary to expectations less lianas were seen in the 2 cm diameter class in the logged forest compared to the untouched forest although average numbers were slightly higher in almost all other classes after logging. Big lianas were even absent in the 7 and 9 cm diameter class for the untouched forest while present in the logged one. This leaves us with a confused picture, as logging would seem to favour large lianas.

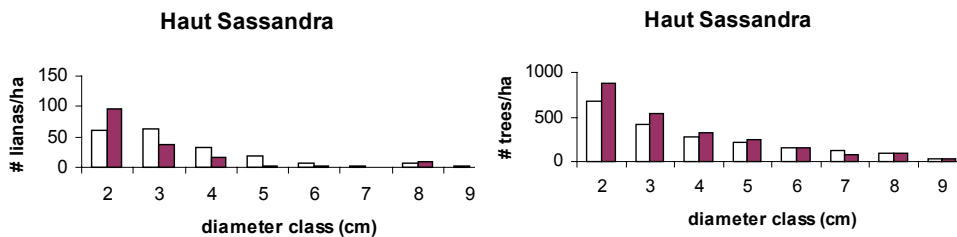


Figure 4.5 Liana (A) and tree (B) diameter distribution (diameter class 2-9 cm) in logged (white bar) and unlogged (black bar) forest in Haut Sassandra, Côte d'Ivoire. The inventoried logged surface encompassed 30 ha (three transects of 50 x 2000 m) while the unlogged surface encompassed 15 ha (three transects of 50 x 1000 m). The transects are 500 m apart, while each unlogged transect (western section) is continuous with a logged one (eastern section).

4.6. DISCUSSION

West African forests have a long logging history and several silvicultural schemes have been tried out over time in this region. Most of these forests have been repeatedly logged over short felling cycles leading to a substantial loss in biomass and accordingly have given rise to a very open forest structure often aggravated by fires which penetrated them occasionally. An additional feature of these forests is that they are rather small and fragmented giving rise to an increased boundary to surface ratio leading to a number of edge effects (see Laurance 1997, *et al.* 2000, *et al.* 2002). It can be expected that liana abundance increases significantly near forest edges and increases with higher disturbance regimes and decreases with better-structured forest (Laurance *et al.* 2001). We saw that lianas are quite abundant in the West African forests although tree infestation by lianas is relatively low compared with forests in other continents. This is in contrast with what we expect from these West African forests which have repeatedly been disturbed. The few West African examples provided are mostly from well-structured and sometimes unlogged forests.

So this is merely reflecting the past situation, of natural dynamics of late secondary unlogged forests with abundant and many large lianas present. The picture will most likely change when more liana inventories will be available in future. This is already confirmed by Kokou *et al.* (2002) for 53 forest fragments in southern Togo varying in size from 1 ha to 3658 ha. Almost all forest fragments had relatively closed lower strata that impeded human penetration with a quarter of the lianas inventoried growing along the ground and very few (9%) lianas were large and up in the canopy of trees greater than 8 m in height. Most climbing plants were herbaceous and climbing shrubs and not lianas (woody climbing plants), indicating relatively low forest stature and having an irregular canopy. The silvicultural experiments as applied at Mopri forest show the same problems with lianas interfering or even blocking the development of tree regeneration. A critical basal area under-limit, below which stand development is seriously delayed, seems to be $15 \text{ m}^2\text{ha}^{-1}$ for these West African forests. This is about half of unlogged late secondary forests. This suggests that any interference should not create more open conditions. However, this is something, which still has to be tested experimentally.

Forest fires and liana cutting interventions both seem to have a long lasting effect on the liana populations in fragmented forests. Frequently occurring forest fires diminish liana numbers on the short term, although with time they restore to original numbers as was seen at the La Téné forest. This is confirmed by the post-fire findings of Gerwing (2001) in the Brazilian Amazon where he noticed a steep reduction in liana stems just after the fires but restoring to the old figures later on. Cochrane and Schulze (1999) and Pinard *et al.* (1999) noticed especially a steep reduction in large lianas after fire in the Amazon. At first the liana population looks quite healthy as stumps resprout vigorously immediately after liana cutting. However, on the longer term the numbers do not matter but the species diversity. With time you can see a shift in species composition most likely eliminating species vulnerable to fire and/or liana cutting, a shift in favour of shade-tolerant species. In Bolivia Kennard *et al.* (2002) found that after burning just 10% of all seedlings and sprouts consisted of lianas. Most striking was that regeneration of lianas in high-intensity burning was mostly from seed and not sprouts. More studies will have to be conducted in which the character (strategy; temperament) of the liana species is investigated, as well as their abundance and composition before and after treatment.

A restoration of biomass and crown cover will be essential for the well being of all Ivorian closed moist forests. National production targets should be set at a minimum and not at a maximum as they are at present. A production halt such as that in FC Bossematié is probably a necessity to restore the forest ecosystem and a conservative production target for the next felling cycle may be the best option. Forest management should aim at facilitating the future production potential by guarantying that sufficient numbers of PCTs would be present. Finegan *et al.* (1999) noticed that not only liana coverage influenced diameter increments but also silvicultural treatments that allow more growing space. Development of PCTs benefit from logging activities, but if found to be insufficient, additional liberation thinning should be applied with liana cutting in case of liana hindrance. That such interventions are beneficial we saw at the Bossematié forest where the mean diameter increment almost doubled. This is in accordance with findings by Gerwing (2001) in the Amazon where PCTs responded similar after liana cutting. Also here

we have to be careful with liana cutting since, although lianas resprout vigorously and might restore to their original stem levels, we might find ourselves left with only liana cutting resistant species (Parren and Bongers 2001). It looks like lianas will play a more prominent role in West African forest dynamics the coming decades since disturbance regimes will be more intensive and frequent. So it will be a challenge to study the interface of forest management consisting of logging and silvicultural treatments sometimes combined with fires on the one hand and liana behaviour of which we have scant knowledge on the other hand.

5. ABUNDANCE AND DISTRIBUTION OF LIANAS AND RATTANS IN A LOWLAND TROPICAL RAIN FOREST IN SOUTHERN CAMEROON

5.1. INTRODUCTION

Woody climbers are a prominent feature in most tropical forests. However, in many forest inventories during the last decades lianas are ignored (e.g. Dallmeier and Comiskey 1998a,b), in contrast with some early botanical collection studies where herbs, shrubs and climbers received full attention while trees were almost entirely ignored (Mayer 1951, Voorhoeve 1965). The overall low attention to lianas is most probably due to their low macro-economic importance. Even though some liana species attracted some special attention such as *Landolphia spp.* as a source of wild rubber in West- and Central Africa (Bourret 1949, Sutton 1983) or *Strophanthus spp.* in Liberia (Baldwin, cited in Voorhoeve 1965) and *Ancistrocladus korupensis* in Cameroon (Thomas *et al.* 1994, Foster and Sork 1997) for medicinal use. Also, difficulties in delimiting individuals (Parren *et al.* in review), overall lower minimum size limit in enumerations (often 10 cm diameter at breast height), and general lack of taxonomic studies resulted in exclusion of lianas in many inventories. More recently, lianas have been included in some systematic sampling programmes (e.g. Hubbell and Foster 1983, Hawthorne 1996, Makana *et al.* 1998).

Lianas add significantly to vascular plant species diversity as their contribution to species richness ranges from 12% in Puerto Rico (Smith 1970) to 31% in Ghana (Hall and Swaine 1981). Lianas make up 2 to 7 % of total woody biomass, but as much as 6 to 36% of the total leaf biomass (Caballé 1986b). Rattans are climbing palms and are thus considered as lianas as well. They vary in growth form as some species occur as solitary stems whilst others produce clumps of stems. In contrast to S.E. Asian and Latin American forests, palms are not very conspicuous in African forests (Dransfield 1978).

In general, ecological information on lianas and rattans is scarce. Abundance and spatial distribution patterns can give an impression of habitat requirements, past events and ecological processes. African moist forests are relatively species-poor when compared with Neotropical and Australasian moist forests. Palms, bamboos, ferns, and epiphytes are not abundant in African forests, but lianas however, are quite common (Reitsma 1988, Gentry 1991). Regional distribution of lianas is strongly related to overall forest type and forest location (Grubb 1987). White (1978) suggested that lianas are less common in the Afromontane forests than in the lowland Guineo-Congolian forests. This is confirmed by Gentry (1992) who showed that the most liana-rich forests on the African continent are in the wetter areas of west Central Africa, from near the base of Mt. Cameroon southeast into Gabon.

The spatial plant distribution pattern affects future processes, both of plants themselves and of a range of other organisms with which they interact. Successional processes result in a mosaic of patches (cf. Aubréville 1938, Watt 1947) and the size and spacing of those patches are important characteristics of the vegetation (Dale 1999). Morphological factors, based on the size and growth pattern of the plants,

which for lianas are atypical, influence spatial patterns next to environmental and phyto-sociological factors.

In South Cameroon we inventoried trees and lianas in 33 1-ha plots of lowland rain forest, within the framework of a study on ecological effects of logging and improved logging techniques. In this paper we focus on the lianas and report on liana abundance, and on size distributions and spatial distribution patterns of (selected) liana and rattan species.

5.2. STUDY SITE

This study was conducted in a logging concession 100 km east of Kribi, Cameroon (3°N, 10°E). The concession area covers about 2,000 km². The study area was located in the north-eastern part near the village Ebom at the Minwo catchment area, in a part that never had been commercially logged before. The mean annual rainfall is 2000 mm with two distinct wet seasons (March – May and August – November), associated with the movement of the intertropical convergence zone over the area (Waterloo *et al.* 1997). The study area is located on a Pre-Cambrian shield resulting in clayey soils and classified as a Xanthic or Plinthic Ferralsol. The topography ranges from undulating to rolling with isolated hills with elevations between 350 m and 600 m a.s.l. (Waterloo *et al.* 1997). The forests of the area are evergreen and can be characterised as late secondary forests of the Biafrian type (*sensu* Letouzey 1968) with a more or less closed canopy layer between 25-40 m with emergent trees 50-55 m in height towering above. Climbers are abundant in the canopy and in gaps where light conditions are favourable to their growth. The omnipresence of the tree species *Pycnanthus angolensis* (Myristicaceae) and *Lophira alata* (Ochnaceae) indicates that the forest has been quite degraded, probably by human activities in the past (see also Letouzey 1968 p. 153).

5.3. METHODS

Plot selection and layout. Research plots 1 ha in size were located in more or less flat terrain avoiding sites with aberrant conditions such as sites with a steep slope, rock outcrops, riversides and valley bottoms. In total 33 plots were established, arranged in a stratified design, in a 500-ha block of forest. In principle each plot had an 8-ha bufferzone allowing for a minimum distance between plots of at least 200 m at each side. This design was chosen to enable the evaluation of silvicultural treatments such as an experiment with climber cutting (see Parren and Bongers 2001).

Liana and rattan abundance. We determined liana abundance in the study area by counting all lianas in 33 1-ha plots. All liana stems ≥ 2 cm in diameter cutting through the imaginary surface at breast height were counted in subplots of 10 x 10 m and their exact positions and dbh was measured. Lianas < 2 cm dbh were only counted in these subplots. We investigated whether liana density was related to tree density. All trees with a diameter at reference height (drh), i.e. at breast height (1.3 m) or 30 cm above buttresses, of over 10 cm were counted and their drh measured. For 32 of the 33 plots we determined the rattan abundance. The total number of stems was counted for each morphospecies per 10 x 10 m subplot. Based on these

data, clumps were located for each morphospecies. The dominant rattan genera *Laccosperma* and *Eremospatha* that form clumps and make up the bulk of the rattans present in our research area were investigated in more detail.

Size distribution. In many inventories the dbh of liana stems are measured and a lower dbh limit is used to include or exclude an individual. In most studies lower dbh limits of 10, 5, 2.5, 2 or 1 cm are used (Parren *et al.* in review). The lower minimum sizes are often very important for the relative dominance of different liana families. Since in our silvicultural experiment we were mainly interested in woody lianas we opted for a lower size cut-off limit at 2 cm for all lianas. In case of irregularly shaped liana stems the diameter was based on both minimum and maximum diameter measurements at breast height. This diameter was then used for liana basal area calculations. Smaller lianas reaching up to breast height were just counted. As the number of very large lianas in an unlogged forest is seen as an indicator of the maturity of the forest (Gardette 1998) we additionally calculated the contribution of large and very large lianas, respectively at the 5 and 10 cm cut-off limits.

Spatial patterns. Spatial patterns of lianas (≥ 2 cm dbh) were described at two spatial levels based on quadrat counts. Over a wide area of 500 ha a sample of 33 1-ha plots is used to determine whether lianas and rattans as a lifeform have a clumped, a random, or a uniform distribution. Over the same area, the distribution of selected liana species (i.e. *Cissus dinklagei*, *Manniophyton fulvum*, *Strophanthus spp.*, *Tetracera alnifolia*) were described based on 26 1-ha plots while the distribution of rattan species (i.e. *Eremospatha spp.*, *Laccosperma spp.*) were described based on 32 1-ha plots.

At a smaller spatial scale, we determined the distribution patterns of the above mentioned liana and rattan species within the 1-ha plots. This was only tested for those hectares with more than ten stems of a particular species present. Within these 1-ha plots we analysed the distribution using quadrats of 0.01 ha following Synnott's (1979) recommendations for plot shape and size.

Spatial distribution patterns were determined using the Morisita index of dispersion (Morisita 1959, 1962; later improved by Smith-Gill 1975). The null hypothesis of random distribution of individuals over plots is tested by comparing the actual distribution with a chi-square distribution. The Morisita's index of dispersion (I_δ) is relatively independent of population density and sample size and can range from 0 to the total number of quadrats.

Smith-Gill (1975) developed the standardised Morisita index of dispersion (I_p) that ranges from -1 to $+1$, and can best be considered as a test statistic (Hurlbert 1990). An I_p of zero indicates a random pattern, an I_p above zero indicates a clumped pattern and an I_p below zero indicates an uniform pattern, with 95% confidence limits at $+0.5$ and -0.5 .

5.4. RESULTS

Liana and rattan abundance. Lianas are very abundant in the area (Table 5.1). In 33 1-ha plots a total of 13,458 liana stems (≥ 2 cm) were measured encompassing all liana species. On average, 408 lianas ≥ 2 cm dbh and 4370 smaller ones were found per ha. The abundance varied considerably, however: both large and small lianas showed roughly a factor 5 between the lowest and the highest density. Really large lianas were quite common as well, as on average 113 lianas ≥ 5 cm dbh and 10 lianas ≥ 10 cm dbh were present (Table 5.1).

Table 5.1 Liana and rattan abundance in 1-ha plots, for 33 liana and 32 rattan plots, Ebom

	Mean	SD	MIN	MAX
Lianas				
< 2 cm	4370	2264	1870	10451
≥ 2 cm	408	200	187	1092
≥ 5 cm	113	58	39	293
≥ 10 cm	10	6	1	25
Rattans				
Stems	184	245	6	1137
Clumps	6	5	1	21

Also for selected species the spatial variation in abundance at the 500 ha scale was high. *Cissus dinklagei* is a common species in the 26 1-ha plots with 16 plots represented with more than 10 individuals (Figure 5.1A). The other three species were rarely encountered as often. *Cissus dinklagei* was the only species encountered in all 26 1-ha plots while *Manniophyton fulvum* and *Tetracera alnifolia* were both completely absent in 8 plots or more.

The rattans in the 32 ha comprised 201 clumps (6 clumps ha⁻¹) and a total of 5881 stems (184 stems ha⁻¹). Rattan clumps were encountered in all 1-ha plots. Rattan presence in a plot could be formed by clumps of a single species such as was often seen for the most common genera *Eremospatha spp.* and *Laccosperma spp.* In other plots multiple clumps were present by a mixture of morphospecies. In a single 1-ha plot even 21 clumps of more than one species could be found (Figure 5.1B). Abundance of *Eremospatha spp.* (3868 stems) was twice as high as *Laccosperma spp.* (1951 stems). *Eremospatha spp.* averaged 3.7 clumps per ha (SD 2.8, max 14 clumps per ha and max 225 stems per clump). *Eremospatha spp.* were absent in just 2 plots. *Laccosperma spp.* had on average 3.4 clumps per ha (SD 2.6, max 10 clumps per ha and max 236 stems per clump). *Laccosperma spp.* was absent in 6 plots and present but not forming clumps, i.e. growing as solitary ramets, in 8 plots (Figure 5.1B). Three taxonomically unidentified rattan morphospecies were relatively rare. Two of these were each recorded in a single plot (one had only a single stem, the other had two closely located stems), while the third was recorded having a total of 59 stems in four different plots forming 7 clumps (Figure 5.1B).

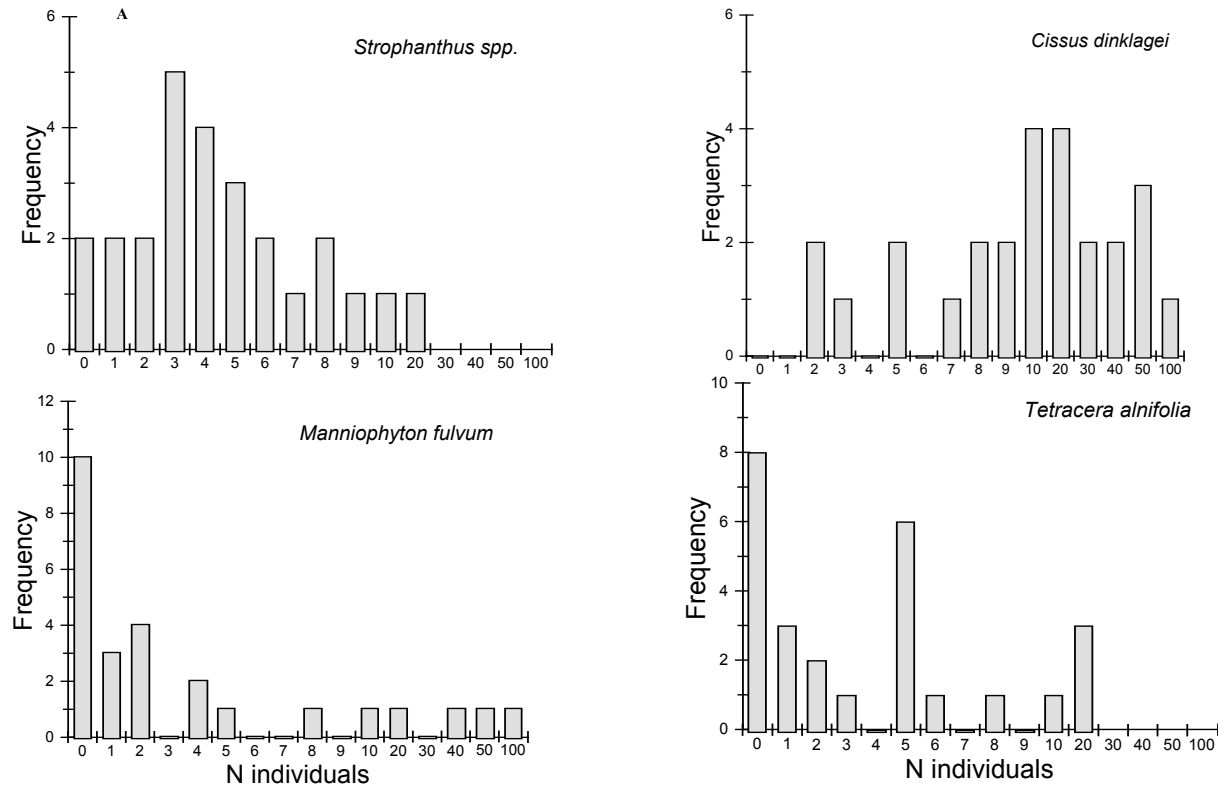


Figure 5.1. (A) Frequency distribution of the abundance of the liana species *Cissus dinklagei*, *Manniophyton fulvum*, *Tetracera alnifolia* and *Strophanthus spp.* in 1-ha plots (N = 26). Abundances are grouped into classes: class 0 = 0 individuals, class 1 to class 9 = 1 to 9 individuals, class 10 = 10-19 individuals, class 20 = 20-29 individuals, class 30 = 30-39 individuals, class 40 = 40-49 individuals, class 50 = 50-99 individuals, class 100 = 100 or more individuals.

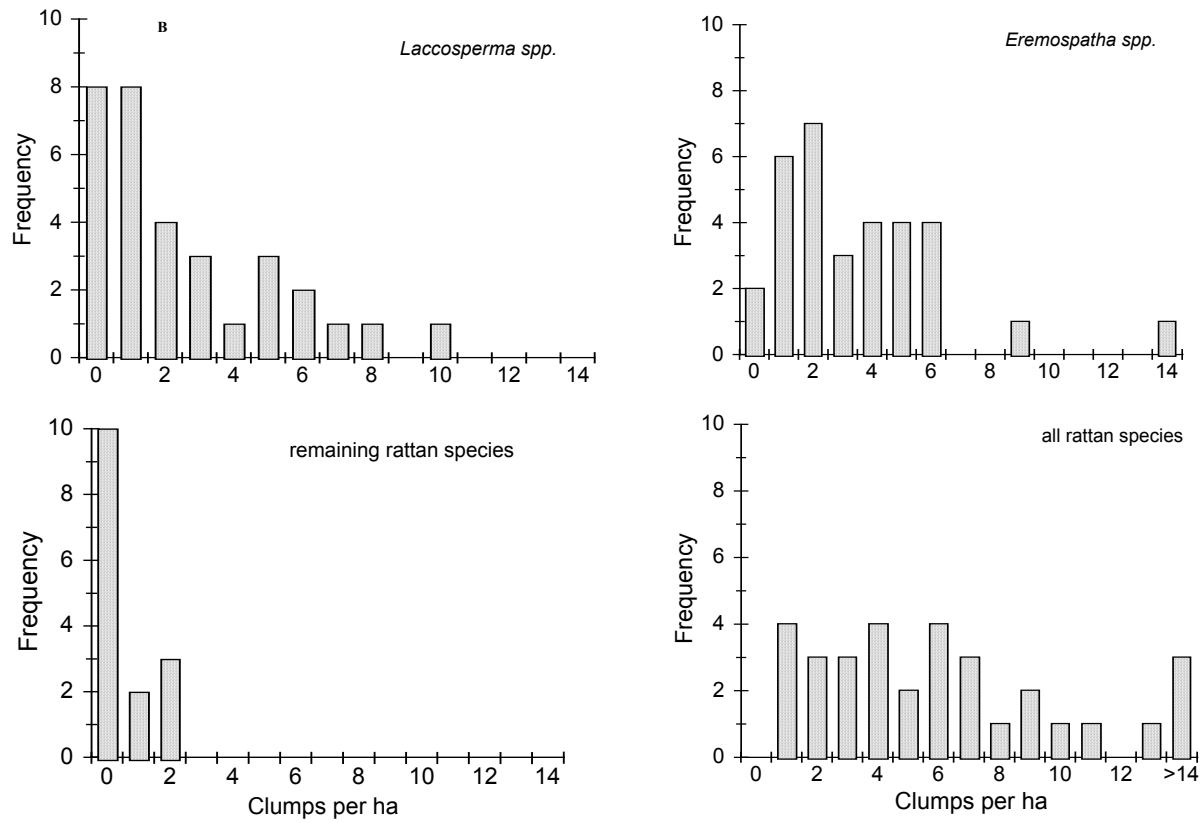


Figure 5.1. (B) Frequency distribution of the abundance of clumps of rattans consisting of five different Bulu names per 1-ha plot (N = 32): the most common genera (a) *Laccosperma spp.* and (b) *Eremospatha spp.*, (c) the remaining rattan species and (d) all rattan species together.

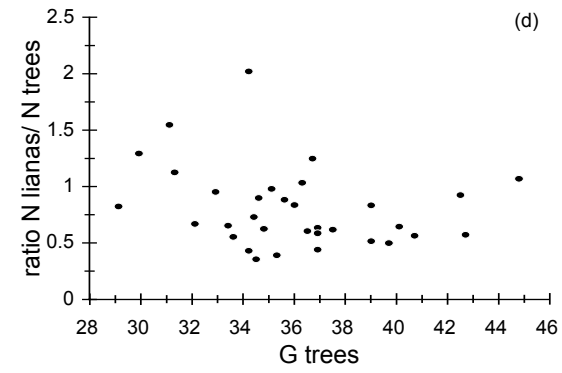
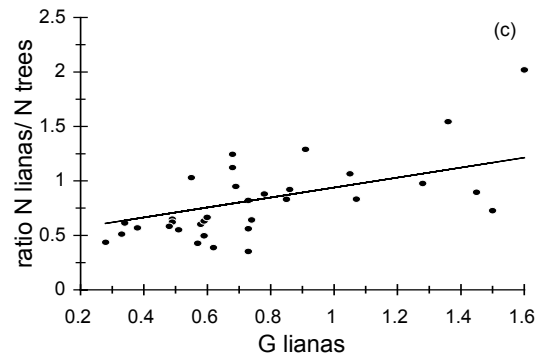
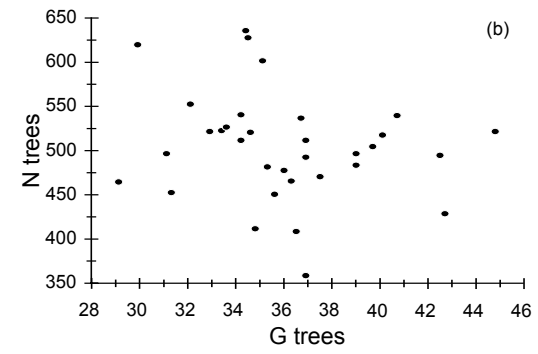
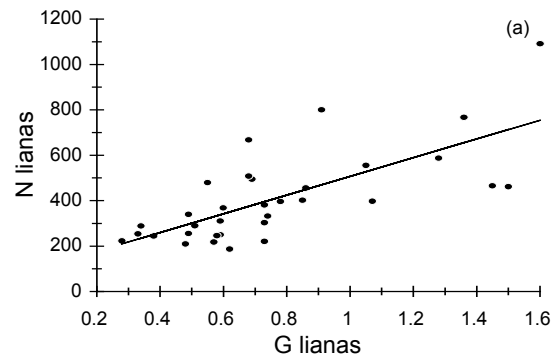


Figure 5.2. Relation between total number (N) and basal area (G in m^2) of lianas (≥ 2 cm dbh) and trees (≥ 10 cm dbh) and the ratio of number of lianas and trees in 33 1-ha plots, in the Minwo catchment area. Note that axes do not always start at zero.

The basal area of lianas (excluding rattans) ≥ 2 cm dbh varied between 0.3 and 1.6 $\text{m}^2 \text{ha}^{-1}$ while that of trees ≥ 10 cm dbh varied between 29.1 and 44.8 $\text{m}^2 \text{ha}^{-1}$. As expected there is a linear relationship between the number of lianas ≥ 2 cm dbh and their total basal area (Figure 5.2a; number of lianas = $94 + 412.8 \times$ basal area lianas, $r^2 = 0.51$, $P < 0.0001$). Such a linear relationship does not exist for trees (Figure 5.2b). The ratio of numbers of lianas and trees was positively related to liana basal areas (Figure 5.2c; ratio of numbers of lianas and trees = $0.29 + 0.68 \times$ basal area lianas, $r^2 = 0.44$, $P < 0.0001$) but not to tree basal area (Figure 5.2d). At tree basal areas over 35 $\text{m}^2 \text{ha}^{-1}$ the ratio oscillates around 1 and can be considered to be more or less constant. The lower tree basal areas ($< 35 \text{m}^2 \text{ha}^{-1}$) show much more variation: the lianas sometimes even outnumbered trees.

Size distribution. The diameter distribution of all liana individuals over 2 cm in 33 1-ha plots for all species showed an inversed J shape (Figure 5.3). In total 344 individuals had a diameter larger than 10 cm dbh, of which 26 in the 20-30 cm dbh class, 12 in the 30-40 cm dbh class, just one in the 40-50 diameter class and even three individuals larger than 50 cm dbh were present. The largest individual had a diameter of 56 cm. A similar distribution pattern was seen in 26 1-ha plots for *Manniophyton fulvum* (max 11 cm), *Cissus dinklagei* (max 31 cm) and *Strophanthus spp.* (max 9 cm) except for the lowest diameter class which is rather underrepresented for the latter two taxa. However, *Tetracera alnifolia* (max 23 cm) did not show this distribution pattern.

Spatial patterns. Lianas have a clumped distribution over an area of 500 ha: the Morisita index (I_δ) for this total number of lianas (at the 1 ha scale) is 1.2315 (with $I_p \geq 0.5$, $p \leq 0.05$). At the same large spatial scale the selected liana species also all showed clumped distributions: *Cissus dinklagei* has an I_δ of 6.853, *Manniophyton fulvum* an I_δ of 2.032, *Tetracera alnifolia* an I_δ of 2.927 and *Strophanthus spp.* an I_δ of 1.870 (all four $I_p \geq 0.5$, $p \leq 0.05$, Appendix 1). Also the selected rattan genera have clumped distributions over the 500 ha: *Eremospatha spp.* had a Morisita index (I_δ) of 3.345 and *Laccosperma spp.* an I_δ of 4.416 (both $I_p \geq 0.5$, $p \leq 0.05$, Appendix 1).

The analyses of more fine-scaled dispersion patterns within the 1-ha plots show the same results (Appendix 1). Within all 33 1-ha plots all lianas together have a clumped distribution. In all plots where the studied liana (morpho)species had ≥ 10 individuals their distributions were clumped ($I_p \geq 0.5$, $p \leq 0.05$) at the 0.01 ha scale (Appendix 1). The Morisita index (I_δ) varied between 2.283 and 15.789 for *Cissus dinklagei* ($N = 16$), between 3.950 and 47.619 for *Manniophyton fulvum* ($N = 5$), between 12.987 and 20.9 for *Tetracera alnifolia* ($N = 4$) and between 4.096 and 20.290 *Strophanthus spp.* ($N = 2$). Only in one case (*Cissus dinklagei* in plot 20) the distribution was apparently random ($I_\delta = 1.818$ and $I_p = 0.139$, $p \geq 0.05$; Fig. 5.4D). Also the two rattan genera show a clumped distribution ($I_p \geq 0.5$, $p \leq 0.05$) at a 0.01 scale in all plots where they were represented by ≥ 10 individuals. The values for *Eremospatha spp.* range from 7.095 to 94.646 ($N = 25$) and for *Laccosperma spp.* they range from 9.167 to 100 ($N = 20$). Since the Morisita index (I_δ), has a potential range up to 100 (N of quadrats), the maximum value for *Laccosperma spp.* indicates

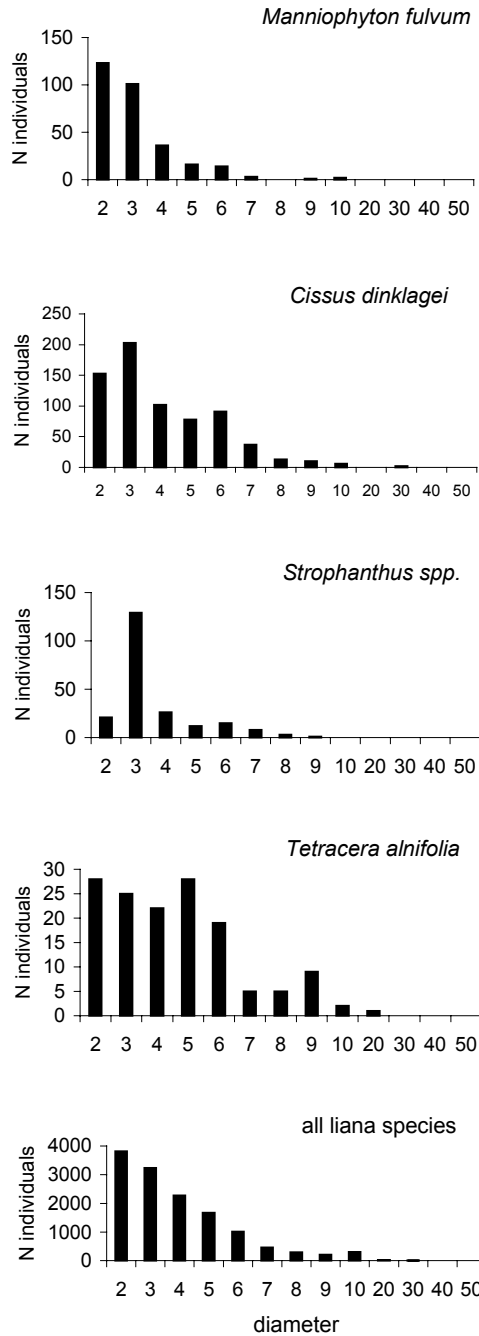


Figure 5.3. Diameter frequency distribution over 33 1-ha plots for all liana species together and for the liana species *Cissus dinklagei*, *Manniophyton fulvum*, *Tetracera alnifolia* and *Strophanthus spp.* (26 1-ha plots) separately. Diameter classes are per cm from 2 to 9 cm, and per 10 cm from 10 to 50 cm.

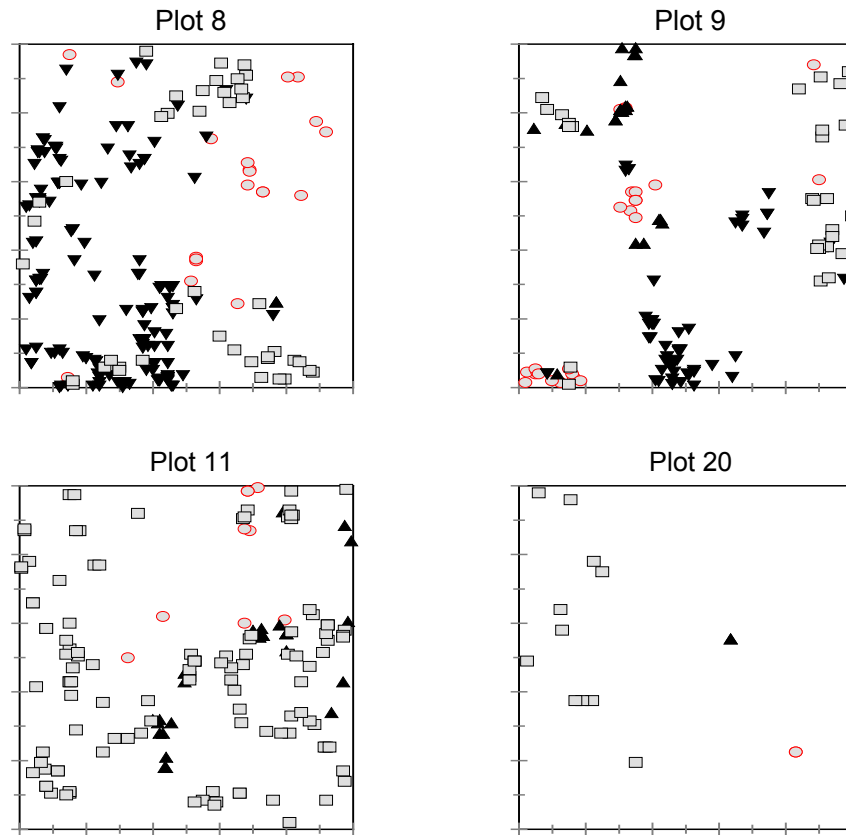


Figure 5.4. Liana stem maps of four selected 1-ha plots in the Minwo catchment area in southern Cameroon. Stems ≥ 2 cm dbh of the liana species *Cissus dinklagei* (\square), *Manniophyton fulvum* (∇), *Tetracera alnifolia* (Δ) and *Strophanthus spp.* (O) are presented.

optimal clumping which in this case is formed by the presence of one multiple stemmed clump of *Laccosperma* spp. in a single 0.01 ha subplot.

At the level of 1 ha there is a large variation in both abundance (see Table 5.1) and spatial distribution. As an example we show the distribution of four species (*Cissus dinklagei*, *Manniophyton fulvum*, *Tetracera alnifolia* and *Strophanthus* spp.) in four plots showing different patterns (Fig. 5.4, see also Appendix 1). Ranging from a plot where all four species studied have a highly clumped distribution (plot 9), to a plot where one species (*Cissus dinklagei*) is abundant (plot 11) but not clumped, while in plot 20 *Cissus dinklagei* is dominant with a random distribution ($I_\delta = 1.818$ and $I_p = 0.139$) while *Manniophyton fulvum* is absent and the other two species each represented by only one individual.

5.5. DISCUSSION

Abundance and size distribution of lianas. Compared to many other forest sites in the tropics (see Gentry 1991b, Hegarty and Caballé 1991) the forest studied shows abundant lianas, especially the number of small lianas. Many large liana stems of over 5 cm dbh (113 liana stems ha⁻¹) grow there but this is not exceptional compared to other continents (Figure 5.5, Appendix 2). Appanah and Putz (1984) in Pahang, Malaysia (13 ha inventoried) found equal numbers of liana stems ≥ 5 cm dbh in their forest compared to ours. In Para State, Brazil, Vidal *et al.* (1997) estimated that some 100 lianas ≥ 5 cm dbh per ha (only 0.42 ha inventoried) were present in mature forest. In a forest at Ituri, D.R. of Congo, Makana *et al.* (1998) found some 67 lianas ≥ 5 cm dbh per ha (3 ha inventoried), but in a monodominant forest type only 24 lianas ≥ 5 cm dbh per ha (3 ha inventoried) were found. That classifies these African forests even as poor concerning large lianas.

