Modelling anthropogenic impacts on the growth of tropical rain forests

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using an individual-oriented forest growth model for analyses of logging and fragmentation in three case studies

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Der Andere Verlag, Osnabrück, Germany, 2000
ISBN 3-934366-99-6
Zugl.: Kassel, Univ., Diss., 2000

Cover:
Dawn in Danum Valley, Sabah (Borneo), Malaysia
October 1997
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Modellierung anthropogener Einflüsse auf das Wachstum tropischer Regenwälder
-
Analyse von Holznutzung und Fragmentierung in drei Fallstudien unter Verwendung
eines individuen-orientierten Waldwachstumsmodells

Inaugural-Dissertation
zur
Erlangung des akademischen Grades eines
Doktors der Naturwissenschaften (Dr. rer. nat.)
im Fachbereich Physik
der Universität Gesamthochschule Kassel

vorgelegt von
Dipl.-Phys.

Peter Köhler

aus Kassel
Kassel, den 01.11.2000

Als Dissertation vom Fachbereich Physik angenommen am 01.11.2000

Erster Gutachter: Prof. Dr. Hartmut Bossel
Zweiter Gutachter: Prof. Dr. Burkhart Fricke
Drittes Mitglied der Promotionskommission: Dr. habil. Andreas Huth
Viertes Mitglied der Promotionskommission: Prof. Dr. Albrecht Goldmann

Tag der mündlichen Prüfung: 01.11.2000

"If everyone complains bitterness,
then to whom is the world?"

Zainal Abidin Jaafar

Overview

For answering questions concerning anthropogeneous impacts on tropical forest development the individual-oriented and process-based forest growth model FORMIND2.0 was developed. It simulates the spatio-temporal dynamics of uneven-aged mixed forest stands in areas of one hectare to several km^2. The model describes forest dynamics as a mosaic of interacting forest patches of 20 m^2×20 m^2 in size. Within these patches trees are not spatial-explicitly distributed, and thus all compete for light and space following the gap model approach. Tree species diversity is aggregated into 5-20 plant functional types (PFT) on the basis of species maximum tree height and successional status. The carbon balance of each individual tree incl. photosynthesis and respiration is modelled explicitly. Thus, we can match measured diameter increment for different PFT, size and light conditions accurately. Allometric relationships connect above-ground biomass, stem diameter, tree height and crown dimensions. Beside increasing mortality through self-thinning in dense plots one of the main processes of mortality is gap creation by falling of large trees. This process as well as seed dispersal from mature trees interlinks neighbouring plots with each other.

The model was parametrised for three different sites in South-East Asia and south-America: Sabah (Malaysia), Venezuela, and French Guiana. Model accuracy is tested with growth data from permanent sampling plots in Sabah. Sensitivity of various result variables on variation of most parameter values is tested and gives important insights into general model behaviour.

Two examples of anthropogeneous impacts on tropical forest dynamics are management practise and fragmentation, both of major concern. Following applications are performed:

Growth and yield of Venezuelan rain forest under various logging methods, intensities and cycles are analysed for their sustainability.

Effects of logging (methods and cycles), fragmentation and recruitment assumptions on forest dynamics in Sabah are discussed.

Finally, fragmentation impacts on mortality and recruitment are simulated and their effects on forest dynamic and biomass loss are evaluated for a forest site in French Guiana.

Keywords: abandoned land; basal area; dipterocarp forest; edge effects; forest growth model; FORMIND; fragmentation; French Guiana; functional groups; individual-oriented model; logging impacts; logging scenarios; Malaysia; maximum height; model; mortality; plant functional types; rain forest; recruitment; secondary succession; simulation; successional status; sustainable timber harvest; tropical rain forest.

Contents

Account

Chapters of this thesis have been published as follows:

Chapter 3:

Köhler, P., Ditzer, T., & Huth, A. 2000b. Concepts for the aggregation of tropical tree species into functional types and the application on Sabah's lowland rain forests. Journal of Tropical Ecology, **16(4)**, 591-602.

Chapter 5:

Köhler, P., Ditzer, T., Ong, R. C., & Huth, A. 2001. Comparison of measured and simulated growth on permanent plots in Sabah's rain forests. Forest Ecology and Management, **142(1-3)**, in press.

Chapter 6:

Kammesheidt, L., Köhler, P., & Huth, A. 2000. Sustainable timber harvesting in Venezuela: a modelling approach. Journal of Applied Ecology, in press.

Chapter 7:

Köhler, P., Ditzer, T., & Huth, A. 2000c. The effects of logging, fragmentation and recruitment on growth of dipterocarp forest. Journal of Ecology, submitted.

Chapter 8:

Köhler, P., Chave, J., Riera, B., & Huth, A. 2000a. Long-term response of tropical rain forests to the effects of fragmentation: a simulation study. To be submitted.

Other publications by the author related to the topics of this thesis:

Ditzer, T., Glauner, R., Förster, M., Köhler, P., & Huth, A. 2000. The process-based stand growth model FORMIX3-Q applied in a GIS-environment for growth and yield analysis in a tropical rain forest. Tree Physiology, **20**, 367–381.

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Chapter 1

Introduction

Introduction

The use of natural resources change our environment directly and indirectly through effects which are not fully understood so far. Climate change and an increase in mean global temperature, the amount of carbondioxide in the atmosphere, or rising sea levels are some examples of occurring effects (Fan et al. 1998; Chavez et al. 1999; Malhi & Grace 2000). These anthropogeneous influences will change our environment for centuries. Plants might react adaptivly to their changing environment (Pastor & Post 1988; Friend 1997; Cao & Woodward 1998; Tian et al. 1998; DeLucia et al. 1999; Pounds et al. 1999; Stil et al. 1999; Hashimotio et al. 2000). Huge ecosystems like forests might buffer changes, caused for example by extraction of timber woods over a long period. But if natural catastrophes occur in ecosystems, which have already been weakened, damage is more dramatic than ever thought before (Phillips & Gentry 1994; Laurance et al. 1997; Phillips et al. 1998; Peres 1999; Gascon et al. 2000). Thus, forest fires in the Amazonian rain forest and the Indo-Malayan archipelago in the years 1997/1998 spread very fast. El Niño, the Great Southern Oscillation, caused serious dry periods (Leighton & Wirawan 1986; Walsh 1996; Hartshorn & Bynum 1999), in which human made fires for land clearing could spread easily to adjacent areas. These forest were already highly disturbed through logging and forest management, and available dead wood fuelled the fires further (Brown 1998; Kellman et al. 1998; Cochrane et al. 1999; Goldammer 1999; Laurance & Fearnside 1999; Nepstad et al. 1999; Hashimotio et al. 2000).

With 36 000 000 km^2 of forests, covering a quarter of the total land surface on earth, beside the oceans forests are the biggest ecosystems on our planet. About 475 to 825 billion tons of carbon are bound in the forests and thus they are the biggest above-ground carbon storages (Murphy 1975; Enquete-Kommission 1990; Grace et al. 1995; Fan et al. 1998; Prentice & Lloyd 1998; Alexandrov et al. 1999b, 1999b). A further reduction of woodland and, following this, an increasing release of carbon in the form of carbondioxide would certainly intensify climate changing effects. Currently, annual release of carbon and its input in the atmosphere are estimated at seven billion tons. About 20 % of the release is caused by global deforestation (Enquete-Kommission 1994; Houghton et al. 2000).

There are various reasons which make forests worth protecting and sustainable management desirable. Forests produce timber, firewood and food, act as local climate regulator, prevent erosion, and are important water storages. Additionally, tropical rain forests are remarkable for their enormous biological species diversity (Tuomisto et al. 1995; Hubbell 1997; Tilman 1999). It is assumed that 50-75 % of all existing species are found in the tropical wet forests (Terborgh 1993). In a survey to identify global extinction threats tropical regions were endangered the most (Sisk et al. 1994). For the conservation of as many different species as possible the approach of biodiversity hotspots is proposed (Myers 1989; 1990; Reid 1998 Myers et al. 2000; Cincotta et al. 2000). Thus, areas with highest diversity are considered most valuable for protection.

Tropical rain forests covered roughly 18 000 000 km^2 in the year 1990, corresponding to 13 % of earth's land surface. Characteristics of tropical climate are a constant high temperature with monthly averages above 18 °C and high precipitation ($>$ 100 mm per month) with no, or only short, dry seasons. Areas with those climatic conditions are found in a belt of 40° latitude around the equator (Whitmore 1998). There are three regions where tropical rain forests occur: South and Central America, central Africa and South-East Asia.

Logging of timber, land clearing, slash-and-burn cultivation, high population pressure and ongoing forest fragmentation are threatening tropical forests (Aiken & Leigh 1993; Cannon et al. 1998; Brown 1998; Grainger 1998; Foster et al. 1999; Rosenzweig 1999; Hughes et al. 2000). Reducing those impacts and changing to sustainable development is needed to stop the extinction of various animal and plant species (Terborgh 1993; Laurance et al. 1997; Bowles et al. 1998; Whitmore 1998). The Food and Agriculture Organisation of the United Nations (FAO) estimated the annual loss of tropical forests at 169 000 km^2 in 1990 with increasing tendency (Riswan & Hartanti 1995; Laurance 1999b). If these trends of deforestation continue most tropical forest will be destroyed within the 21st century.

From an ecological point of view it might be desirable to declare as many forest areas as possible as protection zones with a total ban of timber logging (Whitmore & Sayer 1992). Very often those idealistic conservation ideas conform with public opinion and policy making in developed countries, but neglect local needs for fuel, timber for construction and labour. With a detailed planning effort it might be possible to manage tropical forests in a way that ecosystems have a realistic chance for sustainable regeneration. On the global scale this is especially of interest, as case studies have shown that forests under reduced-impact management will act as a sink for carbondioxide, compared to those under commercial logging (Putz & Pinard 1993; Pinard & Putz 1996, 1997). However, the most important motivation for sustainable management are economic profit on a short time scale (Plumptre 1996). Economic studies have verified increasing profit in well planned management (Barreto et al. 1998). Certification of tropical timber wood is one of the possibilities to support sustainable management strategies (Hahn-Schilling et al. 1994; Boot & Gullison 1995). Non-governmental organisations like the World Wildlife Found for Nature (WWF) are promoting this approach (Liedeker 1999; Forest-Stewardship-Council 2000). The controversial discussion about criteria of sustainability is certainly not finished (Johns 1985, 1997; Fölster et al. 1986; Brown & Lugo 1990, 1994; Bruenig 1996; Ong et al. 1996; Putz & Viana 1996; Weidelt 1996; Rice et al. 1997; Bowles et al. 1998).

For an estimate of annual allowable cuts (AAC) knowledge on the main processes of forest dynamics is essential. In temperate forests, management planning was based on modelling and computer simulations over some decades (e.g. Botkin et al. 1972; Shugart 1984, 1998; Battaglia & Sands 1998; Borgesa & Hoganson 2000). Thus, long-term tendencies of forest dynamics can be estimated under changing conditions.

Modelling of tropical rain forests started in the early nineties with models of various complexity (e.g. Adlard et al. 1989; Alvarez-Buylla & Garcia-Barrios 1991, 1993; Bossel & Krieger 1991, 1994; Alder 1992; Howard & Valerio 1992; Vanclay 1994; Osho 1995, 1996; Albers 1996; Alder & Silva

2000). Available data sets from long-term ecological research plots, (Nakashizuka et al. 1999; Smithsonian-Tropical-Research-Institute 2000) and simulation studies in the context of international climate protection programmes (IGBP 1990) led to an increasing interest in rain forest models in recent years (Liu & Ashton 1998, 1999; Chave 1999a, b; Pinard & Cropper 2000). Another motivation for developing models for tropical forest growth was management planning, very often with the cooperation of European developing projects and local governmental institutes, e.g. the British government in Indonesia (van Gardingen & Phillips 1999) or the German *Gesellschaft für Technische Zusammenarbeit* (gtz) in Malaysia (Ong & Kleine 1995, 1996; Ditzer 1999; Ditzer et al. 2000; Huth & Ditzer 2000a,b). The focus of these schemes was in South-East Asia, where deforestation rates were highest in the last decade (Plumptre 1996). Current rates of forest loss in Latin-America (7.4 million ha y^{-1}) are nearly twice as high as those in Asia (3.9 million ha y^{-1}) (FAO 1997). Modelling approaches depend on available field data used for model development. Thus, the SYMFOR model was developed in tight cooperation with logging companies and for instant application in forest management planning and depends mainly on inventory data collected by the companies (Young & Muezelfeldt 1998; van Gardingen & Phillips 1999), while Chave and colleagues (Chave et al., unpublished manuscript) are interested in long-term development of rain forest migration and try to understand seed dispersal patterns found in paleoecological research.

Various projects of the research group *Ecosystem Modelling* at the Center of Environmental Research, University of Kassel, Germany, for the Deramakot Forest Reserve showed dependency of simulation results on the chosen modelling approach (Haupt 1995; Kaspar 1996; Köhler 1996; Kürpick et al. 1997; Ditzer 1999; Huth 1999). While some models are difficult to parametrise (e.g. the model FORMAL (Kürpick et al. 1997) needs the maximum tree age as an input parameter, which can be estimated only roughly) others come up with elegant mathematical equations (Kaspar 1996). Models, which are not only used for testing ecological hypothesis, but for model application in forestal management planning are of special interest (Ditzer 1999; Ditzer et al. 2000).

Problems of these approaches arise because they are mostly based on an aggregation of tree species in a few (3-5) species groups, which are easy to parametrise, but simplify ecological processes of rain forests greatly. Concepts of species grouping in tropical rain forests based on a more systematic approach were developed only recently (Gitay et al. 1999; Köhler et al. 2000b; Phillips et al. 2000). They are the most important for all further work of this thesis. Furthermore, analysis in Kassel showed the largest potential for data based model development in individual-based models (Huston et al. 1988; DeAngelis & Gross 1992; Judson 1994; Liu & Ashton 1995), as computation time was not a limiting factor anymore, because of improvements in computer capabilities.

The model FORMIND developed by the author in previous studies (Köhler 1996; Köhler & Huth 1998a, 1998b) was the basis of the further research and development presented in this thesis. FORMIND is an individual-based model, while the parallel development of FORMIX3-Q (Ditzer et al. 2000) is still based on a simple matrix approach, incl. transition rates between classes of different tree size. As result of the chosen approach, the model structure of FORMIND was more flexible and an application with different numbers of species groups was easy to perform (Köhler & Huth 1998a).

Two main targets are the focus of this work. First, no existing model of rain forests growth was applied to tropical forests in various regions[1]. This work tries

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[1] Ditzer (1999) was developing a concept of site

to show that, with a model structure covering all main processes, sites in various regions can be simulated. Second, most previous work was based on a forest recruitment module covering only simple principles. Ongoing forest fragmentation will determine recruitment as one limitating factor in rain forest dynamics (Ribbens et al. 1994; da Silva & Tabarelli 2000). Thus, beside general model improvement and enhancement the development of new approaches for modelling of recruitment is one of the main focuses of this work. The resulting new model FORMIND2.0 will be used to answer various questions:

1. Is there a general approach for classifing several hundred tree species in different rain forest sites into a few groups?
2. Does simulated tree growth match measured data sets with acceptable accuracy?
3. Which logging method and rotation length can be called sustainable depending on the forest site?
4. How does recruitment determine forest growth and yield?
5. Can tropical rain forests buffer the effects of ongoing fragmentation?

For this purpose three different rain forest sites, in South-East Asia (Sabah, Malaysia) and South-America (Venezuela and French Guiana), were parametrised (Fig. 1.1)[2]

Besides the introduction, this thesis consists of seven further chapters from which only Chapters 2 and 4 have not been published or submitted for publication. The Chapters are arranged in chronological order to allow a comprehensible understanding of model improvement.

An introduction to rain forest dynamics is given in Chapter 2. A general approach to tree species grouping, based on available data sets, follows thereafter (Chapter 3, Köhler et al. 2000b). The model FORMIND2.0 used in this thesis is completely described in Chapter 4. Chapter 5 consists of a validation of the model in its version FORMIND1.1 with field data from Sabah (Köhler et al. 2001). Additional analysis of the same data with current versions of the model close this Chapter. Besides an intensive sensitivity analysis of model behaviour, various logging methods and intensities in a Venezuelan rain forest are analysed in Chapter 6 (Kammesheidt et al. 2000). An application of the model to a rain forest site in Sabah (Malaysia) is performed in Chapter 7. The influence of various recruitment modules and their impacts on timber logging are analysed in detail (Köhler et al. 2000c). The model application to French Guiana contains an analysis of the effects of forest fragmentation on further forest dynamics (Chapter 8, Köhler et al. 2000a).

Finally, the methods and most important results related to questions posed are summarised incl. an outlook. This summary is written in both German and English.

Data collections (inventory data and lists of tree species), which were needed for simulations, are found in the Appendix.

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depending parametrisation, but was restricted to dipterocarp lowland rain forests in South-East Asia.

[2] At the time of planning this research project a cooperation with a project in Kenya (Africa) existed. Thus, it seemed possible to apply the model to all three global rain forest regions. Unfortunately the leader of the gtz-project was shot dead two days before cooperation started and the project was closed thereafter.

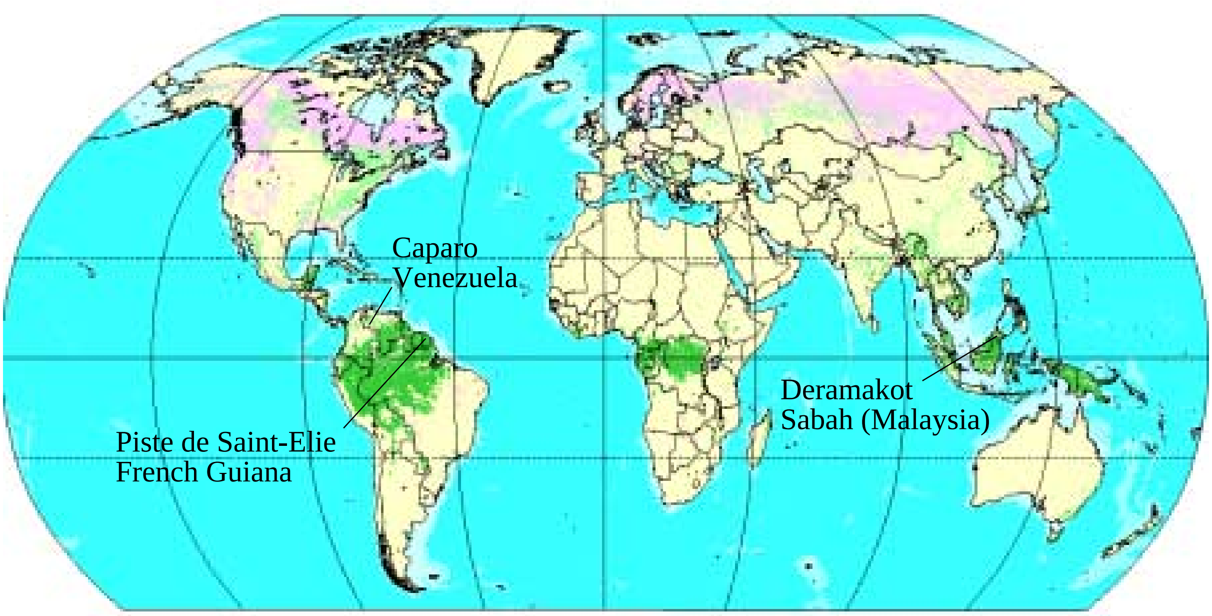

Figure 1.1: Global distribution of forests, including research plots used in this thesis. The map is based on data collected between 1980 and 1990 (from WWF 1997).

Chapter 2

An introduction to tropical rain forests

In the following chapter some fundamental characteristics of tropical rain forests are described. I focus on processes which are important to understand growth dynamics of the forest trees and their species composition. A more detailed description of the ecology of tropical forests is found in several informative text books (Richards 1952, 1996; Whitmore 1984, 1993, 1998; Jacobs 1988; Lieth & Werger 1989; Terborgh 1993; MacKinnon et al. 1996; Huth 1999). The objective of the current chapter is not to go into the details of the ecological processes, but to explain some basic facts about the ecology of tropical rain forests. Thus, the following introduction will be rather brief.

Evergreen lowland rain forest

The tropics are mostly defined by their climate conditions. In tropical regions daily temperature fluctuations exceed average annual temperature variability. Thus, tropical regions are extended north and south of the equator until daily and annual temperature variability match each other (Lamprecht 1986; Enquete-Kommission 1990).

The most important site factors for vegetation formations are temperature, precipitation, light, and soil conditions. For an explicit differentiation of several tropical forest formations, climate, soil water, soil quality and elevation are considered (see Table 2.1). In Central America vegetation is classified after a scheme of Holdridge, which is based on systematic combination of information on temperature and water availability (Terborgh 1993; Shugart 1998). Currently, a framework for a worldwide comparison of tropical woody vegetation types is developed (Blasco et al. 2000).