Rollet (1974) presented pan-tropical data for really large lianas of over 10 cm dbh in 27 1-ha plots (Figure 5.5). Latin America and Africa showed almost equal numbers of large lianas, nine plots in Latin-America showed on average 9 large lianas (range 3-20 stems ha⁻¹), seven plots on Africa had on average 9.4 large lianas (range 6-15 stems ha⁻¹) and ten plots in S.E. Asia had on average 5.6 large lianas (range 1-17 stems ha⁻¹). The latter indicates rather low presence of very large lianas in S.E. Asia compared to the other two major moist forest blocks. Our mean of 10 very large lianas (range 1-25 stems ha⁻¹) is in accordance with what Rollet found for other African moist forests. For S.E. Asian forest, Gardette (1998) showed equal numbers of very large lianas in unlogged forest but noted a drastic change in abundance of these lianas 40 years after logging when very large lianas were almost absent and a few families had markedly fewer individuals in the logged forest. These individuals are often animal dispersed and have a low reiteration potential. Since we worked in forests that had never been commercially logged before the impact of past disturbance has either been minor or taken place very long ago. Gardette's (1998) study area in S.E. Asia has a more intense logging history with up to 14 trees harvested per ha and volumes up to 150 m³ per ha (Webb 1997) as opposed to Cameroon where on average one tree was harvested per ha and a volume of 10 m³ per ha (G.J.R. van Leersum pers. comm.). We conclude that this type of logging

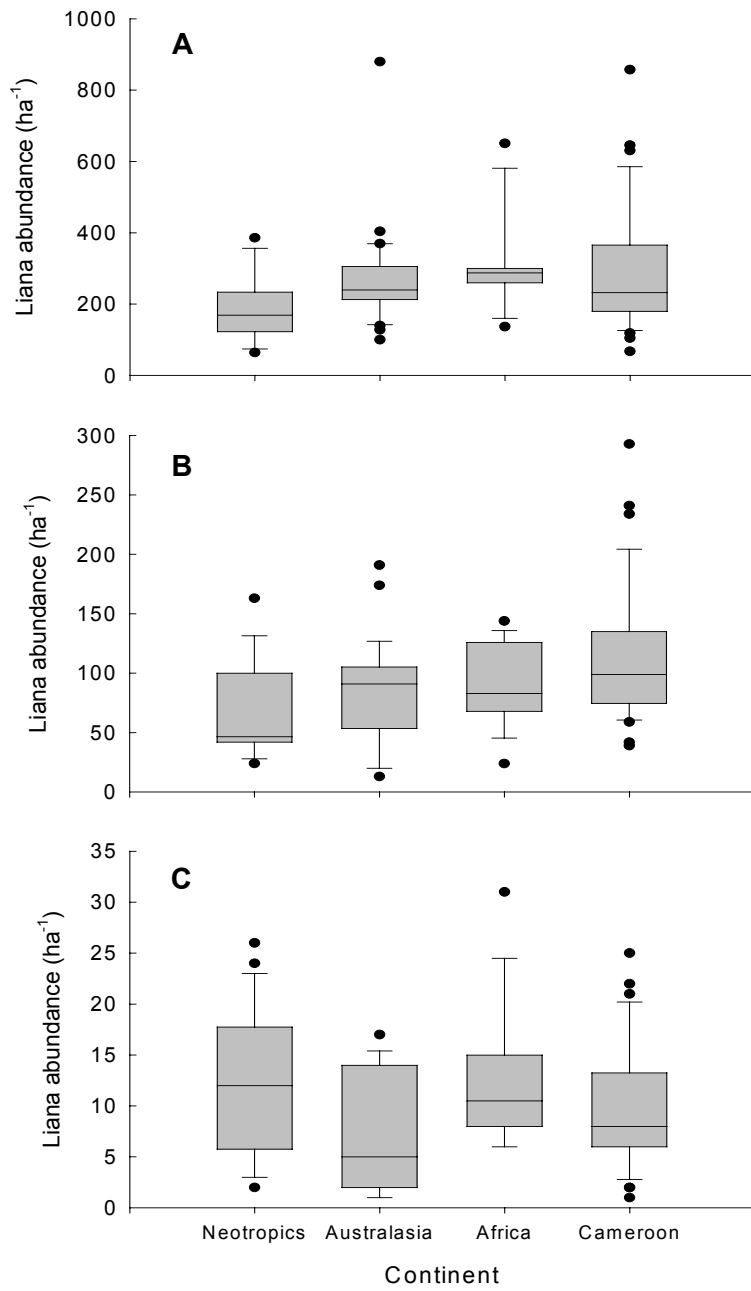


Figure 5.5. Box plots of liana abundance in tropical moist forest plots in three different continents and at Ebom, Cameroon (see Appendix 2). Total number of lianas per ha; (a) in the 2-5 cm dbh class, (b) large lianas: > 5 cm dbh, (c) very large lianas: > 10 cm dbh. The upper and lower border of the box are the 75th and 25th percentiles, respectively, the black horizontal line within the box is the median and the error bars are the 10th and 90th percentiles. The closed circles represent outlier values.

might leave more very large lianas intact. The short term dangers of logging and climber cutting on liana diversity have been demonstrated (Parren and Bongers 2001) but the long term effects of these interventions on the large lianas have not been proven yet for Cameroon.

Spatial patterns. Most lianas as a group or at a species level showed a clumped distribution either at a 0.01 ha or 1-ha level. Local variation in liana abundance may be attributed to the proximity of natural gaps. Most lianas are thought to be light demanding (Caballé 1984, Putz 1984a) and thus are expected to abound in gaps and at gap edges (Caballé 1986b, Hegarty and Caballé 1991). Clonal growth by ramets is quite common by lianas and may also account for the clumping patterns found (Caballé 1977, 1980a, 1994, Peñalosa 1984, Putz 1984a).

Even though Myers (1978) and Krebs (1989) found the standardised Morisita index of dispersion (I_p) established by Smith-Gill (1975) to be one of the best measures of dispersion, we used the original Morisita index of dispersion (I_δ). Hurlbert (1990) showed convincingly that the standardised Morisita index of dispersion (I_p) indicates only the statistical reliability of the original Morisita index of dispersion (I_δ) and not the level of clumping itself. Also in contrast to I_δ I_p is strongly affected by sample size. High values of I_δ indicate that the lianas or rattans are highly concentrated in just a few subplots.

Parthasarathy and Sethi (1997), in a sacred grove consisting of dry evergreen forest in India also found a clumped distribution for most liana species represented by ≥ 5 individuals at both 0.01 ha and 0.25 ha. However, at seven out of 21 cases the pattern changed from uniform to clumped or visa-versa with a change in scale. Such changes were hardly seen in our forest (Appendix 1). The difference might be due to the fact that the sacred grove was rather small (< 17 ha) and with limited initial diversity while our forest was part of an extensive forest area (several thousand ha) with high diversity. Also, plots represented by less than 10 individuals might account for some of the uniform patterns.

Even though most liana species investigated had a clumped distribution at all examined levels, in many cases the species were present only at low numbers or even completely absent within 1-ha plots (see Figure 5.4, Appendix 1). The underlying factors were not investigated. According to Hegarty and Caballé (1991) aggregation is seen where changes in landscape occur. Changes in landscape such as 'steep catena positions in and along edges of tracks and water courses' (see also Van Rompaey 1993) were, however, excluded in our study. The soil in the study area is very uniform (G. Hazeu pers. comm.) and does not help explain the spatial patterns found. Detailed information is needed on species life history characteristics like phenological patterns, seed dispersal, and vegetative propagation in combination with gap dynamics to be able to explain the liana aggregation patterns found. Continued research at both landscape and plant ecological levels will be critical for understanding the spatial patterns in liana abundance at different spatial scales.

Acknowledgements

This is a contribution of the Tropenbos Cameroon Programme. For the liana identification we thank F.J. Breteler, C.C.H. Jongkind and A.J.M. Leeuwenberg of the Herbarium Vardense and for their contribution in the field G. Caballé and M. Elad Epah. For their fieldwork in the liana and rattan inventory we are grateful to J. Ango, J. Etoundi, B. Mva, P. Nkolo and A.P. Nkomo under the supervision of M. Elad Epah. The fieldwork of MP was financially supported by the Tropenbos Foundation, The Netherlands.

6. DOES CLIMBER CUTTING REDUCE FELLING DAMAGE IN SOUTHERN CAMEROON?

6.1. INTRODUCTION

Lianas are an important structural component of tropical forests. Their life form has specific characteristics that have consequences for forest management. A first aspect is their growth habit. Lianas ascend to the forest canopy using trees or other lianas as a host. Their exploration for available space and light may lead to growth from one tree crown to another (Putz and Chai 1987, Clark and Clark 1990, Balfour and Bond 1993, Pinard and Putz 1994). As a result of this process, lianas often intertwine tree crowns and stems. This has two major consequences. Firstly, their finding force may lead to an increase in canopy openings once a tree or major branch falls down. The chance of a falling tree pulling over other neighbouring trees increases. Secondly, the lianas that interconnect tree crowns provide arboreal pathways for canopy vertebrates (Charles-Dominique *et al.* 1981). A second aspect is their resilience. They have a high capacity of resprouting (Kennard 1998) and the many growing points often lead to liana tangles (Putz 1990). Regenerating trees can be covered entirely and lianas may form a blanket hampering them (Neil 1984, Putz *et al.* 1984, Chaplin 1985). In this paper, the focus is on the consequences of both aspects for silviculture.

Lianas are mostly seen as a nuisance by foresters, hence the cutting of liana stems has been an important operation in forest management practices. Pre-logging liana cutting has been applied over several 100,000 ha in both, Ghana and Nigeria, and sometimes even included poisoning of all lianas (Barnard 1955, Gutzwiller 1956, Baidoe 1970, Britwum 1976, Lowe and Walker 1977). This operation is aimed at a reduction of logging damage, an improved precision of felling, an enhancement of the development of the growing stock and a reduction of the regrowth capacity of lianas (Foggie 1960, Lowe 1978). Studies set-up to evaluate the effectiveness of pre-logging climber cutting are scarce, however. What do we need to know? Some of the most important questions are: are lianas strong enough to tear down other trees and branches? Does climber cutting reduce that binding force? Are strong lianas abundant enough to merit climber cutting activities? What is the gain of climber cutting in terms of reduced logging damage, and enhanced development of the growing stock? How resilient are lianas? To what extent liana development in logging gaps is reduced? How different are liana species in these aspects? What is the effect of climber cutting on the movement patterns of animals?

Studies in SE Asia (Fox 1968, Appanah and Putz 1984) and in the Amazon Basin (Vidal *et al.* 1997) have shown positive effects of climber cutting on the reduction of logging damage to residual trees. The African forest is known for its high liana abundance (Hladik 1986, Gentry and Dodson 1987, Reitsma 1988) and climber cutting was prescribed over vast areas. Proper evaluation, however, never took place (Parren and de Graaf 1995). In the present study, we assess whether climber cutting is effective to reduce felling damage. Specifically, we asked the following questions:

- 1 How abundant are lianas in the forest studied?

- 2 To what extent climber cutting results in the death of the lianas and what is their resprouting capacity?
- 3 What is the effect of pre-felling climber cutting on the felling gapsizes, on the number of dead or damaged trees, and on the felling direction?

6.2. STUDY SITE

This study was conducted in a logging concession 100 km east of Kribi, Cameroon (3°N, 10°E). The concession area covers over 2000 km². The study area was located in the north-eastern part near the village Ebom, in a part where large-scale commercial logging never had happened before. The mean annual rainfall is 2000 mm with two distinct wet seasons (March-May and August-November), associated with the movement of the Intertropical Convergence Zone over the area (Waterloo *et al.* 1997). The study area is located on a Pre-Cambrian shield, resulting in clayey soils and classified as a Xanthic or Plinthic Ferralsol. The topography ranges from undulating to rolling, with isolated hills of elevations between 350 and 600 m a.s.l (Waterloo *et al.* 1997). Research plots were located in more or less flat terrain. The forests of the area are evergreen and can be characterised as late secondary forests of the Biafrian type (*sensu* Letouzey 1968) with a more or less closed canopy layer between 25 and 40 m with emergent trees surpassing 60 m in height towering above. Climbers are abundant in the canopy and in gaps where light conditions are favourable to their growth. The omnipresence of *Pycnanthus angolensis* (Welw.) Warb. and *Lophira alata* Banks ex Gaertn. f. indicates that the forest is quite degraded (see also Letouzey 1968, p. 153). In general, forest exploitation in West and Central Africa can be characterised as being highly selective, in the sense that only the best stems of a very limited number of species, in demand on the world market, are felled. Densities of these species are typically low and, as a result, in most areas on average only one to two stems per hectare are removed (Debroux and Karsentry 1997). Average harvest level in our study area is one tree of about 13 m³ per ha and indicates that logging is indeed very selective (G.J.R. van Leersum, personal communication).

6.3. METHODS

In the area, 33 square 1-ha research plots were established, these being spatially dispersed over an area of 500 ha. Around the plots, 100-m wide buffer zones were established. We checked whether the plots to be treated were different from the untreated plots as for tree and liana abundance. The t-test for equality of means showed that there were no significant differences for trees over 10 and 30 cm diameter at reference height (drh), i.e. at breast height (1.3 m) or 30 cm above buttresses, and not even for lianas over 2 or 5 cm in diameter at breast height (dbh). In five control plots, no logging and no silvicultural treatments were applied. The remaining 28 plots were all logged and in 16 of them pre-exploitation climber cutting was applied (May 1995). Felling was carried out 9 months later (February 1996). Climber cutting for each plot was applied in the 1-ha research plot and in the surrounding buffer zone. Harvest levels were set at one tree per ha over 60 cm drh, resembling normal exploitation practice in the region. The baseline of the 1-ha plots was placed perpendicular to the natural inclination of the tree to be felled some 20 m

from the stemfoot to make sure that the entire tree would fall within the plot. Sampling of both, trees and lianas took place. Voucher specimens were deposited at the herbarium in Kribi, Cameroon, and at the Herbarium Vadense in Wageningen, The Netherlands.

6.3.1. Liana abundance and resprouting

Liana stems over 2 cm at dbh were counted in all the thirty-three 1-ha plots (using 10 m x 10 m subplots). All lianas cutting through the imaginary surface at breast height were counted and their dbh measured. Lianas < 2 cm in dbh were only counted per subplot. During Field inventory lianas over 2 cm were identified by their local Bulu name and, at a later stage, herbarium vouchers of each Bulu name were collected and identified in the field (G. Caballé, Montpellier, France), and at Herbarium Vadense. In eight 1-ha plots, a selection of 184 liana individuals were cut and tagged for subsequent monitoring. Resprouting capacity and mortality were assessed regularly for a period of 22 months after climber cutting. Resprouting capacity was expressed as the total number of spots where new sprouts developed on the main stem. This does not concern the actual number of sprouts, as at every spot several sprouts can develop.

At the beginning of the rainy season, we laid down 1-m long climber cuttings on the forest floor to find out their resprouting capacity. We concentrated the experiment on two dominant groups of lianas distinguished by the local Bulu as (a) Avom, consisting of the genera *Landolphia* and *Dictyophleba* of the Apocynaceae family, and (b) Atuk, comprising the genera *Neuropeltis* and *Calycobolus* of the Convolvulaceae family and *Icacina* of the Icacinaceae. Of each group, we collected 1-m cuttings in four diameter classes < 3, 3-6, 6-9 and > 9 cm with 20 cuttings per class. These were equally divided and placed on the forest floor in two different environments, in a cleaned felling gap assuring full sun-exposure and in closed canopy forest, and monitored for resprouting during a period of three months.

6.3.2. Felling gapsizes

We expect climber cutting to result in considerably smaller gaps as a result of removing the binding effects, and lower tree mortality and tree damage levels compared to those without such treatment. To examine this, we selected a total of 161 harvestable trees over 60 cm drh in the 1-ha plots and their buffer zones. This figure of 161 trees is lower than the total of trees that were felled, since some trees were still found to be suspended, hanging in the forks or crowns of surrounding trees, or formed multiple treefall gaps. These anomalous gapsizes were not taken into consideration. The remaining 161 trees consisted of a total of 25 different tree species of which 23 species represented 1-7 individuals, while 17 Tali (*Erythrophleum ivorense*), 24 Padouk (*Pterocarpus soyauxii*) and 48 Azobe (*Lophira alata*) trees were harvested. Of these 161 harvested trees, 81 were located in plots with, and 80 trees in plots without, previous climber cutting. For all these felled trees, the resulting gapsize was determined using the gap definition of Runkle (1981, 1982). Runkle considers trees as part of the surrounding forest canopy when they have a diameter of over 25 cm (and in general reached a height of over 20 m). Runkle's gapsize was calculated using the gap centre as a starting point. Direction

and distance from the gap centre to the bases of all surrounding canopy trees was measured. The gapsize was calculated as the surface of the area enclosed by the bases of the surrounding canopy trees. Runkle's definition is a useful method for measuring gapsize at forest floor level (Van der Meer *et al.* 1994).

Total tree height and crown depth were measured after felling by measuring the distance from the stump to the first main branch or fork and the corresponding distance following the main axis to the treetop (last branches). Crown width was measured perpendicular to the main axes direction, where the tree crown was at its greatest width. Crown volume was calculated as an ellipsoid, $V = 0.167\pi \times (\text{crown width})^2 \times \text{crown depth}$.

6.3.3. Residual stand damage

In the 28 felling gaps of the logged central 1-ha plots, tree mortality as well as bark and crown damage to trees over 10 cm drh were assessed. The damage assessment classification was similar to the one applied in Surinam under the CELOS harvesting system (Jonkers, 1983). In the field, nine different types of damage were distinguished. Stem damage was classified into five classes as: (st1), no stem damage; (st2), minor bark damage (when the stem was damaged less than one third of the circumference of the stem or < 20 cm of the circumference of the stem or over a length of up to 2 m); (st3), severe bark damage (when at least one third of the circumference of the stem or over at least 20 cm of the circumference or over a length of at least 2 m was damaged); (st4), severe stem damage included stems that had split; and (st5), unstable trees resting on others. Crown damage was classified as: (cr1), no crown damage at all; (cr2), minor crown damage when less than half of the crown was broken off; (cr3), severe crown damage when more than half of the crown was broken off; and (cr4), a category where the whole crown was broken off. For analysis, some of the damage classes were grouped into one composite class. Class 1 = cr1(+st2)+cr2(st1/2); Class 2 = cr1(+st3/5)+cr2(+st3/5)+cr3(+st3/4/5); Class 3 = cr3(+st1/2); Class 4 = cr4(+st1/2/3/4/5). The damage classes can be described qualitative as having minor stem and crown damage (Class 1), severe stem damage (Class 2), severe crown damage (Class 3) and entire crowns torn off (Class 4).

6.3.4. Felling

Under normal felling practices, a tree is felled in the direction of the natural lean of a tree. To diminish stand damage, experienced fellers try to change the falling direction (Cedergren 1996). Fellers then predict where the tree would fall down. Strong lianas are expected to influence the falling direction and may lead to a deviation from the predicted direction. We tested our prediction, namely cutting of lianas prior to felling would increase the accuracy of the felling operation. For every felled tree, we calculated the deviation between the predicted felling direction and the actual felling direction. We compared the frequency distributions of these deviations for trees with, and without, previous climber cutting (Kolmogorov-Smirnov test).

6.4. RESULTS

6.4.1. Liana abundance and resprouting capacity

Lianas are very abundant in the area (Table 6.1). On average, there were 408 lianas ≥ 2 cm dbh and 4370 smaller ones per hectare. The abundance varied considerably, however, between 187 and 1092 for the large lianas and between 1870 and 10451 for the small ones, roughly a factor of five between the lowest and the highest density. Lianas that were probably large enough to influence damage levels were quite common as, on average, 113 lianas ≥ 5 cm dbh and 10 lianas ≥ 10 cm dbh were present, but variation was also high among the plots here.

Table 6.1. Liana abundance at breast height in 33 1-ha plots, Ebom, Cameroon

	Mean	S.D.	MIN	MAX
<2 cm	4370	2264	1870	10451
≥ 2 cm	408	200	187	1092
≥ 5 cm	113	58	39	293
≥ 10 cm	10	6	1	25

Table 6.2. Liana performance after climber cutting: mortality, survivorship and resprouting capacity of 184 individuals > 1 cm dbh

	0 Months	6 Months	11 Months	15 Months	22 Months
Dead	0	63 (34%)	92 (50%)	108 (59%)	128 (70%)
Alive	184	121	92	76	56
Total sprouting spots	n.a.	427	403	313	208

During May 1995, we labelled 184 liana individuals ≥ 1 cm dbh that had been cut that same month. In total, 53 morphospecies were distinguished (33 genera and 19 families). Liana mortality increased over time from 34% after 6 months, to half the population after logging (11 months after climber cutting), and 70% almost 2 years later (see Table 6.2). We noticed a slow die-off in most species: first the sprouts closest to the cutting surface died and later those closer to the stem foot. At the end of the monitoring period fungal attack was clearly causing wood rot of the entire stem. The total number of locations along the liana stem with sprouts declined also over time (Table 6.2). The decline was less than expected, based on the number of surviving lianas because these were the more vigorous ones, having many sprouting spots. Some liana genera were flexible and resistant with respect to cutting, while others were vulnerable (Table 6.3). Genera belonging to the Connaraceae, Dilleniaceae, Euphorbiaceae and Papilionoideae families had survival rates of at least 50%. Genera in the Annonaceae, Apocynaceae, Celastraceae and Icacinaceae families had extremely low survival rates. In neither the felling gap nor the closed canopy forest did the 1-m cuttings show any rooting or sprouting after three months. This was contrary to our expectations. In the gap, the cuttings had completely dried out and in the closed canopy forest the cuttings were to a large extent already decomposed.

Table 6.3. Vulnerability of liana genera after climber cutting^a

Morphospecies.	Family	(1) ^b	(2) ^c	(3) ^d	(4) ^e
<i>Rourea</i>	Connaraceae	4	3	75	5
<i>Millettia</i>	Papilionoideae	4	3	75	3.7
<i>Agelaea</i>	Connaraceae	13	9	69	3.8
<i>Dictyophleba</i>	Apocynaceae	3	2	67	1.5
<i>Maniophytum</i>	Euphorbiaceae	8	5	63	5.4
<i>Iodes</i>	Icacinaceae	9	5	56	1.8
<i>Tetracera</i>	Dilleniaceae	9	5	56	2.8
<i>Salacia</i>	Celastraceae	8	4	50	8.3
<i>Artabotrys</i>	Annonaceae	6	2	33	2.5
<i>Acacia</i>	Mimosoideae	3	1	33	4
<i>Combretum</i>	Combretaceae	4	1	25	2
indet. sp1	Icacinaceae	22	1	5	4
<i>Landolphia</i>	Apocynaceae	15	0		
<i>Ancistrocarpus</i>	Tiliaceae	3	0		
<i>Cissus</i>	Vitaceae	3	0		
<i>Icacina</i>	Icacinaceae	3	0		
<i>Strophanthus</i>	Apocynaceae	3	0		
<i>Piper</i>	Piperaceae	3	0		
<i>Strychnos</i>	Loganiaceae	3	0		
<i>Simiristis</i>	Celastraceae	2	2		5.5
indet sp1	Papilionoideae	2	2		3.5
<i>Frisodielsia</i>	Annonaceae	2	2		3.5
<i>Mussaenda</i>	Rubiaceae	2	1		3
indet. sp1	Annonaceae	2	0		
<i>Cnestis</i>	Conneraceae	1	1		5
<i>Lonchocarpus</i>	Papilionoideae	1	1		2
<i>Dalbergia</i>	Papilionoideae	1	1		2
<i>Pyrenacantha</i>	Icacinoceae	1	1		2
<i>Loesenerilla</i>	Celastraceae	1	1		1
<i>Acridocarpus</i>	Malpighiaceae	1	1		3
<i>Calycobolus</i>	Convolvulaceae	1	1		1
<i>Neuropeltis</i>	Convolvulaceae	1	1		4
indet. sp1	Apocynaceae	1	0		
<i>Uncaria</i>	Rubiaceae	1	0		
<i>Sabicea</i>	Rubiaceae	1	0		
<i>Mucuna</i>	Papilionoideae	1	0		
indet. sp1	Euphorbiaceae	1	0		
<i>Afrobrunnichia</i>	Polygonaceae	1	0		
indet. sp1	Celastraceae	1	0		
Unknown		1	0		

^a Top half of the table concern morphospecies with more than three individuals monitored and the lower half with less than three individuals monitored.

^b The initial number of individuals monitored.

^c The number of lianas alive and with sprouting spots after 22 months.

^d The percentage of individuals surviving.

^e The mean number of sprouting spots for alive individuals after 22 months.

6.4.2. Felling gapsizes

Although all felled trees were large canopy trees with a diameter of > 60 cm at reference height, the resulting felling gaps were highly variable in size, ranging from 103 to 1385 m² (Fig. 6.1). The majority of the gapsizes were between 300 and 900 m² (mean 565 m²), irrespective of whether climber cutting had taken place before felling. The logging gaps without climber cutting were more variable and extreme in size. Sizes of felling gaps with (mean 550 m², N=81) previous climber cutting were not smaller than felling gaps without (mean 575 m², N=80) climber cutting. Also the

size distributions of the gapsizes were not significantly different (Kolmogorov-Smirnov two sample test; n.s.). This was contrary to our expectation. Tree size, tree height, and crown size and -form are expected to influence the resulting gapsizes, as well as densities of nearby trees, and numbers and strength of lianas binding the trees together. As our 161 trees consisted of 25 species, and species are expected to be different with respect to their size and form, this was expected to have a large influence on the felling gapsizes. To reduce this variability, we selected all 48 Azobe (*Lophira alata*) felling gaps (Fig. 6.1). Surprisingly, the results were the same: no difference between gapsizes that resulted from logging with (N=27) or without (N=21) previous climber cutting (Kolmogorov-Smirnov two sample test; n.s.). Felled trees of two other species with > 10 individuals, Padouk (*Pterocarpus soyauxii*) and Tali (*Erythrophleum ivorense*) were also tested and showed the same result.

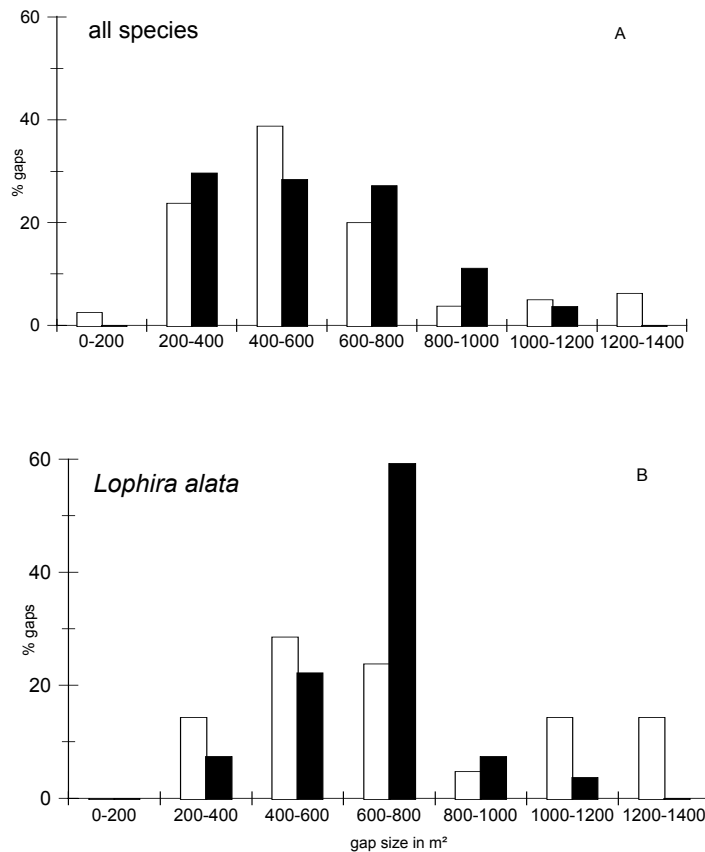


Figure 6.1. Frequency distribution of felling gapsizes (Runkle's method) that result from felling with (black) and without (white) previous climber cutting. (A). All species with (N = 81), and without (N = 80), climber cutting. (B) *Lophira alata*, with (N = 27), and without (N = 21), climber cutting.

When we considered tree height and crown volume for a limited number of individuals this also showed a wide variation. Tree height varied between 33.6 and 57.1 m (N=33) which implies that the largest emergent felled trees were nearly twice as high as the smallest felled trees. Crown volume depended highly on the crown form of the species: especially the height of the first main branch or fork was important. The smallest crown had a volume of 2000 m³, while those with a low fork or branch had a crown volume that could be as large as over 20,000 m³ (N=18). We expected that the gapsize would be determined by the size of the tree, but the results were not statistically significant (Runkle gapsize = 41 + 3 x diameter + 7.2 x height + 0.006*crown volume, r²=0.16, n.s.).

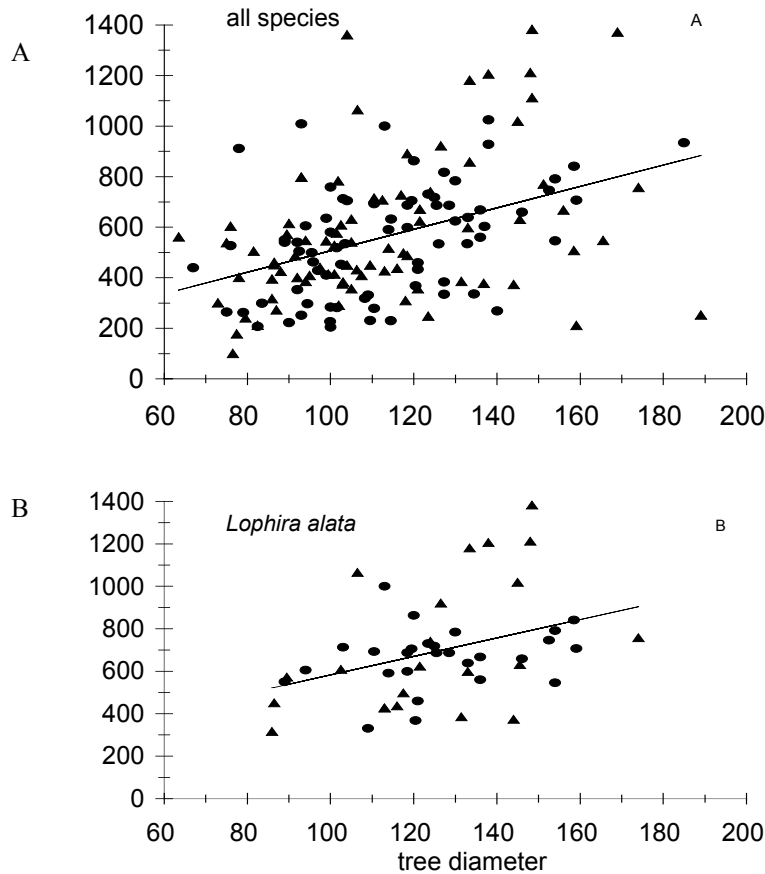


Figure 6.2 The relationship between diameter of felled trees and felling gapsizes (Runkle's method) after pre-felling climber cutting (filled circles) or no climber cutting (filled triangles). (A) All species, N=161 felled trees. Regression line: Runkle gapsize = 83.3 + 4.24 x diameter, r²=0.41, p<0.0001. (B) *Lophira alata*, N=48 felled trees, Regression line: Runkle gapsize = 148.4 + 4.35 x diameter, r²=0.14, p<0.01.

The relationship between felling gapsizes and diameter for the entire group of felled species was linear (Fig. 6.2, Runkle gapsize = $83.3 + 4.24 \cdot \text{diameter}$, $r^2=0.41$, $p<0.0001$). No differences were found for the entire group of felled species with (Runkle gapsize = $80.7 + 4.12 \cdot \text{diameter}$, $r^2=0.19$, $p<0.0001$) and without (Runkle gapsize = $86.6 + 4.35 \cdot \text{diameter}$, $r^2=0.17$, $p<0.0001$) climber cutting. For Azobe (*Lophira alata*), the relationship between felling gapsizes and tree diameter was also linear (Fig. 6.2, Runkle gapsize = $148.4 + 4.35 \cdot \text{diameter}$, $r^2=0.14$, $p<0.01$).

However, for this species, the relationships were different between trees with (Runkle gapsize = $431.9 + 1.85 \cdot \text{diameter}$, $r^2=0.06$, n.s.) and without (Runkle gapsize = $95.5 + 6.63 \cdot \text{diameter}$, $r^2=0.22$, $p<0.05$) climber cutting. No linear relationship was found for Padouk (*Pterocarpus soyauxii*) (Runkle gapsize = $366.3 + 1.24 \cdot \text{diameter}$, $r^2=0.007$, n.s.) and Tali (*Erythrophleum ivorense*) (Runkle gapsize = $400.4 + 0.82 \cdot \text{diameter}$, $r^2=0.003$, n.s.).

6.4.3. Residual stand damage

At a tree felling operation, on average 12 trees died other than the one felled, and slightly more than 20 other trees were damaged, but the variation was large (Fig. 6.3). On average a total of 33 trees were affected for each felled tree. Mortality was not significantly different between trees felled with (mean = 12.3, s.d.=6.9), and without (mean = 12.5, s.d.=6), previous climber cutting (Kolmogorov-Smirnov two sample test; n.s.). The same applies for the damage averages for trees felled with (mean = 24.5, s.d.=11.5), and without (mean = 20.7, s.d.=9.4) climber cutting (Kolmogorov-Smirnov two sample test; n.s.). Seventeen felled trees with climber cutting resulted in mortality of 209 trees and residual stand damage of 416 trees, 11 felled trees without treatment resulted in mortality of 138 trees and residual stand damage of 228 trees over 10 cm drh. The majority of the dead trees were small and medium-sized (Fig. 6.4), and climber cutting had no significant effect on the size distribution (Kolmogorov-Smirnov two sample test; n.s.). Between 16 and 20% of the affected trees belonged to the diameter class that includes potential crop trees (30-60 cm drh) for both, the treated and untreated plots. Damaged harvestable trees (>60 cm drh) made up 9% of the affected trees in treated as well as untreated plots, and mortality of harvestable trees was as low as 2% for treated and 7% for untreated plots.

In general, the damage caused at the felling operation was not severe. Minor stem and crown damage (Class 1) was most common and made up 80% of all damaged trees in untreated plots. Severe stem damage (Class 2) and severe crown damage (Class 3) were equally represented at the felling sites for both treatments but higher when climbers were cut. The most striking aspect was that trees with previous climber cutting showed a three times as high chance of having their crowns torn off (Class 4) as almost 30% of the damaged trees showed such fracture (Fig. 6.5). This was completely contrary to our expectations. The smaller sized trees (Class 10-30 cm drh) were most prone to serious damage: roughly two-third of the total number of damaged trees were in this size class. The mean diameter for all damaged trees was 27.3 cm (N=625 trees) for treated plots and 29.3 cm (N=366 trees) for untreated plots.

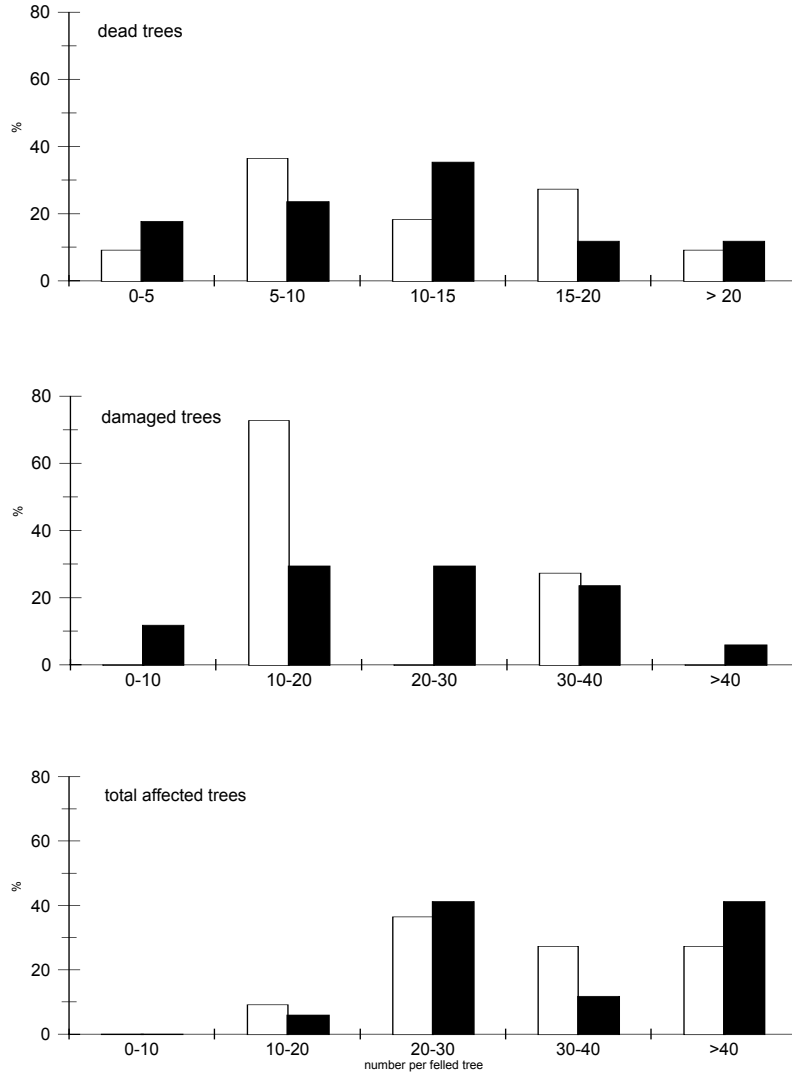


Figure 6.3. Frequency distribution of residual stand damage (mortality, damaged trees and total affected trees) expressed as percentage of felled trees, after felling 17 trees with (black) and 11 trees without (white) climber cutting.

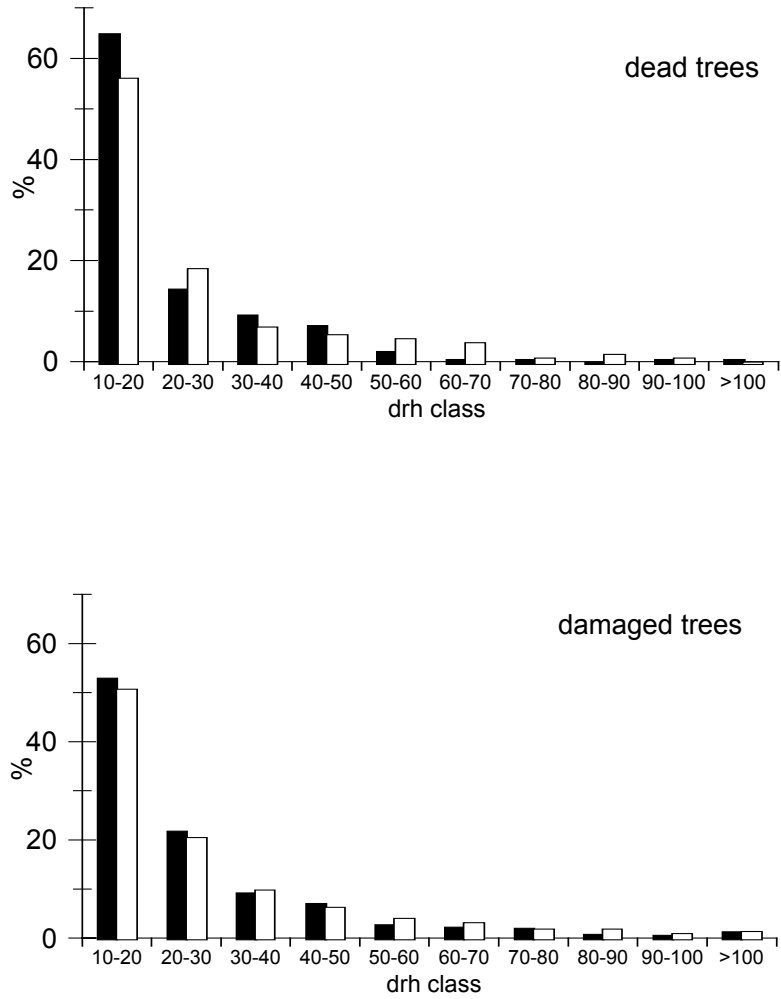


Figure 6.4. Diameter distribution of stand damage after felling of trees with (black) and without (white) climber cutting. Seventeen felled trees with climber cutting resulted in mortality of 209 trees and residual stand damage of 416 trees, 11 felled trees without treatment resulted in mortality of 138 trees and residual stand damage of 228 trees over 10 cm drh.

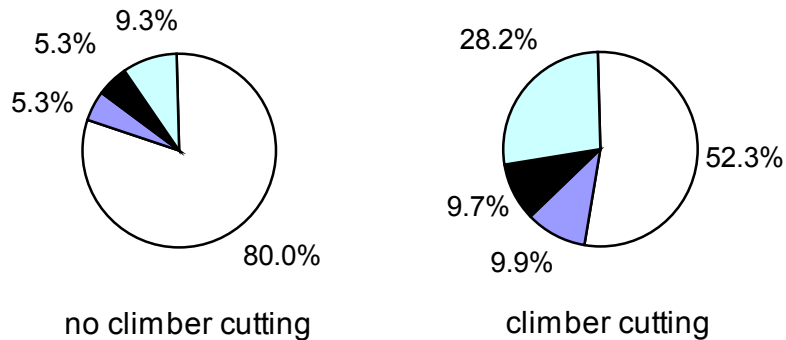


Figure 6.5. Type of damage for trees in an operation (A) with (N = 379) and (B) without (N= 226) previous climber cutting. Damage classes are minor crown and stem damage (white), severe stem damage (dark grey), severe crown damage and hardly any stem damage (black), no crown anymore (light grey).

6.4.4. Felling

Overall the felling deviation, the difference between predicted and actual felling direction, was small (N=100, average 33.6°, S.D.=34.4, min0° and max=170°). The felling deviation for trees with pre-felling climber cutting averaged 37.4° (N=38, s.d.=34.2) and without climber cutting the felling deviation averaged 31.2° (N=62, s.d.=34.7). Thus, contrary to our expectations, climber cutting did not have a significant effect on the reduction of the felling deviation (Kolmogorov-Smirnov two sample test; n.s.).