Classically, the term *rain forest* describes evergreen tropical lowland wet forest up to an elevation of 750 m. Those are closed large growing forests found in latitudes between 10° north and 10° south with high precipitations without seasonal dry periods. Evergreen tropical wet forests covered about 7 million km^2 of land surface in 1993, mainly in the Amazon-Orinoco area (American rain forest formation), at the Gulf of Guinea and in the water catchment of the Congo river (African rain forest formation), in Sri Lanka, Western India, Thailand, Indochina, on the Philippines, in Malaysia, Indonesia, New Guinea (Indo-Malaysian rain forest formation), and on the east coast of Australia (Enquete-Kommission 1994).

Lowland rain forests are by far the most diverse plant communities on earth. Up to 400 different tree species are found in one hectare (Terborgh 1993). The largest trees reach heights of 45 to 60 m, in a few cases up to 70 m. The tree crowns of those large individuals, called emergents, rise above the closed forest canopy, which reaches about 30 m in height. Depending on light conditions small trees and saplings are found below the canopy. Ground vegetation is rare in dense closed forests and consists mainly

Table 2.1: Classification of tropical wet forests (from Whitmore 1998).

Climate	Soil water		Soils	Elevation	Forest formation
Seasonally dry	Strong annual shortage				Monsoon forests (various formations)
	Slight annual shortage				Semi-evergreen forest
Everwet (perhumid)	Dryland		Zonal (mainly oxisols, ultisols)	Lowlands	**Lowland evergreen rain forest**
				(750) 1200-1500 m	Lower montane rain forest
				(600) 1500-3000 m	Upper montane rain forest
				3000 m to tree line	Subalpine forest
			Podzolized sands	Mostly lowlands	Heath forest
			Limestone	Mostly lowlands	Forest over limestone
			Ultrabasic rocks	Mostly lowlands	Forest over ultrabasics
	Water table high (at least periodically)	Coastal saltwater			Beach vegetation, Mangrove forest, Brackish water forest
		Inland freshwater	Oligotrophic peats		Peat swamp forest
			Eutrophic (muck and mineral soils)	±Permanently wet	Freshwater swamp forest
				Periodically wet	Freshwater periodic swamp forest

of recruitment of young trees. Shrubs and bushes are found in single areas (Whitmore 1998). This sort of layer structure is controversially discussed in the literature (Richards 1936; Terborgh & Petren 1991). While a model for light distribution in forest canopies tries to explain the structure (Terborgh 1993), new mathematical analysis of different vertical forest structures for tropical and temperate regions found no differences between them and only a few distinct layers in both regions (Baker & Wilson 2000).

All other rain forest formations differ from this type through simpler structures, lower species diversity and a smaller spectrum of life forms. For means of simplicity we address evergreen tropical lowland rain forest by the short term *rain forest*.

Tree species

Tree species in rain forests can be distinguished, after their successional behaviour, into two or three ecological classes (Denslow 1987; Whitmore 1998; Thomas & Bazzaz 1999). Pioneers and climax species are the extreme positions in a more or less continuous spectrum. While pioneers establish early in succession of available areas, climax or late successional species follow last in a succession process. Most important characteristics of pioneers and climax species are summarised in Table 2.2.

Seeds of climax species germinate and establish in the shade of the own mature community. Therefore, they are called shade-tolerant. They are the dominant plant species in undisturbed primary forests and contribute mainly to the main canopy of a rain forest. The largest individuals normally belong to those species (Whitmore 1998).

The second category are the pioneers. Their seeds depend on light and can only germinate and establish in forest gaps. Height growth is fast, and thus shade-tolerant competitors are suppressed. Pioneer tree species are seldom found in ma-

Table 2.2: Most important characteristics of pioneer and climax species in tropical rain forests (from Whitmore 1998).

	Pioneers	Climax
Common alternative names	Light-demander, (shade-) intolerant, secondary	Shade-bearer, (shade-) tolerant, primary
Germination	Only in canopy gaps open to the sky which receive some full sunlight	Usually below canopy
Seedlings	Cannot survive below canopy in shade, never found there	Can survive below canopy, forming a "seedling bank"
Seeds	Usually small, produced copiously and more or less continuously, and from early in life	Often large, not copious, often produced annually or less frequently and only on trees that have (almost) reached full height
Soil seed bank	Many species	Few species
Dispersal	By wind or animals, often for a considerable distance	By diverse means, including gravity, sometimes only a short distance
Dormancy	Capable of dormancy commonly abundant in forest soil as a seed bank	Often with no capacity for dormancy, seldom found in soil seed bank
Growth rate	Carbon fixation rate, unit leaf rate, and relative growth rates high	these rates lower
Light compensation point	High	Low
Height growth	Fast	Often slow
Branching	Sparse, few orders	Often copious, often several orders
Leaf life	Short, one generation present, viz. high turn-over rate	Long, sometimes several generations present so slow turn-over rate
Wood	Usually pale, low density	Variable, pale to very dark, low to high density
Longevity	Often short	Sometimes very long

ture primary forests, but are most dominant in secondary forest following regrowth of abandoned land, or in highly disturbed forests after logging or catastrophic events. The canopy of those forests is not closed and light demanding plants dominate the sites.

Tree species of medium characteristics, called mid successional species, are also distinguished. They are neither pioneer, nor climax (Whitmore 1998).

Succession and gap dynamics

A forest gap is a not-fully-closed canopy within a mature forest. Gaps are created by the falling of large trees, often causing the destruction of several other, i.e. smaller trees. As mature forest stands are in a dynamic equilibrium, gap creation and regrowth within them balance each other (Shugart 1984, 1998; Brokaw 1985; Brokaw & Scheiner 1989; Platt & Strong 1989; Belsky & Conham 1994).

Gaps are first filled with pioneers. In a second growth cycle, climax seedlings establish themselves underneath the pioneers. After the death of the short-living pioneer species, established climax trees grow and fill the gap. It takes between several decades and some centuries until trees of sizes similar to mature forest dominate those former gap areas (Whitmore 1998).

This growth cycle is called succession. It is essential for the simultaneous coexistence of tree species with different successional behaviour in forests.

In tropical rain forests annual mortality rates of trees with a diameter $\geq$10 cm are about 1-3 % (Swaine 1989; Phillips & Gentry 1994). Mortality rates cover dead standing trees, fallen individuals and those which were smashed by collapsing trees. The causes of tree falls are wind, heavy rain fall and others. Field data show that annually up to 1.5 % of standing trees fall over and thus 90 % of mortality is connected with gap creating events (van der Meer & Bongers 1996).

In the literature the definition of a forest gap is widely discussed (Vandermeer 1994; van der Meer et al. 1994). For example, Brokaw (1982) defined a gap as a missing canopy, which reaches down to 2 m above the forest floor. Others (van der Meer & Bongers 1996) define it as a canopy gap reaching down to 20 m above the floor. For comparing field studies, gap definition is crucial. Thus, the range of gap numbers and gap sizes varies widely (Barden 1989; Runkle 1989). With the second definition given above, a neo-tropical rain forest in Panama would have a gap fraction of 34 % (Hubbell & Foster 1986a).

Disturbance of forests by gap creation can be distinguished in three different areas. In the region of the roots of the falling tree, the forest floor is damaged. Light intensity is increased through the missing tree crown above. Beside the trunk of the falling tree the disturbance is weak. The crown of the falling tree destroys most trees, especially in the understorey (Hubbell & Foster 1986a).

Water and nutrient cycles

As precipitation in the tropics is high and regular (e.g. Sabah on Borneo, Malaysia: 3505 mm per year, Schlensog 1997) without distinct dry seasons, water is not a limiting factor in tree growth (Friend 1993). An explicit description of water cycles within the model is therefore not necessary for accurate modelling results. Applications will show that even in areas with dry seasons of a few months some small, but effective model improvements will lead to acceptable results (Chapter 6). It should be mentioned that dry periods as caused regularly by the Great Southern Oscillation, El Niño, will result in significantly higher tree mortality rates (Walsh 1996).

Soil investigations show that two thirds of all tropical soils have average to very low fertility. Generally, agriculture can only be performed for a very short period of a few years before soils become infertile. It has been shown that above-ground growth of tropical forests depends little on soil fertility (Fölster et al. 1986; Terborgh 1993). Endemic species are very well adapted to nutrient-poor conditions. Plant growth depends on very effective and fast decomposition processes in the top soil layer. Most nutrients are bound in the living biomass, and only about 20 % are depleted and reenter through precipitation and mineral rock erosion. Heavy disturbances of those cycles through clearing, erosion or damage of the humus layer might lead to massive nutrient depletion. Thus, in these soils forests might not grow to their former complexity and size (Terborgh 1993).

Dependence of forest dynamics on soil conditions and slope was analysed in other studies (Biehounek 1999; Clark et al. 1999a; Ditzer 1999; Glauner 1999; Ditzer et al. 2000), and is not the subject of the current thesis. We assume in the following more or less undisturbed nutrient cycles. Investigations of nutrient inputs through air and rain on Borneo support this approach (Weidelt 1993). The implications of this simplification are discussed in Chapter 4.

Chapter 3

Concepts for the aggregation of tropical tree species into functional types and the application to Sabah's lowland rain forests

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Abstract

For analysing field data as well as for modelling purposes it is useful to classify tree species into a few functional types. In this paper a new aggregation of tree species of the dipterocarp rain forests in Sabah (Borneo), Malaysia, is developed. The aggregation is based on the two criteria successional status and potential maximum height. Three classes of successional status (early, mid and late successional species), five classes of potential maximum heights ($\leq$5 m, 5–15 m, 15–25 m, 25–36 m, $>$ 36 m) and their systematic crossing lead up to 15 functional types. The criteria of the developed classification are chosen to fit applications with process-based models, such as FORMIX3 and FORMIND, which are based on photosynthesis production as the main process determining tree growth. The concept is universal and can easily be applied to other areas. With this new method of grouping a more realistic parametrisation of process-based rain forest growth models appears possible.

Keywords: dipterocarp forest, Malaysia, maximum height, model, plant functional types, successional status, tropical rain forest

Journal of Tropical Ecology (2000) **16**(4), 591-602.

Introduction

Tropical rain forests are known for their great tree species diversity with up to several hundred different tree species in one hectare (Groombridge 1992). Their ecology and physiology have been increasingly studied in the last decades (e.g. Bazzaz & Pickett 1980; Mooney et al. 1980; Leigh et al. 1985; Mulkey et al. 1996; Whitmore 1988, 1995, 1998). For generalization of ecological results for single species as well as for modelling purposes different concepts have been developed for aggregating tree species diversity in tropical forests into few plant functional types (PFTs).