6.5. DISCUSSION

6.5.1. Abundance of big lianas

In the forests studied, lianas are highly abundant, compared to many other forest sites (Gentry 1991, Hegarty and Caballé 1991). Gentry (1991) found that, in general, density for lianas ≥ 2.5 cm dbh is greater in Africa (114 stems per 0.1 ha) than in the Neotropics (70 stems per 0.1 ha) and Southeast Asia (70 stems per 0.1 ha). In particular, the number of small lianas is high, but, with respect to climber cutting and its effects, the number of lianas ≥ 5 cm dbh are probably of prime importance. The studied forests harbour many of these large liana stems (113 liana stems ha⁻¹), but this is not exceptional compared to forests in other continents. Appanah and Putz (1984) found equal numbers of liana stems over 5 cm dbh in their forest in Pahang, Malaysia (13 ha inventoried). In Para State, Brazil, Vidal *et al.* (1997) estimated that some 100 large lianas per hectare (only 0.42 ha inventoried) were present in mature forest. In a forest at Ituri, D.R. of Congo, Makana *et al.* (1998) found some 67 large lianas per hectare (3 ha inventoried), but in a monodominant forest type only 24 large lianas per hectare (3 ha inventoried) were found. That classifies these African

forests even as poor concerning large lianas. Unfortunately, no comparable density data were found for very large lianas, such as those of over 10 cm dbh. Still, such very large lianas may be the main cause for tearing off entire tree crowns of surrounding trees.

6.5.2. Sprouting of lianas

The goal of climber cutting is to remove or diminish the strength of the liana, leading to a smaller binding force between trees and tree crowns. We used mortality of lianas after cutting as an indication of weakening. In general, mortality of lianas was high, after climber cutting. For a group of liana morphospecies, mortality was low and, thus, for these species the effect is not very obvious, at least not during the period of observation (22 months). Of course, we cannot prove a positive relation between mortality and a decline of strength of the lianas. For that we need to have knowledge on strength properties of alive and dead lianas.

The fact that cutting had a strong effect on some species, while others were highly resistant, can partly explain the results that we found for the 1-m cuttings. Because the Bulu names do not correspond with one species or genus, the expectations were equivocal. Avom can be both, *Dictyophleba* (high survival) and *Landolphia* (low survival). The same accounts for Atuk, which can be both, *Neuropeltis* and *Calycobolus* (high survival) and *Icacina* (extremely low survival). The choice of the species thus was not the right one. We suggest studying a large number of botanically well-defined ones in this respect. The study performed by Appanah and Putz (1984) is a good example in this respect (32 species), but was performed without taking into account the diameters of the cuttings or the environment (gap or understorey). Over a period of 8 years, Putz (1990) found almost equal mortality rates for liana ramets (1.5%/year) as for canopy trees (1.7%/year). Whereas ramet mortality was high, genet mortality was low (0.3% per year); however, this will result in high genet longevity for most lianas as some parts will stay alive. Recently Pinard *et al.* (1999) showed that burned lianas, one year after a forest fire, displayed resprouting frequencies of only 15-31%, independently of diameter class. The high mortality of over 70% is comparable to our results two years after climber cutting. That the effect of climber cutting can last for a very long time is shown by Rollet (1983). In the Brazilian Amazon, over 1000 ha had their climbers cut. Some 20 years after climber cutting, the number of liana stems were still very low.

6.5.3. Pre-logging and post-logging data

For a proper evaluation of damage levels during felling, pre-logging data should be compared with post-logging data, because trees crushed by the crown are not found (Mensah, 1966, personal observation). In the present study, we followed this procedure (see also White, 1994), in contrast to many other studies where damage levels were assessed only after the logging operation (see, e.g. Appanah and Putz 1984, Uhl and Guimarães Vieira 1989, Vidal *et al.*, 1997). We suspect that the reported damage levels in these studies are underestimated, because many trees are crushed under the felled trees, and thus are not taken into account when looking only at the residual stand after logging. The difference can be analysed when the two methods are used at the same time, but such studies were not found in the literature.

The number of dead trees in this study can be used as an estimate for that difference. In the present study, it was observed that for each felled tree c. 10 trees died and 20 were damaged, hence we can estimate the underestimation of other studies to be between 0 (no tree crushed under the crown of the felled tree) and 50% (all dead trees crushed under that crown).

6.5.4. A tree-based focus

In this study, we followed a felled-tree focus. In most other studies (e.g. White 1994, Vidal *et al.* 1997, but see Appanah and Putz 1984, Cedergren 1996) an area-based procedure is used. These two are hard to combine with respect to residual stand damage. Only in the case of no-overlap between felled trees, the tree-base data can be converted directly into area data. In African forests, until recently, on average one-to-two trees per hectare were taken (Debroux and Karsentry 1997), suggesting no overlap. However, the averages blur the situation in the field. Data from G.J.R. van Leersum (personal communication), for the same area in Cameroon, show that the mean number of felled trees per hectare varied between 0.5 and 1.9 in twelve 25-ha plots (in 7 other plots selected randomly, no trees were felled). A considerable overlap existed within plots, and the tree-based damage data thus cannot be translated directly into area-based data.

6.5.5. Climber cutting effects on gapsize, felling deviation, tree death and damage

This study shows that climber cutting had no effect on the sizes of the felling gaps, contrary to our expectations. Of course, a lot of other factors influence gapsize and, with a small number of gaps, we would not have expected a difference. We studied 161 trees, however, and expected that the large number would have filtered out the variation due to other non-controlled factors. That this was not the case is a strong indicator of the probably very weak role that lianas play in this respect. A drawback of this study, however, may be the fact that we did not count the actual number and sizes of lianas on trees to-be-felled and the liana links to surrounding trees in the upper canopy. Several trees might not have lianas on them at all. Vidal *et al.* (1997) did select individual trees based on the difference in liana load and found that felling trees with many liana connections resulted in canopy gaps that were twice as large as those of liana-free felled trees.

No positive effect was found for the application of pre-felling climber cutting to reduce the felling deviation. The average felling deviation ranged between 31° and 38° whether climber cutting was applied or not and is only slightly less than the average felling deviation of 40° which G.J.R. van Leersum (personal communication) found for 180 trees felled conventionally in the same study area. Similar poor results for climber cutting effects on altering the felling deviation were found by Cedergren (1996) in Sabah, Malaysia. However, the liana abundance in forest in Sabah averaged just 189 individuals ≥ 2 cm dbh, which is rather low in comparison with our results for forest in Cameroon.

Climber cutting had only a very small effect on the number of trees that die and that are damaged during the felling operation (excluding trees that were affected by

skidding operations). This is in contrast to our prediction that the number of affected trees would be lower when climbers were cut some time before the felling of the tree. Also the three times as high chance of having a complete crown torn off after climber cutting, was not as predicted.

The damage levels in our study are in concurrence with studies in Ghana (Mensah 1966) and Gabon (White 1994), but in contrast to studies in Malaysia (Nicholson 1958, Appanah and Putz 1984), Brazil (Uhl and Guimarães Vieira, 1989) and Guyana (Van der Hout 1999) where they found much higher levels. This is probably related to the difference in extraction intensity of 1-2 trees ha⁻¹ in Africa vs. 8-11 trees ha⁻¹ in Southeast Asia and Latin-America. Larger dimensions of harvested trees and comparable dimensions of lianas in African forests may cause less damage compared with smaller dimensions of harvested trees and equal dimensions of lianas for forests in the Neotropics and Southeast Asia.

Crown damage is more abundant than stem damage. Damage assessments in Sabah, Malaysia (Nicholson 1958), Panang, Malaysia (Appanah and Putz 1984) and Ghana (Mensah 1966), following the Nicholson (Nicholson 1958) damage classification, all showed that there was more crown damage than bark damage and that the damage was predominantly of trees in smaller diameter classes. A similar pattern was found in Para, Brazil (Uhl and Guimarães Vieira 1989). These results are consistent with ours.

6.5.6. Is climber cutting cost-effective?

The application of a systematic and large-scale climber cutting operation will strongly depend on the cost and effectiveness of this treatment. Climber cutting was executed by experienced villagers. To assess the costs involved in such an operation a time study was made over a treated area of 90 ha. The cost of cutting was expressed as the number of man-days spent per hectare. The average time required cutting all lianas over 1 cm dbh in a 9-ha plot with a team of 13 labourers was ≈1 day (with 5 efficient working hours per day). On average this is 0.7 man-days of work per hectare. At a daily wage of CFA 1000 (US\$ 1=CFA 600) this would approximately equal US\$ 1 per ha. This amount excludes the costs of transport and other additional costs, which probably are considerably higher. Compared to other costs in the whole logging operation, this is very minor (Van der Hout and Van Leersum 1998, Van der Hout 1999, Van Leersum 1999).

Although these costs are very low (US\$ 1 per ha, compared to US\$ 4 in Guyana, Van der Hout (1999), and US\$ 16 in Brazil, Vidal *et al.* (1997)), we believe that it is not worthwhile to do a general climber cutting operation, because of the paucity of results. In addition, climbers have important ecological functions, particularly those that bear fruit (as noted below). Climber cutting, if at all applied, should be much more selective on a tree-by-tree basis. We suggest that, during the tree inventory prior to logging, the liana situation of every potentially-to-be-felled tree should be verified. Only in the cases that very large lianas are present on the tree, these should be cut. Ideally, we should know which big woody liana species have the greatest strength properties, both alive and dead, to be able to be more selective with climber cutting. This would require additional research.

6.5.7. Ecological relevance

Climber cutting can have strong negative effects on the forest community, because of a number of specific qualities that lianas have. Firstly, lianas, compared to trees, show a different temporal pattern of flowering and fruiting. While trees, as a life form, generally show peak flowering and peak fruiting (Van Schaik *et al.* 1993), lianas either show no peaks (Leighton and Leighton 1983, Putz and Windsor 1987, Heideman, 1989) or peaks clearly separated in time from trees (Putz and Windsor, 1987, Ibarra-Manriquez *et al.* 1991). This implies that, in times of scarcity of flowers and fruits, lianas might form an essential part of the diet of many animals. Many of these animals are essential for dispersal of tree seeds (Alexandre 1980, Charles-Dominique *et al.* 1981, Howe and Smallwood 1982, Corlett 1998, Guariguata and Pinard 1998), including the bulk of commercially interesting species (Jansen and Zuidema, in press).

Secondly, from the arboreal vertebrate viewpoint the canopy consists largely of open space through which lianas offer the only structural continuity over any appreciable distance. The presence of more lianas in African forests than in forests in other tropical continents may help animals to cross canopy gaps since life forms, such as prehensile tailed vertebrates in the Neotropics and gliding vertebrates in Asia, hardly exist on the African continent (Emmons and Gentry 1983). This, again, may also have consequences for seed dispersal. Thirdly, lianas contribute considerably to the plant diversity in moist forests (Gentry and Dodson 1987, Gentry 1991, Hegarty and Caballé 1991). Their vulnerability to cutting could lead to a reduction of general diversity in the forest.

These expected negative effects of liana cutting, combined with the absence of the expected positive effects on damage reduction, lead to the conclusion that general climber cutting prior to logging should not be applied.

Acknowledgements

This is a contribution of the Tropenbos Cameroon Programme. For the liana identification, we like to thank F.J. Breteler, C.C.H. Jongkind and A.J.M. Leeuwenberg of the Herbarium Vadense, Wageningen, and for their contribution in the field G. Caballé and M. Elad Epah. G.J.R. van Leersum and S. Okie as well as several students who made it possible to guide the logging operations. For their field work in the liana monitoring experiment, we are grateful to M. Elad Epah and S. Mutsaers. A.P. Nkomo, M. van Breugel and T. Wanders were of great help with gap-size determinations and J. Voeten and co-workers for damage assessments. The fieldwork of Marc Parren was financially supported by the Tropenbos International, The Netherlands. J.J. Jansen is thanked for statistical advise. Valuable comments on the manuscript were provided by two anonymous reviewers.

7. RECRUITMENT OF LIANAS INTO LOGGING GAPS AND THE EFFECTS OF PRE-HARVEST CLIMBER CUTTING IN A LOWLAND FOREST IN CAMEROON

7.1. INTRODUCTION

The detrimental impact of climbing plants on trees is a widely recognized phenomenon in both natural and managed tropical forests. Climbing plants, particularly lianas (woody vines), compete intensely with trees for both above- and below-ground resources and therefore can significantly decrease tree fecundity, growth rate, and survivorship in closed-canopy forest, treefall gaps, and open fields (Putz 1984a, Stevens 1987, Clark and Clark 1990, Dillenberg *et al.* 1993, Schnitzer and Bongers 2002). Lianas are particularly abundant in disturbed forests or in disturbed areas of natural forests, such as treefall gaps, where they can recruit rapidly and abundantly, and subsequently suppress tree regeneration for many years (Putz 1984a, Babweteera *et al.* 2000, Schnitzer *et al.* 2000, Tabanez and Viana 2000, Schnitzer and Carson 2000, 2001). For example, Schnitzer *et al.* (2000) demonstrated that high liana abundance in natural treefall gaps in Panama could suppress tree regeneration for more than 13 years. During tree extraction in managed and logged forests, lianas can substantially increase the damage and mortality of neighboring trees (collateral damage) and increase the size of logging gaps by binding the trees together, thus pulling down multiple trees in addition to the one being harvested (Appanah and Putz 1984, Putz 1985; but see Parren and Bongers 2001). Lianas also impact tree regeneration detrimentally following tree extraction by suppressing the growth and regeneration of valuable timber trees, as well as causing bending of the tree trunks and thus reducing their value as timber (Putz 1985, Pinard and Putz 1994, Vidal *et al.* 1997). Furthermore, the effects of lianas on trees are likely to become more intensified in the near future, because lianas appear to be increasing in abundance in response to global climate change (Phillips *et al.* 2002).

To minimize the effects of lianas on tree regeneration in managed forests, pre-harvest climber cutting has been used as a silvicultural tool throughout the tropics, costing many millions of dollars annually worldwide (Guigonis 1978, Appanah and Putz 1984, d'Oliveira and Braz 1995, Pinard *et al.* 1995, Pinard and Putz 1996, Amaral *et al.* 1998, Sist *et al.* 1998, Pérez-Salicrup *et al.* 2001a). Pre-harvest climber cutting can reduce the amount of collateral tree damage and thus post-felling canopy gap sizes, and it is commonly assumed that pre-harvest liana cutting results in a long-term reduction of the number of climbers in the forest after timber extraction (Appanah and Putz 1984, Putz *et al.* 1984, Putz 1985, Vidal *et al.* 1997, Gerwing 2001, Parren and Bongers 2001, Gerwing and Vidal 2002). However, pre-harvest climber cutting may be a double-edged sword, sometimes resulting in a net increase in liana stems. Climbers may respond to cutting by rapidly producing many new stems, which can eventually dominate logging gaps and logged forests (Gerwing and Vidal 2002). Even stems as small as 1 m in length can resprout vigorously, giving rise to many young, vegetatively-derived stems (Appanah and Putz 1984), particularly in the high light environment of a gap (Putz 1984a, 1991, Schnitzer *et al.* 2000). For example, in a study in a forest in Cameroon, Parren and Bongers

(2001) followed the fate of 184 experimentally cut liana stems and found that although 70% of the stems died after 22 months (n=184), the 56 surviving individuals vigorously produced many new vegetative offshoots, ultimately resulting in a net increase in the number of living stem sprouts after two years (n=208). Even if climber cutting is initially successful in reducing the number of lianas, the additional number of vegetatively-produced liana stems in logging gaps may actually increase the total number of liana stems following climber cutting (Putz *et al.* 1984), potentially reducing the vitality of the remaining trees in the gap. Consequently, lianas may have an equally detrimental effect on the remaining trees in logging gaps, regardless of pre-harvest cutting.

To date, the exact process and speed by which lianas recruit into gaps is poorly understood. In addition, the long-term effectiveness of pre-harvest climber cutting in reducing the number of lianas that recolonize logging gaps has also not been resolved (Parren and Bongers 2001, Pérez-Salicrup *et al.* 2001a, Schnitzer and Bongers 2002). We used a six-year chronosequence of logging gaps to determine the effectiveness of pre-harvest climber cutting and the speed of liana recruitment in a forest concession in Cameroon. We tested the hypotheses that: 1) lianas recruit into logging gaps very early after gap creation, mostly through stem sprouting while the gap is still open; and 2) pre-harvest liana cutting will significantly reduce liana stem abundance, including stem spouts, in logging gaps. We further investigated the mechanism by which lianas recruit into gaps by examining whether the speed of liana recruitment differs in different zones of the gap (crown, root and bole). Knowing the speed and process by which lianas recruit into gaps and the specific zones of the gap that they invade is essential for understanding how lianas affect regeneration in gaps and for formulating effective liana management plans.

7.2. METHODS

Study site. We initiated this study in 1996, in and around a 500 ha area within a 2000 km² forest logging concession 100 km east of Kribi, Cameroon (3⁰ North, 10⁰ East). The 500 ha study area was located within a relatively flat, homogeneous area of the forest, although the topography of the entire forest ranges from undulating to rolling with some relatively small, isolated hills (Waterloo *et al.* 1997). The forest is evergreen, with a 25-40 m closed canopy and emergent trees surpassing 60 m in height (Parren and Bongers 2001). The mean annual rainfall in this area is approximately 2000 mm, with two distinct dry seasons that last from May until August and from December until March (Waterloo *et al.* 1997). Climbers were abundant in the forest, with 408 stems (> 2 cm in diameter) per ha, comparable to other tropical forests (e.g., Gentry 1991b, Mascaro *et al.* 2003), particularly for large lianas greater than 5 cm in diameter (~ 113 stems per ha; Appanah and Putz 1984, Vidal *et al.* 1997, Parren and Bongers 2001). Logging tends to be relatively selective and light in this forest; on average only one tree over 60 cm in diameter is harvested per ha per year (Parren and de Graaf 1995, Jonkers and Van Leersum 2000).

Establishing a chronosequence of logging gaps. We established a chronosequence of logging gaps in areas of the forest that had been previously logged without pre-harvest liana cutting. We located six new (year 0) and six one-year-old (year 1) gaps

by following the progress of the logging company and marking new gap sites within several weeks of timber harvest. We used logging records to accurately determine six logging gaps that were approximately six years old. These gaps gave a chronosequence of six years in which we could examine liana infestation into logging gaps in which there had been no pre-harvest liana cutting. We selected gaps that were approximately the same size (mean gap size = $810 \text{ m}^2 \pm 314 \text{ s.d.}$), according to the Runkle method for gap size determination (Runkle 1981, 1982, Van der Meer *et al.* 1994). The six-year-old gaps were located about 6 km from the zero- and one-year old gaps in the same expanse of forest, which had similar tree and liana abundance (Parren unpublished data).

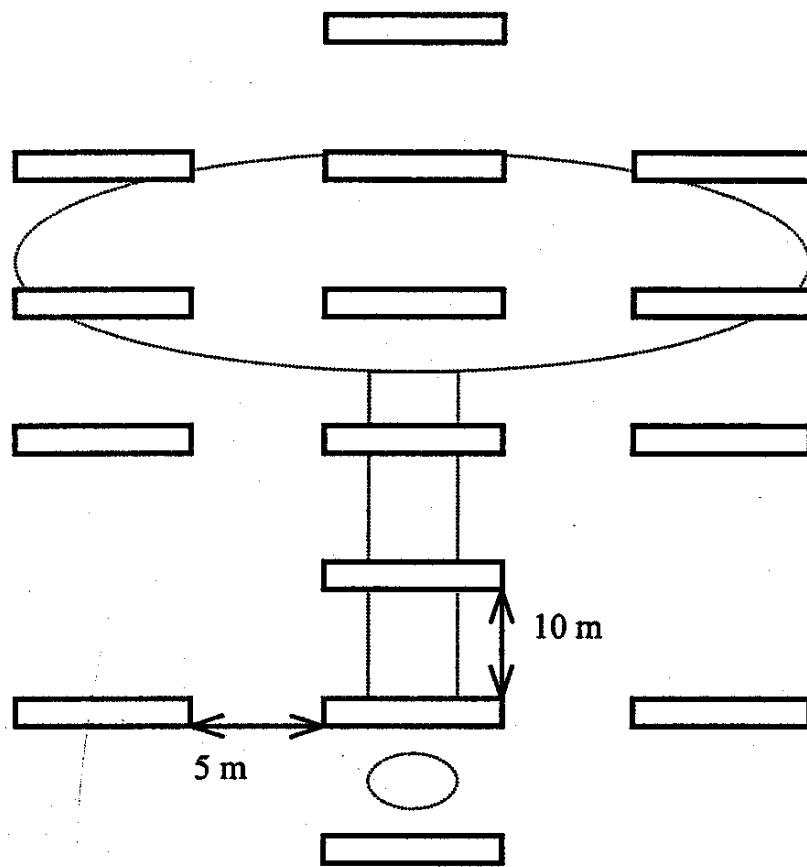


Figure 7.1. Sampling design for each treefall gap. Each rectangular box represents a 1 x 5 m subplot in which we sampled all lianas and trees > 1 cm dbh and taller than 1 m. We sub-sampled all liana ramets > 1 mm dbh in the leftmost 1 x 1 m section of each 1 x 5 m subplot. We divided the gap into two zones: the root/bole zone consisted of the bottom seven subplots and the canopy zone consisted of the top seven subplots.

We divided each of the gaps into the crown and the root/bole zone (Fig. 7.1). Using logging records, we could accurately locate tagged stumps of the felled trees and knowing the tree heights, we were able to accurately determine the locations of the

root/bole and crown zones. We combined the root and the bole zones because it was not always possible to distinguish between these two zones, whereas the distinction between the canopy and bole zones was, in nearly all cases, very clear. In each of these two zones, we established up to eight 1 x 5 m subplots, in which we censused all trees and lianas > 1 m in height. The grid layout was designed to accurately estimate the entire gap area affected by the treefall (Fig. 7.1).

Pre-harvest liana cutting gap selection. Within the 500 ha study area, we established six square 1 ha plots surrounded by a 100 m buffer zone. Nine months prior to logging, we cut all lianas in these plots and in the surrounding buffer zones. We used gaps from the six, one-year old gaps from the chronosequence study in which the lianas were not cut, to serve as control plots. The one-year-old liana-cut and uncut gaps were logged at approximately the same time to control for temporal differences in liana and tree recruitment, and each treatment was located in nearby adjacent areas of the forest. Prior to cutting, liana abundance did not differ between the blocks (Parren unpublished data). One year following tree harvest, we located six similar-sized logging gaps in each of the liana-cut and control plots. The mean gap size was $658 \text{ m}^2 \pm 200$ (sd), and mean gap sizes did not significantly differ among the liana-cut and control plots (669 m^2 and 641 m^2 , respectively). We partitioned the gaps into root/bole and canopy zones using the same methodology that we had used for the chronosequence gaps described above (Fig. 7.1).

Gap censuses. One year following tree harvest (21 months after liana cutting), we censused the lianas and trees within each of the 1 x 5 m subplots of the liana-cut and control gaps as well as the chronosequence gaps. We measured the abundance as well as the diameter 130 cm from the roots (dbh) of all liana individuals and trees > 1 cm dbh that broke the plane of the 1 x 5 m subplots 1 m above the ground, as well as the height for the trees meeting these criteria. We considered a liana to be a distinct individual (genet) if it was independently rooted and was not obviously attached to any other liana stem (methods follow Schnitzer and Carson 2001, Burnham 2002, Mascaro *et al.* 2003). We acknowledge, however, that we were not always able to distinguish liana ramets from genets because of current or previous underground connections between stems (see Schnitzer and Carson 2001, Gerwing and Vidal 2002, Mascaro *et al.* 2003). We also counted all liana stem sprouts > 1 mm diameter (ramets), including all multiple stems of each individual. Because of the large number of liana sprouts, we restricted our sampling of these small stems to the leftmost 1 x 1 m section of each 1 x 5 m subplot (looking up the tree from the root zone; Fig. 1), but we present the stem sprout data in units of 5 m^2 so that they are comparable to the liana genet data. For each of the above-mentioned variables, we averaged the number of subplots per zone and used the gap as our unit of replication (n=6). For each tree, we visually estimated the level of infestation of lianas into the tree's crown. For liana infestation of the tree's crown, we used the following scale: 1 = no lianas in tree; 2 = lianas on stem only; 3 = at least one liana in the crown, but no lianas connecting crown with any other trees; 4 = at least one, but typically more, lianas in crown and lianas connecting crown with other trees; and 5 = lianas completely covering tree crown (methods modified from Clark *et al.* 1993). To estimate canopy openness, we visually assessed the amount of open sky above the center of each of the 1 x 5 m subplots in the gap, 2 m above the ground. We assigned canopy openness as one of four categories: **1** = 0-10%; **2** = 11-50%; **3**

= 51-90%; and 4 = 91-100% openness. We used relatively broad liana infestation and canopy openness classes in order to minimize our estimation error.

Data analyses. We analyzed recruitment of lianas and trees into the six-year chronosequence of logging gaps and the response of lianas and trees to pre-harvest liana cutting using two-way analysis of variance (ANOVA; SAS institute 2000). For the chronosequence analysis, we included the gap age (0, 1, and 6) and zone (crown vs. root/bole) as the independent variables; and liana abundance (> 1 cm dbh), number of liana stem sprouts, tree abundance, tree dbh, tree height, tree infestation, and canopy openness as the dependent variables. We divided the trees into either saplings (1-4 cm dbh) and trees (>4 cm dbh); however, we concentrated our analyses on the saplings in order to capture the dynamics of gap-phase regeneration following logging (Schnitzer and Carson 2001). For the pre-harvest liana cutting experiment, we used an ANOVA similar to the other analyses, but we substituted the liana cutting treatment (liana-cut vs. control) for gap age. We analyzed the data to ensure that they conformed to the assumptions of ANOVA and log-transformed the number of lianas and canopy openness so that their distribution was normal. Because the large tree data were not normally distributed even with log-transformations, we analyzed them using Kruskal-Wallis non-parametric analyses, which do not assume a normal distribution (Sokal and Rohlf 1995).

7.3. RESULTS

The speed of liana recruitment into logging gaps. Liana abundance was initially low in logging gaps, but lianas recruited heavily within one year, mostly as ramets via stem sprouting, and they remained in high abundance throughout the six-year study period. Within several weeks of timber extraction (year 0), there was an average of 20.7 liana stem sprouts > 1 mm dbh per 5 m² subplot throughout all zones of the gap (Fig. 7.2a). By year one, however, the number of liana stem sprouts was significantly higher, averaging 34.7 per 5 m² ($P = 0.003$; Table 7.1; Fig. 7.2a) and remained essentially unchanged by year six (31.1 liana stems per 5m²). The number of larger lianas (genets > 1 cm dbh) remained the same between years zero and one (1.5 and 1.6 stems per 5m², respectively), but increased significantly to 3.7 by year six ($P = 0.002$; Table 7.1, Fig. 7.2b). These findings suggest that liana stem sprouts recruit into gaps within the first year and that many of these stems are able to persist and grow into the 1 cm dbh size-class by year six, at which point many of them may become indistinguishable from genets. Although most of the regeneration that we observed was from ramets, lianas probably also recruited into the gaps from seed; however, we cannot quantify the proportion of liana ramets and genets.

Liana colonization in relation to gap zone. Both liana ramet and genet abundance were significantly greater in the root/bole zone than the crown zone. There were 32.5 ± 1.8 (se) liana stem sprouts per 5 m² in the root/bole zone compared to 25.1 ± 2.5 in the crown zone ($P = 0.02$; Fig. 7.2a; Table 7.1). For individual liana stems (genets > 1 cm dbh), there was an average of 2.6 ± 0.3 per 5m² in the root/bole zone and 2.0 ± 0.4 in the crown zone (Fig. 7.2b); these differences, however, were not statistically significant ($P = 0.54$; Table 7.1). The lack of a significant interaction between liana colonization and gap zone suggests that lianas were consistently more abundant in the root/bole zone than the crown zone.

Table 7.1. Analysis of variance for the chronosequence plots (0, 1, and 6 years after tree felling) and for the pre-harvest liana cutting vs. control plots. An interaction term was used in the model but was not shown here because it was not significant for all cases except canopy openness for the liana-cut vs. control plots ($p = 0.05$). The number of degrees of freedom was two for the tests among the chronosequence plots and one for the tests between the liana-cut and control plots.

Source	<i>Treatment</i>			<i>Zone</i>		
	ss	F	P	ss	F	P
	Chronosequence plots					
# Liana stem sprouts	1265.79	7.28	0.003	497.85	5.73	0.02¹
#Lianas (>1cm dbh) ²	7.98	7.72	0.002	0.20	0.39	0.54
# Saplings (1-4 cm dbh)	410.72	6.28	0.005	1.78	0.05	0.82
Sapling dbh	0.70	3.32	0.05	0.12	1.14	0.29
Sapling height	0.46	1.66	0.30	0.07	0.38	0.54
Sapling infestation	2.02	0.19	0.19	0.01	0.01	0.48
Canopy Openness ²	1.95	13.01	< 0.0001	0.33	4.44	0.04¹
	Liana-cut vs. Control plots					
# Liana stem sprouts	796.95	13.55	0.002	534.40	9.10	0.007¹
#Lianas (>1cm dbh)	534.40	9.10	0.03	0.16	0.24	0.63
# Saplings (1-4 cm dbh)	3.76	0.14	0.71	49.59	1.83	0.19
Sapling dbh	0.27	2.00	0.17	0.08	0.60	0.45
Sapling height	2.18	8.86	0.008	0.15	0.63	0.44
Sapling infestation	9.68	29.97	< 0.0001	1.15	3.56	0.07
Canopy Openness	2.91	8.64	0.008	0.05	0.15	0.70

¹ In each case the mean number of trees and lianas was greater in the root/bole zone than in the crown zone.

² Log transformed to normalize data.

Table 7.2. Kruskal-Wallis analyses for the number and the level of liana infestation of big trees (> 4 cm dbh) in chronosequence plots (0, 1, and 6 years after tree felling) and for the pre-harvest liana cutting vs. control plots. The number of degrees of freedom was two for the tests among the chronosequence plots and one for the tests between the liana-cut and control plots.

Source	<i>Treatment</i>		<i>Zone</i>	
	Chi-Square	P	Chi-Square	P
Chronosequence plots				
# Trees (> 4 cm dbh)	4.66	0.10	4.33	0.04¹
Tree infestation	5.30	0.07	3.28	0.07
Liana-cut vs. Control plots				
# Trees (> 4 cm dbh)	0.001	0.97	4.09	0.04¹
Tree infestation	8.25	0.004	0.62	0.43

¹ In each case the mean number of trees and lianas was greater in the root/bole zone than in the crown zone.

Figure 7.2.

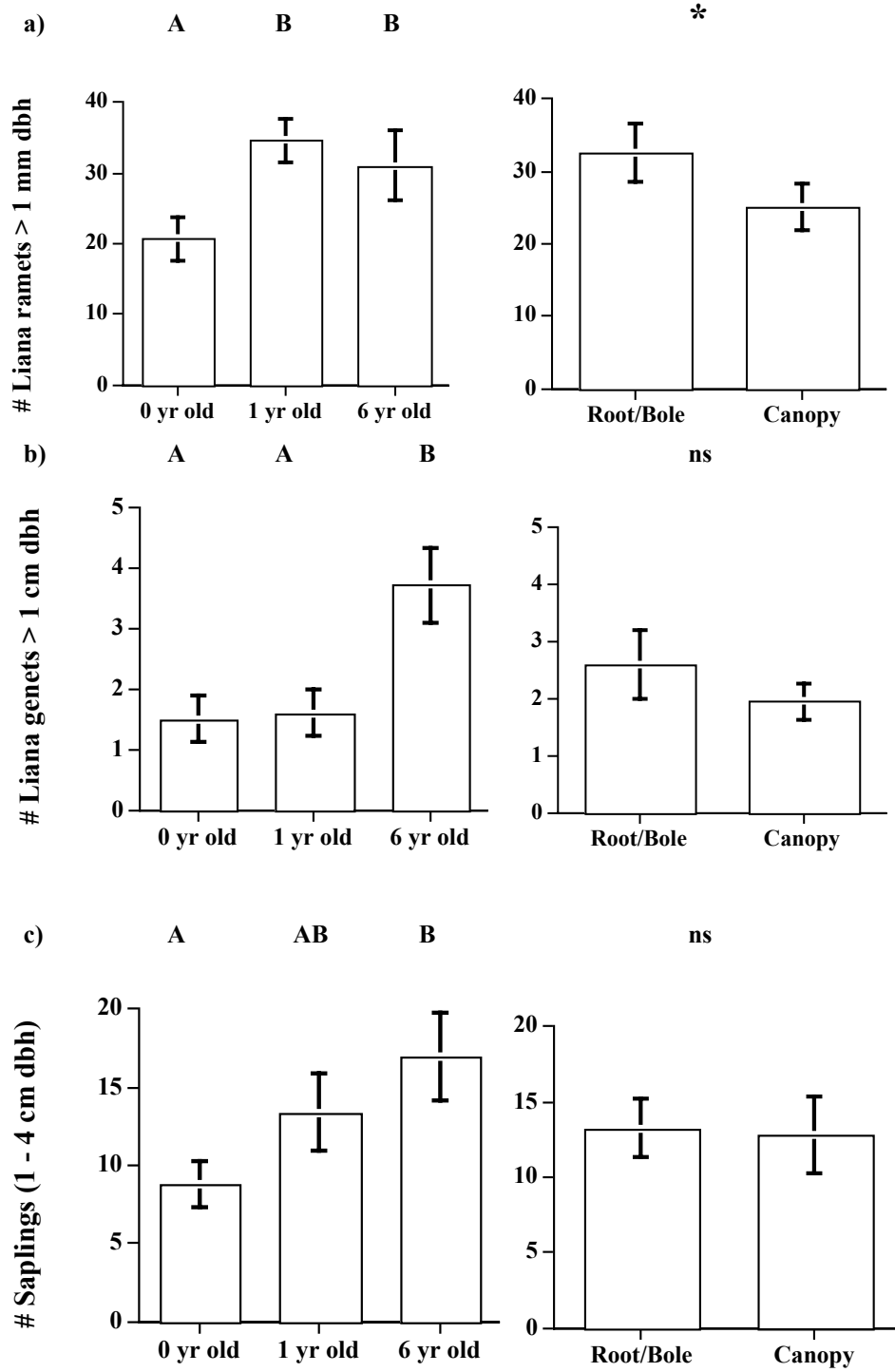


Figure 7.2. continued

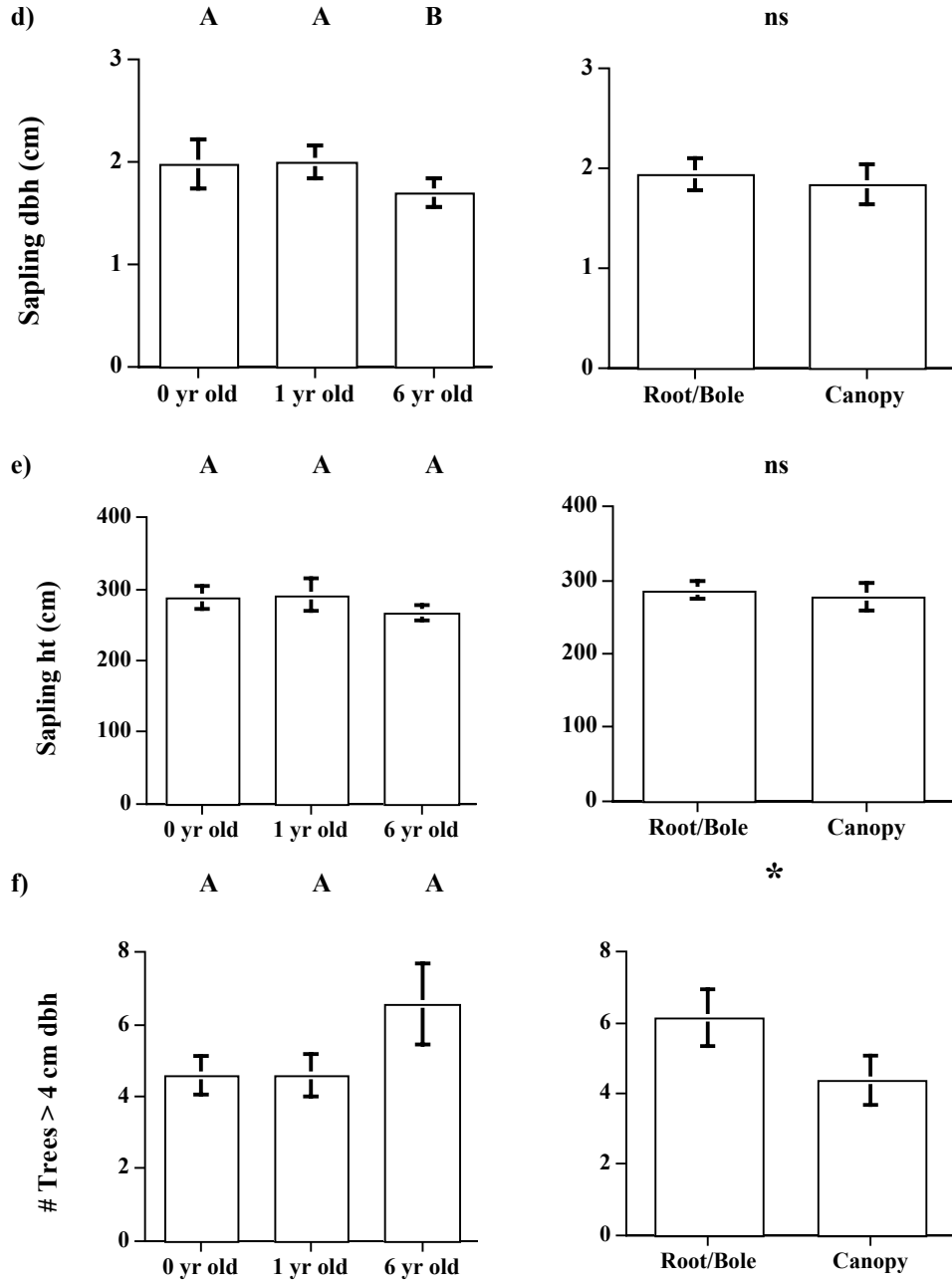


Figure 7.2. continued

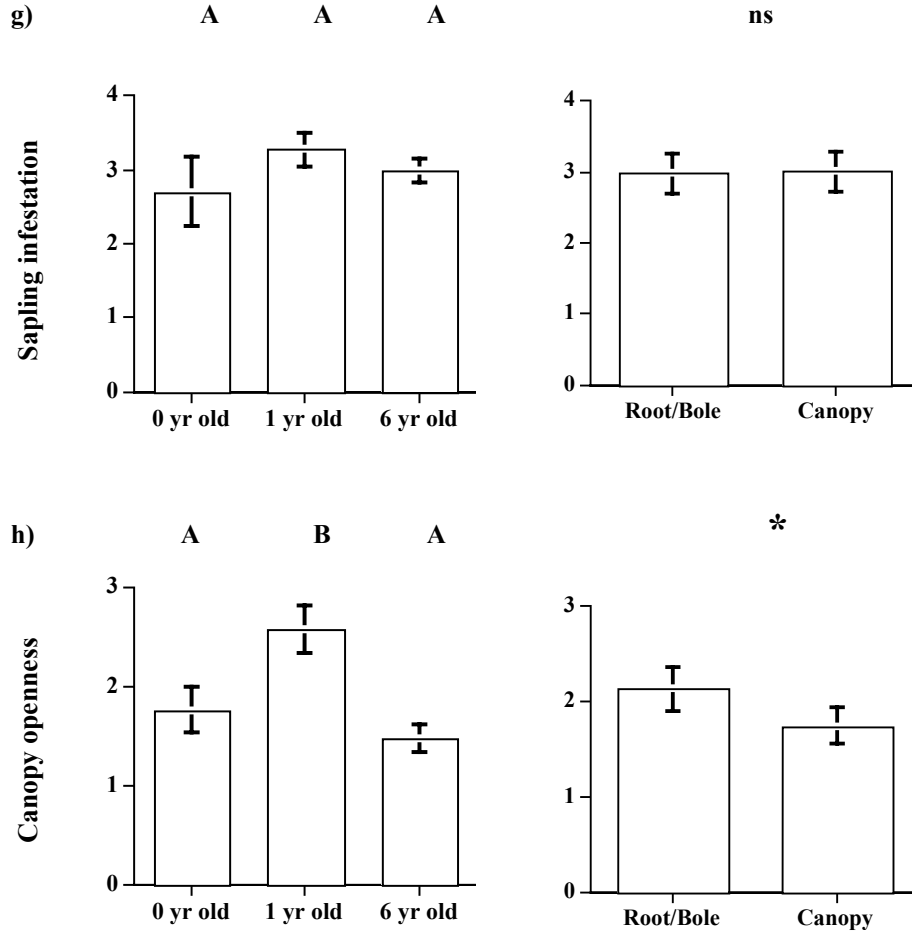


Figure 7.2. Mean liana and tree recruitment per 5 m² area into new (0 yr old), 1-, and 6-year old single-tree timber extraction gaps (column 1) and the zone of the gap (root/bole and canopy) into which the lianas recruited (column 2). We classified trees as either saplings (1 - 4 cm dbh) or trees (> 4 cm dbh). We divided lianas into two groups: 1) liana stem sprouts (ramets) > 1 mm dbh; and 2) liana individuals (genets) > 1 cm dbh. Different letters denote significant differences among the different aged logging gaps. Asterisks denote significant differences between the gap zones. Errors bars represent ± 1 standard error. Data for the number of large lianas (> 1 cm dbh) and sapling canopy openness were log transformed to normalize the data; non-transformed data are presented.

Sapling and tree colonization in logging gaps

Mean sapling abundance increased significantly in logging gaps by year six, suggesting that relatively small, sapling-sized trees continued to recruit into the gaps after the first year (Fig. 7.2c; Table 7.1). Mean sapling diameter, however, decreased between years one and six (Fig. 7.2d), possibly because many of the larger saplings grew out of the 1 - 4 cm size class and were replaced by smaller ones. Indeed, larger trees (> 4 cm dbh) increased slightly, but not significantly by year six ($P = 0.10$; Fig. 7.2f; Table 7.2).

There were no differences in the mean height of saplings or the amount of liana infestation among the different aged gaps (Figs. 7.2e, g), even though liana abundance had increased significantly (Figs. 7.2a, b). Canopy openness, however, was significantly higher in year one than in years zero or six; the latter two years were not significantly different from each other (Fig. 7.2h, Table 7.1). Canopy openness also differed significantly between the treefall zones, with an average openness index of 2.1 ± 0.1 (se) in the root/bole compared to 1.8 ± 0.2 (se) the canopy zone ($P = 0.04$; Table 7.1). The higher light levels in the root/bole zone may have enhanced the recruitment of trees into the larger size class, with large trees being significantly more abundant in the root/bole zone compared to the crown zone ($P = 0.04$; Fig. 7.2f; Table 7.2).

The effects of liana cutting in logging gaps

Pre-harvest liana cutting reduced the number of lianas in logging gaps one year after timber extraction. The average number of liana stem sprouts (> 1 mm dbh) and liana individuals (> 1 cm dbh) were both significantly lower in the liana-cut than the control gaps (Figs. 7.3a, b; Table 7.1). For liana stem sprouts, there were 36.7 ± 2.4 (se) per 5 m^2 in the control plots, while only 24.3 ± 2.4 (se) in the liana-cut plots. There was twice the number of lianas > 1 cm dbh per 5 m^2 in the control gaps compared to the liana-cut gaps (1.6 ± 0.3 se vs 0.8 ± 0.3 se, respectively). As in the chronosequence gaps, liana stem sprouts were significantly more abundant in the root/bole zone than in the canopy zone, but liana genets did not differ between the gap zones.

These findings demonstrate that even though lianas sprout vigorously after cutting, pre-harvest liana cutting still significantly reduced the number of liana stems, including multiple stem sprouts, in logging gaps. Correspondingly, the average amount of liana infestation on both saplings and trees was significantly lower in the liana-cut compared to the control gaps (Figs. 7.3f, g; Tables 7.1, 7.2). Surprisingly, both the average sapling height and the amount of canopy openness were significantly lower in the liana-cut plots (Figs. 7.3e, h; Table 7.1). The abundance and diameter of saplings and trees and the height of trees, however, did not differ significantly between the liana-cut and the control gaps (Figs. 7.3 c, d; Tables 7.1, 7.2).

Figure 7.3.

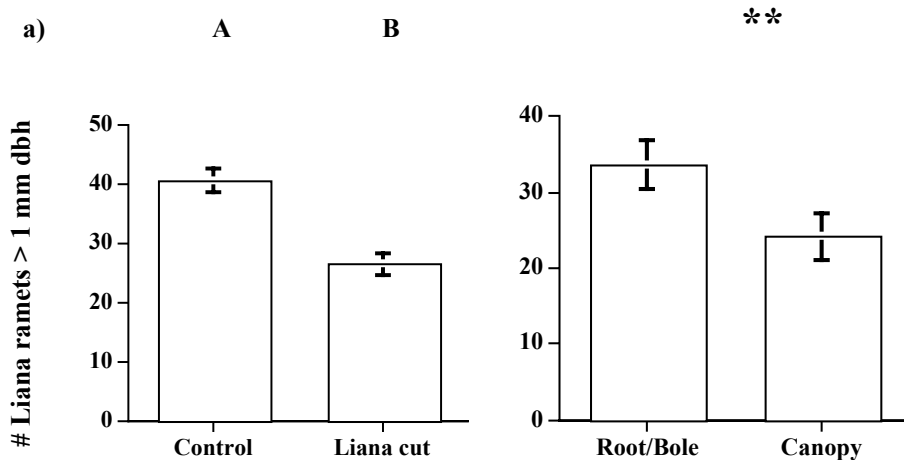


Figure 7.3. continued

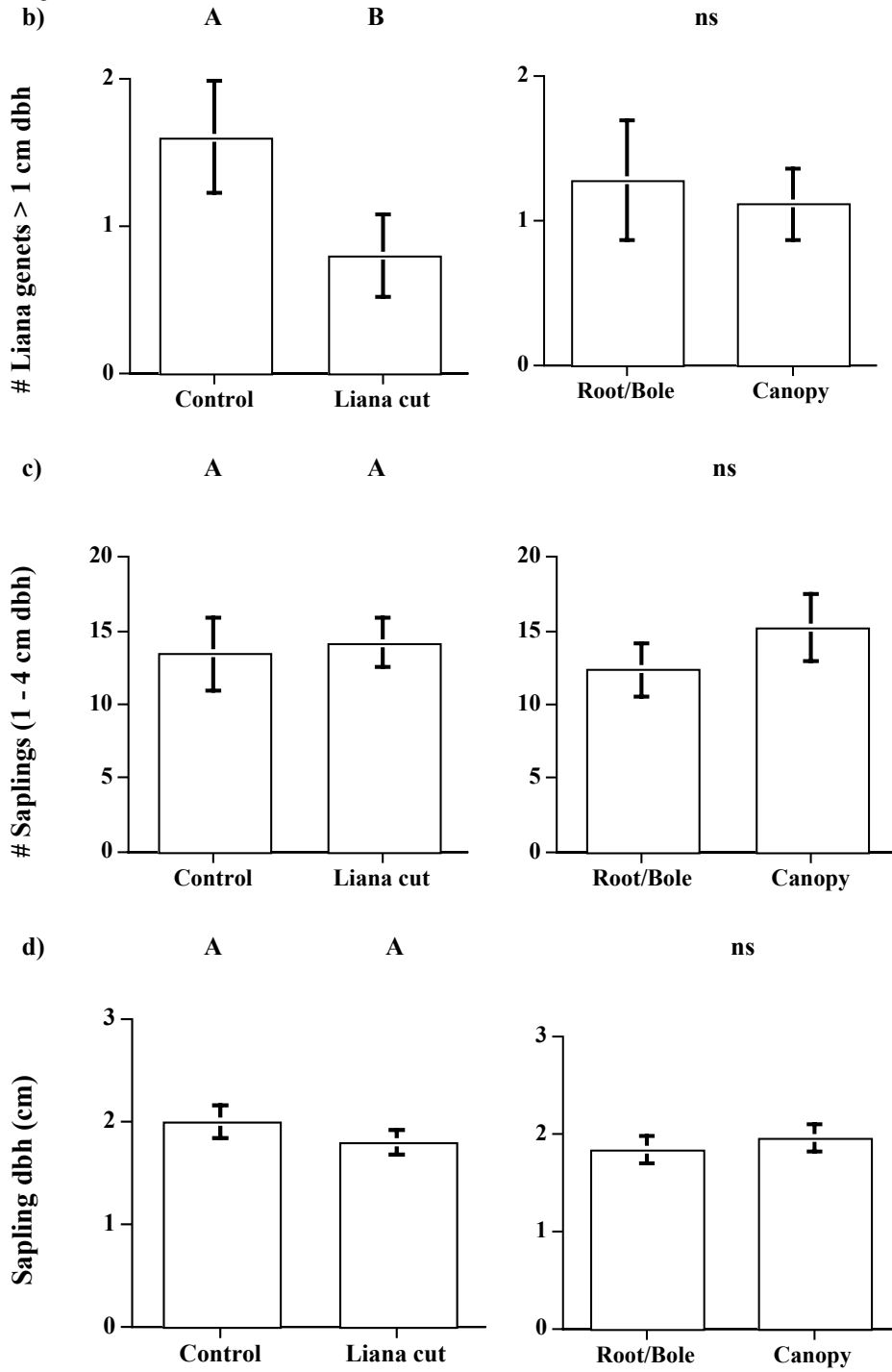
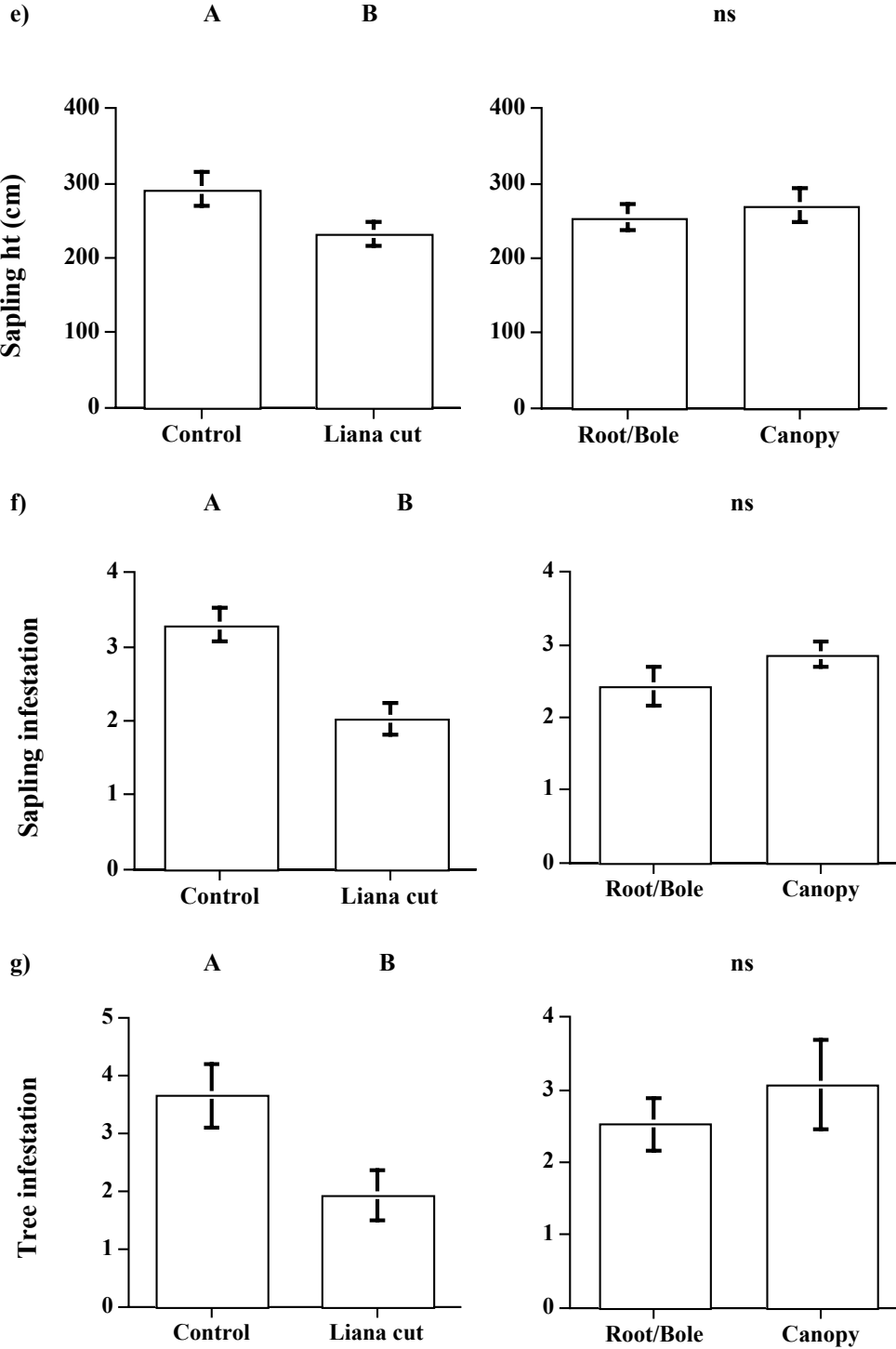


Figure 7.3 continued



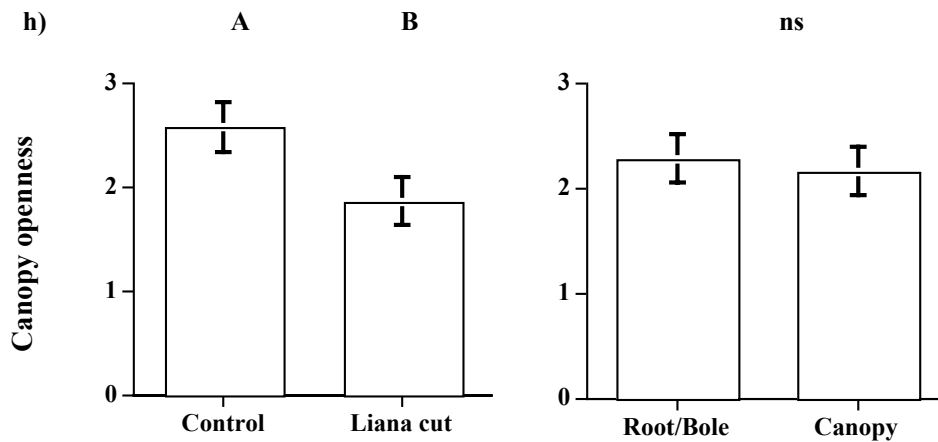


Figure 7.3. Liana and tree recruitment in one-year old, single-tree timber extraction gaps in which lianas were either left uncut (Control) or all lianas were cut 9 months prior to timber extraction (column 1) and the zone of the gap into which the lianas recruited (column 2). We classified trees as either saplings (1 - 4 cm dbh) or trees (> 4 cm dbh). We divided lianas into two groups: 1) liana stem sprouts (ramets) > 1 mm dbh; and 2) liana individuals (genets) > 1 cm dbh. Different letters denote significant differences among the control and liana-cut logging gaps. Asterisks denote significant differences between the gap zones. Error bars represent ± 1 standard error.

7.4. DISCUSSION

How lianas colonize logging gaps

Lianas recruited into logging gaps in very high abundance within one year of gap formation. The majority of these lianas were ramets, sprouting from fallen liana stems. These liana ramets appeared to persist in the gaps for many years, eventually reaching the one cm dbh size-class within six years. Our findings are consistent with those of other studies of liana invasion in both natural and logging gaps (Putz 1984a, Babweteera *et al.* 2000, Schnitzer *et al.* 2000, Tabanez and Viana 2000, Gerwing and Vidal 2002); although Kennard (1998) suggested that climber infestation is mainly a colonizing process, rather than being predominated by stump sprouts of surviving lianas. For example, in natural treefall gaps, Putz (1984a) found that lianas were very abundant in young gaps and decreased only after many years. Schnitzer *et al.* (2000) also reported that lianas recruited en masse into natural treefall gaps, reaching very high abundance and often completely suppressing tree regeneration within five years of gap formation. In Brazil, Thomson *et al.* (1998) monitored small trees and lianas over a period of four years in different gap sizes and concluded that liana densities in large gaps were twice those of interior forest. In a selectively logged forest in Uganda, Babweteera *et al.* (2000) also found that lianas recruited rapidly and abundantly into large logging gaps (> 400 m²). Similarly, lianas recruit in extremely high abundance into such large-scale disturbances as abandoned pastures and areas affected by hurricanes (Horvitz *et al.* 1998, DeWalt *et al.* 2000).

Interestingly, we found the majority of liana stems, particularly ramets, in the root/bole zone of the gap (~33 stems per 5 m²; Table 7.1). This zone may have had the most ramets because stem sprouts can originate along the entire length of a fallen

liana stem. If the liana is rooted at the base of the fallen tree, which many of the lianas were, then most of the stem sprouts will also be at the base and along the bole of the fallen tree. In addition, the root/bole zone may have had the most light and least amount of competition for below-ground resources. However, there were still a substantial number of stem sprouts in the canopy zone (~ 25 stems per 5 m²), demonstrating that lianas can recruit into both zones in high abundance. Identifying the zone of the gap into which the majority of the lianas recruit is important for devising strategies to control lianas in managed forests.

Pre-harvest liana cutting as a method for reducing liana load on trees

Our findings demonstrate that pre-harvest liana cutting significantly reduces liana abundance in post-logging gaps (see also Gerwing and Vidal 2002), which resulted in significantly lower rates of liana infestation of trees. The detrimental effects of lianas on trees are well established in the literature (Nicholson 1958, Putz 1984a, Stevens 1987, Dillenberg *et al.* 1993, Schnitzer *et al.* 2000, Pérez-Salicrup and Barker 2000, Schnitzer and Bongers 2002), and thus we expect that in the long run, trees with high liana infestation will have less vigorous growth and reproduction. After one year, however, canopy openness was significantly higher and saplings were taller in the control plots, which had substantially more lianas (Figs. 7.3e, h). The positive relationship between liana abundance and canopy openness was probably due to the ability of lianas to keep the gap open for long periods of time. Schnitzer *et al.* (2000) reported that lianas favor the growth of some trees, primarily pioneers, at the expense of shade-tolerant trees, possibly by keeping gaps open for many years, thus giving the pioneers a chance to grow into the canopy (see also Putz 1984a). In this current study, the large number of lianas may have also inhibited canopy closure (Fig. 7.3h) and thus both the lianas and saplings grew slightly more in the higher-light environment. We suspect, however, that this benefit of increased light during the first year will be short-lived, and that the saplings with lower liana infestation will eventually surpass the height and vigor of trees that have more lianas in their crowns. If competition with lianas for below-ground, rather than above-ground resources in gaps is the mechanism that ultimately limits sapling growth, as has been suggested by a number of recent studies (Dillenberg *et al.* 1993, Pérez-Salicrup and Barker 2000, Schnitzer *et al.* in review), then sapling growth should also decrease as the surrounding lianas increase in abundance and size.

Managing lianas in tropical forests

The decision to cut climbers in managed forests is complex, with a number of factors to consider. Treefall gaps, whether they are natural or anthropogenic in origin, appear to provide the optimal regeneration site for lianas (Putz 1984a, Babweteera *et al.* 2000, Schnitzer *et al.* 2000, Schnitzer and Carson 2001). Consequently, managing lianas in gaps may be the key to controlling liana abundance in logged forests. Although it is likely that no reasonable management plan will be able to completely eradicate lianas from managed forests because of the ability of lianas to resprout copiously from cut and fallen stems, our findings suggest that pre-harvest climber cutting reduces the number of regenerating stem sprouts, which ultimately should lead to more rapid canopy tree regeneration. Pre-harvest climber cutting also provides a number of other beneficial results, including reducing the collateral damage to other trees and reducing the size of logging gaps, (Appanah and Putz 1984, Putz 1984a, 1985, Pinar and Putz 1994, Vidal *et al.* 1997,

but see Parren and Bongers 2001). A potentially important long-term result of logging and liana cutting (which is sometimes followed by fire) may be a change in the composition of the liana community, favoring those species that can readily resprout in response to disturbance, while putting at a disadvantage those species that rely primarily on sexual reproduction (Bell 2001, Bond and Midgley 2001, del Tredici 2001, Gerwing and Vidal 2002). For instance, Parren and Bongers (2001) reported that some species of liana resprouted readily after cutting, while others were much more vulnerable (see also Videl *et al.* 1997). To date, however, the potential changes in liana communities in response to cutting have received very little attention (Gerwing and Vidal 2002).

Post-harvest liana cutting may also be beneficial for controlling liana regeneration in logging gaps. Although Putz (1985) argued that there was very little benefit of post-harvest liana cutting and that it is very difficult to kill the multiple stems of recumbent lianas, a combination of selective pre- and post-harvest climber cutting might be the best option for controlling liana regeneration after logging. The costs versus benefits of post-harvest climber cutting, of course, must be assessed for specific regions in the tropics (e.g., Pérez-Salicrup *et al.* 2001a). Some of the considerations of this analysis most certainly will include: the cost of labor, the amount of effort for post-harvest climber cutting, and, most importantly, the effectiveness of post-harvest climber cutting in controlling liana resprouting and regeneration from seed.

Knowing the zone of the gap into which lianas recruit provides additional information on how lianas invade logging gaps and thus will be instrumental in devising management plans on how to control liana regeneration after logging. For example, if lianas regenerate exclusively into the crown zone, then pre-harvest liana cutting may be necessary both around the bole of the target tree, where many of the lianas in the canopy originate, as well as in a larger area of forest around the target tree. The rationale for this latter treatment is that large lianas in the canopy of a tree may actually be rooted quite far from the base of that tree (Putz 1984a), and thus if the above ground portion is cut and subsequently dies, then it cannot sprout from its recumbent stem after the tree is felled. Conversely, if lianas recruit exclusively into the root and bole zones, then pre-harvest liana cutting around the base of the target tree may be the most efficient method for limiting liana regeneration and therefore cutting in a larger area would not be necessary.

We found that liana sprouts consistently recruited into the root/bole zone in much higher abundance than in the crown zone (Fig. 7.2a), supporting the management strategy of cutting the lianas found around the base of the tree. However, lianas were still abundant in the crown zone, albeit in somewhat lower density, suggesting that both management strategies have some merit. Overall, we suggest that cutting lianas located in the area beneath the canopy of the target tree may be the best overall strategy for reducing liana infestation in logging gaps and promoting tree regeneration. This strategy will certainly remove most of the lianas in the canopy of the regenerating trees as well as greatly reduce below-ground competition, which may be important for liana-tree competition (Dillenberg *et al.* 1993, Pérez-Salicrup and Barker 2000, Schnitzer *et al.* in review).

Conclusions

Lianas recruit rapidly into logging gaps in high abundance, within the first year of gap formation. Recruitment was mostly from stem sprouts; many of which apparently became independently rooted individuals that were indistinguishable from genets within six years. Most of the liana recruitment was into the root/bole zone of logging gaps, but lianas were still in fairly high abundance in the canopy zone. Our findings demonstrate that pre-harvest liana cutting significantly reduced the number of lianas that regenerated in logging gaps, resulting in saplings that were infested with fewer lianas and were significantly taller than in the gaps where lianas were not cut prior to logging. Based on our findings and those of other studies, we recommend pre-harvest liana cutting in the area beneath the canopy of the target tree for controlling liana regeneration and promoting tree regeneration in logging gaps.

Acknowledgements

This study is a contribution to the Tropenbos-Cameroon Programme. We thank the Tropenbos Foundation and IRAD, Cameroon, for their support, and Wijma for being able to work in their logging concession. S. Mutsaers, M. Elad, S. Okie and J. Ango collected a large part of the field data. We thank A. Ercoli, D. Pérez-Salicrup, F. Sterck, and one anonymous reviewer for helpful comments on this manuscript.

8. SYNTHESIS

The relation between lianas and logging is largely dependent on the condition and species composition of the forest. In West Africa the forests are strongly influenced by events (disturbances) that took place in the recent past. The forests in Cameroon were quite unique for West Africa because they had never been logged before, unlike most other parts of this region where the second or more felling cycles have already occurred. This unlogged forest then provides a glimpse of the past by providing information on long-lived lifeforms such as trees and lianas, on species dominance (light-demanding vs. shade-tolerant) and species abundance. On the African continent very few liana studies have been made, even though it is claimed that lianas are very dominant in most forests. Their dominance also means that lianas are often regarded as a hindrance in logging operations, and that lianas can retard the development of the residual vegetation. This study investigated the role of lianas, the extent to which they are dominant in this region, and what options are available to reduce their negative impact. So far, little attention has been paid to lianas in sustainable forest management at the operational level. Recommendations are made here to address their importance.

8.1. PRESENT FOREST REFLECTS DYNAMICS OF THE PAST

West and Central African forests show the footprints of the past not only by the presence of charcoal and pottery but also by their species composition. Most commercially large-sized trees in the upper canopy are light demanding tree species due to prior disturbances. The rain forests of Africa witnessed major Bantu migrations in pre-colonial periods in which recurring fires and tree extraction led to forest conversion (Oslisly 2001, Vansina 1990). To what extent shifting cultivation for food crops played a role is still under debate, but it is certain that all these activities have altered the species composition in favour of commercially interesting light demanding species. The omnipresence of *Pycnanthus angolensis* and *Lophira alata* in the Ebom study site reveals large-scale disturbance in the past followed by a period in which the forest had time to recover with hardly any human interference (Chapter 1). This is confirmed by analysing the species composition and regeneration strategy of 16 one-ha plots in the Ebom forest. In nine of these plots the older trees preferred shifting cultivation fields for recruitment, while younger trees preferred gaps and closed forest conditions. This indicates that these plots once experienced large-scale disturbances (Van Gernerden *et al.* 2003). However, little is known about the length of the building period. Recently, Worbes *et al.* (2003) determined growth rates and the subsequent age of trees in a moist semi-deciduous forest in Cameroon. The unlogged forest investigated was determined as a very late secondary forest and would have taken about 200 years to reach the beginning of a mature forest stage after clear cutting. Most interestingly, Oslisly (2001) observed a period between 600 – 1,200 A.D. in which the forests in Gabon became depopulated. So the present forests might be no more than several hundred years old.

Nowadays, it is evident that rain forest boundaries are not stable, but depend on climatic cycles as the forest boundary either expands into savanna areas or retreats in the opposite direction (Maley 2001, White 2001). It currently appears as if forests in West and Central Africa are expanding northwards in countries extending from

Guinea to the Central African Republic (Fairhead and Leach 1998, Maley and Chepstow-Lusty 2001), while savanna enclosures are gradually disappearing in countries such as Gabon and the Democratic Republic of Congo (Tutin and White 1998). This forest expansion at the cost of savanna intrusion is at the same time counterbalanced by renewed forest fragmentation as a result of logging activities and forest conversion for other land uses. Notably, these West and Central African forests are currently rich in commercial timber species and have characteristic high liana abundance. To a large extent the natural vegetation dynamics are dictated by climate, mainly rainfall. Human activity associated with migration patterns resulting from changes in climate, pre-colonial wars and limited soil fertility is superimposed on this. The present day species composition and abundance reflect forest disturbance regimes of the past, aggravated by recent disturbances. These natural and human induced processes have led to intensive forest fragmentation, clearings in the forest and thus to an increase in forest edges. The abundance of lianas suggests that this lifeform in particular has benefited most from this situation.

8.2. LIANA ABUNDANCE

In harvesting and silvicultural systems in West Africa, lianas play a dominant role. Dawkins (1960) noted that liana-tangles reign supreme in West Africa and North Borneo. Dawkins also remarked that lianas form the greatest drawback in tropical silviculture, where steps have to be taken to control their proliferation and interference with trees. In West Africa (Chapter 4), tangles of herbs, shrubs and climbers are found to block tree regeneration after too drastic a canopy opening in silvicultural experimental sites such as Mopri in Côte d'Ivoire. In Ghana, Foggie (1960) and Osafo (1970) noted that any treatment designed to give more light to the regeneration would also stimulate growth of lianas since many West African liana species are light demanders. Nevertheless, very little research has been conducted on the ecology of lianas in Africa and seems to be limited to the work done by Caballé (1986) in Gabon and Kokou *et al.* (1999, 2002) in Togo. Caballé worked in primary moist forest while Kokou worked in a highly fragmented landscape with rather small (< 4000 ha) forest fragments left in the savanna intrusion which penetrates deep into the African moist forest belt, the so-called Dahomey Gap. Their work might provide an insight into liana-tree interactions as a consequence of edge effects by different forest sizes and statures. Furthermore, these studies may be comparable to the work done in South America by Oliveira-Filho *et al.* (1997), Gerwing and Lopes Farias (2000) and Laurance *et al.* (2001) that show the aggregation of lianas at forest edges compared to the forest interior. Recently, Kuzee (in prep.) analysed the role lianas play in the recovery of degraded forests in southern Côte d'Ivoire. She studied liana-tree interactions showing that below-ground competition is more important than above-ground competition (Schnitzer *et al.* in review).

Liana assessment forms no special part of forest inventory and has received little attention compared to trees. Problems related to liana assessment are (1) to define the point of measurement, (2) the risk of remeasuring the same individual (ramets), (3) the fact that it is not always clear whether other types of climbing lifeforms are also included, such as hemi-epiphytes and climbing palms (Chapter 3). The different definitions of what is considered to be a liana and the different ways of measurement mean that comparisons between different sites and continents are difficult to make

and may over- or under-estimate liana numbers at certain sites. Comparisons are also difficult to make since often different lower limits are used: most researchers measure all lianas over 2 cm but Gentry (1982, 1989, Gentry and Dodson 1987) for instance measured everything over 2.5 cm (Chapter 3). Also a wide variation of plot sizes is used, thus making it hard to provide species richness at standard sizes. The level of disturbance, although a very important factor influencing liana abundance, is not always well described. Whether logging took place, whether lianas were harvested as non-timber forest products or whether the site underwent shifting cultivation in the past all seriously influence liana abundance and diversity (e.g. Zagt *et al.* 2003). Seasonality determined by rainfall patterns and altitudinal gradients can also influence liana abundance but are rarely taken into account (but see Balfour and Bond 1993, Heaney and Proctor 1990).

It is generally assumed that lianas in West African forests are more abundant than elsewhere and, accordingly, that liana infestation rates are higher. However, liana abundance in West African forests is not extremely high (Chapter 5), while liana infestation is rather low (Chapter 4). Only seasonal forests in the Indian subcontinent and floodplain forests in the Neotropics show similar low infestation levels. The Ebom forest can be considered to have abundant lianas with 408 stems (> 2 cm in diameter) per ha and large lianas 113 stems (\geq 5 cm in diameter) per ha (Chapter 5). This is not particularly high compared to other tropical forests. With the many recent studies on the Neotropics, we now see that the proportion of infested trees in South American forests is extremely high (Chapter 4), as is liana abundance (Chapter 5), compared with African and Asian forests. Overall, the African and Asian moist forest studies with liana inventories are under-represented. Phillips *et al.* (2002) noted a marked increase in large lianas (> 10 cm) in unlogged Amazonian forests during the last few decades and attributed this to an increase of carbon dioxide in the atmosphere. Whether this is the real cause is still uncertain, however. In general, human activities in the forest have increased during the last few centuries so there are hardly any undisturbed forests left in the African moist forests (White and Oates 1999, Mbida Mindzie *et al.* 2001) and this is probably a major factor in explaining the increasing abundance of lianas. Similarly in 'liana forests' in South America, potsherds and charcoal have been found (Putz 1983, Alvira Reyes 2002, Kennard *et al.* 2002). To what extent an increase in large lianas (> 10 cm) in African forests will be detectable is not evident. Unlogged forests that have been monitored over long timespans are few in number, while overall logging and forest conversion is increasing. This leads to liana proliferation, but mostly in the smaller diameter classes (Chapter 4).

8.3. LIANAS AND THE NEED TO CONTROL LOGGING DAMAGE

Does climber cutting reduce felling damage?

The abundance of lianas and their capacity to connect multiple tree crowns is often associated with high damage levels when liana-laden trees are felled during logging. To reduce such logging damage it has often been advocated that liana cutting prior to logging is a worthwhile silvicultural treatment. Most of the initial experiences with liana cutting were gained in Southeast Asia. Fox (1968) and Appanah and Putz (1984) in Malaysia showed that logging damage could be reduced by almost half after pre-harvest liana cutting operations. Liana cutting was optimal in combination with

poisoning of the cutting edge of lianas by the herbicide 2,4,5-T butyl ester (Appanah and Putz 1984). Since the 1980s however, poisoning of lianas and trees has been almost completely banned. The growing deforestation and growing concern for improved management of tropical forests in the 1990s resulted in the growth of reduced-impact logging (RIL). Many experiments were initiated, mostly comparing conventional operations with RIL. These experiments are concentrated in South America and most often include the prescription of liana cutting. Examples are the studies in the Amazon by d'Oliveira and Braz (1995), Barreto *et al.* (1998), Vidal *et al.* (1997), Pérez-Salicrup *et al.* (2001), Gerwing (2001), Gerwing and Vidal (2002), in the Mata Atlantica by Viana *et al.* (1997), and in the Guyana Shield by Van der Hout (1999). In general, lower losses at the felling site were recorded (less splitting and higher volumes per felled tree) and less residual stand damage which could be partly attributed to pre-harvest liana cutting.

Other experiments, however, did not result in a significant reduction of damage levels. The experiment in the Ebom forest, Cameroon, found liana cutting to be hardly beneficial in reducing gapsizes and felling damage (Chapter 6). Similarly, experiments in Borneo showed that liana cutting did not alter felling deviation and did not reduce felling damage (Cedergren 1996, Sist *et al.* 2003). This shows that forest heterogeneity may play an important role, that is, the density of trees and lianas and overall forest structure, as well as harvesting aspects, such as the number (or density) of trees to be harvested per hectare, whether or not only emergent trees are harvested, and the minimum exploitable diameter for each species to be harvested.

Post-harvest liana proliferation

Lianas are often reported to swarm *en masse* into treefall gaps, reaching very high abundance and often completely suppressing tree regeneration (Schnitzer *et al.* 2000, Schnitzer and Bongers 2002). Pre-harvest liana cutting can significantly reduce the number of lianas in felling gaps, as discussed in Chapter 7 and confirmed by a study by Alvira Reyes (2002) for a Bolivian forest. Most of these studies were done at relatively low harvesting intensities. However, the effect of liana cutting has not been tested yet at very drastically opened forests, where less than half of the basal area of unlogged forest conditions sometimes remain, leading to prolonged (decades) hampering of tree regeneration development (i.e. see Chapters 2 and 4 for Côte d'Ivoire, Kasenene 2001). We expect the effects of liana cutting to be even stronger in those cases. In Nigeria, Okali and Ola-Adams (1987), showed that repeated liana cutting after tree harvesting instead of pre-harvest liana cutting combined with canopy opening was beneficial for diameter increment of released trees and improved stocking of saplings. To date, too few detailed studies analysing the effect of liana cutting on the regeneration in felling gaps have been done in order to draw definite conclusions, but we expect that liana cutting generally will be effective.

Liana mortality and resprouting capacity

In addition to the negative effects of lianas on logging damage, liana cutting might also have an impact on the total liana population of the forest. Cut lianas can produce many sprouts which can then dominate and form blankets; but at the same time mortality of cut stems is high, which could negatively influence species diversity. Liana density can increase due to the high capacity of liana stems to

survive injuries and produce new sprouts (Peñalosa 1983, 1984, Fisher and Ewers 1991). In a liana forest in Bolivia, Pérez-Salicrup *et al.* (2001) observed that originally about 86% of all trees (≥ 10 cm dbh) were infested by lianas, while two years after liana cutting only 22% of these trees were still infested. The cut lianas present produced on average two sprouts two months after that treatment. The most vigorous individuals were large lianas (≥ 5 cm dbh). This percentage is rather low compared with the 66% of all individuals that were observed resprouting six months after liana cutting in Cameroon (Chapter 6) and 70% after seven months at another Bolivian site (Fredericksen 2000). In Cameroon, two years after liana cutting just 30% of the lianas survived (Chapter 6). Most studies that monitored the resprouting capacity of cut lianas lasted less than a year after liana cutting and found rather high resprouting capacities (Appanah and Putz 1984, Fredericksen 2000, Alvira Reyes 2002). From our findings we conclude that the mortality of sprouting lianas still increases the following year. However, those still alive produced a great number of sprouts per liana stump, with the potential to infest more than one support, thus increasing the chance of tree infestation.

Twenty years after liana cutting, Rollet (1983) found evidence of significant lower liana abundance in Amazonian forest. However, Dekker and de Graaf (2003) showed that this is not always the case in a forest of the Guyana Shield where liana cutting had been applied 20 years earlier. Surprisingly, lianas were sometimes found to be more abundant in treated plots than in control plots. This contrasting effect might be due to the forest's natural heterogeneity resulting in original differences in density of both lianas and palms at plot level. Palms can be quite dominant in Neotropical forests in contrast to African forests where palms are almost absent. Where palm density was high, lianas were found to be less abundant, and *visa versa*. It would seem that a heavy palm cover suppressed the development of lianas.

Effects on species composition

The effect of logging and liana cutting as a silvicultural treatment on liana composition has not been investigated in depth. The danger exists that in opened up forests, liana species composition will be reduced to liana species that are resistant to liana cutting and fire (Chapter 4). In Bolivia, Kennard *et al.* (2002) monitored tree and liana regeneration in felling gaps for 18 months after heavy disturbance (clearing, fire). A small group of lianas and sprouts of non-commercial tree species were found to dominate the post-disturbance gaps. This highlights the danger of increased disturbance regimes that might lead to unwanted species composition. In Guyana, Zagt *et al.* (2003) found that both liana species density and diversity increased four years after RIL application. This was most profound in heavily logged forest compared to moderately and lightly logged forest. A limited group of liana species responded negatively to increasing logging intensity and disturbances and they can be considered vulnerable. These species were far outnumbered by a group of species which showed a positive response and which started to dominate, while a great number of species were considered to be indifferent to changes. Since so few species appear to be strongly negatively affected by logging, no liana species were found to be good indicators for old growth forest, while those that responded positively to logging disturbances were found to be reasonable indicators for logging damage (mainly for skid trail areas). Nevertheless, care should be taken with logging

and liana cutting to avoid elimination of those species that respond negatively to these interventions.

Costs of liana cutting

Liana cutting could take up to 24 person-hours per ha in the Amazon since lianas are abundant in many of these forests, while in Cameroon only 4 person-hours were involved (Chapter 6). Not surprisingly, liana cutting could make up 25% of the additional costs to be made in RIL operations in the Amazon compared with conventional logging. However, this was compensated by higher volumes per ha recovered and a less dense skid trail network (better operational planning). So the overall costs remained mostly comparable with those involved in conventional logging operations. In the Bolivian Amazon, a trial with herbicide application on cut lianas at an additional cost of \$0.24 per ha meant that 60% of all cut liana stems were killed after seven months (Fredericksen 2000). Such a treatment is efficient but also indiscriminate in that it might eradicate most large lianas present. It remains questionable whether such treatment should be applied at an operational level.