The principles of species aggregation into PFTs have been discussed widely (Botkin 1975; Smith et al. 1993, 1997; Box 1996; Gitay & Noble 1997; Lavorel et al. 1997). As pointed out by Gitay & Noble (1997) there is no universal classification or concept for the development of PFTs, the type of classification depends on the context of the performed aggregation. PFTs are often used in global vegetation models (Cramer 1997; Leemans 1997) and climate change analysis (Bugmann 1996a). For forest ecosystems the following conceptual approaches can be distinguished:

(1) *Grouping based on physiological criteria such as shade tolerance at different life stages* (Hubbell & Foster 1986b; Whitmore 1988, 1989, 1998). This concept varies from the rough distinctions whether species are early or late successional ones (Shugart 1997) to more exact differentiations of several aspects of plant behaviour and growth strategies for light demanding pioneer species and shade-tolerant climax species (Whitmore 1989). While Swaine & Whitmore (1988) state that it is difficult to distinguish more than the mentioned two groups, Kammesheidt (2000) distinguishes early, mid and late successional species. However, Swaine & Whitmore suggest to subdivide the two major ecological groups into further sub-groups.

(2) *Classification based on differences in potential maximum height.* Richards (1936) was the first to derive a grouping concept in tropical rain forest research when he described the layering structure of rain forest canopy and distinguished tree species according to potential canopy layers. This approach was developed further by various researchers (Hubbell & Foster 1986a; Swaine & Whitmore 1988; Poker 1995; Condit et al. 1996; Denslow 1996).

(3) *Intensive statistical data analysis of diameter growth pattern,* for a specific site to derive groups with significant different diameter increment behaviour (Host & Pregitzer 1991; Vanclay 1991; Ong & Kleine 1995).

(4) *Approaches which combine several concepts together.* Lieberman et al. (1985 1990) combine diameter growth analysis with maximum size, Acevedo et al. (1995), Condit et al. (1996) shade-tolerance with maximum height, Shugart (1984, 1997) gap requirements for regeneration with maximum size. Kammesheidt's (2000) classification is based on all available data concerning different criteria as growth form, establishment, phenology, etc. In single case studies pioneer species are distinguished from other tree species, which are further subdivided (Manokaran & Kochummen 1987; Manokaran & Swaine 1994; Bossel & Krieger 1991; Köhler & Huth 1998a, b).

Within the context of modelling, grouping concepts become important for integrating field data in terms of parameter values in models and for comparing typical simulation results with observations (Vanclay & Skovsgaard 1997). Interpretation of results is easier with a small number of functional types, where by with increasing number of PFTs accuracy increases as well.

Approaches already published are unsatisfactory for the purpose of process-based modelling for two reasons. First, the balance between adequate and necessary ac-

Table 3.1: Successional status (SS) of 468 of Sabah's lowland tree species. No: Number of species per SS. Ab: Abundance of trees with diameter > 10 cm in forest inventories in Deramakot, Lingkabau, Kalabakan and Ulu Segama.

Successional status	SS	No	Ab [%]
Early successional spp.	1	31	24.8
Mid successional spp.	2	317	63.4
Late successional spp.	3	120	11.9

curacy has so far not been dealt with satisfactorily. Most approaches use very few (e.g. five) or many (20–50) PFTs, where 10 to 20 PFTs seems to be more appropriate, if both interpretation and accuracy is of concern. Second, no approach is generic in its concept and easily applicable to different forest sites using available data to derive the appropriate number of PFTs. We therefore develop a universal approach, based on the systematic combination of well established classifications into different successional status and maximum height at maturity to derive about 10–20 PFTs, and apply the concept to tropical lowland rain forests in Sabah, Malaysia.

Methods

Criteria for the development of plant functional types

We choose as grouping criteria successional status (as defined in detail below) and attainable maximum height.

We distinguish early, mid and late successional species. We are aware of several different nomenclatures for these classes (e.g. pioneers, non-pioneers), but find this the most appropriate (for alternatives see Swaine & Whitmore 1988). In the context of modelling we define different successional status as (a) different light requirements for the establishment of seedlings, (b) different growth rates in a given light regime for trees of similar size, and (c) differences in mortality rates. While early successional species grow fast they tend to build low-density stems, in contrast to the slow growing late successional species which have higher wood densities. Based on the correlation between wood density and growth rate a data set of Ong & Kleine (1995) on wood density covering 468 tree species was used to derive species successional status. Apart from typical pioneers (classified as early successional spp. in our context), Ong & Kleine distinguish timber groups of light, medium and heavy hardwood species. We classify those light and medium hardwood species as mid-successional, and heavy hardwoods as late successional species. In a few cases (including an undefined group, called OTHERS), grouping differs due to additional knowledge on successional behaviour (Rundi, pers. comm.). The quality of the timber group classification is verified through a literature survey on wood density (Meijer & Wood 1964; Burgess 1966;

Table 3.2: Aggregation of 468 of Sabah's lowland tree species into five height groups (HG). Corresponding canopy layer. H: Height range at maturity. No: Number of species per HG. Ab: Abundance of trees with diameter > 10 cm in forest inventories in Deramakot, Lingkabau, Kalabakan and Ulu Segama.

Canopy layer	H [m]	HG	No	Ab [%]
Shrubs	0- 5	1	15	5.7
Understorey	5-15	2	97	13.5
Lower canopy	15-25	3	119	32.9
Upper canopy	25-36	4	117	21.9
Emergents	>36	5	120	26.0

Table 3.3: Autecological characteristics of 13 plant functional types (PFTs) of Sabah's lowland tree species. Height at maturity. SS: related successional status (Table 3.1). HG: related height group (Table 3.2). No: number of species per PFT. Ab: Abundance of trees with diameter > 10 cm in forest inventories in Deramakot, Lingkabau, Kalabakan and Ulu Segama.

Plant functional type	Height [m]	PFT	SS	HG	No	Ab [%]
Shrub mid successional spp.	0-5	1	2	1	15	5.7
Understorey early successional spp.	5-15	2	1	2	5	0.4
Understorey mid successional spp.	5-15	3	2	2	28	4.7
Understorey late successional spp.	5-15	4	3	2	65	8.3
Lower canopy early successional spp.	15-25	5	1	3	14	19.0
Lower canopy mid successional spp.	15-25	6	2	3	92	13.6
Lower canopy late successional spp.	15-25	7	3	3	13	0.3
Upper canopy early successional spp.	25-36	8	1	4	10	4.1
Upper canopy mid successional spp.	25-36	9	2	4	89	16.0
Upper canopy late successional spp.	25-36	10	3	4	18	1.8
Emergent early successional spp.	>36	11	1	5	3	1.2
Emergent mid successional spp.	>36	12	2	5	93	23.3
Emergent late successional spp.	>36	13	3	5	24	1.5

Fox 1970; Cockburn 1980; Keating & Bolza 1982; PROSEA 1994).

The maximum potential height $h_{\max}$ of trees is grouped into five classes for Sabah's rain forests. The classes can be named according to their canopy layers as emergents ($h_{\max} > 36$ m), upper main canopy (25 m $< h_{\max} \leq 36$ m), lower main canopy (15 m $< h_{\max} \leq 25$ m), understorey (5 m $< h_{\max} \leq 15$ m) and shrubs ($h_{\max} \leq 5$ m) (nomenclature according to Manokaran & Swaine 1994, Poker 1995). The identification of the class limits is based on observations of typical canopy heights and mean maximum tree heights of different species in Sabah's dipterocarp lowland forests (Forestal-International-Limited 1973, unpublished data from forest inventories). Maximum heights of Sabah's dipterocarp lowland rain forest tree species were determined using the literature (Meijer & Wood 1964; Burgess 1966; Fox 1970; Whitmore & Ng 1972; Cockburn 1980; Keating & Bolza 1982; PROSEA 1994). In some cases, where no data on maximum height were available maximum girth or diameter was used to determine maximum height by using height-to-diameter functions calculated by Forestal-International-Limited (1973). With the assumption that the two criteria for grouping are independent the use of both species classification leads up to 3 × 5 = 15 different PFTs.

Application to Sabah's dipterocarp lowland rain forests

We use the species list for Sabah's dipterocarp lowland rain forest compiled by Ong & Kleine (1995), plus some additional tree species described in several forest inventories. In total we have 468 tree species (Table B.2 in Appendix of thesis, http://www.usf.uni-kassel.de/usf/archiv/dokumente.en.htm). For technical reasons sometimes only a species code, to which several tree species belong is stated and only the timber group can be determined. Data from the inventory of four Forest Management Units (FMUs) in Deramakot, Kalabakan, Lingkabau, and Ulu Segama were used to calculate the relative abundance of different PFTs (Kilou et al. 1993 and unpublished data of the Forestry Department Sabah). In the inventory 2023 systematically scattered sampling units, each 0.25 ha in size, were enumerated. For details concerning the inventory methods see Chai et al. (1991).

As mentioned by Grime et al. (1997) a testing of the grouping concept is very important because of various possible conceptual approaches. In our case study the chosen concept is determined mainly by the needs of model development and its application and the existence or availability of field data (Gitay & Noble 1997). However, for the proposed groupings there are possibilities to estimate the quality of the classification. In particular, different successional status can be checked against field data in the criteria we defined above for our classification. Specifically, we (1) check growth rates in terms of diameter increment and photosynthesis measurements, and (2) discuss mortality rates, the latter for both successional status and grouping of potential maximum heights.

Mortality and diameter increment rates calculated from permanent sampling plots (PSPs) in three different forests reserves in Sabah (Garinono, Segaliud Lokan and Sepilok) are taken to validate the resulting grouping. The PSPs differ in size (2 to 7 ha), observations length (9 to 20 y), number of (3–10) and time between recordings (1–5 y). Analysis of these data can be found in Köhler (1998) and Köhler et al. (2000).

Results

Successional status

The resulting classification of species distribution according to successional status is found in Table 3.1. Thus, 31 species were classified as early, 120 species as mid, and 317 species as late successionals. In the forest management inventories the abundance of mid successional spp. was highest (64%), whereas late successionals were rarest (12%).

Maximum potential height

The number of species (Table 3.2) distributed over the five height groups was similar within groups 2 to 5 (97–120 species per group). Only the lowest group containing the shrub species was occupied by a smaller number of species (15). The abundance of trees in the FMU inventories however was not equally distributed. Lower main canopy species were most abundant (33%), followed by emergent species (26%), upper main canopy species (22%), understorey species (14%) and shrub species (6%).