What to do?

The conservation and maintenance of biological diversity should form part of any logging operation. Information on the flora of the concession should be clearly documented and verified by the results of a forest inventory. Protection and conservation of biodiversity, with particular consideration of the preservation of rare, threatened and endangered plant species, should be incorporated in management plans. Liana diversity is high in West Africa, since around 25% of the over 1000 species present in the Upper Guinea forest block are rare and/or endemic (Bongers *et al.* 2002). With the recent taxonomic work on West African trees and lianas by Hawthorne and Jongkind (in press), it should be possible to list all rare, threatened and endangered liana species in a country. Forest inventory teams should be trained to identify and map these liana species and to compare them with the West African distribution maps (Poorter *et al.* in press) so as to be able to set priorities. This should result in a zonation in timber and non-timber forest products of productive areas, protective areas, and areas to be restored which are degraded and poorly stocked. Fine-grained protection measures will also have to be introduced in productive areas, banning logging in a restricted zone surrounding all rare, threatened and endangered liana species (Hawthorne and Abu-Juam 1995, Hawthorne 1996). At the same time, the forest inventory teams can indicate trees to be felled on the compartment map, with their felling direction and indicate whether they possess abundant lianas on their trunk and crown.

Considering the above, it appears relevant to investigate whether liana cutting operations can be reduced in size and be made more selective. This may be cost effective and may reduce some negative ecological effects. Such recommendations have also been made by Vidal *et al.* (1997). Most likely a limited number of species that attain greater diameters are the agents for most of the damage. Some large size lianas will probably be more resistant to breakage and will cause crowns or branches to break off and to uproot entire trees in the process of treefall. Others will hardly contribute to this phenomenon on their own, but intertwined with other lianas in a kind of web structure they can cause similar problems. Large-sized liana species should be tested for their mechanical strength properties by the application of tests such as a tension tensile strength test, a torsion test, an impact bending test and a

rotting process test. This should lead to a ranking of liana species contributing to damage control after liana cutting. So far, biomechanical tests are limited to tests with some Neotropical liana species (Putz and Holbrook 1991, Rowe and Speck 1996, Gallenmüller *et al.* 2000, 2001).

In a Bolivian forest dominated by lianas, Alvira Reyes (2002) observed that 90% of the lianas on trees rooted below the tree crown. Therefore she recommended liana cutting to be applied within an imaginary circle of half the tree crown's diameter (or c. 4 m) from the tree's liana-laden stemfoot. Liana cutting in such so-called 'liana forest' seems to be a good measure to control prolific liana presence, although at high initial costs. Whether lianas mainly root under the tree crown remains to be investigated in the African conditions, but it suggests limiting the operation to liana-laden trees only. A tree-by-tree approach for such a treatment might not reduce the abundance of large lianas in the forest, as Zagt *et al.* (2003) observed.

While maintenance and enhancement of the forest ecosystem productivity is mainly concerned with selection of trees to be harvested (i.e. no more than 3 trees per hectare to be felled), and their felling direction (simple RIL guidelines), most forest operations in West Africa do not include lianas in their management. At the same time, limits are to be set on minimum spacing of felled trees (density of felling) to avoid too large treefall gaps. Harvesting guidelines should contain: (1) minimum number and size of trees to be retained as seed bearers; (2) maximum number (or density) of trees to be harvested per hectare; (3) the minimum exploitable diameter for each species to be harvested; (4) techniques for avoiding large gaps; (5) measures to be taken to minimise the impact of harvesting on the physical structure of the area, topography, soils, water resources and post-harvesting tree crop and vegetative cover; and (6) fine-grained protection measures. The last three points all concern lianas, and liana cutting on a limited scale could form part of management operations to improve the precision of felling, to enhance the development of the growing tree stock and to overcome some of the problems related to tangles of herbs, shrubs and climbers that can block tree regeneration in felling gaps. These measures will also improve the safety of the forest workers since logging operations are dangerous and are often aggravated by the occurrence of liana tangles.

8.4. CONCLUSIONS

The heterogeneity in tropical forests on the one hand, and harvesting aspects on the other, do not allow for liana regulating prescriptions that are universally applicable. Based on the present study, however, some clear conclusions can be drawn and recommendations can be made:

- Lianas are abundant and will play a more prominent role in West African forest dynamics in the coming decades since disturbance regimes will be more intensive and frequent.
- More liana inventories are needed in tropical forests to counterbalance the general lack of information on this plant lifeform. Standardisation of liana inventories can be helpful for drawing general worldwide conclusions of the contributions of lianas to forest structure and diversity.

- Liana assessments should form part of forest inventories and the preservation of rare, threatened and endangered liana species should be incorporated in management plans. These species should also get extra protection during liana cutting operations.
- Pre-harvest liana cutting is recommended in the area beneath the canopy of the target tree with abundant lianas for controlling the deviation of the predicted felling direction of the tree to be felled. This will result in reduced damage to the tree felled and to the residual stand, and increase the safety of forest workers.
- Pre-harvest liana cutting is recommended for controlling liana regeneration and promoting tree regeneration in felling gaps. Also post-harvest liana cutting can be beneficial in this respect.
- Development of immature commercial trees of selected species benefit from logging activities, but if found to be insufficient, additional liberation thinning should be applied with liana cutting in case of liana hindrance.
- Lianas restore to original densities within ten years after pre-harvest liana cutting. However, large-sized lianas (≥ 5 cm diameter) are mostly absent.
- Pre-harvest liana cutting might reduce liana diversity. Selective cutting is of great importance: only those species which cause most damage should be cut, and as many harmless species as possible should be left intact. This may also ensure that many large-sized lianas will remain present in the forest.

9. REFERENCES

- Aferdi Dadebo, M. & T. Shinohara (1999). Forest resources and timber production of Ghana: current instruments for sustainable development. *J. For. Res.* 4: 1-12.
- Aïdara, G.L. (1992). Sylviculture et aménagement des forêts tropicales humides: l'expérience ivoirienne. Dans: Cleaver, K., M. Munasinghe, M. Dyson, N. Egli, A. Peuker and F. Wencélius (eds.), *Conservation de la forêt dense en Afrique Central et de l'Ouest*. World Bank Environment Paper No. 1. Washington D.C., U.S.A., World Bank, pp. 119-126.
- Alder, D. (1989). Natural forest increment, growth and yield. In: Wong, J.L.G. (ed.), *Ghana Forest Inventory Project seminar proceedings* (Accra 1989). Kumasi, Ghana, Forest Inventory Project, pp. 47-52.
- Alder, D. (1993). *Growth and yield research in Bobiri Forest Reserve*. Consultancy Report No. 14. Denis Alder (Consulting) Ltd., Oxford, U.K., 71 p.
- Alexandre, D.Y. (1980). Caractère saisonnier de la fructification dans une forêt hygrophile de Côte d'Ivoire. *Revue d'Ecologie (la Terre et la Vie)* 34: 335-350.
- Alvarez, J., Guevara, S.S., 1985. Caida de hojarasca en la selva. In: Gomez-Pompa, A. and R.S. del Amo (eds.), *Investigations on the regeneration of high forests in Vera Cruz, Mexico*. Volume 2. Mexico D.F., Mexico, Editorial Alhambra Mexicana, pp. 171-189.
- Alvira Reyes, D.C. (2002). *Liana loads and post-logging densities after liana cutting in a lowland forest in Bolivia*. MSc thesis, University of Florida, Gainesville, USA.
- Amaral, P., Verissimo, A., Barreto, P. & E. Vidal (1998). *Floresta para sempre. Um manual para a produção de madeira na Amazônia*. IMAZON, Belém, Brazil.
- Anon. (1996). *Rapport d'éclaircie sélective par dévitalisation*. SODEFOR, Centre de Gestion de Gagnoa, Division de Niegré, Gagnoa, Côte d'Ivoire.
- Anon. (2001). *Taylor-made. The pivotal role of Liberia's forests and flag of convenience in regional conflict*. Global Witness Ltd., London, UK, International Transport Workers Federation, London, UK.
- Appanah, S. and F.E. Putz (1984). Climber abundance in virgin dipterocarp forest and the effect of pre-felling climber cutting on logging damage. *Malaysian Forester* 47: 335-342.
- Appanah, S., Gentry, A.H. & J.V. LaFrankie (1993). Liana diversity and species richness of Malaysian rain forests. *Journal of Tropical Forest Science* 6: 116-123.
- Arnaud, J.-C. and G. Sournia (1980). Les forêts de Côte d'Ivoire. *Annales de l'Université d'Abidjan series G*, 9: 6-93.
- Aubréville, A. 1938. *La forêt coloniale. Les forêts de l'Afrique occidentale française*. Annales de l'Acad. des Sciences Coloniales, Tome IX. Société d'Editions Géographiques, Maritimes et Coloniales, Paris, France, 244 p.
- Aviau de Piolant, J. de (1952). Rapport de la Côte d'Ivoire. *Actes de la Première Conférence Forestière Inter africaine (Abidjan, 1951)*. Paris, France, Commission de Coopération Technique en Afrique au Sud de Sahara (CCTA); Nogent-sur-Marne, France, Centre Technique Forestier Tropical, pp. 163-186.
- Babweteera, F., Plumptre, A., Obua, J. (2000). Effect of gap size and age on climber abundance and diversity in Budongo Forest Reserve, Uganda. *African Journal of Ecology* 38: 230-237.
- Baidoe, J.F. (1970). The selection system as practised in Ghana. *Commonwealth Forestry Review* 49: 159-165.

- Balfour, D.A. and W.J. Bond (1993). Factors limiting climber distribution and abundance in a southern African forest. *Journal of Ecology* 81: 93-99.
- Balslev, H., Luteyn, J., Ollgaard, B. & L.B. Holm-Nielsen (1987). Composition and structure of adjacent unflooded and floodplain forest in Amazonian Ecuador. *Opera Botanica* 92: 37-57.
- Barker, M.G. and D.R. Pérez-Salicrup (2000). Comparative water relations of mature mahogany (*Swietenia macrophylla*) trees with and without lianas in a subhumid, seasonally dry forest in Bolivia. *Tree Physiology* 20: 1167-1174.
- Barnard, R.C. (1955). Silviculture in the tropical rain forest of Western Nigeria compared with Malayan methods. *Malayan Forestry* 18: 173-190
- Barreto, P., Amaral, P., Vidal, E. & C. Uhl (1998). Costs and benefits of forest management for timber production in eastern Amazonia. *Forest Ecology and Management*. 108: 9-26.
- Bawa, K.S. and R. Seidler (1998). Natural forest management and conservation of biodiversity in tropical forests. *Conservation Biology* 12: 46-55.
- Beekman, F. (1981). *Structural and dynamic aspects of the occurrence and development of lianas in the tropical rain forest*. Department of Forestry, Wageningen Agricultural University, Wageningen, The Netherlands, 45 p.
- Bell, D.T. (2001). Ecological response syndromes in the flora of southwestern Australia: fire resprouters versus reseeders. *Botanical Review* 67: 417-440.
- Bennett, E.L. and J.G. Robinson (2000). *Hunting of wildlife in tropical forests. Implications for biodiversity and forest peoples*. Environment Department Papers No 76. Biodiversity Series - Impact Studies. Environment Department, World Bank, Washington DC, USA.
- Berg, J. van den and K. Biesbrouck (2000). *The social dimension of rainforest management in Cameroon: issues for co-management*. Tropenbos-Cameroon Series 4. Tropenbos-Cameroon Programme, Kribi, Cameroon.
- Bertault, J.G. (1986). *Etude de l'effet d'interventions sylvicoles sur la régénération naturelle au sein d'un périmètre expérimental d'aménagement en forêt dense humide de Côte d'Ivoire*. These doctoral, Nancy, France, Université de Nancy, 254 p.
- Bertault, J.G., Dupuy, B. & H.F. Maître (1993). Silvicultural research for sustainable management of rain forest. In: Wood, P.J., Vanclay, J.K. & Wan Razali Wan Mohd (Eds.), *Proceedings of the Tropical Silviculture Workshop IUFRO Centennial Conference (Berlin, 1992)*. Kuala Lumpur, Malaysia, Forest Research Institute Malaysia, pp. 1-14.
- Bertault, J.G., Miézan, K., Dupuy, B., Durrieu de Madron, L. & I. Amsallem. (1999). *Croissance et productivité en forêt dense humide après incendie. Le dispositif de La Téné - Côte d'Ivoire (1978-1993)*. Série FORAFRI Document 20. CIRAD-Forêt, Montpellier, France.
- Blanc, P. (2002). *Etre plante à l'ombre des forêts tropicales*. Nathan, Paris, France.
- Bledoumou, A., Fickinger, H. & B. Birkenhäger (1994). *Plan d'aménagement de la Forêt Classée de la Bossematié (22.200 ha) 1995-2014*. Programme d'Aménagement des Forêts Classées de l'Est et de Protection de la Nature (Taï). Abengourou, Côte d'Ivoire, SODEFOR-GTZ, 86 pp.
- Bobadilla, U.L. and S.F. Ferrari (2000). Habitat use by *Chiropotes satanas utahicki* and *Syntopic platyrrhines* in Eastern Amazonia. *American Journal of Primatology* 50: 215-224.

- Bond, W.J. and J.J. Midgley (2001). Ecology of sprouting in woody plants: the persistence niche. *Trends in Ecology and Evolution* 16: 45-51.
- Boom, B.M. and S.A. Mori (1982). Falsification of two hypotheses on liana exclusion from tropical trees possessing buttresses and smooth bark. *Bulletin of the Torrey Botanical Club* 109: 447-450.
- Bongers, F., Popma, J., del Castillo, J.M. & J. Carabias (1988). Structure and floristic composition of the lowland rain forest of Los Tuxtlas, Mexico. *Vegetatio* 63: 13-34.
- Bourret, F.M. (1949). *The Gold Coast. A survey of the Gold Coast and British Togoland 1919-1946*. The Hoover Library on War, Revolution and Peace Publication no. 23. Oxford University Press, London, U.K., 231 p.
- Brevet, R. (1994a). *Evolution du diamètre moyen initial des essences principales 10 années après éclaircies par dévitalisation en forêt dense sempervirente de Côte d'Ivoire (périmètre d'Irobo)*. Abidjan, Côte d'Ivoire, IDEFOR/DFO, 15 p.
- Brevet, R. (1994b). *Evolution du diamètre moyen initial des essences principales 10 années après éclaircies par dévitalisation en forêt dense humide semi-décidue de Côte d'Ivoire (périmètre de Mopri)*. Abidjan, Côte d'Ivoire, IDEFOR/DFO, 18 p.
- Brevet, R. & A. Diahuissie (1994). *Amenagement de la Forêt Classée de Yapo. Etude de l'évolution de quelques placeaux permanents 6 années après intervention sylvicole. 4ième campagne de mensuration*. Abidjan, Côte d'Ivoire, IDEFOR/DFO, 20 pp.
- Brevet, R., Tuo, N. & A. Diahuissié (1993). *Régénération naturelle acquise en forêt sempervirente*. Abidjan, Côte d'Ivoire, IDEFOR/FDO, 10 p.
- Brinkmann, K. (2000). *Untersuchung zur Struktur und Dynamik eines exploitierten immergrünen Feuchtwaldes im Südosten der Côte d'Ivoire*. Diplomarbeit der Forstwissenschaftlichen Fakultät, Albert- Ludwigs- Universität, Freiburg im Breisgau, Deutschland.
- Britwum, S.P.K. (1976). Natural and artificial regeneration practices in the high forest of Ghana. *Ghana Forestry Journal* 2: 45-49
- Brcic, T. (2003). *Ecology and patch dynamics of Megaphrynium macrostachyum (Benth.) Milne-Redh. (Marantaceae) in the south-west Central African Republic*. Doctoral thesis. Oxford University, Oxford, U.K.
- Brüning, E.F. and J. Poker (1991). Is sustainable utilization of the tropical evergreen moist forest possible?. In: Erdelen, W., Ishwaran, N. & P. Müller (eds.), *Proceedings of the international and interdisciplinary symposium Tropical Ecosystems (Saarbrücken, 1989)*. Weikersheim, Germany, Margraf Scientific Books: pp. 1-10.
- Burghouts, T.B.A., Campbell, E.J.F. & P.J. Kolderman (1994). Effects of trees species heterogeneity of leaf fall in primary and logged dipterocarp forest in the Ulu Segama forest reserve, Sabah, Malaysia. *Journal of Tropical Ecology* 10: 1-26.
- Burnham, R.J. (2002). Dominance, diversity and distribution of lianas in Yasuni, Ecuador: who is on top? *Journal of Tropical Ecology*. 18: 845-864.
- Caballé, G. (1977). Multiplication végétative en forêt dense du Gabon de la liane *Entada scelerata* (Mimosoideae). *Adansonia*, sér. 2, 17: 215-220.
- Caballé, G. (1980a). Caractéristiques de croissance et multiplication végétative en forêt dense du Gabon de la "liane à eau" *Tetracera alnifolia* Willd. (Dilleniaceae). *Adansonia*, sér. 2, 19: 467-475.

- Caballé, G. (1980b). Caractères de croissance et déterminisme chorologique de la liane *Entada gigas* (L.) Fawcett and Rendle (Leguminosae-Mimosoideae) en forêt dense du Gabon. *Adansonia*, sér. 2, 20: 309-320.
- Caballé, G. (1984). Essai sur la dynamique des peuplements de lianas ligneuses d'une forêt du nord-est du Gabon. *Revue d'Ecologie (la Terre et la Vie)* 39: 3-35.
- Caballé, G. (1986a). *Sur la biologie des lianes ligneuses en forêt gabonaise*. Doctorat d'état en Sciences, Université de Montpellier II Sciences et Techniques du Languedoc, Montpellier, France.
- Caballé, G. (1986b). Les peuplements de lianes ligneuses dans une forêt du Nord-est du Gabon. Mémoire. Mus. Nat. Hist. Nat. (Paris). *Nouvelle série, Série A Zoologie* 132: 91-96.
- Caballé, G. (1993). Liana structure, function and selection: a comparative study of xylem cylinders of tropical rainforest species in Africa and America. *Botanical Journal of the Linnean Society* 113: 41-60.
- Caballé, G. (1994). Ramet proliferation by longitudinal splitting in the Gabonese rain forest liana *Dalhousiea africana* S. Moore (Papilionaceae). *Biotropica* 26: 266-275.
- Caballé, G. (1998). Le port autoportant des lianes tropicales: une synthèse des stratégies de croissance. *Canadian Journal of Botany* 76: 1703-1716
- Caballé, G. and A. Martin (2001). Thirteen years of change in trees and lianas in a Gabonese rainforest. *Plant Ecology* 152: 167-173
- Cabrera Gaillard, C. (1988). *Aménagement de la forêt dense humide sempervirente: contribution à une étude des traitements sylvicoles, cas de la forêt de Yapo, Côte d'Ivoire*. Mémoire ESAT 1. Montpellier, France, Ecole Supérieure d'Agronomie Tropicale, 64 p.
- Campbell, E.J.F. and D. McC. Newbery (1993). Ecological relationships between lianas and trees in lowland rainforest in Sabah, East Malaysia. *Journal of Tropical Ecology* 9: 469-490.
- Cannon, C. H., Peart, D. R. & M. Leighton (1998). Tree species diversity in commercially logged Bornean rainforest. *Science* 281: 1366-1368.
- Carrière, S.M., Letourmy, P. & D.B. McKey (2002). Effects of remnant trees in fallows on diversity and structure of forest regrowth in a slash-and-burn agricultural system in southern Cameroon. *Journal of Tropical Ecology* 18: 375-396.
- Carse, L.E., Fredericksen, T.S. & J.C. Licona (2000). Liana-tree species associations in a Bolivian dry forest. *Tropical Ecology* 41: 1-10.
- Carsten, L.D., Juola, F.A., Male, T.D. & S. Cherry (2002). Host associations of lianas in a south-east Queensland rain forest. *Journal of Tropical Ecology* 18: 107-120.
- Castellanos, A.E., Duran, R., Guzman, S., Briones, O. & M. Ferial (1992). Three-dimensional space utilization of lianas: a methodology. *Biotropica* 24: 396-401.
- Catinot, R. (1965). Sylviculture tropicale en forêt dense Africaine. *Revue Bois et Forêts des Tropiques* 100: 5-18; 101: 3-16; 102: 3-16; 103: 17-29.
- Cedergren, J. (1996). *A silvicultural evaluation of stand characteristics, pre-felling climber cutting and directional felling in a primary dipterocarp forest in Sabah, Malaysia*. Ph.D. thesis, Umeå, Sweden, Swedish University of Agricultural Sciences. Acta Universitatis Agriculturae Sueciae, Silvestria 9.
- CENADEFOR (1988a). *Forest resource inventory of Cameroon: summary report*. Yaoundé, Cameroon, CENADEFOR.

- CENADEFOR (1988b). *Inventaire des ressources forestières du Cameroun: résultats d'inventaire étape 1*. Yaoundé, Cameroun, CENADEFOR.
- Chalmers, A.C. and J.C. Turner (1994). Climbing plants in relation to their supports in a stand of dry rainforest in the Hunter Valley, New South Wales. *Proceedings of the Linnean Society of New South Wales* 114: 73-90
- Chaplin, G.E. (1985). An integrated silvicultural solution to weedy climber problems in the Solomon Islands. *Commonwealth Forestry Review* 64: 133-139.
- Charles-Dominique, P., Atramentowicz, M., Charles-Dominique, M., Gérard, H., Hladik, A., Hladik, C.M. & M.F. Prévost (1981). Les mammifères frugivores arboricoles nocturnes d'une forêt Guyanaise: Inter-relations plantes-animaux. *Revue d'Ecologie (la Terre et la Vie)* 35: 341-435.
- Chevalier, A. et D. Normand (1946). *Forêts vierges et bois coloniaux*. Série <Que sais-je?>. Paris, France, Presses Universitaires, 127 p.
- Chittibabu, C.V. and N. Parthasarathy (2001). Liana diversity and host relationships in a tropical evergreen forest in the Indian Eastern Ghats. *Ecological Research* 16: 519-529.
- Clark, D.B. and D.A. Clark (1990). Distribution and effects on tree growth of lianas and woody hemiepiphytes in a Costa Rican tropical wet forest. *Journal of Tropical Ecology* 6: 321-331.
- Clark, D.B. and D.A. Clark (1991). The impact of physical damage on canopy tree regeneration in tropical rain forest. *Journal of Ecology* 79: 447-457
- Clark, D.B. and D.A. Clark (2000). Landscape-scale variation in forest structure and biomass in a tropical rain forest. *Forest Ecology and Management* 137: 185-198
- Cleuren, H. (2001). *Paving the road for forest destruction. Key actors and driving forces of tropical deforestation in Brazil, Ecuador and Cameroon*. Leiden Development Studies, New Series 1. Research School of Asian, African and Amerindian Studies (CNWS), Leiden University, Leiden, The Netherlands.
- Cochrane, M.A. and M.D. Schulze (1999). Fire as a recurrent event in tropical forests of the eastern Amazon: effects on forest structure, biomass, and species composition. *Biotropica* 31: 2-16.
- Colwell, R.K. and Coddington, J.A. (1994). Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London* 345: 101-118.
- Condit, R., Hubbell, S.P., Lafrankie, J.V., Sukumar, R., Manokaran, N., Foster, R.B. & P.S. Ashton (1996). Species-area and species-individual relationships for tropical trees: a comparison of three 50-ha plots. *Journal of Ecology* 84: 549-562.
- Corlett, R.T. (1998). Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) Region. *Biological Reviews* 73: 413-448.
- Costa, F.R.C. and W.E. Magnusson (2003). Effects of selective logging on the diversity and abundance of flowering and fruiting understory plants in a Central Amazonian forest. *Biotropica* 35: 103-114.
- Côté, S. (1993). *Plan de zonage du Cameroun forestier méridional*. Québec, Canada, Poulin Thériault Inc., 62 p.
- Coudurier, T. (1992). *Sur la place des lianes dans la forêt guyanaise. Une approche qui utilise l'architecture végétale*. Doctorat de l'Université de Montpellier II Sciences et Techniques du Languedoc, Montpellier, France.
- Cremers, G. (1973). Architecture de quelques lianes d'Afrique tropicale. 1. *Candollea* 28: 249-280.

- Creemers, G. (1974). Architecture de quelques lianes d'Afrique tropicale. 2. *Candollea* 29: 57-110.
- Croat, T.B. (1978). *Flora of Barro Colorado Island*. Stanford University Press, Stanford, California, USA.
- Dale, M.R.T. (1999). *Spatial pattern analysis in plant ecology*. Cambridge studies in ecology. Cambridge University Press, Cambridge, U.K., 326 p.
- Dallmeier, F. and J.A. Comiskey (eds.). (1998a). *Forest biodiversity research, monitoring and modelling. Conceptual background and Old World case studies*. Man and the Biosphere Series Volume 20. UNESCO, Paris, France; Parthenon Publishing Group, New York, New York, 671 p.
- Dallmeier, F. and J.A. Comiskey (eds.). (1998b). *Forest biodiversity in North, Central and South America, and the Caribbean: research and monitoring*. Man and the Biosphere Series Volume 21. UNESCO, Paris, France; Parthenon Publishing Group, New York, New York, 768 p.
- Darwin, C. (1867). On the movements and habits of climbing plants. *Journal of the Linnean Society of London (Botanical)* 9: 1-118.
- Dawkins, H.C. (1958). *The management of natural tropical high-forest with special reference to Uganda*. Imperial Forestry Institute Paper No. 34. Oxford, U.K., University of Oxford, 155 p.
- Dawkins, H.C. (1960). *New methods of improving stand composition in tropical forests*. Proceedings of the 5th World Forestry Congress (Seattle): pp. 441-446.
- Debroux, L. and A. Karsenty (1997). L'implantation des sociétés forestières asiatiques en Afrique Centrale. *Revue Bois et Forêts des Tropiques* 254: 80-85.
- Del Tredici, P. (2001). Sprouting in temperate trees: a morphological and ecological review. *Botanical Review* 67: 121-140.
- Dewalt, S. J. & J. Chave (in review). Structure and biomass of four lowland Neotropical forests. *Biotropica*.
- Dewalt, S.J., Schnitzer, S.A. & J.S. Denslow (2000). Density and diversity of lianas along a chronosequence in a central Panamanian lowland forest. *Journal of Tropical Ecology* 16: 1-19.
- Dillenburg, L.R., Whigham, D.F., Teramura, A.H. & I.N. Forseth (1993). Effects of below- and aboveground competition from the vines *Lonicera japonica* and *Parthenocissus quinquefolia* on the growth of the tree host *Liquidambar styraciflua*. *Oecologia* 93: 48-54.
- Doumbia, F. (1993). *Caractéristiques de la régénération naturelle en forêt dense semi décidue au sein du dispositif d'expérimentation sylvicole SODEFOR de Mopri 14 années après intervention*. Abidjan, Côte d'Ivoire, IDEFOR/DFO, 29 p.
- Dransfield, J. (1978). Growth forms of rain forest palms. In: Tomlinson, P.B. and M. H. Zimmermann (eds.), *Tropical trees as living systems*. Cambridge University Press, Cambridge, U.K., pp. 247-268
- Duivenvoorden, J.F. (1994). Vascular plant species counts in the rain forests of the middle Caqueta area, Colombian Amazonia. *Biodiversity and Conservation* 3: 685-715.
- Dunn, R.M., D.O. Otu and J.L.G. Wong (1994). *Report of the reconnaissance inventory of high forest and swamp forest areas in Cross River State, Nigeria*. Calabar, Nigeria, Cross River State Forestry Project, 8 p.
- Durrieu de Madron, L. et E. Forni (1997). Aménagement forestier dans l'est du Cameroun. *Revue Bois et Forêts des Tropiques* 254: 39-50.

- Durrieu de Madron, L., Favrichon, V., Dupuy, B., Bar Hen, A. & H.F. Maître (1998a). *Croissance et productivité en forêt dense humide: bilan des expérimentations dans le dispositif d'Irobo, Côte d'Ivoire (1978-1990)*. Document 2 Série FORAFRI. CIRAD-Forêt, Montpellier, France, 69 p.
- Durrieu de Madron, L., Favrichon, V., Dupuy, B., Bar Hen, A., Houde, L. & H.F. Maître (1998b). *Croissance et productivité en forêt dense humide: bilan des expérimentations dans le dispositif de Mopri, Côte d'Ivoire (1978-1992)*. Document 3 Série FORAFRI. CIRAD-Forêt, Montpellier, France, 73 p.
- Durrieu de Madron, L., Forni, E. & M. Mekok (1998c). *Les techniques d'exploitation à faible impact en forêt dense humide camerounaise*. Document 17 Série FORAFRI. CIRAD-Forêt, Montpellier, France, 28 p.
- Dykstra, D.P. and R. Heinrich (1996). *Code modèle FAO des pratiques d'exploitation forestière*. FAO Forest Harvesting, Trade and Marketing Branch, Rome, Italy.
- Eba'a Atyi, R. (1997). La certification des forêts. Le cas du Cameroun. *Revue Bois et Forêts des Tropiques* 253: 62-67.
- Eba'a Atyi, R. (1998). *Cameroon's logging industry: structure, economic importance and effects of devaluation*. Occasional Paper No. 14. Jakarta, Indonesia, CIFOR, 40 p.
- Eba'a Atyi, R. (2000). *TROPFOMS, a decision support model for sustainable management of South-Cameroon's rain forests*. Tropenbos-Cameroon Series 2. Tropenbos-Cameroon Programme, Kribi, Cameroon.
- Ek, R.C. (1997). *Botanical diversity in the tropical rain forest of Guyana*. Tropenbos-Guyana Series 4. Georgetown, Guyana, Tropenbos-Guyana Programme. Ph.D. thesis, Departments of Botanical Ecology and Evolutionary Biology and Theoretical Biology, Utrecht University, The Netherlands.
- Emmons, L.H. and A.H. Gentry (1983). Tropical forest structure and the distribution of gliding and prehensile-tailed vertebrates. *American Naturalist* 121: 513-523.
- Ewers, F.W. and J.B. Fisher (1991). Why vines have narrow stems: histological trends in Bauhinia (Fabaceae). *Oecologia* 88: 233-237.
- Fairhead, J. and M. Leach (1998). *Reframing deforestation. Global analysis and local realities: studies in West Africa*. Global Environmental Change Series. London, UK; New York, USA, Routledge, 238 p.
- Fairhead, J. and M. Leach (1998). Reconsidering the extent of deforestation in twentieth century West Africa. *Unasylva* 192: 38-46
- Favrichon, V. (1997). Réaction de peuplements forestiers tropicaux à des interventions sylvicoles. *Revue Bois et Forêts des Tropiques* 254: 5-24
- Faure, J.-J. (1993). Un essai de solution globale au problème de la déforestation en forêt dense africaine: l'aménagement pilote intégré (API) de Dimako (Est Cameroun). *Le Flamboyant* 26: 10-16.
- Fickinger, H. (1992). *Zur Verjüngung einiger Wirtschaftsbaumarten in selektiv genutzten Feuchtwäldern der Republik Kongo*. Göttinger Beiträge zur Land- und Forstwirtschaft in den Tropen und Subtropen. Heft 75. Göttingen, Deutschland, Georg-August-Universität, 203 pp.
- Fickinger, H. (1995). *Les effets de l'éclaircie sélective en Forêt Classée de Bossematié sur l'accroissement des arbres d'avenir*. Paper presented at 'Atelier de sylviculture et d'aménagement' Yamoussoukro.

- Finegan, B., Camacho, M. & N. Zamora (1999). Diameter increment patterns among 106 tree species in a logged and silviculturally treated Costa Rican rain forest. *Forest Ecology and Management* 121: 159-176.
- Fisher, J.B. and F.W. Ewers (1989). Wound healing in stems of lianas after twisting and girdling injuries. *Botanical Gazette* 150: 251-265.
- Fisher, J.B. and F.W. Ewers (1991). Structural responses to stem injury in vines. In: Putz, F.E. & Mooney, H.A. (eds.). *The biology of vines*. Cambridge, U.K., Cambridge University Press, pp. 99-124
- Foggie, A. (1960). Natural regeneration in the humid tropical forest. *Caribbean Forester* 21: 73-81.
- Foster, P.F. and V.L. Sork (1997). Population and genetic structure of the West African rain forest liana *Ancistrocladus korupensis* (Ancistrocladaceae). *American Journal of Botany* 84: 1078-1091.
- Fox, J.E.D. (1968). Logging damage and the influence of climber cutting prior to logging in the lowland dipterocarp forest of Sabah. *Malayan Forester* 31: 326-347.
- F.P.R.I. (1968). *F.P.R.I. annual report 1968*. Kumasi, Ghana, Forest Products Research Institute, 53 p.
- F.P.R.I. (1970). *F.P.R.I. annual report 1969-70*. Kumasi, Ghana, Forest Products Research Institute, 66 p.
- Franqueville A. (1973), *Atlas régional Sud-Ouest 1*. République du Cameroun. ORSTOM, Yaounde, Cameroun.
- Gallenmüller, F., Müller, U., Rowe, N. & Speck, T. (2001). The growth form of *Croton pullei* (Euphorbiaceae)- Functional morphology and biomechanics of a neotropical liana. *Plant Biology* 3: 50-61.
- Gardette, E. (1998). The effect of selective timber logging on the diversity of woody climbers at Pasoh. In: Lee, S.S., Dan, Y.M., Gauld, I.D. and J. Bishop (eds.), *Conservation, management and development of forest resources*. Proceedings of the Malaysia-United Kingdom programme workshop (Kuala Lumpur 1996). Forest Research Institute Malaysia, Kuala Lumpur, Malaysia, pp. 115-125.
- Gartner, B.L. (1991). Structural stability and architecture of vines vs. shrubs of poison oak, *Toxicodendron diversilobum*. *Ecology* 72: 2005-2015.
- Gautier-Hion, A., Gautier, J.P. & R. Quris (1981). Forest structure and fruit availability as complementary factors influencing habitat use by a troop of monkeys (*Cercopithecus cephus*). *Revue d'Ecologie (la Terre et la Vie)* 35: 511-536.
- Gemerden B.S. van and G.W. Hazeu (1999). *Landscape ecological survey (1:100,000) of the Bipindi - Akom II - Lolodorf region, southwest Cameroon*. Tropenbos-Cameroon Documents 1. Tropenbos Foundation, Wageningen, the Netherlands.
- Gemerden B.S. van, Olf, H., Parren, M.P.E. & F. Bongers (2003). The pristine rain forest? Remnants of historical human impacts on current tree species composition and diversity. *Journal of Biogeography* 30: 1381-1390.
- Gentry, A.H. (1982). Patterns of Neotropical plant species diversity. *Evolutionary Biology* 15: 1-84.
- Gentry, A.H. (1985). An ecotaxonomic survey of Panamanian lianas. In: Dárcy, W. and M. Correa (eds.), *Historia natural de Panamá*. Monographs of Systematic Botany, Missouri Botanical Garden, Saint Louis, U.S.A., pp. 29-42.
- Gentry, A.H. (1988). Tree species richness of upper Amazonian forests. *Proceedings of the National Academy of Sciences of the USA* 85: 156-159.

- Gentry, A.H. (1989). Speciation in the forest. In: Holm-Nielsen, L.B., Nielsen, I. & Balslev, H. (eds.). *Tropical forest: Botanical dynamics, speciation and diversity*. London, U.K., Academic Press, pp. 113-134.
- Gentry, A.H. (1991a). Breeding and dispersal systems of lianas. In: Putz, F.E. and H.A. Mooney (eds.), *The biology of vines*. Cambridge Univ. Press, Cambridge, U.K., pp. 393-423.
- Gentry, A.H. (1991b). The distribution and evolution of climbing plants. In: Putz, F.E. and Mooney, H.A. (eds.). *The biology of vines*. Cambridge University Press, Cambridge, U.K., pp. 3-49
- Gentry, A.H. (1992). Tropical forest biodiversity: distributional patterns and their conservational significance. *Oikos* 63: 19-28.
- Gentry, A.H. (1993). *A field guide to the families and genera of woody plants of Northwest South America*. Conservation International, Washington D.C. Reprinted by University of Chicago Press in 1996.
- Gentry, A.H. and C. Dodson (1987). Contribution of non trees to species richness of a tropical rain forest. *Biotropica* 19: 149-156.
- Gerwing, J.J. (2001). Testing liana cutting and controlled burning as silvicultural treatments for logged forest in the eastern Amazon. *Journal of Applied Ecology* 38: 1264-1276.
- Gerwing, J.J. (2002). Degradation of forests through logging and fire in the eastern Brazilian Amazon. *Forest Ecology and Management* 157: 131-141.
- Gerwing, J. (in press). Life history diversity among six species of canopy lianas in an old-growth forest of the eastern Brazilian Amazon. *Forest Ecology and Management*.
- Gerwing, J.J. and D.L. Farias (2000). Integrating liana abundance and forest stature into an estimate of total aboveground biomass for an eastern Amazonian forest. *Journal of Tropical Ecology* 16: 327-335.
- Gerwing, J.J. and E. Vidal (2002). Changes in liana abundance and species diversity eight years after liana cutting and logging in an eastern Amazonian forest. *Conservation Biology* 16: 544-548.
- Ghartey, K.K.F. (1989). Results of the inventory. In Wong, J.L.G. (ed.), *Ghana Forest Inventory Project seminar proceedings (Accra 1989)*. Kumasi, Ghana, Forest Inventory Project, pp. 32-46.
- Ghartey, K.K.F. (1990). *The evolution of forest management in the tropical high forest of Ghana*. Paper presented at the conference on conservation and the rational utilization of the high forest of Central and West Africa (Abidjan 1990), 11 p.
- Grauel, W. and F.E. Putz (in press). Effects of lianas on growth and regeneration of *Prioria copaifera* in Darien, Panama. *Forest Ecology and Management*.
- Grieser Johns, A. and B. Grieser Johns (1995). Tropical forest primates and logging : long-term coexistence ? *Oryx* 29: 205-211.
- Grubb, P.J. (1987). Global trends in species-richness in terrestrial vegetation: a view from the northern hemisphere. In: Gee, J.H.R. and P.S. Giller (eds.), *Organization of communities: Past and present*. Blackwell Scientific Publications, Oxford, UK., pp. 23-27.
- Guariguata, M.R. and M.A. Pinard (1998). Ecological knowledge of regeneration from seed in neotropical forest trees: Implications for natural forest management. *Forest Ecology and Management* 112: 87-99.

- Guariguata, M.R., Rosales Adame, J.J. & B. Finegan (2000). Seed removal and fate in two selectively logged lowland forests with contrasting protection levels. *Conservation Biology* 14: 1046-1054.
- Guigonis, E.R. (Ed.). 1978. *Mémento du forestier*. 2ème Edition. Techniques rurales en Afrique. Ministère de la Coopération, Paris, France.
- Gutzwiller, R. (1956). Principales pratiques sylvicoles en vue de la production de bois d'oeuvre en forêt dense équatoriale. Sylvicultures au Congo belge, Cameroun, Nigeria, en Gold Coast et en Côte d'Ivoire. *Schweizerische Zeitschrift für Forstwesen* 107: 175-194.
- Hall, J.B. and M.D. Swaine (1981). *Distribution and ecology of vascular plants in a tropical rain forest. Forest vegetation in Ghana*. Geobotany 1. Dr. W. Junk Publishers, The Hague, Netherlands, 383 pp.
- Hallé, F. et R.A.A. Oldeman (1970). *Essai sur l'architecture et la dynamique de croissance des arbres tropicaux*. Paris, France, Masson et Cie.
- Hallé, F., Oldeman, R.A.A. & P.B. Tomlinson (1978). *Tropical trees and forests: an architectural analysis*. Berlin, Germany, Springer Verlag.
- Hawthorne, W.D. (1993). *Forest regeneration after logging. Findings of a study in the Bia South Game Production Reserve, Ghana*. ODA Forestry Series No. 3. Chatham Maritime, U.K., Natural Resources Institute, 52 p.
- Hawthorne, W.D. (1994). *Fire damage and forest regeneration in Ghana*. ODA Forestry Series No. 4. Chatham Maritime, U.K., Natural Resources Institute, 53 p.
- Hawthorne, W.D. (1995). *Ecological profiles of Ghanaian forest trees*. Tropical Forestry Papers 29. Oxford, U.K., Oxford Forestry Institute, Department of Plant Sciences, 345 p.
- Hawthorne, W.D. (1996). Holes and the sums of parts in Ghanaian forest: regeneration, scale and sustainable use. In: Alexander, I.J., Swaine, M.D. & R. Watling (eds.), *Essays on the ecology of the Guineo-Congo rain forest. Proceedings of the Royal Society of Edinburgh* 104B: 75-176.
- Hawthorne, W. and C. Jongkind (in press). *A guide of the woody plants of western African forests*. Royal Botanic Gardens, Kew, U.K.
- Hawthorne, W.D., Grut, M. & M. Abu-Juam (1998). *Forest production and biodiversity conservation in Ghana, and proposed international support of biodiversity conservation*. CSERGE Working Paper 98-18. Norwich, UK, CSERGE, 30 p.
- Heaney, A. and J. Proctor (1990). Preliminary studies on forest structure and floristics on Volcán Barva, Costa Rica. *Journal of Tropical Ecology* 6: 307-320.
- Hecketsweiler, P. (1992). *Phénologie et saisonnalité en forêt gabonaise. L'exemple de quelques espèces ligneuses*. Doctorat de l'Université de Montpellier II Sciences et Techniques du Languedoc, Montpellier, France, 2 vol.
- Hegarty, E.E. (1990). Leaf life-span and leafing phenology of lianes and associated trees during a rainforest succession. *Journal of Ecology* 78: 300-312.
- Hegarty, E.E. (1991). Leaf litter production by lianes and trees in a sub-tropical Australian rain forest. *Journal of Tropical Ecology* 7: 201-214.
- Hegarty, E.E. and G. Caballé (1991). Distribution and abundance in forest communities. In: Putz, F.E. and H.A. Mooney (eds.), *The biology of vines*. Cambridge University Press, Cambridge, U.K., pp. 313-335
- Heideman, P.D. (1989). Temporal and spatial variation in the phenology of flowering and fruiting in a tropical rainforest. *Journal of Ecology* 77: 1059-1079.

- Henderson-Howat, D., Johnson, A., Thompson, D. & P. Tweneboah (1995). *Policy recommendations for sustainable management of the forest resource in Ghana*. Edinburgh, U.K., Forestry Commission, 44 p.
- Henderson, J. (1990). *Damage-controlled logging in managed tropical rainforest in Suriname*. Ecology and Management of Tropical Rain Forest in Suriname 4. Agricultural University, Wageningen, Netherlands.
- Hladik, A. (1974). Importance des lianes dans la production foliaire de la forêt équatoriale du Nord-Est du Gabon. *Comptes Rendus de l'Académie des Sciences* 278(D): 2527-2530.
- Hladik, A. (1978). Phenology of leaf production in rain forest of Gabon: distribution and composition of food for folivores. In: Montgomery, G. (ed.), *The ecology of arboreal folivores*. Smithsonian Institution Press, Washington D.C., U.S.A., pp. 51-71
- Hladik, A. (1986). Données comparatives sur la richesse spécifique et les structures des peuplements des forêts tropicales d'Afrique et d'Amérique. *Mémoires du Muséum National d'Histoire Naturelle, Nouvelle Série A*, 132: 9-17.
- Hladik, A. et P. Blanc (1987). Croissance des plantes en sous-bois de forêt dense humide (Makokou, Gabon). *Revue d'Ecologie (la Terre et la Vie)* 42: 209-234.
- Holmes, T.P., Bate, G.M., Zweede, J.C., Pereira Jr., R., Barreto, P., Boltz, F. & R. Bauch (2002). Financial and ecological indicators of reduced impact logging performance in the eastern Amazon. *Forest Ecology and Management*. 163: 93-110.
- Holmgren, M., Scheffer, M., Ezcurra, E., Gutiérrez, J.R. & G.M.J. Mohren (2001). En Nino effects on the dynamics of terrestrial ecosystems. *Trends in Ecology & Evolution* 16: 89-94.
- Horvitz, C., Pascarella, J.B., McMann, S., Freedman, A. & R.H. Hofstetter (1998). Regeneration guilds of invasive non-indigenous plants in hurricane-affected subtropical hardwood forests. *Ecological Applications* 8: 947-974.
- Hout, P. van der (1999). *Reduced impact logging in the tropical rain forest of Guyana. Ecological, economic and silvicultural consequences*. Ph.D. Dissertation, Utrecht University, Utrecht, The Netherlands. Tropenbos-Guyana Series 6. Georgetown, Guyana, Tropenbos-Guyana Programme, 335 p.
- Hout, P. van der and G.J.R. van Leersum (1998). Reduced impact logging: a global panacea? Comparison of two logging studies. In: Boddens Hosang, J., Roche, M. & R.J. Zagt (eds.), *Research in tropical rain forests: Its challenges for the future*. Proceedings Tropenbos seminar (Wageningen, 1997). Tropenbos Foundation, Wageningen, The Netherlands, pp. 185-203.
- Howe, H.F. and J. Smallwood (1982). Ecology of seed dispersal. *Ann. Rev. Ecol. Syst.* 13: 201-228.
- Hubbell, S.P. and R.B. Foster (1983). Diversity of canopy trees in a neotropical forest and implications for conservation. In: Sutton, S.L. Whitmore, T.C. & A. C. Chadwick (eds.), *Tropical rain forest: Ecology and management*. Special publications series of the British Ecological Society No. 2. Blackwell Scientific Publications, Oxford, U.K., pp. 25-41.
- Hurlbert, S.H. (1990). Spatial distribution of the montane unicorn. *Oikos* 58: 257-271.
- Ibarra-Manríquez, G. & M. Martínez-Ramos (2002). Landscape variation of liana communities in a Neotropical rain forest. *Plant Ecology* 160: 91-112.

- Ibarra-Manriquez, G., Sanchez-Garfias, B. & L. Gonzalez-Garcia (1991). Fenología de lianas y arboles anemocoros en una selva calido-humeda de México. *Biotropica* 23: 242-254.
- Ibrahima, A., Schmidt, P., Ketner, P. & G.J.M. Mohren (2002). *Phytomasse et cycle des nutriments dans la forêt dense humide du sud Cameroun*. Tropenbos-Cameroon Documents 9. Tropenbos-Cameroon Programme, Kribi, Cameroon.
- Jackson, S.M., Fredericksen, T.S. & J.R. Malcolm (2002). Area disturbed and residual stand damage following logging in a Bolivian tropical forest. *Forest Ecology and Management* 166: 271-283.
- Jans, L., Poorter, L., Rompaey, R.S.A.R. Van & F. Bongers (1993). Gaps and forest zones in tropical moist forest in Ivory Coast. *Biotropica* 25(3): 258-269.
- Jansen, P.A. and P.A. Zuidema (2001). Logging, seed dispersal by vertebrates, and natural regeneration of tropical timber trees. In: Fimbel, R., Grajal, A., Robinson, J. (eds.), *The cutting edge*. Conserving wildlife in logged tropical forests. Columbia University Press, New York, U.S.A., pp. 35-59.
- Johns, A.D. (1988). Effects of "selective" timber extraction on rain forest structure and composition and some consequences for frugivores and folivores. *Biotropica* 20: 31-37.
- Johns, A.D. (1992). Vertebrate responses to selective logging: implications for the design of logging systems. *Philosophical Transactions of the Royal Society of London Serie B* 335: 437-442
- Johns, A.D. and J.P. Skorupa (1987). Responses of rain forest primates to habitat disturbance: a review. *International Journal of Primatology* 8: 157-191.
- Jong, W. de, Melnyk, M., Alfaro, L., Rosales, M. & M. Garcia (2000). A concerted approach to Una de gato development in Peru. *International Tree Crops Journal* 10: 321-336.
- Jongkind, C.C.H. and R.H.M.J. Lemmens (1989). *The Connaraceae, a taxonomic study with emphasis on Africa*. Doctoral thesis, Agricultural University Wageningen Papers 89-6. Agricultural University, Wageningen, Netherlands.
- Jonkers, W.B.J. (1983). *Exploitation, natural regeneration and increment. Experiment plan and progress report on experiment 78/5*. CELOS Rapporten 141. Anton de Kom Universiteit van Suriname, Paramaribo, 17 p.
- Jonkers, W.B.J. (1987). *Vegetation structure, logging damage and silviculture in a tropical rain forest in Suriname*. Doctoral thesis, Wageningen, Netherlands, Agricultural University, 172 pp.
- Jonkers, W.B.J. (2002). Reduced impact logging in Sarawak, Guyana and Cameroon: the reasons behind differences in approach. In: Enters, T., Durst, P.B., Applegate, G.B., Kho, P.C.S. & G. Man (eds.), *Applying reduced impact logging to advance sustainable forest mananagement*. RAP Publication 2002/14. Asia-Pacific Forestry Commision, FAO Regional Office for Asia and the Pacific, Bangkok, Thailand, pp. 199-207.
- Jonkers, W.B.J. and P. Schmidt (1984). Ecology and timber production in tropical rainforest in Suriname. *Interciencia* 9: 290-297.
- Jonkers, W.B.J. and G.J.R. van Leersum (2000). Logging in south Cameroon: current methods and opportunities for improvement. *International Forestry Review* 2: 11-16.
- Kam, M. de, Fines, J.-P. & G. Akogo Mvogo (eds.) (2002). *Schéma directeur pour le développement de l'unité technique opérationnelle de Campo-Ma'an*,

- Cameroun. Camp Ma'an Serie 1. Projet d'Aménagement et de Conservation de la Biodiversité de Campo-Ma'an, Kribi, Cameroun.
- Kammesheidt, L. (1999). Liana infestation of trees: some observations in a Neotropical lowland forest. *Ecotropica* 5: 217-220.
- Karani, P.K. (1970). *Silvicultural systems as practiced in Ghana and species trial in Nigeria*. Uganda Forest Department Technical Note No. 163, 20 p.
- Kasran, B. (1989). Effect of logging on sediment yield in a hill Dipterocarp forest in Peninsular Malaysia. *Journal of Tropical Forest Science* 1: 56-66.
- Kennard, D.K. (1998). Biomechanical properties of tree saplings and free-standing lianas as indicators of susceptibility to logging damage. *Forest Ecology and Management* 102: 179-191.
- Kennard, D.K., Gould, K., Putz, F.E., Fredericksen, T.S. & F. Morales (2002). Effect of disturbance intensity on regeneration mechanisms in a tropical dry forest. *Forest Ecology and Management* 162: 197-208.
- Kennedy, J.D. (1935). The group method of natural regeneration in the rain forest at sapobe, Southern Nigeria. *Empire Forestry Journal* 14: 19-24.
- Killeen, T.J., Jardim, A., Mamani, F. & N. Rojas (1998). Diversity, composition and structure of a tropical semideciduous forest in the Chiquitania region of Santa Cruz, Bolivia. *Journal of Tropical Ecology* 14: 803-827.
- Kio, P.R.O. (1978). Effect of silvicultural treatments on growth in the natural high forest. *Nigerian Journal of Forestry* 8: 8-13.
- Kio, P.R.O., Ekwebelam, S.A., Ola-Adams, B.A., Ladipo, D.O. & F.O.C. Nwonwu (1986). Natural regeneration technology in use in African high forests. *Proceedings of the 18th IUFRO World Congress, Division 1, Vol. II*. Ljubljana, Yugoslavia, pp 424-437.
- Kio, P.R.O., Abu, J.E. & R.G. Lowe (1993). High forest management in Nigeria. In: Wood, P.J., Vanclay, J.K. & W.R.W. Mohd (eds.), *Proceedings of the tropical silvicultural workshop IUFRO centennial conference (Berlin 1992)*. Kuala Lumpur, Malaysia, Forest Research Institute Malaysia, pp. 112-144.
- Klerk, M. de (1991). *Regeneration strategies of some emergent tree species in Côte d'Ivoire*. MSc thesis, Wageningen, Netherlands, Department of Forestry, Wageningen Agricultural University, 60 p.
- Knight, D.H. (1975). A phytosociological analysis of species-rich tropical forest on Barro Colorado Island, Panama. *Ecological Monographs* 45: 259-284.
- Kokou, K., Couteron, P., Martin, A. & G. Caballé (2002). Taxonomic diversity of lianas and vines in forest fragments of southern Togo. *Revue d'Ecologie (la Terre et la Vie)* 57: 3-18.
- Koné, S. (1996). *Rapport de l'essai d'éclaircie sélective par dévitalisation en forêt naturelle dans la Forêt Classée du Haut-Sassandra*. SODEFOR, Centre de Gestion de Daloa, Division de Haut-Sassandra, Daloa, Côte d'Ivoire.
- Kotey, N.A., Francois, J., Owusu, J.G.K., Yeboah, R., Amanor, K.S. & L. Antwi (1998). *Ghana. Falling into place*. Policy that works for forests and people Series No. 4. London, U.K., International Institute for Environment and Development, 138 pp.
- Krebs, C. J. (1989). *Ecological methodology*. Harper Collins Publishers, New York, New York, 654 p.
- Kuppen, I.G.W.M., Rompaey, R.S.A.R. van. & R.P. van der Zwan (1992). *Jaarringonderzoek aan boorkernen van zes tropische boomsoorten uit Côte d'Ivoire*. Wageningen, Netherlands, Hinkeloord Report Series 10, 39 p.

- Laburthe-Tolra, P. (1981). *Les seigneurs de la forêt. Essai sur le passé historique, l'organisation social et les normes éthiques des anciens Beti du Cameroun*. Série NS Recherche 48. Publications de la Sorbonne, Université René Descartes-Paris 5e, Paris, France.
- Lanly, J.P. (1969). Regression de la forêt dense en Côte d'Ivoire. *Revue Bois et Forêts des Tropiques* 127: 45-59.
- Laurance, W.F. (1997). Hyper-disturbed parks: edge effects and the ecology of isolated rainforest reserves in tropical Australia. In: Laurance, W.F. and R.O. Bierregaard, Jr. (eds.), *Tropical forest remnants: Ecology, management, and conservation of fragmented communities*. Chicago, USA, University of Chicago Press, pp. 71-83.
- Laurance, W.F., Delamônica, P., Laurance, S.G., Vasconcelos, L. & T.E. Lovejoy (2000). Rain forest fragmentation kills big trees. *Nature* 404: 836.
- Laurance, W.F., Pérez-Salicrup, D., Delamonica, P., Fearnside, P.M., Agra, S., Jerzolinski, A., Pohl, L. & T.E. Lovejoy (2001). Rain forest fragmentation and the structure of amazonian liana communities. *Ecology* 82: 105-116.
- Laurance, W.F., Lovejoy, T.E., Vasconcelos, H.L., Bruna, E.M., Didham, R.K., Stouffer, P.C., Gascon, C., Bierregaard, Jr., R.O., Laurance, S.G. & E. Sampaio (2002). Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conservation Biology* 16: 605-618.
- Leersum, G.J.R. van (1999). Logging research for the design of a sustainable forest management plan in south Cameroon. In: Jonkers, W.B.J and M. Wessel (eds.), *Forest management related studies of the Tropenbos-Cameroon Programme*. Tropenbos-Cameroon Reports 99-1. Tropenbos Foundation, Wageningen, The Netherlands, pp. 37-53.
- Leighton, M. and D.R. Leighton (1983). Vertebrate responses to fruiting seasonality within a Bornean rain forest. In: Sutton, S.L., Whitmore, T.C. & A.C. Chadwick (eds.), *Tropical Rain Forest: Ecology and Management*. Special Publications Series of the British Ecological Society No. 2. Oxford, UK, Blackwell Scientific Publications, pp. 181-196.
- Lennertz, R. (1993). *Inventaire des Forêts Classées de l'Est de la Côte d'Ivoire*. FC Mabi. Rapport IFCE No. 7. SODEFOR/KfW/GTZ, Abengourou, Côte d'Ivoire.
- Letouzey R. (1968). *Etude phytogéographique du Cameroun*. Encyclopédie Biologique 69. Ed. P. Lechavelier, Paris, France, 511 p.
- Lowe, R.G. (1978). Experience with the Tropical Shelterwood System of regeneration in natural forest in Nigeria. *Forest Ecology and Management* 1: 193-212.
- Lowe, R.G. and P. Walker (1977). Classification of canopy, stem, crown status and climber infestation in natural tropical forest in Nigeria. *Journal of Applied Ecology* 14: 897-903.
- McGraw, W.S. (1998). Tree monkeys nearing extinction in the forest reserves of eastern Côte d'Ivoire. *Oryx* 32: 233-236.
- Maginnis, S. (1994). Understorey condition scoring of Ghanaian lowland tropical moist forest during stock survey: a technique for regulating the allowable cut in ecologically and structurally degraded production forest. *Forest Ecology and Management* 70: 89-97
- Maître, H.F. (1986a). Dynamique et production des peuplements naturels de forêt dense humide en Afrique. *Revue Bois et Forêts des Tropiques* 213: 3-12.

- Maître, H.F. (1986b). Recherches sur la dynamique et la production des peuplements naturels en forêt dense tropicale d'Afrique de l'Ouest. *Proceedings of the 18th IUFRO World Congress, Division 1, Vol. II*. Ljubljana, Yugoslavia, pp. 438-450.
- Maître, H.F. (1991). Silvicultural interventions and their effects on forest dynamics and production in some rain forest of Côte d'Ivoire. In: Gomez-Pompa, A., Whitmore, T.C. & M. Hadley (eds.), *Rain forest regeneration and management*. Man and the Biosphere Series, Vol. 6. Paris, France, UNESCO; Carnforth, U.K., Park Ridge, U.S.A., Parthenon Publishing Group, pp. 383-392 [English translation: BFT 213, 1986].
- Maître, H.F. et M. Hermeline (1985). *Dispositifs d'étude de l'évolution de la forêt dense Ivoirienne suivant différentes modalités d'intervention sylvicole. Présentation des principaux résultats après quatre années d'expérimentation*. Abidjan, Côte d'Ivoire, SODEFOR, 83 p.
- Makana, J.-R., Hart, T.B. & Hart, J.A. (1998). Forest structure and diversity of lianas and understory treelets in monodominant and mixed stands in the Ituri forest, Democratic Republic of the Congo. In: Dallmeier, F. and J.A. Comiskey (eds.), *Forest biodiversity research, monitoring and modelling. Conceptual background and Old World case studies*. Man and the Biosphere Series Volume 20. Paris, France, UNESCO, Carnforth, UK, Parthenon Publishing Group Ltd, pp. 429-446
- Mamede-Costa, A. C. and N. Gobbi (1998). The black lion tamarin *Leontopithecus chrysopygus* - its conservation and management. *Oryx* 32: 295-300.
- Martin, C. (1989). *Die Regenwälder Westafrikas. Ökologie, Bedrohung und Schutz*. Basel, Switzerland, Birkhäuser Verlag, 235 pp.
- Mascaro, J., Schnitzer, S.A. & W.P. Carson (in press). Liana diversity, abundance and mortality in a tropical wet forest in Costa Rica. *Forest Ecology and Management*.
- Mason, D. (1996). Responses of Venezuelan understory birds to selective logging, enrichment strips and vine cutting. *Biotropica* 28: 296-309.
- Mayer, K.R. (1951). *Forest resources of Liberia*. Agricultural Information Bulletin No. 67. U.S. Department of Agriculture.
- Mbida Mindzie C., Doutrelepont H., Vrydaghs L., Swennen R.L., Swennen R.J., Beeckman H., de Langhe E. & de Maret P. (2001). First archaeological evidence of banana cultivation in central Africa during the third millennium before present. *Vegetation History and Archaeobotany* 10: 1-6.
- M'Bla, K. et A. Diahuissie (1993). *Note de mise en place d'un dispositif d'étude du déliantage dans la forêt classée de Yapo*. Abidjan, Côte d'Ivoire, IDEFOR/DFO.
- Meer, P.J. van der, Bongers, F., Chatrou, L. & B. Riéra (1994). Defining canopy gaps in a tropical rain forest: effects on gap sizes and turnover time. *Acta Oecologica* 15: 701-714.
- Mengin-Lecreux, P. (1990). *Simulation de la croissance d'un peuplement de forêt dense. Le cas de la forêt de Yapo (Côte d'Ivoire)*. Paris, France, CTFT; Abidjan, Côte d'Ivoire, SODEFOR, 55 p.
- Mensah, K.O.A. (1966). An analysis of logging damage in compartment 4 of Tano Suhien Forest Reserve, Ghana. *Ghana Journal of Science* 6: 63-69.
- Mielot, F. et J.G. Bertault (1980). *Etude dynamique en vue de l'aménagement de la forêt dense de Côte d'Ivoire*. Abidjan, Côte d'Ivoire, Direction des Inventaires et de l'Aménagement, SODEFOR, 166 p.

- Moloney, A. (1887). *Sketch of the forestry of West Africa: with particular reference to its present principal commercial products*. London, U.K., Sampson Low, Marston, Searle & Rivington, 533 p.
- Mooney, J.W.C. (1963). Silviculture in Ghana. *Commonwealth Forestry Review*: 159-163.
- Morellato, P.C. and H.F. Leitao-Filho (1996). Reproductive phenology of climbers in a southeastern Brazilian forest. *Biotropica* 28: 180-191.
- Mori, S.A., Boom, B.M., de Carvalho, A.M. & T.S. dos Santos (1983). Southern Bahian moist forests. *Botanical Review* 49: 155-232.
- Morisita, M. (1959). Measuring of the dispersion of individuals and analysis of the distributional patterns. *Mem. Fac. Sci., Kyushu Univ., Ser. E (Biol.)* 2: 215-235.
- Morisita, M. (1962). I_s -index, a measure of dispersion of individuals. *Res. Popul. Ecol.* 4: 1-7
- Muthuramkumar, S. and Parthasarathy, N. (2000). Alpha diversity of lianas in a tropical evergreen forest in the Anamalais, Western Ghats, India. *Diversity and Distributions* 6: 1-14.
- Muthuramkumar, S. and N. Parthasarathy (2001). Tree-liana relationships in a tropical evergreen forest at Varagalaiar, Anamalais, Western Ghats, India. *Journal of Tropical Ecology* 17: 395-409.
- Myers, J.H. (1978). Selecting a measure of dispersion. *Environmental Entomology* 7: 619-621.
- Nabe-Nielsen, J. (2000). *Liana community and population ecology in a neotropical rain forest*. Ph.D. dissertation, University of Aarhus, Denmark.
- Nabe-Nielsen, J. (2001). Diversity and distribution of lianas in a neotropical rain forest, Yasuni National Park, Ecuador. *Journal of Tropical Ecology* 17:1-19.
- Nabe-Nielsen, J. (2002). Growth and mortality rates of the liana *Machaerium cuspidatum* in relation to light and topographic position. *Biotropica* 34: 319-322.
- Nascimento, H.E.M. and W.F. Laurance (2002). Total aboveground biomass in central Amazonian rainforests: a landscape-scale study. *Forest Ecology and Management* 168: 311-321.
- Neil, P.E. (1984). Climber problems in Solomon Islands forestry. *Commonwealth Forestry Review* 63: 27-34.
- Nicholson, D.I. (1958). An analysis of logging damage in tropical rain forest, North Borneo. *Malayan Forester* 21: 235-245.
- Nolan, T.M. (1989). Increment, annual cut and the growth of the forest. In: Wong, J.L.G. (ed.), *Ghana Forest Inventory Project seminar proceedings (Accra 1989)*. Kumasi, Ghana, Forest Inventory Project, pp. 53-58.
- Nolan, T.M. and K.K.F. Gartey (1992). Management of the tropical high forest of Ghana. In: Miller, F.R. and K.L. Adam (eds.), *Wise Management of Tropical Forests (Oxford 1992)*. Oxford, U.K., Forestry Institute, pp. 225-234.
- Nuys, G.J., Wijers, R.G., & A. Frühwald (1992). *Wood residues and logging damage in Nkrabia Forest Reserve, Ghana*. ITTO-Project PD 74/90: Better utilization of tropical timber resources in order to improve sustainability and reduce negative ecological impacts. University of Hamburg, Hamburg, Germany.
- Oates, J.F. (1995). The dangers of conservation by rural development: a case study from the forests of Nigeria. *Oryx* 29: 115-122.
- Okuda, T., Suzuki, M., Adachi, N., Quah, E.S., Hussein, N.A. & N. Manokaran (2003). Effect of selective logging on canopy and stand structure and tree species

- composition in a lowland dipterocarp forest in peninsular Malaysia. *Forest Ecology and Management* 175: 297-320.
- d'Oliveira, M.V.N. and E.M. Braz (1995). Reduction of damage to tropical moist forest through planned harvesting. *Commonwealth Forestry Review* 74: 208-210.
- Oliveira-Filho, A.T., Marcio de Mello, J. & J.R.S. Scolforo (1997). Effects of past disturbance and edges on tree community structure and dynamics within a fragment of tropical semideciduous forest in south-eastern Brazil over a five-year period (1987-1992). *Plant Ecology* 131: 45-66.
- Olivry J.C. (1986). *Fleuves et rivières du Cameroun*. Collection Monographies Hydrologiques d'ORSTOM 9. MESRES-ORSTOM, Paris, France.
- Opler, P.A., Baker, H.G. & G.W. Frankie (1991). Seasonality of climbers: a review and example from Costa Rican dry forest. In: Putz, F.E. and H.A. Mooney (eds.), *The biology of vines*. Cambridge, U.K., Cambridge University Press, pp. 377-391.
- Osafo, E.D. (1968). *The application of the Tropical Shelterwood System in coupe 2 of the Bobiri Research Centre*. Technical Note No. 3. Kumasi, Ghana, Forest Products Research Institute, 6 p.
- Osafo, E.D. (1969). Obstacles to natural regeneration in the high forest of Ghana. *F.P.R.I. Technical Newsletter* 3: 4-8.
- Osafo, E.D. (1970). *The development of silvicultural techniques applied to natural forests in Ghana*. Technical Note No. 13. Kumasi, Ghana, Forest Products Research Institute, 15 p.
- Oslisly, R. (2001). The history of human settlement in the middle Ogooué valley (Gabon). In: Weber, W., White L.J.T., Vedder, A. & L. Naughton-Treves (eds.), *African rain forest ecology and conservation. An interdisciplinary perspective*. Yale University Press, New Haven, U.S.A., pp. 101-118.
- Parren, M.P.E. (1994). *French and British colonial forest policies: past and present implications for Côte d'Ivoire and Ghana*. Working Papers in African Studies no. 188. Boston, U.S.A., African Studies Center, Boston University, 25 p.
- Parren, M. and F. Bongers (2001). Does climber cutting reduce felling damage in southern Cameroon? *Forest Ecology and Management* 141: 175-188.
- Parren, M.P.E. and N.R. de Graaf (1995). *The quest for natural forest management in Ghana, Côte d'Ivoire and Liberia*. Tropenbos Series 13. Tropenbos Foundation, Wageningen, The Netherlands.
- Parren, M.P.E., Van den Berg, J., Biesbrouck, K. and G.J.R. van Leersum (2001). A collaborative approach to forest management: the case of production forests in Southern Cameroon. In: Foahom, B., Jonkers, W.B.J., Nkwi, P.N., Schmidt, P. & M. Tchatat (eds.), *Seminar proceedings 'Sustainable management of African rain forests' (Kribi 1999). Part I: Workshops*. Wageningen, Netherlands, Tropenbos International, pp. 17-33.
- Parren, M.P.E., Bongers, F., Caballé, G., Nabe-Nielsen, J. & S.A. Schnitzer (in review). On censusing lianas: A review of the common methodologies. *Journal of Tropical Ecology*.
- Parrotta, J.A., Francis, J.K. & O.H. Knowles (2002). Harvesting intensity affects forest structure and composition in an upland Amazonian forest. *Forest Ecology and Management* 169: 243-255.
- Parthasarathy, N. and P. Sethi (1997). Trees and liana species diversity and population structure in a tropical dry evergreen forest in south India. *Tropical Ecology* 38: 19-30.

- Parthasarathy, N., Muthuramkumar, S. & M. Sridhar Reddy (in press). Patterns of liana diversity in tropical evergreen forests of peninsular India. *Forest Ecology and Management*.
- Paz y Miño C.G. Balslev, H. & R. Valencia (1995). Useful lianas of the Siona-Secoya Indians from Amazonian Ecuador. *Economic Botany* 49: 269-275.
- Pereira Jr., R., Zweede, J., Asner, G.P. & M. Keller (2002). Forest canopy damage and recovery in reduced-impact and conventional selective logging in eastern Para, Brazil. *Forest Ecology and Management* 168: 77-89.
- Peñalosa, J. (1983). Shoot dynamics and adaptive morphology of *Ipomoea phillomega* (Vell.) House (Convolvulaceae), a tropical rainforest liana. *Annals of Botany* 52: 737-754.
- Peñalosa, J. (1984). Basal branching and vegetative spread in two tropical rain forest lianas. *Biotropica* 16: 1-9.
- Pereira Jr., R., Zweede, J., Asner, G.P. & M. Keller (2002). Forest canopy damage and recovery in reduced-impact and conventional selective logging in eastern Para, Brazil. *Forest Ecology and Management* 168: 77-89.
- Pérez-Salicrup, D.R. (2001). Effect of liana cutting on tree regeneration in a liana forest in Amazonian Bolivia. *Ecology* 82: 389-396.
- Pérez-Salicrup, D.R. and M.G. Barker (2000). Effect of liana cutting on water potential and growth of adult *Senna multijuga* (Caesalpinioideae) trees in a Bolivian tropical forest. *Oecologia* 124: 469-475.
- Pérez-Salicrup, D.R., Claros, A., Guzman, R., Licona, J.C., Ledezma, F., Pinard, M.A. & F.E. Putz (2001a). Cost and efficiency of cutting lianas in a lowland liana forest of Bolivia. *Biotropica* 33: 324-329.
- Pérez-Salicrup, D.R., Sork, V.L. & F.E. Putz (2001b). Lianas and trees in a liana forest of Amazonian Bolivia. *Biotropica* 33: 34-47.
- Pérez-Salicrup, D.R., Schnitzer, S.A. & F.E. Putz (eds.) (in press). The community ecology and management of lianas. *Forest Ecology and Management*.
- Phillips, O. (1991). The ethnobotany and economic botany of tropical vines. In: Putz, F.E. and H.A. Mooney (eds.). *The biology of vines*. Cambridge, U.K., Cambridge University Press, pp. 427-475
- Phillips, O.L., Vasquez Martinez, R., Arroyo, L., Baker T.R., Killeen, T., Lewis, S.L., Malhi, Y., Monteagudo Mendoza, A., Neill, D., Nunez Vargas, P., Alexiades, M, Ceron, C., Di Fiore, A., Erwin, T., Jardim, A., Palacios, W., Saldia, M. & B. Vinceti (2002). Increasing dominance of large lianas in Amazonian forests. *Nature* 418: 770-774.
- Pinard, M. A. and F.E. Putz (1994). Vine infestation of large remnant trees in logged forest in Sabah, Malaysia: Biomechanical facilitation in vine succession. *Journal of Tropical Forest Science* 6: 302-309.
- Pinard, M.A. and F.E. Putz (1996). Retaining forest biomass by reducing logging damage. *Biotropica* 28: 278-295.
- Pinard, M.A., Putz, F.E. & J.C. Licona (1999). Tree mortality and vine proliferation following a wildfire in a subhumid tropical forest in eastern Bolivia. *Forest Ecology and Management* 116: 247-252.
- Pinard, M.A., Putz, F.E., Tay, J. & T.E. Sullivan (1995). Creating timber harvest guidelines for a reduced-impact logging project in Malaysia. *Journal of Forestry* 93: 41-45.

- Plumptre, A. J. (1996). Changes following 60 years of selective timber harvesting in the Budongo Forest Reserve, Uganda. *Forest Ecology and Management* 89: 101-113.
- Poker, J. (1989). *Struktur und Wachstum in selektiv genutzten Beständen im Grebo National Forest von Liberia*. Abschlußbericht zum GTZ-Projekt Nr. 87.2050.0-01.100. Hamburg, Bundesrepublik Deutschland, Institut für Weltforstwirtschaft und Oekologie, Bundesforschungsanstalt für Forst- und Holzwirtschaft, 274 p.
- Poorter, L., Bongers, F., Rompaey, R.S.A.R. Van & M. de Klerk (1996). Regeneration of canopy tree species at five sites in West African moist forest. *Forest Ecology and Management* 84: 61-69.
- Prabhu, R. & Lay-Cheng Tan (eds.) (1995). *Testing criteria and indicators for the sustainable management of forests. Final report test Côte d'Ivoire June 2-30, 1995*. Bogor, Indonesia, CIFOR, 26 p.
- Prabhu R., Maynard, W., Eba'a Atyi, R., Colfer, C.J.P., Shepherd, G., Venkateswarlu, P. & F. Tiayon (1998). *Testing and developing criteria and indicators for sustainable forest management in Cameroon: the Kribi test. Final report*. Bogor, Indonesia, CIFOR, 122 p.
- Proctor, J., Haridasan, K. & G.W. Smith (1998). How far north does Lowland Evergreen Tropical Rain Forest go? *Global Ecology and Biogeography Letters* 7: 141-146.
- Putz, F.E. (1983). Liana biomass and leaf area of a "tierra firme" forest in the Rio Negro Basin, Venezuela. *Biotropica* 15: 185-189.
- Putz, F.E. (1984a). The natural history of lianas on Barro Colorado Island, Panama. *Ecology* 65: 1713-1724.
- Putz, F.E. (1984b). How trees avoid and shed lianas. *Biotropica* 16: 19-23.
- Putz, F.E. (1985). Woody lianas and forest management in Malaysia. *Commonwealth Forestry Review* 64: 359-65.
- Putz, F.E. (1991). Silvicultural effects of lianas. In: Putz, F.E. & H.A. Mooney (eds.). *The biology of vines*. Cambridge, U.K., Cambridge University Press, pp. 493-501.
- Putz, F.E. (1990). Liana stem diameter growth and mortality rates on Barro Colorado Island, Panama. *Biotropica* 22: 103-105.
- Putz, F.E. (1995). Vines in treetops: consequences of mechanical dependence. In: Lowman, M.D. and N.M. Nadkarni (eds.), *Forest canopies*. San Diego, U.S.A., Academic Press, pp. 311-323.
- Putz, F. E. and P. Chai (1987). Ecological studies of lianas in Lambir National Park, Sarawak, Malaysia. *Journal of Ecology* 75: 523-531.
- Putz, F.E. and N.M. Holbrook (1991). Biomechanical studies of vines. In: Putz, F.E. and H.A. Mooney (eds.), *The biology of vines*. Cambridge, U.K., Cambridge University Press, pp. 73-97.
- Putz, F.E. and H.A. Mooney (eds.) (1991). *The biology of vines*. Cambridge, U.K., Cambridge University Press, 526 pp.
- Putz, F.E. and D.M. Windsor (1987). Liana phenology on Barro Colorado Island, Panama. *Biotropica* 19: 334-341.
- Putz, F.E., Lee, H.S. & R. Goh (1984). Effects of post-felling silvicultural treatments on woody vines in Sarawak. *Malaysian Forester* 47: 214-226.
- Ramírez, N. (1993). Producción y costo de frutos y semillas entreformas de vida. *Biotropica* 25: 46-60.

- Reitsma, J.M. (1988). Forest vegetation of Gabon. Tropenbos Technical Series No 1. Tropenbos Foundation, Ede, The Netherlands, 142 p.
- Richards, P. W. (1996). The tropical rain forest: an ecological study. Second edition. Cambridge University Press, Cambridge, U.K.
- Rollet, B. (1974). L'architecture des forêts denses humides sempervirentes de plaine. Centre Technique Forestier Tropical, Nogent-sur-Marne, France, 298 p.
- Rollet, B. (1983). La régénération naturelle dans les trouées. Un processus général de la dynamique des forêts tropicales humides. *Revue Bois et Forêts des Tropiques* 201: 3-34.
- Runkle, J.R. (1981). Gap regeneration in some old-growth forests of the eastern United States. *Ecology* 62: 1041-1051.
- Runkle, J.R. (1982). Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology* 63: 1533-1546.
- Sabatier, D., Grimaldi, M., Prévost, M.-F., Guillaume, J., Godron, M., Dosso, M., and P. Curmi (1997). The influence of soil cover organization on the floristic and structural heterogeneity of a Guianan rain forest. *Plant Ecology* 131: 81-108.
- Sargent, C., Husain, T., Ashie Kotey, N., Mayers, J., Prah, E., Richards, M. & T. Treue (1994). Incentives for the sustainable management of the tropical high forest in Ghana. *Commonwealth Forestry Review*. 73(3): 155-163.
- SAS Institute (2000). *JMP statistics and graphics guide*, Version 3.1. SAS Institute Inc., Cary, NC.
- Schäfer, C. (1997). Sekundärwaldentwicklung in Gebiet eines teilweise laubabwerfendn Waldes in Süd-Benin. Göttinger Beiträge zur Land- und Forstwissenschaft in den Tropen und Subtropen Heft 120. Fakultät für Forstwissenschaften und Waldökologie, Georg-August-Universität, Göttingen, Germany.
- Schenck, H. (1892-1893). Beiträge zur Biologie und Anatomie der Lianen, im Besonderen der in Brasilien einheimischen Arten. In Botanische Mitteilungen aus den Tropen. Schimper, Jena, Deutschland, 2 Vol.
- Schmidt, R.C. (1987). Tropical rain forest management. *Unasylva* 39(156): 2-17.
- Schnell, R. (1950). La forêt dense. Introduction à l'étude botanique de la région forestière d'Afrique occidentale. Manuels Ouest-Africains, Vol. I. Paris, France, Lechevalier, 330 p.
- Schnitzer, S.A. and F. Bongers (2002). The ecology of lianas and their role in forests. *Trends in Ecology and Evolution* 17: 223-230.
- Schnitzer, S.A. and W.P. Carson (2000). Have we missed the forest because of the trees? *Trends in Ecology and Evolution* 15: 375-376.
- Schnitzer, S.A. and Carson, W.P. (2001). Treefall gaps and the maintenance of diversity in a tropical forest. *Ecology* 82: 913-919.
- Schnitzer, S.A., Dalling, J.W. & Carson, W.P. (2000). The impact of lianas on tree regeneration in tropical forest canopy gaps: Evidence for an alternative pathway of gap-phase regeneration. *Journal of Ecology* 88: 655-666.
- Schnitzer, S.A., Dewalt, S.J. & Chave, J. (unpublished manuscript). Censusing and measuring lianas: a quantitative comparison of the common methods.
- Schnitzer, S.A., Kuzee, M. & Bongers, F. (in review). Disentangling above- and below-ground competition between lianas and trees in a tropical forest. *Ecology*.
- Schnitzer, S.A., Parren, M.P.E. & Bongers, F. (in press). Recruitment of lianas into logging gaps and the effects of pre-harvest liana cutting. *Forest Ecology and Management*.