Plant functional types

An independent application of both classification criteria led to a maximum of 15 PFTs. We did not distinguish the shrub species in their successional status, because of the lack of information on them. The resulting 13 PFTs and their autecological characteristics are shown in Table 3.3. Numbers of species per PFT varied from 3 to 93. Again the FMU inventories as one possible species distribution for Sabah showed different abundances between 0.4% and 23.3%. From the characteristics of the aggregation one can easily identify various important species, e.g. most dipterocarps are within PFT 9, 10, 12 and 13, *Macaranga spp.* are found in PFT 5.

Discussion

Successional status

For 259 species (of 468 species in total), data on wood density were found. This incompleteness was the reason to group the species list not according to values on density but on the more general concept of quality differences in wood density as done by Ong & Kleine (1995). Another reason for not using detailed values as the basis for grouping is the fact that often wide ranges of densities are found in the literature for individual species. Therefore dividing up the range of wood densities would become difficult if not impossible. However the data available enable us to validate the timber grouping of Ong & Kleine (1995). Because of the incomplete data set, comparing medians (not means) seems to be the appropriate statistic. We found wood density ρ_{median} of 455, 657 and 921 kg m^{-3} for early, mid, and late successional species, respectively. Thus, the concept of timber groups by Ong & Kleine (1995) seems to be based on wood densities.

Growth rates in terms of diameter increments show trends, expected by our grouping concept (Table 3.4). In Sepilok and Segaliud Lokan 1 & 2 average growth rates are highest in early successional, and lowest in late successional species, although differences are not significant (χ^2 test; $P > 0.7$). In Garinono, average growth rate of early successionals is lower than growth rates of mid successionals. It is not surprising to find no significance in the differences of growth rates. They are averaged over both different light regimes and diameter ranges. A more detailed analysis considering growth rates as function of PFT, light regime and diameter range might find significant differences between groups. The data set of PSP is not appropriate for this analysis for several reasons. Time between two enumerations was 5 y in most cases, and thus light regimes might change extremely within this time step. Low growth rates of early successional spp. in Garinono can be explained with the high density of this stands (basal area BA = 31.3 m^2 ha^{-1}, all other stands BA < 30 m^2 ha^{-1}). Thus, average light regimes might have suppressed growth of early successional spp. Plotting frequency distribution of diameter increment data for different successional status is another possibility to gain comprehensive information (not shown). It can be seen, in individuals showing high diameter increment rates, that early successionals had the highest share, late successional species the lowest.

Data of photosynthesis measurement for testing our PFTs are rare (Eschenbach et al. 1998) or not appropriate to our problems (Moad (1992) measured only photosynthesis of dipterocarp seedlings, all belonging to PFTs 12 and 13 in our concept and thus giving no information about differences between PFTs; the measurements of Koyama (1981) were on excised leaves). Testing of nine species against photosynthesis data of Eschenbach et al. (1998) supported that early successional species have a higher saturation point in photoproduction. From the nine measured species, one was an early, six mid, and two were late successional species. Their average maximum assimilation rates (ranges in parentheses) were 19.4, 9.3 (5.7–16.7) and 6.8 (6.8) μmol m^{-2} s^{-1} respectively estimated by fitting a rectangular hyperbola (Thornley 1976). Recent research on the relationship of photosynthesis characteristics and asymptotic tree heights (Thomas & Bazzaz 1999) found significant differences in photosynthetic production for trees of the same successional status but with different maximum heights.

As a last test of the classification of successional status we analyse mortality rates measured in PSPs. The average annual

Table 3.4: Diameter increment rates [mm y^{-1}] for different successional status SS (early (1), mid (2) and late (3) successional spp.). N: sample size. P-values of χ^2-test.

Location	SS 1	 2	 3	N	χ^2	P
Garinono	3.3	4.1	2.8	7694	0.33	0.85
Sepilok	4.8	3.9	2.9	6435	0.43	0.81
Segaliud Lokan1	5.0	4.9	4.2	6132	0.11	0.95
Segaliud Lokan2	6.6	5.4	4.6	2213	0.47	0.79

Table 3.5: Average annual mortality rates [% y^{-1}] for different successional status SS (A: early (1), mid (2) and late (3) successional spp.). Sample size see Table 3.4. P-values of χ^2-test. B only distinguishes between early (1) and non-early (4) successional spp.

Location	mean	A SG 1	 2	 3	 χ^2	 P	B SG 4	 χ^2	 P
Garinono	2.6	3.8	1.9	2.7	0.75	0.69	3.2	0.68	0.41
Sepilok	5.1	6.6	4.7	7.5	1.6	0.45	5.0	2.68	0.10
Segaliud Lokan1	5.1	8.4	4.4	3.9	2.54	0.28	6.4	2.48	0.12
Segaliud Lokan2	6.3	9.8	3.4	2.9	5.15	0.08	4.8	2.24	0.13

mortality rates differ in the different PSPs (Garinono: 2.6 % y^{-1}; Segaliud Lokan1: 5.1 % y^{-1}; Segaliud Lokan2: 6.3 % y^{-1} and Sepilok: 5.1 % y^{-1}) and over time, indicating changes with dry years as observed in Sabah in 1982/83 (Walsh 1996). Mortality is unexpectedly high in all observations, compared to normally observed annual mortality rates of 1–2 % y^{-1} in tropical rain forests (e.g. Manokaran & Swaine 1994). Mortality rates decline from early to late successional species in the two areas in Segaliud Lokan, whereas in Garinono and Sepilok, beside highest mortality rates in early successional spp., mid-successionals have lowest rates (Table 3.5A). The grouping might not resolve the differences between mid- and late successional species easily. However, differences between early and non-early successional spp. are seen clearly (Table 3.5B). Differences between groups increase as analysis is focused on two groups only.

The discussion (by Hubbell et al. (1999)) about recruitment limitations and abundances of seedling in canopy gaps cannot be broadened to include our concepts yet, because data available on recruitment patterns (FMU inventories) lack information on canopy structure.

Table 3.6: Average annual mortality rates [% y^{-1}] of mid- and late successional spp. for different height groups (shrubs (1), understorey(2), lower main canopy (3), upper main canopy(4) and emergent (5)). N: sample size. P-values of χ^2-test.

Location	mean	Height group 1	2	3	4	5	N	χ^2	P
Garinono	2.0	3.4	3.0	1.6	1.6	0.9	4867	2.28	0.68
Sepilok	5.0	9.2	7.0	4.1	4.4	4.3	5825	4.63	0.33
Segaliud Lokan1	4.4	6.2	3.7	2.9	3.4	4.9	4752	1.69	0.79
Segaliud Lokan2	3.3	6.3	3.6	2.7	3.5	2.9	952	38.05	0.56

Maximum potential height

Because the list underlying our classification concentrates on tree species it is not surprising to find very few shrub species in it. In our context, missing shrubs are unimportant. It might be necessary, however, to consider those shrubs for analysis of slash-and-burn-techniques practised by indigenous people (Whitmore 1998).

The height limits chosen were already used (with small differences) in the FORMIX3 model (Huth et al. 1998; Ditzer et al. 2000). Thus, model application and former data analysis have shown them to be very practical. Nevertheless, one might define a different number of height groups at different height limits.

As some verification of the height group classification we again analyse trends in the mortality rates for different groups. We only consider differences between height groups of mid and late successional species, knowing that early successional species have higher mortality rates. Taller-growing trees, in general, should have longer life-times than shorter-growing trees (Manokaran & Swaine 1994). This tendency is found in their mortality rates (Table 3.6), although differences from the average are not significant (χ^2 test; $P > 0.3$). Again the test verifies our classification.

It should be noted finally that any PFTs defined lie on a continuum and dividing it up is a matter of convenience based on arbitrary divisions.

Plant functional types

In previous model applications (Huth et al. 1998; Köhler & Huth 1998a; Ditzer et al. 2000) the non-existence of a principal approach to grouping has been a crucial point. Thus, within only five groups, which were distinguished by maximum tree heights, one contained all early successional species. This implied that all mid or late successional species with similar maximum heights were grouped to slightly incorrect height groups. From this experience, the optimal number of derived PFTs was between 10 and 20. At the upper end, parametrization already becomes difficult, but modelling the complex system of the tropical rain forest with less than ten PFTs might include assumptions leading to biased results.

Conclusions

We presented a generic concept for the aggregation of tree species into plant functional types which can be applied to forests in different regions. The concept was developed in the context of process-based modelling of forest dynamics and therefore was focused on criteria which are essentially influencing tree growth in the models FORMIX3 and FORMIND: successional status and potential height. In the application for Sabah's lowland rain forests successional status was classified into three groups, potential height into five groups. Thirteen plant functional types in total were distinguished for this application, a number which we consider as very practical for further forest growth analysis. Within this concept it is and will be difficult to rely on published data sets for all species in this respect. In this case it is important to test the classification with all available field data. We have shown different possibilities for testing using field data on diameter increment, mortality rates, photosynthesis production and wood densities.

As a consequence of the final PFTs derived in this paper a new parametrization of the forest growth models FORMIX3 and FORMIND will be elaborated. Simulations and model analysis with the new parametrization will show whether and in what ways the quality and accuracy of the results are improved.

Acknowledgements

We would like to thank all members of the Malaysian–German Sustainable Forest Management Project, and the Forest Research Center, Sandakan, Sabah, Malaysia, responsible for data collection, for their kind cooperation, especially M. Rundi for sharing his knowledge on the successional status of trees, R. Ong and M. Kleine for making data available for us and R. Glauner for information on height-to-diameter-relations. We also owe a debt of gratitude to D. Newbery and an anonymous reviewer for very helpful comments on a former version of the manuscript. Thanks to L. Kammesheidt for critical reading.

Additional remarks, not included in the article

We think that the aggregation of tree species to plant functional types is absolutely necessary in the modelling of tropical forest dynamics. In the meantime a model called FORMOSAIC was developed (Liu & Ashton 1998, 1999), which tried to quantify the dynamic of species richness for the large and long-term research area of Pasoh, Malaysia (50 ha, inventoried for now 15 years). The approach of FORMOSAIC was to model the dynamic of individual species, but the abundance of many of these tree species was too low - even in this area of 50 ha - to gain statistically well supported results for recruitment, growth and mortality.

Simultaneously to the development of our grouping concept different approaches were proposed for tropical rain forest in Ghana, Africa (Atta-Boateng & Moser 1998), Australia (Gitay et al. 1999) and Kalimantan, Indonesian Borneo (Phillips et al. 2000). The first approach was focused on commercial tree species and based on typical diameter increment rates with the emphasis on model construction. In the second case, various theoretical considerations about principle differences of ecological characteristics, which might be used for the identification of plant functional groups were discussed (Pillar 1999; Weiher et al. 1999). To identify timber groups was the main targets in the species grouping in Indonesia. However, application and validation possibilities of the concepts were also of central interest (McIntyre et al. 1999b). More general considerations concerning different applications in global vegetation models and for analysing field data were found in a special issue of *Journal of Vegetation Science* (McIntyre et al. 1999a) and in the standard text book of Smith and colleagues (Smith et al. 1997).

Chapter 4

The model FORMIND2.0

Because model descriptions in articles need to be very brief, a complete description of the model used is contained in this chapter.

An individual-oriented cohort model (Uchmański & Grimm 1996) is described, which is able to simulate growth dynamics in mixed tropical rain forests. The model includes all important growth processes. Thus, the model can be applied to different rain forest sites, if parametrisation is adapted to specific conditions. After some more general thoughts about models, the principles of the modelling approach are described. Spatial and temporal resolutions are described. Individual physiological submodel and their mathematical implementations are explained in detail. Following this, the main differences to a former version of FORMIND (Köhler 1996; Köhler & Huth 1998a, 1998b) are discussed. Similar features of various versions of the model FORMIX3 (Ditzer et al. 2000; Huth & Ditzer 2000a) are also mentioned. A discussion of the chosen model approach closes the chapter.

General concepts about models

One of the basic approaches in physics is the description of physical phenomena with mathematical models.

Modelling of ecological systems uses a similar approach. A system is described with a model, which initially might be verbal describing main interactions. However, to obtain quantitative answers to questions of interest, mathematical equations are needed. From the first more general description of interactions, qualitative conclusions about modelled systems can be drawn. Two general types of models can be distinguished: Those describing behaviour and those explaining the system. Descriptive models try to match system behaviour with model behaviour. Very often regression functions are used in this context. Explanatory models try to extract essential structures of the system correctly and rebuild them in the model. The advantage of the latter approach is the possibility to study systems with different environmental conditions (Bossel 1992).

Often models describe very complex systems. Thus, it is necessary to reduce the number of modelled processes. One inevitably has to make simplifying assumptions which will not enable all possible questions to be answered with the same modelling approach.

To gain an overview over the quality of a model, several criteria in respect to the aim of modelling should be fulfilled. The dynamic behaviour of the model should qualitatively fit to that of the real system. Numerical and logical model results should correspond to those of the original if environmental or boundary conditions are comparable. Differences should be explainable through assumptions made during model building. Simulation results should be useful with respect to potential applications of the model and with respect to the aim of modelling.

Basic structure of model

In the following section spatial and temporal resolutions are described. Furthermore, the technical realisation of the model as an individual-oriented cohort model is explained.

The individual-oriented approach

Individual-based modelling is one of the main concepts in recent theoretical ecology (DeAngelis & Gross 1992; Judson 1994; Liu & Ashton 1995; Grimm 1999; Lett et al. 1999; Haefner & Dugaw 2000). However, there are various researchers who emphasize the importance of different modelling approaches. Thus, it is desirable to combine the advantages of different concepts (Bolker et al. 1997; Uchmański & Grimm 1996). Advantages of individual-based modelling with those of the cohort approach (Vanclay 1994) are optimised and unified in the current study. Thus, our approach is called *individual-oriented* according to the rather narrow definition of Uchmański & Grimm (1996).

The biological criteria, which underlie this classification of different approaches are as follows (Uchmański & Grimm 1996):

1. the degree to which complexity of individual's life cycles is reflected in the model;
2. whether or not the dynamics of the resources (e.g. food, space) is explicitly taken into account;
3. the use of numbers of individuals or densities in representing the size of populations; and
4. the extent to which variability of individuals of the same age is considered.

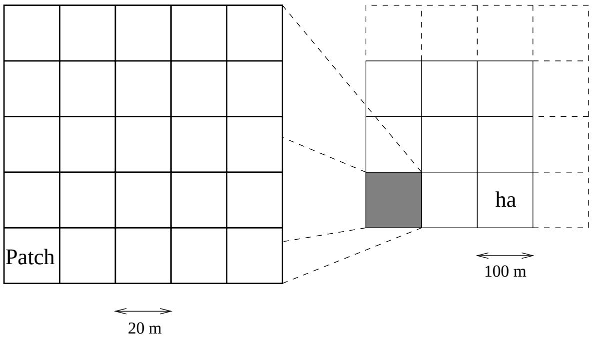

Figure 4.1: Spatial resolution of simulated area.

FORMIND2.0 uses simple assumptions concerning nutrient and water cycles. For higher computing efficiency, small individuals are packed together into cohorts. Thus, models are highly flexible because cohorts can be added and removed easily. According to Vanclay (1994) the three main components of tree growth are modelled in the following way within a cohort model:

1. Diameter increment is modelled by incrementing the size of a representative tree;
2. mortality is simulated by reducing the expansion factor (the number of trees represented by each cohort); and
3. recruitment is accommodated by initiating new cohorts from time to time.

Within one cohort the growth of one tree is modelled, which interacts through complex functional relationships with trees of its own and the other cohorts.

A strict individual-based model corresponds to a cohort model with an expansion factor of one. Aggregating trees to cohorts is an effective optimisation of computing time. For initialisation, trees of the same species group, same commercial status and within the same spatial subunit are aggregated into cohorts in diameter classes of 5 cm. Within the cohorts of the small trees

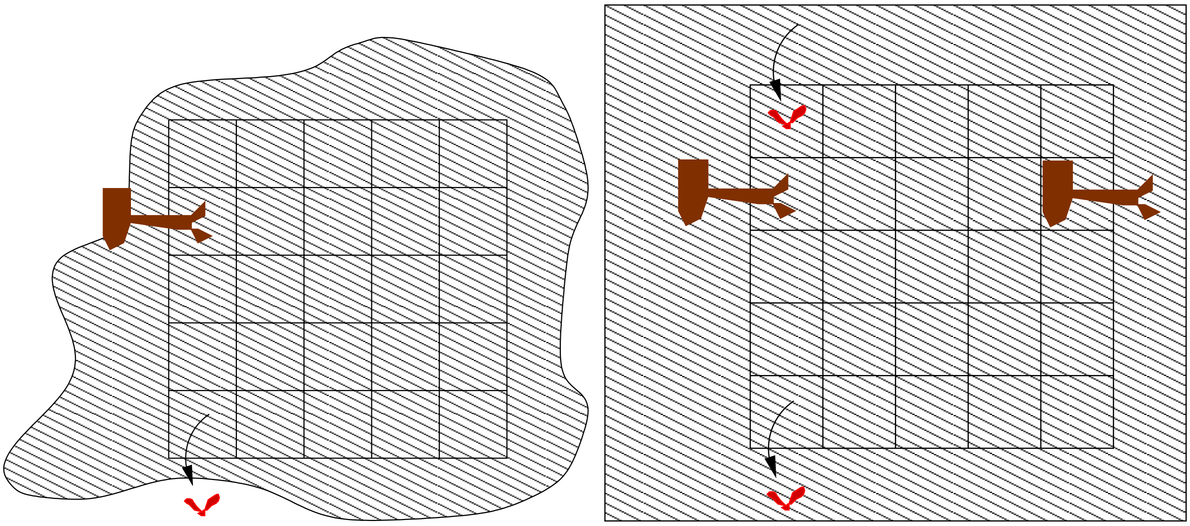

Figure 4.2: Different boundary conditions and their ecological meaning. Left: Open boundaries represent a highly fragmented situation. Right: With periodic boundaries the simulated area is assumed to be surrounded by similar forest structure. Falling trees and seed dispersal are shown as possible interlinking processes between neighbouring patches.

some hundred individuals might be packed together. In general, trees with a diameter larger than 20 cm are simulated individually as a result of mortality and self-thinning.

Spatial resolution

A simulation area of one hectare of rain forest is divided into 5 × 5 subareas (so-called *patches*), each 20 m × 20 m in size (Fig. 4.1). Within the patches trees do not have explicit positions. This corresponds to the spatial resolution of available inventory data and has been proven practical in various different so-called gap models for temperate forests (Botkin et al. 1972; Shugart 1984, 1998; overview at recent applications in Liu & Ashton 1995). In recent years spatial explicit rain forest models have been developed (Liu & Ashton 1998; Chave 1999b; van Gardingen & Phillips 1999), but they all use much simpler formulations for describing tree growth compared to FORMIND2.0.

All individuals in one patch are considered as direct neighbours and compete for light and space. Interlinking processes between neighbouring patches are the falling of trees and an explicit modelling of seed dispersal. In a third minor interacting process, crowns of large trees might extend into neighbouring areas if they exceed the size of their own patch.

We distinguish between open and periodic (or toroidal) boundary conditions. Open boundaries correspond to forest islands in a heavily fragmented landscape. Thus, e.g. seed dispersal leaving the simulation area will get lost. We do not consider any migration effects, which might enter simulation in open boundaries. Periodic boundaries assume the area of interest to be embedded in a larger area of similar structure. Any action leaving the simulation area will thus enter it on the opposite side (Fig. 4.2).

Several field inventories were performed with the same spatial resolution of 400 m^2. Distribution of trees to single patches was thus easily possible. In other cases only average tree densities, without spatial information, was recorded. In the later case, trees are randomly distributed into single patches.

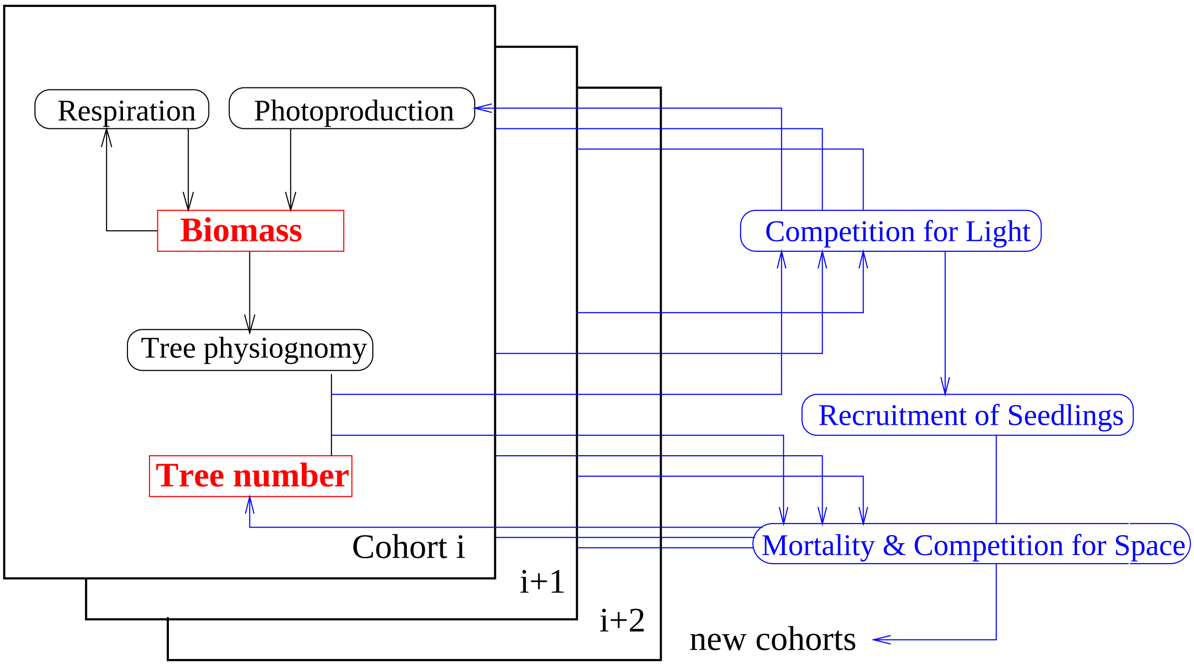

Figure 4.3: Overview of the interactions of the submodels and the dependencies on the main variables biomass B and tree number N. Arrows indicate whether the results of a submodel influence the calculations of another submodel.