- Schwartz, D. (1992). Assèchement climatique vers 3000 B.P. et expansion Bantu en Afrique cantrale atlantique: quelques réflexions. *Bull. Soc. géol. France* 163: 353-361.
- Schwarzkopf, L. & B. Rylands (1989). Primate species richness in relationship to habitat structure in Amazonian rainfores fragments. *Biological Conservation* 48: 1-12.
- Shafer, C.L. (1990). *Nature Reserves. Island theory and conservation practice.* Washington, USA, Smithsonian Institution Press, 189 p.
- Shanmughavel, P., Zheng, Z., Liqing, S. & C. Min (2001). Floristic structure and biomass distribution of a tropical seasonal rain forest in Xishuangbanna, southwest China. *Biomass and Bioenergy* 21: 165-175.
- Siebert, S.F. (1993). The abundance and site preferences of rattan *Calamus exilis* and *Calamus zollingeri* in two Indonesian national parks. *Forest Ecology and Management* 59: 105-113.
- Siebert, S.F. (2000). Abundance and growth of *Desmoncus orthacanthos* Mart. (Palmae) in response to light and ramet harvesting in five forest sites in Belize. *Forest Ecology and Management* 137: 83-90.
- Sist, P., Dykstra, D. & R. Fimbel (1998). *Reduced-impact logging guidelines for lowland and hill dipterocarp forests in Indonesia.* CIFOR Occasional Paper No 15. CIFOR, Bogor, Indonesia.
- Sivha, M., Mühlenberg, M. & J. Slowik, 1993. *Manuel des espèces de mammifères et d'oiseaux choisies pour le programme de suivi écologique en forêt classée de Bossematié (FCB).* Oekologische Station der Universität Würzburg, Rauhenebrach, Allemagne, 86 pp.
- Sizer, N. and D. Plouvier (1999). *Increased investment and trade by transnational logging companies in Africa, the Caribbean and the Pacific: implications for the sustainable management and conservation of tropical forests.* WWF, Brussels, Belgium; WRI Forest Frontiers Initiative, Washington DC, USA.
- Skorupa, J.P. (1986). Responses of rain forest primates to selective logging in Kibale Forest, Uganda: a summary report. in K. Benirschke (ed.), *Primates: the road to self-sustaining populations.* Berlin, Germany, Springer Verlag: 57-70.
- Smith, R.F. (1970). The vegetation structure of a Puerto Rican rain forest before and after short-term gamma irradiation. In H. T. Odum (Ed.). *A tropical rain forest*, pp. D103-D140. U.S. Atomic Energy Commission, Oak Ridge.
- Smith-Gill, S.J. (1975). Cytophysiological basis of disruptive pigmentary patterns in the leopard frog *Rana pipiens*. II. Wild type and mutant cell specific patterns. *Journal of Morphology* 146: 35-54.
- SODEFOR, (1986). *Projet d'aménagement pilote de la forêt classée de Yapo. Compte rendu de mission d'appui technique (20 au 28 janvier 1986).* Abidjan, Côte d'Ivoire, SODEFOR.
- SODEFOR, (1996). *Sylviculture en forêt naturelle. Protocole d'éclaircie sélective par dévitalisation.* Abidjan, Côte d'Ivoire, SODEFOR.
- Sokal, R.R. and F.J. Rohlf (1995). *Biometry.* W.H. Freeman and Company, New York.
- Stevens, G. C. (1987). Lianas as structural parasites: the *Bursera simaruba* example. *Ecology* 68: 77-81.
- Stevenson, D.S. (1952). *Report on the Gold Coast. Actes de la Première Conférence Forestière Interafricaine (Abidjan, 1951).* Paris, France, Commission de

- Coopération Technique en Afrique au Sud du Sahara (CCTA), Nogent-sur-Marne, France, CTFT: 247-256.
- Stockdale, M.C. & Wright, H.L. (1996). Rattan inventory: determining plot shape and size. Pp. 523-533 in Edwards, D.S., Booth, W.E. & Choy, S.C. (eds.). *Tropical rainforest research - Current issues*. Monographiae Biologicae Vol. 74. Dordrecht, The Netherlands, Kluwer Academic Publishers.
- Struhsaker, T.T. (1997). Ecology of an African rain forest. Logging in Kibale and the conflict between conservation and exploitation. University Press of Florida, Gainesville, U.S.A.
- Sunderland, T.C.H. (1999). Recent research into African rattans (Palmae): A valuable non-wood forest product from the forests of Central Africa. In Sunderland, T.C.H., Clark, L.E. & P. Vantomme (eds.), *Non-Wood Forest Products of Central Africa. Current research issues and prospects for conservation and development*. FAO, Rome, Italy: 87-97.
- Sutton, I. (1983). Labour in commercial agriculture in Ghana in the late nineteenth and early twentieth centuries. *Journal of African History* 24: 461-483.
- Suzuki, W. (1989). Tree damage caused by climbing plants and the mechanism of their development in Hinoki (*Chamaecyparis obtusa*) plantations. *Journal of the Japanese Forestry Society* 7: 395-404.
- Swaine, M.D. (1992). Characteristics of dry forest in West Africa and the influence of fire. *Journal of Vegetation Science* 3: 365-374.
- Swaine, M.D., Agyeman, V.K., Kyereh, B., Orgle, T.K., Thompson, J. & E.M. Veenendaal (1997). Ecology of forest trees in Ghana. ODA Forestry Series 7. O.D.A., London, U.K.
- Synnott, T.J. (1979). A manual of permanent plot procedures for tropical rainforests. Tropical Forestry Papers No. 14. Commonwealth Forestry Institute, University of Oxford, UK.
- Tabanez, A.A.J. and Viana, V.M. (2000). Patch structure within Brazilian Atlantic forest fragments and implications for conservation. *Biotropica* 32: 925-933.
- Technical Working Group (1999). Quality management of the forests of Ghana: forest standards, principles and specification. Accra, Ghana, Ministry of Lands & Forestry, 59 p.
- Thomas, D.W., Boyd, M.R., Cardellina, J.H., Gereau, R.E., Jato, J., and P. Symonds (1994). Sustainable harvest of *Ancistrocladus korupensis* (Ancistrocladaceae) leaf litter for research on HIV. *Economic Botany* 48: 413-414.
- Thompson, J., Proctor, J., Scott, D.A., Fraser, P.J., Marrs, R.H., Miller, R.P. & V.M. Viana (1998). Rain forest on Maraca Island, Roraima, Brazil: artificial gaps and plant response to them. *Forest Ecology and Management* 102: 305-321.
- Tra Bi, F.H. (1997). Utilisations des plantes, par l'homme, dans les Forêts Classées du Haut-Sassandra et du Scio, en Côte d'Ivoire. Thèse Doctorat. Université de Cocody, Abidjan.
- Troy, A.R., Ashton, P.M.S. & B.C. Larson (1997). A protocol for measuring abundance and size of a Neotropical liana, *Desmoncus polyacanthus* (Palmae), in relation to forest structure. *Economic Botany* 51: 339-346.
- Uhl, C. and I.C. Guimarães Vieira (1989). Ecological impacts of selective logging in the Brazilian Amazon: a case study from the Paragominas region of the state of Pará. *Biotropica* 21: 98-106.
- Uhl, C., Clark, K., Dezzeo, N. & Maquirino, P. (1988). Vegetation dynamics in Amazonian treefall gaps. *Ecology* 69: 751-763.

- Van Rompaey, R.S.A.R. (1993). Forest gradients in West Africa. A spatial gradient analysis. Ph.D. Dissertation, Wageningen Agricultural University, Wageningen, The Netherlands, 142 p.
- Van Schaik, C.P., Terborgh, J.W. & S.J Wright (1993). The phenology of tropical forests: Adaptive significance and consequences for primary consumers. *Annu. Rev. Ecol. Syst.* 24: 353-377.
- Viana, V.M., Tabanez, A.A.J. & J.L.F. Batista (1997). Dynamics and restoration of forest fragments in the Brazilian Atlantic moist forest. In Laurance, W.F. & R.O. Bierregaard, Jr. (eds.), *Tropical forest remnants: Ecology, management, and conservation of fragmented communities*. University of Chicago Press, Chicago, U.S.A.: 351-365.
- Vidal, E., Johns, J., Gerwing, J.J., Barretto, P. & C. Uhl (1997). Vine management for reduced-impact logging in eastern Amazonia. *Forest Ecology and Management* 98: 105-114.
- Vogelezang, L. (1998). Eco-management and botanical biodiversity conservation in forest reserves in Ivory Coast. A series of three case studies: Bossematié, Yaya and Yapo-Abbé. MSc thesis. Wageningen, Netherlands, Sub-Department of Forestry, Wageningen Agricultural University, 99 p.
- Vooren, A.P. (1992). Harvest criteria for tropical forest trees. in Cleaver, K., M. Munasinghe, M. Dyson, N. Egli, A. Peuker and F. Wencélius (eds.), *Conservation of West and Central African rainforests*. World Bank Environment Paper No. 1. Washington D.C., U.S.A., World Bank: 134-140.
- Vooren, A.P. (1999). Introduction de la bionomie dans la gestion des forêts tropicales denses humides. Doctoral thesis, Wageningen University, Wageningen, The Netherlands, 220 p.
- Vooren, A.P. and D.M.J. Offermans (1985). An ultralight aircraft for low-cost, large-scale stereoscopic aerial photographs. *Biotropica* 17: 84-88.
- Voorhoeve, A.G. (1965). Liberian high forest trees. Ph.D. Dissertation, Wageningen Agricultural University. PUDOC, Wageningen, The Netherlands, 416 p.
- Vries, H. de (1880). Sur les causes des mouvements auxotoniques des organes végétaux. *Archives Néerlandaises des Sciences Exactes et Naturelles* 15. 295 pp.
- Waitkuwait, W.E. (1992). Restauration d'un écosystème forestier: contribution de l'aménagement de la faune. dans Vooren, A.P., Schork, W., Blokhuis, W.A. et A.J.C. Spijkerman (éds.), *Compte rendu séminaire sur l'aménagement intégré des forêts denses humides et des zones agricoles périphériques* (Abidjan, 1991). Tropenbos Series 1. Wageningen, Pays-Bas, Fondation Tropenbos: 203-214.
- Waterloo, M.J., Ntonga, J.C., Dolman, A.J. & A.B. Ayangma (1997). Impact of land use change on the hydrology and erosion of rain forest land in South Cameroon. Report 134. Winand Staring Centre, Wageningen, The Netherlands, 89 p.
- Watt, A.S. (1947). Pattern and process in the plant community. *Journal of Ecology* 35: 1-22
- Webb, E.L. (1997). Canopy removal and residual stand damage during controlled selective logging in lowland swamp forest of northeast Costa Rica. *Forest Ecology and Management* 95: 117-129.
- Weingart, J.B. (1990). Tätigkeitsbericht und waldbauliche Ergebnisse des Forest Management Unit Bomi Hills/ Liberia: 1988-1990. Eschborn, Bundesrepublik Deutschland, Gesellschaft für Technische Zusammenarbeit, 11 p.
- Whigham, D. (1984). The influence of vines on the growth of *Liquidambar styraciflua* L. (sweetgum). *Canad. J. For. Res.* 14: 37-39.

- White, F. (1978). The afro-montane region. In M. J. A. Werger (Ed.). *Biogeography and ecology of Southern Africa*, pp. 436-513. Dr. W. Junk Publishers, The Hague, The Netherlands.
- White, L.J.T. (1994). The effects of commercial mechanised selective logging on a transect in lowland rainforest in the Lopé Reserve, Gabon. *Journal of Tropical Ecology* 10: 313-322.
- White, L.J.T. (2001). Forest-savanna dynamics and the origins of Marantaceae Forest in central Gabon. in Weber, W., White L.J.T., Vedder, A. & L. Naughton-Treves (Eds.), *African rain forest ecology and conservation. An interdisciplinary perspective*. Yale University Press, New Haven, U.S.A.: 165-182.
- White L.J.T. and J.F. Oates (1999). New data on the history of the plateau forest of Okomu, southern Nigeria: an insight into how human disturbance has shaped the African rain forest. *Global Ecology and Biogeography* 8 : 355-361.
- White L.J.T. and C.E.G. Tutin (2001). Why chimpanzees and gorilla respond differently to logging. A cautionary tale from Gabon. In Weber, W., White L.J.T., Vedder, A. & L. Naughton-Treves (eds.), *African rain forest ecology and conservation. An interdisciplinary perspective*. Yale University Press, New Haven, U.S.A. : 449-46
- Whitmore, T.C. (1984). *Tropical rain forests of the Far East*. 2nd ed., Oxford, U.K., Clarendon Press, 352 p.
- Wirth, R., Weber, B. & Ryel, R.J. (2001). Spatial and temporal variability of canopy structure in a tropical moist forest. *Acta Oecologia* 22: 235-244
- Wöll, H.J. (1981). *Silvicultural evaluation. Diagnostic sampling 1978-1980*. Monrovia, Liberia, German Forestry Mission, 66 p.
- Wöll, H.J. (1986). *Bildung einer Forest Management Unit (FMU) innerhalb des Vorhabens "Holzwirtschaftliches Ausbildungszentrum Bomiwood" in Liberia*. Eschborn, Deutschland, Gesellschaft für Technische Zusammenarbeit, 62 p.
- Wöll, H.J. (1991). *Forêt Classée de la Bossematié (FCB). Plan d'aménagement élaboré pour quelques parcelles d'une série de production*. Abidjan, Côte d'Ivoire, GTZ-SODEFOR, 30 p.
- Wöll, H.J. (1992). *Le projet "Rehabilitation de la Forêt Classée de Bossematié", Côte d'Ivoire, Région d'Abengourou*. dans Vooren, A.P., Schork, W., Blokhuis, W.A. et A.J.C. Spijkerman (éds.), *Compte rendu séminaire sur l'aménagement intégré des forêts denses humides et des zones agricoles périphériques* (Abidjan, 1991). Tropenbos Series 1. Wageningen, Pays-Bas, Fondation Tropenbos: 163-179.
- Woods, P. (1989). Effects of logging, drought, and fire on structure and composition of tropical forests in Sabah, Malaysia. *Biotropica* 21: 290-298.
- Wright, D.D., Jessen, J.H., Burke, P. & H.G. de Silva Garza (1997). Tree and liana enumeration and diversity on a one-hectare plot in Papua New Guinea. *Biotropica* 29: 250-260.
- Wright, S.J., Calderón, O., Hernández, A. & Paton, S. (in review). Are lianas increasing in importance in tropical forests? A 16-year record from Barro Colorado Island, Panamá. *Ecology*.

APPENDIX 1

Morisita index (I_{δ}) for liana (morpho)species at two spatial levels at two spatial levels of 1-ha plots over an area of 500 ha and within 1-ha plots. For the latter spatial level species should be represented by ≥ 10 individuals (≥ 2 cm dbh) in 33 1-ha plots. This has been worked out for 0.01 ha and sometimes 0.04 ha scales. The total number of liana stems (N) present are presented too.

Plot #	All spp	All spp	N	<i>Cissus dinklagei</i>	N	<i>Manniophyton fulvum</i>	N	<i>Tetracera alnifolia</i>	N	<i>Strophanthus spp</i>	N	<i>Eremospatha spp.</i>	N	<i>Lacosperma spp.</i>	N
1-ha scale				6.85	680	2.03	296	2.927	142	1.870	141	3.35	3868	4.42	1951
Scale within 1-ha's	0.01 ha	0.04 ha		0.01 ha		0.01 ha		0.01 ha		0.01 ha		0.01 ha		0.01 ha	
1	1.37	1.14	588									42.48	267	29.36	88
2	1.52	1.19	462									20.06	158		0
3	1.50	1.20	466												
4	1.54	1.20	250										4	26.14	18
5	2.83	1.61	221									31.04	55	21.66	136
6	1.65	1.36	218									31.27	250	36.14	75
7	1.47	1.14	187									56.13	295		0
8	1.44	1.16	1092	4.76	42	3.95	134		1	4.1	19	20.16	23	23.39	19
9	1.66	1.22	495	8.74	30	22.05	52	16	24	20.29	26	71.23	56		3
10	1.89	1.30	402		9		4		6		1	71.41	38	9.17	16
11	1.69	1.36	767	2.28	118		0	20.9	30		8	59.09	12	39.78	92
12	1.72	1.31	556	4.33	27	47.62	11		5		7	38.43	395	52.94	18
13	1.73	1.17	340		7		2	12.99	23		4		5	12.49	99
14	2.04	1.53	456	11.91	28	17.33	25		0		4	78.92	27	31.95	41
15	1.67	1.24	508		5	6.04	42		5		9	94.65	219	24.7	73
16	1.34	1.13	668	3.09	81		5		0		6	46.12	133		4
17	1.87	1.40	256		2		0		0		2		6		0

Lianas and logging in West Africa

18	1.79	1.20	254		3	4	0	3	7	0			
19	1.67	1.33	398	6.21	30	2	5	5	40.76	163	1		
20	1.94	1.31	303	1.82	11	0	1	1	19.31	30	0		
21	1.58	1.30	332		5	0	5	2	72.53	14	0		
22	1.53	1.15	480	4.65	50	1	2	3	28.99	178	52.54	36	
23	1.98	1.34	223		2	2	0	6	53.33	10		9	
24	1.61	1.28	290	4.76	21	1	1	3		0	100	25	
25	1.30	1.19	800	2.33	64	1	5	0	55.81	313	56.88	24	
26	1.65	1.29	246	10.99	14	0	2	5		8		2	
27	1.21	1.07	382	3.52	47	0	3	0	69.25	54		8	
28	1.95	1.19	289		9	0	0	3		0	52.94	18	
29	1.79	1.29	311		8	0	0	3	23.08	13	100	21	
30	2.11	2.32	209		8	2	5	4	48.22	83	24.51	100	
31	1.40	1.22	368	4	26	0	8	4	7.1	749	22.41	388	
32	1.95	1.39	244	8.79	14	0	0	5	26.38	34	14.73	93	
33	1.80	1.36	397	15.79	19	8	14.55	11	8	17.87	269	24.590	544

All I_s values are significant at $p \leq 0.05$, standardized Morisita index (I_p) ≥ 0.5 except for the bold values which are n.s.

APPENDIX 2

Liana abundance in tropical moist forest plots in three different continents. Total number of lianas per ha; (a) in the 2-5 cm dbh class, (b) large lianas: ≥ 5 cm dbh, (c) very large lianas: ≥ 10 cm dbh.

Continent	Site	2-5 cm	≥ 5 cm	≥ 10 cm	References
Africa	Cameroon – Ebom	347	241	7	
	Cameroon – Ebom	169	293	25	
	Cameroon – Ebom	269	197	20	
	Cameroon – Ebom	135	115	3	
	Cameroon – Ebom	119	102	19	
	Cameroon – Ebom	105	113	7	
	Cameroon – Ebom	68	119	11	
	Cameroon – Ebom	858	234	18	
	Cameroon – Ebom	420	75	6	
	Cameroon – Ebom	308	94	22	
	Cameroon – Ebom	631	136	19	
	Cameroon – Ebom	479	77	14	
	Cameroon – Ebom	268	72	9	
	Cameroon – Ebom	352	104	21	
	Cameroon – Ebom	409	99	11	
	Cameroon – Ebom	575	93	6	
	Cameroon – Ebom	186	70	10	
	Cameroon – Ebom	212	42	8	
	Cameroon – Ebom	261	137	13	
	Cameroon – Ebom	225	78	12	
	Cameroon – Ebom	258	74	7	
	Cameroon – Ebom	408	72	5	
	Cameroon – Ebom	184	39	2	
	Cameroon – Ebom	229	61	8	
	Cameroon – Ebom	646	154	7	
	Cameroon – Ebom	156	90	3	
	Cameroon – Ebom	283	99	10	
	Cameroon – Ebom	230	59	1	
	Cameroon – Ebom	211	100	7	
	Cameroon – Ebom	128	81	8	
	Cameroon – Ebom	233	135	6	
	Cameroon – Ebom	161	83	2	
Cameroon – Ebom	216	181	5		
Cameroon – Edea			8	Rollet 1974	
Côte d'Ivoire - San Pedro	256	68	8	Rollet 1974	
Côte d'Ivoire – Banco			15	Rollet 1974	
Gabon - A4	288	78	6	Rollet 1974	
Gabon - C4	272	86	6	Rollet 1974	
Gabon – Montagne de Sable	292	121	13	Rollet 1974	
Gabon – Makokou	304	126	10	Rollet 1974	
Gabon – Makokou		144	11	Caballé 1984	
Gabon – Makokou		128		Caballé 1984	
Gabon – Makokou		80	31	Caballé 1984	
D.R. of Congo – Lenda	137	24		Makana <i>et al.</i> 1998	
D.R. of Congo – Edoro	651	67		Makana <i>et al.</i> 1998	
Australasian	India – Haldibari			5	Proctor <i>et al.</i> 1998
	Malaysia – Pahang	286	127		Appanah & Putz 1984
	Malaysia – Pahang	213	81		Appanah & Putz 1984
	Malaysia – Pahang	227	121		Appanah & Putz 1984
	Malaysia – Pahang	221	101		Appanah & Putz 1984
	Malaysia – Pahang	197	92		Appanah & Putz 1984

Malaysia – Pahang	262	106		Appanah & Putz 1984
Malaysia – Pahang	321	174		Appanah & Putz 1984
Malaysia – Pahang	232	102		Appanah & Putz 1984
Malaysia – Pahang	370	191		Appanah & Putz 1984
Malaysia – Pahang	226	98		Appanah & Putz 1984
Malaysia – Pahang	292	105		Appanah & Putz 1984
Malaysia – Pahang	306	88		Appanah & Putz 1984
Malaysia – Pahang	272	84		Appanah & Putz 1984
Malaysia – Pasoh	404	102	6	Rollet 1974
Malaysia – Rengam	248	91	3	Rollet 1974
Sarawak – Semengoh	100	54	1	Rollet 1974
Sarawak – Bintulu	328	13	2	Rollet 1974
Sarawak – Lambir	296	52	2	Putz & Chai 1987
Sarawak – Lambir	162	2	2	Putz & Chai 1987
Sabah – Sepilok	168	46	6	Rollet 1974
Sabah – Mile 81	204	54	2	Rollet 1974
Indonesia – Sumatra 1	128	21	1	Rollet 1974
Indonesia – Sumatra 2	228	20	4	Rollet 1974
Indonesia – Kalimantan 1	368	78	14	Rollet 1974
Indonesia – Kalimantan 2	220			Rollet 1974
Philippines – Mindanao	880	109	17	Rollet 1974
PNG – Crater Mountain			14	Wright <i>et al.</i> 1997
Australia – Queensland			15	Hegarty & Caballé 1991
Neotropics				
Costa Rica – Volcan Barva		42	2	Heaney & Proctor 1990
100 m altitude				
Costa Rica – Volcan Barva		32	7	Heaney & Proctor 1990
500 m altitude				
Panama – BCI	386	43	3	Putz 1984
Panama			13	Rollet 1974
Venezuela	144	51	3	Rollet 1974
Guyana	64	24	7	Rollet 1974
Fr. Guyana – Piste St. Elie	169	49	16	Beekman 1981
Fr. Guyana – Piste St. Elie			9.8	Sabatier <i>et al.</i> 1997 ¹
Brazil – Caxuana	215	100	5	Rollet 1974
Brazil – Manaus	116	44	12	Rollet 1974
Brazil – Jari 1			6	Rollet 1974
Brazil – Jari 2			7	Rollet 1974
Brazil – Pilão			3	Rollet 1974
Brazil – Santarem			20	Rollet 1974
Brazil – Para	240	100		Vidal <i>et al.</i> 1997
Brazil – Olho d’Agua, Para			10	Cochrane & Schulze 1999
Brazil – Olho d’Agua, Para			22	Cochrane & Schulze 1999
Bolivia – Las Trancas		163	3.6	Killeen <i>et al.</i> 1998 ²
Peru – Yanamono			26	Gentry 1988
Peru – Mishana			16	Gentry 1988
Peru – Cocha Cashu			23	Gentry 1988
Peru – Cabeza de Mono			24	Gentry 1988
Peru – Tambopata			14	Gentry 1988
Peru – Tambopata			17	Gentry 1988
Peru – Neblina			20	Gentry 1988
Peru			16	Rollet 1974

¹Average of transects totalling 19 one-hectare plots

²Average of total of one hundred 500 m² plots (total 5 ha)

SUMMARY

In this dissertation the role of lianas in the tropical forest ecosystem in relation to logging activities is analysed. Lianas (woody vines) are an abundant, diverse, and conspicuous growth form in nearly all tropical forests. Foresters mostly see lianas as a nuisance. Cutting of liana stems is an important technique in some forest management practices. Pre-harvest liana cutting is aimed at reduction of logging damage, improved felling precision, enhancement of the growth of the remaining trees, and reduction of the regrowth capacity of lianas. However, studies investigating the effectiveness of pre-harvest liana cutting are scarce. Most studies in SE Asia and in the Amazon Basin established during the last half of the 20th century pointed towards positive effects of liana cutting. They concluded that liana-cutting leads to reduction of logging damage to residual trees reduced size of logging gaps and more rapid development of tree regeneration in logging gaps.

In the past, liana cutting was prescribed over vast areas of the African continent, although a proper evaluation never took place. For this purpose, a large-scale experiment was set up as part of the study reported here, to test liana cutting as a pre-harvest silvicultural treatment. The silvicultural treatment formed part of a larger project that aimed at increasing stand productivity by applying silvicultural treatments to favour desired species. The study was conducted in a logging concession 100 km east of Kribi, Cameroon (3^o N, 10^o E). The concession area covers more than 2,000 km². The study area was located in the northeastern part near the village Ebom, in a part of the forest where large-scale commercial logging had not happened before. 33 one-hectare research plots, surrounded by a 100-m wide bufferzone, were located in mostly flat terrain. In 5 control plots no logging or silvicultural treatments were applied. The remaining 28 plots were all logged and in 16 of them pre-harvest liana cutting was applied (May 1995). Felling was carried out nine months later (February 1996). Liana cutting was applied in the research plots and in the surrounding buffer zone. Harvest levels were set at one tree per ha over 60 cm dbh, resembling normal exploitation practise in the region.

An important aspect of this study was to assess the influence of physical damage of felling to the remaining vegetation, and the response of the remaining trees to the changed conditions. By harvesting trees the light climate at the felling sites changes drastically. Field measurements on various aspects of responses of individual trees and lianas in relation to logging activities took place at several stages of harvesting, such as during the pre-harvest, actual felling and post-harvest period. An initial inventory of all lianas ≥ 2 cm diameter at breast height (dbh) and trees ≥ 10 cm dbh took place within the 1-ha plots. As a pre-harvest treatment liana cutting was applied in order to assess the role of lianas in the ecosystem and to analyse their response to stress and disturbance. Lianas have a high capacity to re-sprout, but the potential changes in liana composition in response to cutting have received little attention. Re-sprouting capacity and mortality were assessed regularly for a period of 22 months after climber cutting. In this study it was also assessed whether liana cutting is effective in reducing felling damage to residual trees and to reduce logging gap sizes significantly. A six-year chronosequence of logging gaps was used to determine the speed by which lianas develop into logging gaps. The effectiveness of pre-harvest

liana cutting in reducing the number of lianas that re-colonise logging gaps was also assessed.

The following questions were asked to investigate the role of lianas in relation to logging:

1. How to inventory lianas?
2. How abundant are lianas in the forest studied?
3. What are the spatial distribution patterns of the lianas?
4. To what extent does liana cutting result in the death of the lianas, and what is their re-sprouting capacity?
5. What is the effect of pre-harvest liana cutting on felling gap size, on the number of dead or damaged trees, and on felling direction?
6. How and at what speed do lianas recruit into gaps and how effective can pre-harvest liana cutting be to reduce the number of lianas that re-colonise logging gaps?

Chapter 1 introduces the topic of the dissertation and describes the role and importance of lianas in relation to logging activities. Chapter 2 provides an overview of silvicultural systems applied in the past in Côte d'Ivoire, Ghana and Nigeria, as well as more recent developments since the 1970s in these countries and in Liberia and Cameroon. Over the past decades, several new ideas and developments in forestry can be seen in West Africa, and a selection of them is presented in this chapter. Most West African forests can be characterised as depleted of their timber. These over-exploited forests, often invaded by farmers after their exploitation, require some form of restoration before they can be exploited sustainably. Some of these forests are seriously degraded and have so many large logging gaps that hardly any canopy cover is left. In these forests, often the development of tree regeneration is seriously hampered by liana mats and tangles for decades (see also Chapter 4). The best examples of forest restoration in West Africa can be seen in eastern Côte d'Ivoire where ecological knowledge has been collected and incorporated into the management plan. Notably, harvesting guidelines for senescent trees as developed in research work in Taï National Park can be applied in buffer zone management, whereby a 'close-to-nature' method. At national level, Côte d'Ivoire neighbouring country Ghana has made most progress by trying to match the biological production potential of the forests to the national sawmill capacity, thereby aiming at sustainable resource supply. In Ghana, also a multi-scale approach to the protection of forests has been implemented, based on botanical inventories covering the entire moist forest zone of the country. Innovative plans at the level of the forest reserve can be seen in Cameroon, Côte d'Ivoire and Nigeria. These plans focus on collaborative forest management and restoration processes by integrating fauna conservation in timber production forests. However, these plans are mostly still to be embedded in a national forest strategy as can be seen in Ghana.

Chapter 3 reviews many of the methodological problems related to the study of lianas. Because of their growth habits, the inclusion of lianas in forest censuses is often complicated, as they cannot be assessed in the same way as trees. A list of recommendations for assessment of lianas is presented, which should be considered when comparing previous liana studies and in conducting future censuses. It is suggested to divide lianas into 'true' woody climbers and non-woody climbers; with

epiphytes and hemi-epiphytes not classified as lianas or vines. Apart from this, apparent genets (individual lianas not connected to any other liana stem) and ramets should be included in forest censuses, with the data separated as (1) apparent genets only and (2) all liana stems. In a census, the shape of the plot will, to some extent, influence the number, basal area and biomass of lianas present and preferably only similar-shaped plots should be compared. When deciding where to measure the stem diameter of lianas, consistency is most important. All climbers should be measured at a fixed distance from the rooting point. It is recommended to avoid the irregular and anomalous parts of the stem. Different measurement positions will yield different results, so only similar measurement methods should be compared among studies. Liana growth can be measured by either the size increment of a given stem or by the change in the number of stems in the community.

Only very few studies provide quantitative data on liana abundance of the moist forest zone in West Africa, as discussed in Chapter 4. A comparison of liana infestation in the tropics showed that on the African continent notably less trees are infested, with up to 40% of the trees occupied by lianas. Since the 1950s, pre-harvest liana cutting has been applied over several 100,000 ha in both Ghana and Nigeria and at a lesser scale in Côte d'Ivoire. A decade after such intervention liana abundance appears to be back to original numbers but liana diversity might still be reduced. This phenomenon can also be seen after the passage of fire, which have become more frequent due to forest fragmentation after intensive logging. As a result, the remaining lianas may be more resistant to cutting and fire, while species vulnerable to fire and liana cutting may have diminished to low numbers. It could be noticed that large lianas (≥ 5 cm dbh) remained absent long after interventions took place. The combined effect of logging and fire greatly enhanced invasive grasses such as Marantaceae and Zingiberaceae, as well as liana proliferation in repeatedly logged forests. This is especially the case when logging occurs over short time spans, often leading to a high fragmented canopy of low stature. This may result in forest types that are often associated with recurring fires. These forests, which are typically called Marantaceae-forest already, occupy about 30% of the moist forest formations in Ghana.

Liana and rattan abundance and distribution patterns were determined in the study area by counting all lianas and rattans in 33 1-ha plots (Chapter 5). Vernacular (Bulu) names were used to identify individuals. For all names, specimens were collected and, if possible, botanically identified. Of all lianas over 2 cm dbh we measured location in the plot and dbh. Smaller individuals were counted in 10 x 10 m subplots. Lianas and rattans were very abundant in the area with an average of 408 lianas ≥ 2 cm dbh of which over 100 large ones (≥ 5 cm dbh) per ha. In the area 4370 smaller ones were found per ha, together with 6 clumps and 184 rattan stems. Abundance of lianas and rattans varied considerably over ha plots. Diameter distributions of all lianas together as well as of selected species showed inversed J shaped curves. Spatial pattern analysis (using Morisita's index) showed that lianas have a clumped distribution, both at the larger 1 ha scale over an area of 500 hectares and at the smaller 0.01 ha scale within each of the plots studied. The same was found for rattans. Liana abundance at the level of 1 ha was compared with other tropical lowland forests. The Cameroonian forest has a high number of lianas,

especially small ones, but lianas over 5 cm dbh are comparable to forests on other continents.

The abundance of lianas and the detrimental impact that they have on tropical moist forest trees is discussed in Chapter 6. Lianas are particularly abundant in disturbed areas of the forest, such as logging gaps, and pre-harvest liana cutting has been widely recommended throughout the tropics to reduce the impact of lianas during and following tree harvest. The effectiveness of forest-wide liana cutting, however, is currently unresolved, particularly for reducing liana abundance in logging gaps. Lianas can be very abundant: up to 5000 individuals (at breast height) per ha. Some 70% of monitored lianas had died 22 months after cutting. Re-sprouting capacity was high but variable among species. Felling gap sizes (average 550 m² per felled tree) tree mortality (12 trees per felled tree) and damage (20 trees per felled tree) were not significantly affected by pre-harvest liana cutting, although a small part of the damage was severe. Smaller trees were most prone to destruction and damage. Nevertheless, the results show that pre-harvest liana cutting in this study had no significant effect on resulting gap sizes, tree mortality and damage levels. We conclude that liana cutting before a logging operation does not contribute to damage reductions at the felling sites in African moist forests where the logging intensity is low. We suggest that liana cutting should be applied on a tree-by-tree basis only, and after careful judgement of the tree's liana load.

Our understanding of the dynamics and rate of liana colonisation in gaps is limited. In Chapter 7 we tested (1) the speed at which lianas recruit into logging gaps and their subsequent development; and (2) whether pre-harvest liana cutting reduces the abundance of lianas after logging. We established a chronosequence of logging gaps in areas of the forest that had been previously logged without pre-harvest liana cutting, and we compared liana recruitment in new, one-year-old and six-year-old logging gaps. In addition, we compared liana abundance and tree infestation by lianas in one-year-old logging gaps in which all lianas had been cut nine months prior to tree felling, with one-year old logging gaps in which lianas had not been cut. We found that lianas recruited heavily into logging gaps within one year, mostly by means of stem sprouts, and many of these new stems were able to persist for longer than six years. Lianas were significantly more abundant in the root and lower stem zones of gaps than in the canopy zone, mostly due to the vigorous regeneration of stem sprouts. Canopy openness was highest in gaps one year after logging, possibly due to the smothering effect of the lianas on developing trees. Although liana abundance increased significantly over the six-year gap chronosequence, direct liana infestation of trees remained the same. Pre-harvest liana cutting significantly reduced the number of lianas, and the number of liana-infested trees in logging gaps. Consequently, liana cutting appears to be an effective method to reduce the abundance of lianas and thus minimise their detrimental effects on regenerating trees in logging gaps.

In summary, lianas are abundant and will continue to play a prominent role in West African forest dynamics in coming decades since disturbance regimes can be expected to increase in intensity and frequency. Pre-harvest liana cutting is recommended in the area beneath the canopy of the target tree when lianas are abundant, to reduce felling damage and to avoid problems related to liana tangles in

logging gaps after felling. However, it all depends on the logging intensity and frequency. To avoid negative impacts of liana cutting and fire on liana species diversity, it is recommended to apply this treatment only selectively. Spatially, treatments should be limited to zones where lianas are heavily interfering with trees to be felled, thereby taking into account felling direction. Treatments also should be species-specific, by limiting liana cutting to those species, which cause most of the damage. In general, a balance has to be sought between optimising the production potential of the forests and limiting the negative impact of liana cutting on liana populations. We conclude that lianas play an important role in the West African moist forests and that their detrimental effects in relation to logging can be brought under control.

RESUMÉ

Dans cette dissertation, le rôle des lianes dans les écosystèmes forestières tropicaux en relation avec les activités de l'exploitation forestière a été analysé. Les lianes sont abondantes, diverses avec des formes variées dans presque toutes les forêts tropicales. Les forestiers ont le plus souvent considéré les lianes comme des plantes nuisibles. Dans certains types d'aménagements forestiers, le délianage constitue une technique importante. Cette méthode a pour but de réduire les dégâts causés par l'exploitation forestière, d'améliorer la précision dans la chute des arbres, de favoriser le développement des arbres laissés sur pieds, et de réduire le développement des lianes. Cependant les études sur l'efficacité de cette méthode sont rares. Plusieurs études faites en Asie du Sud Est et en Amazonie pendant la dernière moitié du 20^e siècle montrent des aspects positifs du délianage, avec la conclusion selon laquelle le délianage contribue à la réduction des dégâts causés sur les petits arbres lors de l'exploitation forestière, la réduction de la taille des trouées et permet une régénération rapide des arbres.

Dans le passé, le délianage était recommandé sur le continent africain, malgré le fait qu'aucune évaluation propre n'a jamais été réalisée. C'est pour cette raison qu'une expérimentation a été réalisée dans la zone de notre étude afin de tester le délianage comme traitement sylvicoles avant l'exploitation forestière. Ce traitement fait partie d'un ensemble de pratiques visant à augmenter la productivité des arbres et à favoriser certaines espèces prisées. Cette étude était réalisée dans une concession forestière, située à 100 km est de Kribi au Cameroun (3°N, 10°E). Cette concession couvre plus de 2,000 km². Le site de l'étude est localisé dans la partie nord-est près du village Ebom dans une forêt ayant connue une intense activité d'exploitation forestière dans le passé. 33 parcelles permanentes ayant 1-ha chacune entourée par une zone tampon de 100 m de longueur étaient réalisées le plus souvent en terrain plat. Dans 5 parcelles témoins aucune activité forestière ou de traitement sylvicoles n'a été réalisée. Le reste des 28 parcelles avaient été exploitées et 16 d'entre elles avaient subies le délianage avant l'exploitation (mai 1995). L'abattage a eu lieu 9 mois après (février 1996). Le délianage était fait dans les parcelles de recherche et dans la zone tampon. Le taux d'exploitation était de un arbre par ha pour tout arbre ayant un diamètre supérieur à 60 cm.

Un aspect important de cette étude était de mesurer l'influence des dégâts causés sur la végétation et la réponse des autres arbres après l'exploitation. En prélevant les arbres, l'intensité de lumière dans le chablis change drastiquement. La collecte des données sur les différents aspects liés à la réponse des arbres et des lianes a eu lieu à différents stades de l'exploitation : avant, pendant et après l'abattage. Un inventaire préliminaire de toutes les lianes ayant un diamètre ≥ 2 cm et tous les arbres ≥ 10 cm a été réalisé dans une parcelle de 1 ha. Le délianage a été effectué avant l'exploitation afin d'étudier le rôle des lianes dans l'écosystème et d'analyser leur réponse au stress et à la perturbation. Les lianes avaient une grande capacité de régénération, mais le changement survenu dans la composition de ces lianes a connu une faible attention. La capacité de régénération et de mortalité étaient étudiées régulièrement pendant une période de 22 mois après le délianage. Dans cette étude, l'efficacité de la méthode de délianage avant l'exploitation sur la réduction des

dégâts causés sur les autres arbres sur pied et la réduction de la taille des trouées a été également analysée.

Les études ont été réalisées dans des trouées liées à l'exploitation forestière ayant une chronosequence de 6 ans afin de déterminer la vitesse de régénération et de développement des lianes.

Les questions suivantes ont été posées pour permettre l'investigation du rôle des lianes en relation avec l'exploitation forestière:

7. Comment inventorier les lianes ?
8. Quelle est l'abondance des lianes dans la forêt étudiée ?
9. Quelle est la distribution spatiale des lianes ?
10. Jusqu'à quel niveau le déliantage peut causer la mort des lianes et quelle est leur capacité de produire des rejets ?
11. Quels sont les effets du déliantage avant l'abattage sur la taille des trouées, le nombre des arbres détruit ou endommagé, et sur la direction de chute de l'arbre abattu ?
12. Comment et à quelle vitesse les lianes s'installent dans les chablis et quel est l'impact du déliantage dans la réduction du nombre de lianes qui recolonise les chablis ?