Temporal resolution

Temporal resolution is of importance in dynamic models, as accuracy of modelled processes, numerical solution of differential equations and computing time depend on it.

Various forest growth models include yearly and daily variations in sun angle in their description of light conditions (e.g. TREEDYN3, cf. Bossel 1994). Rain forest growth models in general do not consider a temporal resolution smaller than a year for other than numerical reasons (Vanclay 1994). This is possible because of relatively small variations of daily and seasonal parameters. Day length changes only slightly within a year, dusk and dawn are very short, irradiance is mostly diffuse and not direct as a result of rainy and cloudy weather conditions (Schlensog 1997). Data for a validation of a more detailed description of processes like photosynthesis are not available. Furthermore, all relevant data of basic processes (growth, mortality, recruitment) are very rarely measured with a resolution below one year. Therefore, a temporal resolution of $\mathrm{d}t = 1$ y is chosen here. Solving the system of differential equations with $\mathrm{d}t = 1$ y will lead in most cases to minor, inrelevant, numerical errors (investigated in Köhler 1996). $\mathrm{d}t$ is critical for the numerical solution only for small trees and will be reduced in this case (explained after model description).

Description of plant-physiological submodels

The model is divided into the submodels

- tree physiognomy,
- light competition,
- tree growth (photosynthesis, respiration),
- mortality and spatial competition, and
- recruitment.

An overview on interactions between different submodels and the main variables *biomass* and *tree number* within one cohort can be seen in Fig. 4.3. Photoproduction and respiration are calculated for individual trees. They change their biomass. Tree physiognomic assumptions allow transforming biomass into various other variables like diameter, tree height, leaf area, crown dimensions, and bole volume. Light competition and mortality are interacting processes between trees of the same and different cohorts, and they directly affect individual photoproduction and tree number, respectively. Competition for light regulates, via available irradiance at the forest floor, potential recruitment of seedlings. New recruits will be added to a new cohort.

In the following, parameters with indices s or h depend on species grouping as outlined in Chapter 3, specifically on successional behaviour or maximum tree height, respectively. Parametrisations for different sites are found in the corresponding Chapters 5–8. Variables are calculated for each cohort i.

Tree physiognomy

For calculating competition processes and growth variables such as stem diameter d_i, height h_i, crown length c_i and crown projection area f_i are required (Fig. 4.4). They can be calculated from biomass B_i as follows.

The stem of each tree is assumed to be of conical shape. Its aboveground biomass B_i is calculated via

$$B_i = \frac{\pi}{4} d_i^2 \cdot h_i(d_i) \cdot \frac{\rho_s \cdot \gamma_i(d_i)}{\tau}. \qquad (4.1)$$

with ρ_s: wood density, γ_i: form factor, and τ: fraction of stem biomass to total aboveground biomass. Several field studies in South-East Asia (Kato et al. 1978; Yamakura et al. 1986) indicate a relation between τ and tree height for reference size d_{120} (d =120 cm) at a certain site, also called site index (Ditzer 1999, Fig. 4.5):

$$\tau = \tau_1 + \tau_2 \cdot h(d_{120}), \qquad (4.2)$$

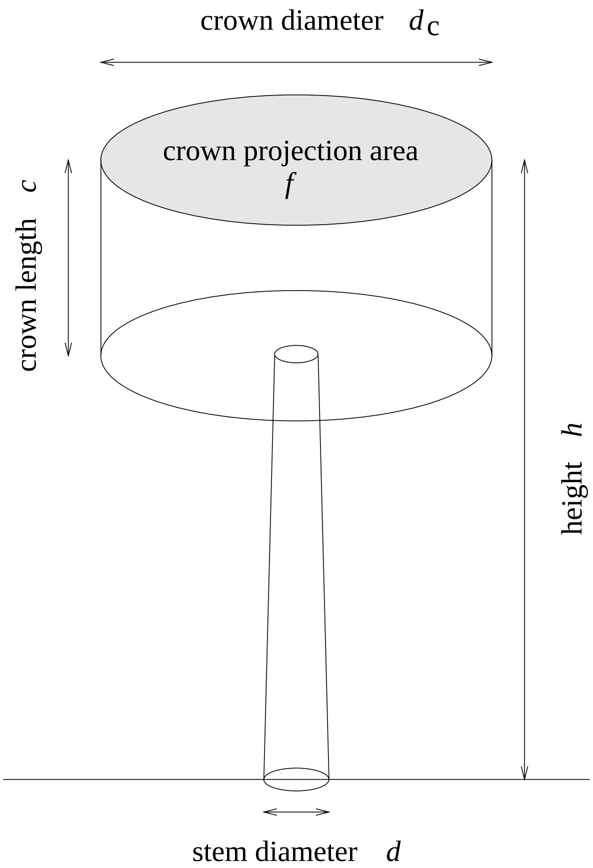

Figure 4.4: A typical tree of the model is shown including the relevant physiognomic dimensions. Stem diameter is measured at breast height (h = 1.3 m.)

τ_1, τ_2: parameters. For sites in South-America we take average values for τ.

A form factor γ_i covers differences of conical stem from a cylindric form (Fig. 4.6A):

$$\gamma_i = \gamma_0 \cdot exp(\gamma_1 \cdot d_i^{\gamma_2}), \qquad (4.3)$$

γ_0, γ_1, and γ_2: parameters.

Tree height h_i is calculated from diameter (Fig. 4.6B).

$$h_i = \frac{d_i}{\frac{1}{h_{0h}} + \frac{d_i}{h_{1h}}}, \qquad (4.4)$$

h_{0h}, and h_{1h}: parameters.

A tree in the model has a cylindrical crown shape. Its crown diameter d_{ci} is calculated from stem diameter:

$$d_\mathrm{c} = (f_0 + f_1 \cdot d^{f_2}) \cdot d, \qquad (4.5)$$

and its circular crown projections area f_i follows from crown diameter ($f_i = \frac{\pi}{4} d_{\mathrm{c}i}^2$), with f_0, f_1, and f_2: parameters.

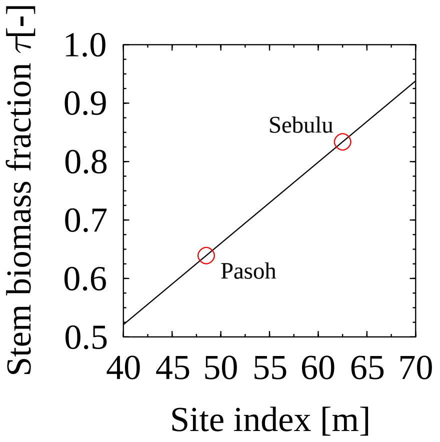

Figure 4.5: Depending of stem wood fraction τ on site index. Field data were taken in Pasoh (Kato et al. 1978) and Sebulu (Yamakura et al. 1986).

Total leaf area l_i of one tree i is a function of stem diameter d_i with an upper threshold LAI_M to avoid unrealistic high values (Ashton 1978).

$$l_i = \max \begin{cases} l_1 \cdot d_i + l_2 \cdot d_i^2 + l_3 \cdot d_i^3 \\ LAI_\mathrm{M} \cdot f_i \end{cases} \tag{4.6}$$

Thus, leaf area index LAI_i of an individual tree is obtained from total leaf area l_I divided by crown projection area (Fig. 4.6AC):

$$LAI_i = \frac{l_i}{f_i} \tag{4.7}$$

Crown length c_i is proportional to tree height h_i (Burgess 1961; Poker 1993):

$$c_i = c_\mathrm{P} \cdot h_i, \tag{4.8}$$

c_P: parameter.

Stem volume V_i can be calculated out of biomass using τ and ρ_s ($V_i = \tau / \rho_s \cdot B_i$). For growth and yield studies only the volume $V_{\mathrm{b}i}$ below the crown is of interest (called bole volume). Using geometric relations of for the frustum of a cone (Bronstein & Semendjajew 1991; Ditzer 1999) $V_{\mathrm{b}i}$ is calculated as:

$$V_{\mathrm{b}i} = \frac{1}{3f_i}(1 + x_i + x_i^2)(1 - c_\mathrm{P})V_i, \tag{4.9}$$

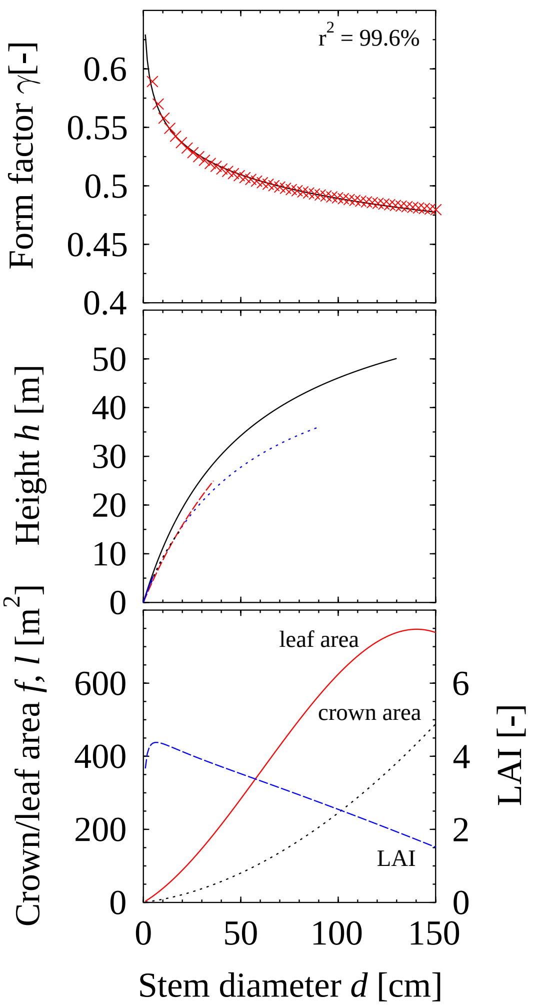

Figure 4.6: Functions depending on stem diameter plotted for parametrisation of Sabah, Malaysia. Top: Form factor $\gamma(d)$ (Kato et al. 1978; Yamakura et al. 1986). Middle: Height-to-diameter-relations $h(d)$. Height is only plotted for achievable diameters of different height groups (Forestal-International-Limited 1973; Köhler 1998). Bottom: Leaf area $l(d)$ (closed line), crown projection area $f(d)$ (broken line), and leaf area index $LAI(d)$ (dotted line) (Kato et al. 1978; Yamakura et al. 1986).

with

$$x_i = 1 - (1 - c_\mathrm{p}) \left(\frac{3}{2} - \sqrt{3 f_i - \frac{3}{4}} \right). \tag{4.10}$$

Light competition

Knowledge about the distribution of leaf area within the canopy is necessary for calculating the light climate in a patch. The description of a single tree crown was already given in the previous subsection.