Le Chapitre 1 introduit le sujet de la dissertation et décrit le rôle et l'importance de lianes en relation avec l'exploitation forestière. Le Chapitre 2 prévu un aperçu des systèmes sylvicoles appliqués dans le passé en Côte d'Ivoire, au Ghana et au Nigeria, de même que les développements plus récents à partir des années 1970 dans ces pays et au Liberia et Cameroun. Durant les décennies passées, plusieurs nouvelles idées et développements en foresterie ont pu être observés en Afrique de l'Ouest, et une sélection d'elles est présentée dans ce chapitre. La plupart des forêts de l'Afrique de l'Ouest ont été démunies de leurs bois. Ces forêts surexploitées, le plus souvent envahies par les agriculteurs après l'exploitation ont besoin d'une forme de restauration avant qu'elles puissent être exploitées de nouveau de façon durable. Certaines de ces forêts sont gravement dégradées et ont tellement des grandes trouées qu'il n'y a plus des forêts à voûtes uniformes et hautes. Dans ces forêts la régénération des arbres est gravement empêchée par des grands agrégats de lianes pendant plusieurs décennies (voir Chapitre 4). De bons exemples de restauration de ces forêts de l'Afrique de l'Ouest s'observent mieux à l'Est de la Côte d'Ivoire où les connaissances écologiques ont été récoltées et incorporées dans le plan d'aménagement. Notamment, un guide des règles d'exploitation des arbres sénescence développé dans le cadre de recherche dans le Parc National de Taï peut être appliqué dans la zone tampon comme une méthode 'de la reproduction fidèle de la nature'. Au niveau national, le Ghana, pays voisin de la Côte d'Ivoire a fait de grand progrès en essayant de combiner le potentiel de la production biologique à la capacité nationale des scieries avec pour but une utilisation rationnelle des ressources. Au Ghana encore, une approche multidimensionnelle pour la protection des forêts a été réalisée à base des inventaires botaniques couvrant la totalité de la zone des forêts humides de ce pays. Des innovations au niveau de la protection des forêts peuvent être observées au Cameroun, à la Côte d'Ivoire et au Nigeria. Ces innovations mettent l'accent sur l'aménagement participatif des forêts et la

restauration des forêts de la production en intégrant la conservation de la faune. Cependant ces innovations ne sont pas encore intégrées dans une stratégie nationale comme observée au Ghana.

Le Chapitre 3 est un compte rendu des problèmes méthodologiques liés à l'étude des lianes parce que leur mode de croissance fait que l'inclusion des lianes lors des inventaires est souvent compliquée car elles ne sont pas recensées de la même façon que les arbres. Une liste de recommandations sur les études des lianes est présentée, qui doit être prise en considération lors des études antérieures. Il est suggéré de diviser les lianes en 'vraie' lianes ligneuses et lianes non-ligneuses et ne faut pas considérer les épiphytes et les hémiepiphytes comme lianes. En dehors de ces catégories, genets en apparence (individu de liane présentant une aberration génétique sans relation d'une autre tige des lianes) et ramets doivent être inclus lors des inventaires avec une définition comme la suivante (1) genets en apparence et (2) toutes les tiges des lianes. Lors de l'inventaire, la forme de la parcelle dans une certaine mesure influence le nombre, la surface terrière et la biomasse des lianes présentes. De préférence seule les parcelles de même forme doivent être comparées. Dans la mesure du diamètre la consistance est importante. Toutes les lianes doivent être mesurées à une hauteur fixe de la base. Il est recommandé d'éviter les parties anormales de la tige. Des mesures prises à des hauteurs différentes vont donner des résultats différents, donc seule des méthodes de mensurations similaires doivent être comparées entre les études. La croissance des lianes peut être mesurée soit par l'accroissement de chaque tige ou par les changements de nombre des tiges ou peuplement.

Seulement très peu d'études ont des données quantitatives sur l'abondance des lianes des forêts humides de l'Afrique de l'Ouest comme discuté dans le Chapitre 4. Une comparaison faite sur l'envahissement des arbres par les lianes dans les tropiques montre que sur le continent africain, peu des arbres sont infestés, avec près de 40% des arbres portant des lianes. Depuis les années 1950 le déliantage avant l'exploitation a été appliqué sur plusieurs 100,000 ha au Ghana et Nigeria et un peu moins en Côte d'Ivoire. Une décennie après cette intervention, l'abondance de ces lianes semble se restituer au niveau original, mais sa diversité reste faible. Ce phénomène peut également être observé après les feux de brousse qui deviennent fréquents à cause de la fragmentation des forêts après d'intenses activités d'exploitation forestière. A cet effet seul les espèces de lianes qui sont résistantes aux incendies et au déliantage persistent pendant que les espèces vulnérables diminuent en nombre. Il a été remarqué que les grandes lianes (≥ 5 cm) restent absentes après l'exploitation forestière. L'effet combiné de l'exploitation et de l'incendie permet l'envahissement des plantes pionnières telles que les Marantacées et les Zingibéracées de même que la prolifération des lianes dans les zones ayant subi des coupes répétées. Tel est le cas lorsque l'exploitation forestière est répétée pendant de courtes durées. Ce qui favorise une grande fragmentation de la canopée et de basse stature. Les types de forêts qui en résultent peuvent être comparés à des forêts issues de l'intervention répétée des incendies. Ces types de forêts qui sont typiquement appelées "les forêts à Marantacées" occupent près de 30% des forêts humides au Ghana.

L'abondance et la distribution des lianes et des rotins étaient déterminées dans la zone d'étude en comptant tous les lianes et rotins dans 33 parcelles de 1-ha chacune (Chapitre 5). Les noms vernaculaires (Bulu) étaient utilisés lors de l'identification des individus. Pour tous les noms des spécimens botaniques furent collectés et si possible identifié. Pour toutes les lianes supérieures à 2 cm de diamètre, nous avons mesuré son diamètre et pris sa position dans la parcelle. Les petits individus furent comptés dans les sous-parcelle de 10x10 m. Les lianes et les rotins étaient très abondant dans la région avec une moyenne de 408 lianes \geq 2 cm parmi les quelles plus de 100 grandes lianes (\geq 5 cm) à l'hectare. Un total de 4370 petites lianes furent récoltés à l'hectare avec 6 touffes et 184 tiges de rotins. L'abondance des rotins et de lianes varie considérablement dans les différentes parcelles de 1-ha. La distribution du diamètre de toutes les lianes inventoriées donne une combe qui a une forme de F inversée. L'analyse spatiale (en utilisant l'index de Morisita) montre que les lianes ont une distribution en motte tant dans les grandes parcelles de 1-ha sur une superficie de 500 ha que dans les petites parcelles de 0.01 ha dans les parcelles permanentes. Les même résultats ont été obtenus pour les rotins. Au niveau de grandes parcelles (1-ha), l'abondance de liane a été comparée avec celle d'autres forêts tropicales de basses altitudes. La forêt camerounaise a un nombre élevé de lianes, surtout de petites lianes, mais les lianes au-dessus de 5 cm de diamètre sont comparables à celles des forêts dans d'autres continents.

L'abondance des lianes et l'impact nuisible aux arbres de forêts tropicales humides est discuté dans le Chapitre 6. Les lianes sont particulièrement abondant dans les zones de forêts perturbées telles que les trouées liées à l'exploitation forestière, et le délianage avant l'exploitation a été largement recommandé à travers les tropiques pour réduire l'impact des lianes lors de l'exploitation. Mais l'efficacité de cette intervention reste cependant sans solution, particulièrement en ce qui concerne la réduction de l'abondance des lianes dans les chablis. Les lianes peuvent être très abondantes : plus de 5000 individus par ha. Quelque 70% de lianes observe pendant 22 mois après la coupe sont mort à la fin. La capacité de régénération fut élevée mais variable parmi les espèces. La taille des chablis (en moyenne 550 par arbre abattu), la mortalité des arbres (12 arbres par arbre abattu) et le dommage causé (20 arbres par arbre abattu) n'étaient pas affecté de manière significative par le délianage, bien qu'une petite partie des endommagement fut sévère. Les arbres de petit diamètre étaient plus susceptibles aux endommagements et destructions. Néanmoins les résultats montrent que le délianage avant l'exploitation n'a pas d'effet significatif sur la taille des trouées, la mortalité et niveau d'endommagé des arbres dans notre site d'étude. Nous arrivons à la conclusion selon laquelle le délianage avant l'exploitation ne contribue pas à la réduction des dégâts causes par les arbres abattus dans les zones d'exploitation forestière des forêts humides africaines où le taux de prélèvement est faible. Nous suggérons que le délianage soit uniquement fait sur le niveau d'arbres individuels après un jugement minutieux de la quantité de liane sur chaque arbre.

Notre entendement sur la dynamique et le taux de développement expansif dans les chablis est limité. Dans le Chapitre 7 nous testons (1) la vitesse avec laquelle les lianes régénèrent dans les chablis et aussi que leur développement ; et (2) si le délianage avant l'exploitation réduit l'abondance des lianes après l'exploitation. Nous établissons une chronosequence des chablis dans les forêts qui n'ont pas subi

de délianage avant l'exploitation et nous comparons la régénération des lianes dans les chablis créés récemment, d'un an et six ans après abattage. En plus nous comparons l'abondance des lianes et l'envahissement des arbres par les lianes dans des chablis d'un an dans les quelles toutes les lianes furent coupées 9 mois avant l'abattage avec celles où les lianes n'étaient pas coupées. Nous observons que les lianes régénèrent abondamment dans les chablis au moins d'un an en produisant de jeunes pousses dont plusieurs sont capables de résister pendant plus de six ans. Les lianes étaient plus abondantes de manière significative au niveau de la souche et les parties basses du fût de l'arbre abattu que dans la zone où la cime de l'arbre était tombée, particulièrement à cause de développement expansif des pousses. La canopée était plus ouverte dans les chablis d'un an après l'exploitation, probablement causé par l'envahissement des jeunes arbres en développement par les lianes. Malgré le fait que l'abondance des lianes augmente de manière significative dans les chablis de six ans, l'envahissement des arbres par les lianes reste presque le même. Le délianage réduit de manière significative le nombre de lianes et le nombre des arbres infestés par les lianes dans les chablis. En conséquence, le délianage semble être une technique efficace pour réduire l'abondance des lianes qui permet de minimiser leur effet nuisible à la régénération des arbres dans les chablis causés par l'exploitation forestière.

En résumé, les lianes sont abondantes et vont continuer de jouer un rôle primordial dans la dynamique des forêts de l'Afrique de l'Ouest pendant les années à venir car les causes de perturbations vont certainement augmenter en intensité et en fréquence. Le délianage avant l'exploitation est recommandée dans la zone en dessous la cime de l'arbre à abattu lorsque les lianes sont abondantes afin de réduire les dégâts causés par la chute de l'arbre et d'éviter les problèmes dans les chablis liées par l'envahissement des jeunes arbres par les lianes. Néanmoins tout dépend du taux de prélèvement et de la fréquence de l'exploitation. Pour éviter l'impact négatif du délianage et d'incendie sur la diversité des espèces de lianes, il est recommandé d'appliquer seulement un traitement sélectif avant l'exploitation forestière. Ce traitement doit être limité dans les zones où l'envahissement des arbres par les lianes empêcherait l'arbre à abattre de tomber dans la direction prévue. Les traitements doivent spécifiquement viser les espèces de lianes qui causent beaucoup plus de dégâts. En général un équilibre doit être fait entre l'optimisation de la production des forêts à exploiter et la limitation des impacts négatifs du délianage sur la population des lianes. Nous concluons que les lianes jouent un rôle important dans des forêts humides de l'Afrique de l'Ouest et que c'est possible de contrôler leur impact nuisible à l'exploitation forestière.

SAMENVATTING

In dit proefschrift wordt de rol van lianen in het boscysteem in relatie tot de houtkap belicht. Lianen (houtige klimplanten) komen in bijna alle tropische bossen overvloedig, en als gevarieerde en opvallende groeivorm voor. Bosbouwers beschouwen lianen vooral als hinderlijk. Het kappen van lianenstammen is in bepaald bosbeheer dan ook een belangrijke activiteit. Lianenkap voorafgaand aan de boomvelling heeft als doel de beperking van de schade bij houtexploitatie, het bereiken van een hogere precisie van de beoogde valrichting, een betere groei van de bomen in de opstand, en een verminderde aanwezigheid van de lianen zelf. Echter studies die de doeltreffendheid van deze lianenkap onderzochten zijn schaars. De meeste lianenkap studies die tijdens de laatste helft van de twintigste eeuw in Zuidoost-Azië en het Amazonebekken zijn uitgevoerd beoordelen deze maatregel positief. Zij concluderen dat lianenkap leidt tot verminderde exploitatieschade aan achterblijvende bomen, kleinere kapgaten en een betere ontwikkeling van boomverjonging in kapgaten.

Lianenkap is in het verleden ook op het Afrikaanse continent over grote oppervlaktes toegepast maar nooit behoorlijk geëvalueerd. Daarom werd er binnen het kader van dit onderzoek een grootschalige proef opgezet om lianenkap als een bosteeltkundige ingreep voorafgaand aan de bosexploitatie uit te testen. Deze bosteeltkundige ingreep maakte deel uit van een veel groter project waarbij een verhoging van de productiviteit van de opstand werd beoogd doormiddel van bosteeltkundige ingrepen. De studie werd uitgevoerd in een kapconcessie met een totaal oppervlak van 2,000 km² ongeveer 100 km ten oosten van Kribi in Kameroen. Het eigenlijke bosteeltkundige onderzoeksgebied lag in het noordoosten van de concessie vlakbij het dorp Ebom in een stuk bos waar nog nooit eerder houtexploitatie had plaatsgevonden. Drieëndertig 1-ha proefperken met 100 m brede bufferzones werden aangelegd in min of meer vlak terrein. In vijf controle proefperken vond geen houtexploitatie en geen bosteeltkundige ingrepen plaats. De overige 28 proefperken werden geëxploiteerd en in 16 van hen vond lianenkap plaats voorafgaand aan de houtexploitatie (in mei 1995). De boomvelling werd negen maanden later uitgevoerd (februari 1996). Daarbij werd de lianenkap zowel in het centrale 1-ha proefperk als in de bufferzone uitgevoerd. De oogstintensiteit was één boom dikker dan 60 cm per hectare, wat vergelijkbaar was aan een normale houtexploitatie in dit gebied.

Een belangrijk onderdeel van deze studie was het bepalen van de invloed van fysieke schade door de velling op de achterblijvende vegetatie en vooral de reactie van de achterblijvende bomen op deze veranderingen. Doordat bomen worden geoogst veranderd het lichtklimaat in de kapgaten drastisch. Daarom werden er verschillende metingen verricht om de reactie van dezelfde bomen en lianen vast te leggen voorafgaand, tijdens en na de exploitatie. Een algemene inventarisatie van alle lianen dikker dan 2 cm en bomen dikker dan 10 cm op borsthoogte vond dan ook plaats in de centrale 1-ha proefperken. Lianenkap werd dan ook voorafgaand aan de kap uitgevoerd om de rol van lianen in het boscysteem te bestuderen en hun reactie op stress en verstoring. Lianen hebben een zeer goed vermogen om weer uit te lopen (vorming van spruiten) na kap. Echter de mogelijke gevolgen van deze ingreep op de verandering in soortensamenstelling in het bos van de lianenpopulatie

hebben tot dusverre weinig aandacht gekregen. De mogelijkheden tot spruitvorming en uitlopen van deze spruiten en het afsterven van gekapte lianen werd over een periode van 22 maanden met regelmatige tussenpozen gevolgd. Er werd in deze studie ook bekeken in hoeverre lianenkap effectief was om de schade bij de velling te verminderen en of dit zou leiden tot kleinere kapgaten. Een tijdserie van kapgaten tot zes jaar oud werd gebruikt om te kijken hoe snel lianen zich ontwikkelen in kapgaten. Daarbij werd tevens gekeken in hoeverre lianenkap een rol kon spelen in het terugdringen van het aantal lianen dat een kapgat kan domineren.

De volgende vragen werden gesteld om de rol van lianen in relatie tot houtexploitatie te onderzoeken:

- Hoe moet je lianen inventariseren?
- Hoe algemeen voorkomend zijn lianen in het bestudeerde bos?
- Wat zijn de verspreidingspatronen van deze lianen?
- In welke mate leidt lianenkap tot het afsterven van lianen, en wat is hun vermogen tot uitlopen?
- Wat is het effect van lianenkap voorafgaand aan de boomvelling op de grootte van de kapgaten, op het aantal dode of beschadigde bomen, en op de valrichting van de te vellen boom?
- Hoe en hoe snel groeien lianen in kapgaten en hoe efficiënt is lianenkap voorafgaand aan de boomvelling om het aantal lianen dat de kapgaten koloniseren te beperken?

Hoofdstuk 1 introduceert het thema van dit proefschrift en beschrijft de rol en het belang van lianen in de bosexploitatie. Hoofdstuk 2 geeft een overzicht van bosteeltkundige systemen uit Côte d'Ivoire, Ghana en Nigeria als ook meer recente ontwikkelingen in Liberia en Kameroen sinds the jaren zeventig. De afgelopen decennia kon men meerdere nieuwe ideeën en ontwikkelingen in de bosbouw in West Afrika waarnemen waarvan een aantal in dit hoofdstuk worden toegelicht. De meeste West Afrikaanse bossen zijn inmiddels verarmd wat betreft kapbare bomen van commerciële houtsoorten. Deze overgeëxploiteerde bossen, waar vaak na de houtkap boeren de bossen binnentrokken, hebben een zeker bosherstel nodig voordat ze duurzaam geoogst kunnen worden. Sommige van deze bossen zijn zo erg verarmd en laten zo veel kapgaten zien dat er bijna geen sprake meer is van een kronendak. In deze bossen wordt de ontwikkeling van de boomverjonging vaak voor een periode van verscheidene decennia gehinderd door een wirwar van lianen die vaak veel weg hebben van complete tapijten (zie ook Hoofdstuk 4). De beste voorbeelden van bosherstel in West Afrika zijn in het oosten van Côte d'Ivoire te zien waar ecologische kennis is geïntegreerd in het beheersplan van enkele bosreservaten. Tevens zijn richtlijnen voor de oogst van aftakelende bomen zoals ontwikkelt in een onderzoeksproject in Taï Nationaal Park toepasbaar in bufferzonebeheer, een 'dicht bij de natuur staande'-methode. Côte d'Ivoire's buurland Ghana heeft de meeste vooruitgang geboekt op nationaal niveau door te proberen om zijn nationale zagerijcapaciteit te combineren met de biologische productiviteit van zijn bossen. Daarmee zou een duurzame aanvoer van hout gegarandeerd moeten zijn. In Ghana heeft men tevens een geheel vernieuwde bosbeschermingsindeling gemaakt met verschillende schaalniveaus gebaseerd op botanische inventarisaties die de hele regenbosgordel van het land omvat.

Vernieuwende plannen op reservaatniveau vinden ook in Côte d'Ivoire, Kameroen en Nigeria plaats. Deze plannen draaien vooral om gemeenschappelijk bosbeheer en processen tot bosherstel waarbij bescherming van de fauna wordt geïntegreerd met houtproductie. Echter deze plannen moeten veelal nog worden opgenomen in een nationale strategie ten aanzien van bossen zoals in Ghana.

Hoofdstuk 3 geeft een overzicht van de vele methodologische problemen betreffende de studie van lianen. Vanwege hun groeiwijze worden lianen vaak niet opgenomen in inventarisaties aangezien ze niet op dezelfde wijze als bomen kunnen worden geïnventariseerd. Een lijst met aanbevelingen hoe men lianen zou moeten inventariseren wordt gepresenteerd. Deze geeft aan waar men rekening mee zou moeten houden indien men wil vergelijken met eerder uitgevoerde lianenstudies en voor het uitvoeren van inventarisaties in de toekomst. Er wordt voorgesteld om lianen te onderscheiden in 'echte' houtige klimplanten en niet-houtige klimplanten, waarbij epifyten en hemi-epifyten niet worden aangemerkt als lianen of klimplant. Daarnaast zou in bosinventarisaties onderscheid moeten worden gemaakt tussen genets (individuele lianen die niet gerelateerd zijn aan enige andere lianenstam) en ramets, waarbij de data gescheiden dienen worden in (1) ogenschijnlijk enkel genets en (2) alle lianenstammen. Tijdens een inventarisatie zal de vorm van een proefperk in zekere mate het aantal aangetroffen lianen, hun grondvlak en biomassa beïnvloeden vandaar dat bij voorkeur enkel proefperken van dezelfde vorm moeten worden vergeleken. De positie van het meetpunt ter bepaling van de diameter van lianen moet van tevoren worden vastgesteld. Alle lianen moeten worden gemeten op een vaste afstand van waar ze wortelen. Wat vooral van belang is dat deze meting steeds op dezelfde wijze wordt toegepast. Daarbij zou moeten worden vermeden om onregelmatige en afwijkende stamdelen te meten. Het gebruik van verschillen in de positie van meetpunten zal dan ook leiden tot andere resultaten, dus enkel studies waarbij dezelfde meetmethodes zijn gehanteerd kunnen worden vergeleken. De groei van lianen kan worden gemeten of door de toename in afmeting van een bepaalde stam of door de verandering in stamtal.

Maar een beperkt aantal studies in de regenbosgordel van West Afrika zoals besproken in Hoofdstuk 4 geven kwantitatieve gegevens betreffende lianendichtheden. Een vergelijking van de mate waarin lianen zich bevinden op bomen in de tropen laat zien dat op het Afrikaanse continent opvallend weinig bomen zijn geïnfesteerd, minder dan 40% van de bomen dragen lianen. Sinds de jaren vijftig werden in honderdduizenden hectaren bos in Ghana en Nigeria, en op kleinere schaal in Côte d'Ivoire, lianen gekapt voorafgaand aan de boomvelling. Tien jaar na een dergelijke ingreep is de lianendichtheid bijna op het oude niveau echter de soortendiversiteit in lianen kon wel eens minder zijn. Dit fenomeen kan ook worden waargenomen na brand. Branden zijn frequenter geworden als gevolg van bosversnippering na intensieve houtexploitatie. Hierdoor kunnen de overblijvende lianen wel eens meer resistent zijn tegen de kap en vuur terwijl kap- en vuurgevoelige soorten wel eens in aantal kunnen zijn afgenomen. Het was opvallend dat grote lianen (dikker dan 5 cm) afwezig bleven lang nadat ingrepen hadden plaatsgevonden. Een combinatie van regelmatig terugkerende houtexploitatie met vuur bevorderde een invasie van grassen zoals Marantaceae en Zingiberaceae alsmede een ongebreidelde toename van lianen. Dit treedt vooral op wanneer de houtexploitatie zeer frequent optreedt in hetzelfde bos en leidt dan vaak

tot een laag bos met een zeer gefragmenteerd kronendak. Dit kan dan ook leiden tot een bostype die geassocieerd wordt met terugkerende bosbranden. Deze bossen die vaak worden aangeduid als Marantaceae-bos bezetten inmiddels al bijna 30% van de regenbosgordel van Ghana.

Lianen- en rotandichtheden en hun verspreidingspatronen werden bepaald in het studiegebied door alle lianen en rotans te tellen in de 33 1-ha proefperken (Hoofdstuk 5). Inheemse (Bulu) namen werden gebruikt om de individuen te identificeren. Voor al deze namen werd herbariummateriaal verzameld en indien mogelijk botanisch geïdentificeerd. Van alle lianen dikker dan 2 cm bepaalden we hun dikte en positie in het proefperk. Kleinere individuen werden slechts geteld per 10 x 10m vlak. Lianen en rotans kwamen zeer algemeen voor in dit gebied met gemiddeld 408 lianen dikker dan 2 cm per ha waarvan meer dan 100 grote lianen (dikker dan 5 cm). Gemiddeld groeiden er zo'n 4370 kleinere lianen per ha alsmede 6 rotankluiten en gemiddeld zo'n 184 rotanstammen. De lianen- en rotandichtheden verschilden enorm per proefperk. De diameterverdeling van alle lianen samen alsmede van een selectie van lianensoorten waren in de vorm van een omgekeerde J-curve. Analyse van de ruimtelijke patronen (gebruikmakend van de Morisita's index) toonden aan dat lianen een gegroepeerde verspreiding hebben zowel op het 1-ha niveau binnen een oppervlak van 500 ha alsmede op het 0.01 ha schaalniveau binnen de bestudeerde proefperken. De rotans lieten hetzelfde patroon zien. Lianendichtheden op het 1-ha niveau werden vergeleken met andere tropische regenbossen. Daaruit bleek dat dit Kameroenese bos rijk was aan lianen, vooral in de kleinere diameters, maar grote lianen (dikker dan 5 cm) waren vergelijkbaar met bossen in andere continenten.

Lianendichtheden en de nadelige gevolgen dat deze hebben op bomen in tropische regenbossen wordt in Hoofdstuk 6 besproken. Lianen komen vooral veel voor in verstoorde delen van het bos, zoals kapgaten, waardoor in de gehele tropen lianekap voorafgaand aan de boomvelling werd aangeraden. Dit beoogde het terugdringen van de negatieve effecten van lianenaanwezigheid tijdens en na de bosexploitatie. In hoeverre deze oppervlaktegewijze lianekap zijn doel bereikte is momenteel nog steeds niet duidelijk, vooral wat betreft het terugdringen van het aantal lianen in kapgaten. Lianen kunnen in grote getale voorkomen: zo'n 5000 individuen per ha (op borsthoogte gemeten). Zeventig procent van de gekapte lianen die werden gevolgd door de tijd waren na 22 maanden afgestorven. De gekapte lianen hadden een goed vermogen om weer uit te lopen maar was wel variabel afhankelijk van de soort. Lianekap voorafgaand aan de boomvelling had geen invloed op de grootte van de kapgaten (gemiddeld oppervlak 550 m² per gevelde boom), boomsterfte (12 bomen per gevelde boom) en schade (20 bomen per gevelde boom) ofschoon een klein gedeelte van de schade was ernstig. Vooral kleinere bomen leden de meeste schade. Vandaar dat geconcludeerd kon worden dat in Afrikaanse regenbossen waar de bosexploitatie relatief licht is systematische oppervlaktegewijze lianekap voorafgaand aan de boomvelling niet leidt tot schadevermindering. Lianekap zou op een individuele boombasis moeten worden uitgevoerd en beoordeeld moeten worden op hoeveel lianen deze boom draagt.

Ons begrip van de dynamiek en snelheid waarmee lianen een kagat kunnen domineren is beperkt. In Hoofdstuk 7 onderzochten we (1) de snelheid waarmee

lianen zich vestigen in kapgaten en ontwikkeling daarna en (2) of lianekap voorafgaand aan de boomvelling het aantal lianen kan beperken dat aanwezig zal zijn na de houtexploitatie. Een tijdserie van kapgaten werd geselecteerd waar geen lianekap voorafgaand aan de boomvelling had plaatsgevonden en we vergeleken de vestiging van lianen in nieuwe kapgaten, één jaar oude en zes jaar oud kapgaten. Tevens werden lianendichtheden en boominfestaties door lianen in één jaar oude kapgaten waar de lianen waren gekapt negen maanden voorafgaand aan de boomvelling vergeleken met één jaar oude kapgaten waar geen lianen waren gekapt. Daarbij werd waargenomen dat lianen massaal in het eerste jaar zich vestigden, vooral doormiddel van uitlopers (spruiten) op de stam, waarbij vele van deze nieuwe stammen langer dan zes jaar overleefden. Lianen werden vooral in grotere getale aangetroffen in de zone van de kapgaten dichtbij de stamvoet van de geveld boom en waar het onderste stamdeel had gelegen en veel minder waar de boomkroon zich bevond. Dit werd vooral bepaald door vitale verjonging van uitlopers (spruiten) op de stam. Het minst gesloten kronendak werd waargenomen in één jaar oude kapgaten, mogelijk doordat lianen, bomen die zich nog ontwikkelden overdekten en platdrukten. Ofschoon lianendichtheden significant toenamen in de tijdserie van kapgaten over zes jaar, toch bleven de aantallen boominfestaties door lianen gelijk. Lianekap voorafgaand aan de boomvelling verminderde de aantallen lianen en het aantal boominfestaties door lianen in de kapgaten aanzienlijk. Vandaar dat lianekap een effectieve methode lijkt om lianendichtheden te verminderen en door het toepassen van deze behandeling kunnen de nadelige gevolgen van lianen op de boomverjonging in kapgaten worden beperkt.

Samenvattend lianen komen algemeen voor en zullen de komende decennia een belangrijke rol blijven vervullen in de West Afrikaanse bosdynamiek aangezien verstoringen zowel in aantal als intensiteit zullen toenemen. Lianekap voorafgaand aan de boomvelling is aan te raden onder de kroon van de te vellen boom indien er veel lianen worden aangetroffen in dit gebied, om de velschade te beperken en om problemen te voorkomen van het ontstaan van een wirwar van lianen in kapgaten. Echter dit is afhankelijk van hoeveel bomen er worden geëxploiteerd per ha en hoe snel men terugkeert in hetzelfde stuk bos. Om de negatieve gevolgen van lianekap en vuur op de soortendiversiteit van lianen te beperken zou lianekap slechts selectief moeten worden toegepast. Ruimtelijk zou deze behandeling beperkt moeten worden tot een zone met veel lianeninfestatie in te vellen bomen, waarbij rekening wordt gehouden met de valrichting. Lianekap zou soortspecifiek moeten zijn door alleen soorten te kappen die de meeste schade veroorzaken. In *het algemeen* moet er een balans gezocht worden tussen het verhogen van de productiviteit van deze bossen en het beperken van de negatieve gevolgen van lianekap op de lianenpopulaties. Er kan worden geconcludeerd dat lianen een belangrijke rol vervullen in het West Afrikaanse regenbos maar dat hun nadelige gevolgen ten opzichte van de bosexploitatie wel onder controle kunnen worden gebracht.

CURRICULUM VITAE

Marcus Peter Emile (Marc) Parren was born on 25 September 1963 in Roermond, the Netherlands. After obtaining the diploma "HAVO" at the Scholengemeenschap Sintermeerten in Heerlen, the Netherlands in 1982, he visited the tropics and more specific Ghana for the first time. In 1985 he obtained the diploma "Atheneum" at the Zuidlimburgs Avondcollege in Heerlen and went to the Wageningen Agricultural University that same year. He obtained his "Ingenieurs" degree in Tropical Forestry in 1991, with majors in Tropical Silviculture, Tropical Forest Ecology and Non-Timber Forest Products. During his study he spent time for practical training and field research in Ghana on agroforestry, silvicultural systems and forest elephants as dispersal agents, in Côte d'Ivoire on silvicultural systems, and Argentina, Paraguay, Brazil on vegetable tannins and the leather industry. At the end of his studies he was one of the organisers of the XIXth International Forestry Students Symposium and editor of the proceedings.

After graduation he was employed by the Wageningen Agricultural University with funding from the Tropenbos Foundation to work out more in detail his thesis on silvicultural systems in West Africa and published as a book in 1995. A shift in working experience towards the Congo Basin was enabled in 1993 when he accepted a position with the Department of Forestry at the Wageningen University to do his doctoral research in Cameroon. Between 1994-1996 he was based in Kribi and engaged in the Tropenbos-Cameroon Programme, studying the ecological effects of logging with a focus on the role of lianas in the forest.

Since 1997 he was engaged in a variety of teaching, research and consultancy activities. These include investigations for forest corridor creation between Ghana and Côte d'Ivoire and a workshop was organised on transboundary cooperation in Accra, Ghana funded by CEPF, USA. The organisation of the Tropenbos-ITTO workshop and symposium 'Sustainable management of African rain forests' in Kribi, Cameroon. The consultancies all concern projects funded by the European Community DG VIII, Brussels and include one by ODI, UK and the BOS Foundation, The Netherlands on nature conservation and biodiversity in Cameroon, one for the ECOSYN project on lianas and logging in Côte d'Ivoire, one for DHV, The Netherlands, on a project coordinated by GTZ, Germany and the International Agricultural Centre, The Netherlands on inter-institutional development of training capacity in forest certification project for ACP countries. Workshops were organised in capacity building in forest certification in Elmina, Ghana for anglophone West Africa and in Grand-Bassam, Côte d'Ivoire for francophone West Africa. On behalf of FFI, UK a mid-term evaluation of the project titled 'Re-assessment of Forest Cover, Updating of the Protected Forest System and Improvement of Environmental Information for Liberia' was made. In 2000 he became tropical forestry lecturer at the University of Professional Education Larenstein, Velp, the Netherlands.

PUBLICATIONS

- Lemmens, R.H.M.J., N. Wulijarni-Soetjpto, R.P. van der Zwan and M.P.E. Parren (1991). Introduction. In: Lemmens, R.H.M.J. and N. Wulijarni-Soetjpto (eds), *Plant Resources of South-East Asia No.3. Dye and tannin-producing plants*. Wageningen, Netherlands, PUDOC, pp.15-34.
- Hummel, J. and M.P.E. Parren (eds.) (1992). *Forests a growing concern*. Proceedings of the XIXth IFSS, September 30- October 7 1991, Wageningen, Netherlands. IUCN Forest Conservation Programme, IUCN, Gland, Switzerland and Cambridge, U.K., 233 p.
- Parren, M.P.E. (1992). *Non-timber forest products: weighing the benefits against the costs*. In Hummel, J. and M.P.E. Parren (eds.). *Forests a growing concern*. Proceedings of the XIXth IFSS, September 30- October 7 1991, Wageningen, Netherlands. IUCN Forest Conservation Programme, IUCN, Gland, Switzerland and Cambridge, U.K., pp. 185-188.
- Aidara, G.L. et M.P.E. Parren (1994). *L'exploitation forestière*. Dans: Riezebos, E.P., Vooren, A.P. et J.L. Guillaumet (éds). *Le Parc National de Taï, Côte d'Ivoire*. I. Synthèse des Connaissances. II. Bibliographie. Wageningen, Pays-Bas, Fondation Tropenbos, pp. 123-132.
- Parren, M.P.E. (1994). *French and British colonial forest policies: past and present implications for Côte d'Ivoire and Ghana*. Working Papers in African Studies No. 188. Boston, U.S.A., African Studies Center, Boston University, 25 p.
- Parren, M.P.E. and N.R. de Graaf (1995). *The quest for natural forest management in Ghana, Côte d'Ivoire and Liberia*. Tropenbos Series 13. Wageningen, Netherlands, Tropenbos Foundation, 199 p.
- Parren, M.P.E. and N.R. de Graaf (1995). *Silviculture with natural regeneration: a comparison between Ghana, Côte d'Ivoire and Liberia*. Proceedings of the Second International Symposium on Environmental Studies of Tropical Rainforests - Forest '92. May 24-29, 1992, Rio de Janeiro, Brazil: 166-169.
- Breugel, M. van and M.P.E. Parren (1997). Forestry in Equatorial Guinea. in *The Congo Basin. Recent developments and alternatives for sustainable development*. *BOS Newsletter* 16(3): 76-83.
- Bongers, F., Poorter, L., van Rompaey, R.S.A.R. & M.P.E. Parren (1999). Distribution of twelve moist forest canopy trees in Liberia and Côte d'Ivoire: response curves to a climatic gradient. *J. Veg. Sc.* 10(3): 371-382.
- Parren, M. & F. Bongers (1999). *Forest lianas and pre-felling climber cutting in southern cameroon: a silvicultural evaluation*. Dans Nasi, R., Amsallem, I. & S. Drouineau (eds.), *La Gestion des Forêts Denses Africaines Aujourd'hui*. Actes du séminaire FORAFRI de Libreville, Gabon, 12-16 octobre. Session 4: exploitation, aménagement, gestion, 12 pp. CD ROM, CIRAD, Montpellier, France.
- Hawthorne, W.D. and M.P.E. Parren (2000). How important are forest elephants to the survival of woody plant species in Upper Guinean forests? *J. Trop. Ecol.* 16(1): 133-150.
- Parren, M.P.E. (2000). Latest trends in West African natural forest management. In: Seydack, A.H.W., Vermeulen, W.J. & C. Vermeulen (eds.), *Proceedings of the Natural Forests and Woodlands Symposium II titled 'Towards sustainable management based on scientific understanding of forests and woodlands'*

- September 5-9, 1999, Knysna, South Africa. Knysna, South Africa, Department of Water Affairs and Forestry, pp. 2-16.
- Zagt, R.J., Van der Hout, P. & M. Parren (2000). Growth and yield prediction: some experiences from the Tropenbos Programme. In: Wright, H.L. and D. Alder (eds.), *Proceedings of a workshop on humid and semi-humid tropical forest yield regulation with minimal data*. O.F.I. Occasional Papers 52. Oxford, U.K., Oxford Forestry Institute, Department of Plant Sciences, pp. 28-34.
- Parren, M. & F. Bongers (2001). Does climber cutting reduce felling damage in southern Cameroon? *Forest Ecology and Management* 141: 175-188.
- Parren, M.P.E. and F.J.J.M. Bongers (2001). Liana diversity and the effects of climber cutting in southern Cameroon. In: Jonkers, W.B.J., Faohom, B. & P. Schmidt (eds.), Seminar proceedings '*Sustainable management of African rain forest*', November 1999, Kribi, Cameroon. Part II: Symposium. Wageningen, Netherlands, Tropenbos International, pp. 89-101.
- Parren, M.P.E., Berg, J. van den, Biesbrouck, K. & G.J.R. van Leersum (2001). A collaborative approach to forest management: the case of production forests in southern Cameroon. In: Faohom, B., Jonkers, W.B.J., Nkwi, P.N., Schmidt, P. & M. Tchatat (eds.), Seminar proceedings '*Sustainable management of African rain forest*', November 1999, Kribi, Cameroon. Part I: Workshops. Wageningen, Netherlands, Tropenbos International, pp. 17-33.
- Parren, M.P.E., Leede, B.M. de & F. Bongers (2002). A proposal for a transnational forest network area for elephants in Côte d'Ivoire and Ghana. *Oryx* 36: 249-256.
- Parren, M.P.E. and M.K. Sam (2003). *Elephant corridor creation and local livelihood improvement in West Africa*. Paper presented at a CIFOR conference titled 'Rural livelihoods, Forests and Biodiversity' in Bonn, Germany, May 19-23. CD ROM, CIFOR, Bogor, Indonesia.

MSc theses from this project

- Bosdijk, T. (1996). Advanced regeneration in an evergreen rainforest in Cameroon. MSc thesis AV 95-38, PT 95-22, Department of Forestry, Wageningen Agricultural University, 90 p.
- Breugel, M. van & T. Wanders (1996). Forestry in Equatorial Guinea. Report P95-24, Department of Forestry, Wageningen Agricultural University, 82 p.
- Breugel, M. van & T. Wanders (1997). Ecological aspects of an African rain forest. Gaps, composition, structure and light. MSc thesis AV 95-39, Department of Forestry, Wageningen Agricultural University, 97 p.
- Mutsaers, A.S. (1999). The liana factor. MSc thesis AV 99-17, Department of Environmental Sciences, Wageningen Agricultural University, 60 p.
- Van Loon, T. (1997). Regeneration in logging gaps in the moist forest of southern Cameroon. MSc thesis, Department of Forestry, Wageningen Agricultural University, 60 p.
- Voeten, J. (1996). Damage and regrowth. Measuring effects of logging on forest regeneration. P97-07, Department of Forestry, Wageningen Agricultural University, 44 p.
- Voeten, J.G.W.F. (1997). Physical soil damage and forest regeneration on skid trails: survey of soil damage afflicted on forest soils and regeneration of the forest on skid trails in South Cameroon, MSc thesis, Department of Forestry, Wageningen Agricultural University, 49 p.