In a vertical direction the canopy is divided with equidistant steps of the width Δz in a finite number of layers. It is now necessary to calculate which leaf areas are found in the various layers between z and $z + \Delta z$ (called z in the following). It is assumed that leaves are distributed homogeneously within the tree crown.

The contribution of each cohort i to crown coverage $F(z)$ of the layer z is calculated out of stem number N_i and the crown projection area f_i of an individual tree normalised to patch area A:

$$F(z) = \sum_i \left(N_i \cdot \frac{f_i}{A} \right), \text{ for some } i. \qquad (4.11)$$

The leaf area L of layer z follows from the summation of all leaf area indices $LAI_i(z)$ of cohorts belonging to layer z multiplied with their crown coverage :

$$L(z) = \sum_i \left(N_i \cdot \frac{f_i}{A} \cdot LAI_i(z) \right), \text{ for some } i. \qquad (4.12)$$

Now, for each individual tree i the leaf area L_i has to be calculated, which is found above its crown and which partially absorbs the incoming irradiance:

$$L_i = \sum_z L(z), \qquad \text{with } z > h_i. \qquad (4.13)$$

Tree growth

For the determination of changes in biomass first

- photosynthetic production, then
- respiration

is calculated.

Photosynthetic production

Photosynthetic production is based on the work of Monsi & Saeki (1953). Incoming irradiance is partially absorbed in the canopy as a function of total leaf area index L. Photosynthetic Active Radiation (PAR) is frequency dependent and called irradiance or light intensity I in the following.

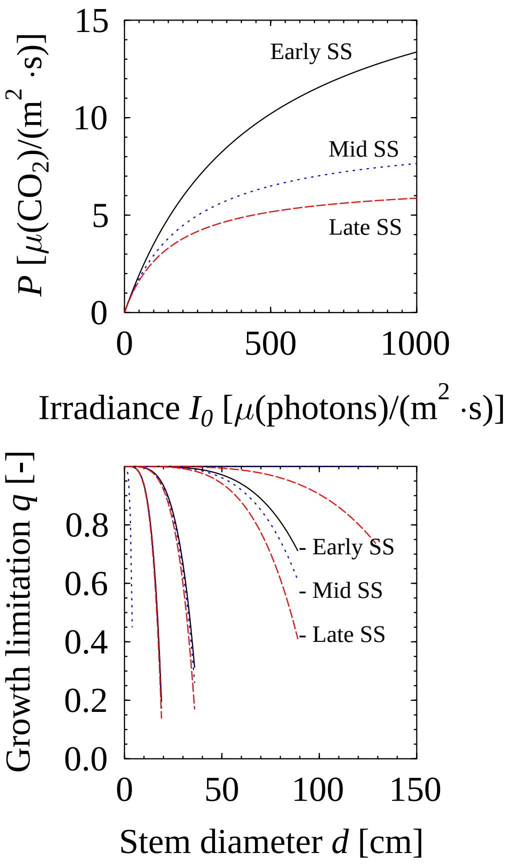

Figure 4.7: Functional dependencies of tree growth at the site Sabah, Malaysia. Top: Light response curve (Eschenbach et al. 1998). Bottom: Growth limitation. For each of the 13 plant functional types one graph is plotted. Height groups have different maximum diameter. For one height group graphs are labelled according to their successional status.

The light response curve of photosynthesis P_i is of Michaelis-Menten type, a typical saturation relationship between light intensity and production:

$$P_i(I_i) = \frac{\alpha_s \cdot I_i}{1 + \frac{\alpha_s}{P_{\mathrm{M}s}} I_i}, \qquad (4.14)$$

with $P_{\mathrm{M}s}$ as maximum photoproduction at saturation, and α_s as quantum use efficiency.

Within the canopy vertical light absorption after the law of Beer-Lambert (Gerthsen et al. 1989) is assumed (Fig. 4.7A):

$$I_i(L_i) = I_{0y} \cdot \mathrm{e}^{-k \cdot L_i}. \qquad (4.15)$$

Individual available light I_i of each tree, as function of its total leaf area index above tree crown L_i, is calculated. I_{0y} corresponds to average light intensity of the photoactive time of day, taking seasonal differences into account. Absorption coefficient k is estimated out of detailed field studies about the microclimate of light within tropical forests (Kira & Yoda 1989).

Actual photoproduction $\tilde{P}_i$ is calculated by integrating P_i over the shading canopy under the assumption of totally closed canopy layers:

$$\tilde{P}_i = \int_0^{L_i} P_i(I_i(L))\mathrm{d}L. \qquad (4.16)$$

Solving the integral (Eq. 4.16) leads to:

$$\tilde{P}_i = \frac{P_{\mathrm{M}s}}{k} ln \frac{\alpha_s k I_i + P_{\mathrm{M}_s}(1-m)}{\alpha_s k I_i e^{(-kLAI_i)} + P_{\mathrm{M}s}(1-m)}, \qquad (4.17)$$

with m as transmission coefficient of the leaves (Thornley 1976).

Different length of wet/dry seasons S_{Sy} and seasonal dependent length of photoactive daytime S_{Dy} determine length of photoactive time and thus contribute to the photoproduction.

Furthermore, a size-dependent growth limitation q caused by water transport deficits is assumed (Fig. 4.7B). Limitation is chosen in a way that trees will stop growing if they reach their maximum diameters D_{M} (Ditzer 1999). Other models incorporate similar limitation factors, but call them age limitation (as done for c_s in Landsberg & Waring 1997):

$$q = 1 - (1 - q_{D_{\mathrm{M}}}) \cdot (\frac{d_i}{D_{\mathrm{M}}})^2 \qquad (4.18)$$

Parameter $q_{D_{\mathrm{M}}}$ corresponds to growth limitation at maximum diameter and is calculated internally from the following condition:

$$\frac{\mathrm{d}d(D_{\mathrm{M}})}{\mathrm{d}t} = 0 \qquad (4.19)$$

Respiration

All biomass losses are summed up under what we call respiration. They are composed of root decay, litter-fall and respiration of tree organs and leaves at night. Daily leaf respiration is implicitly included in the light response curve (Eq. 4.16).

We distinguish between a biomass-dependent maintenance respiration $R_{\mathrm{m}i}$ (Kira 1978; Yoda 1983), and growth respiration $R_{\mathrm{g}i}$, depending on actual photoproduction.

$$R_{\mathrm{m}i} = r_{0s} \cdot B_i^{2/3} + r_{1s} \cdot B_i, \qquad (4.20)$$

r_{0s} and r_{1s}: parameters,

$$R_{\mathrm{g}i} = R_{\mathrm{G}} \cdot q_i \cdot \tilde{P}_i, \qquad (4.21)$$

R_{G}: parameter. Details on respiration are found in the work of Ditzer (Ditzer 1999; Ditzer et al. 2000).

Changes in biomass

With our assumptions concerning photosynthesis and respiration the time dependent changes in biomass are calculated as follows in our main growth equation:

$$\frac{\mathrm{d}B_i}{\mathrm{d}t} = \tilde{P}_i \cdot q(1 - R_{\mathrm{G}}) - R_{\mathrm{m}i} \qquad (4.22)$$

Mortality and spatial competition

Tree mortality in undisturbed tropical rain forest lies on average between 1 and 3 % per year (Swaine 1989; Phillips & Gentry 1994; Condit et al. 1995b; van der Meer & Bongers 1996).

Different types of mortality are included in the model.

Normal mortality: If field data indicate functional relationships between tree mortality and tree size $M_{\mathrm{D}} = f(d)$ (Okuda et al. 1997), or diameter growth $M_{\mathrm{I}} = f(d_{\mathrm{inc}})$

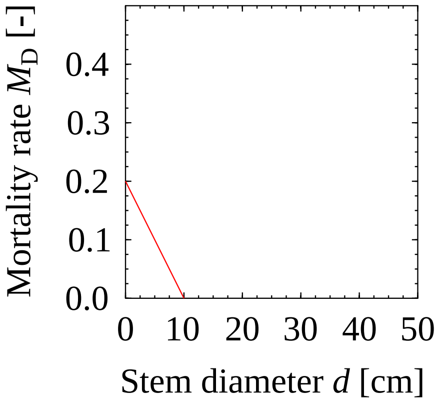

Figure 4.8: Size-depending mortality rate M_D at the site Sabah, Malaysia. For trees with a diameter $d > 10cm$ $M_\mathrm{D} = 0$.

(Swaine 1989) they can be added to the basic mortality $M_{\mathrm{B}s,h}$. Well known significant differences in mortality rates between different successional status and maximum tree height are covered in M_B. Thus, early successionals have shorter lifetimes, and tree mortality is lower in high growing trees. The basic equation for mortality rates is

$$M_i = M_{\mathrm{B}s,h} + M_\mathrm{D} + M_\mathrm{I}. \qquad (4.23)$$

Mortality of small trees is significantly higher than average (Fig. 4.8):

$$M_\mathrm{D} = \left\{ \begin{array}{lcl} M_\mathrm{D0} - M_\mathrm{D0}/M_\mathrm{D1} \cdot d & : & d < M_\mathrm{D1} \\ 0 & : & \text{else} \end{array} \right. \qquad (4.24)$$

M_D0, and M_D1: parameters. In a field study in Pasoh, Malaysia mortality of seedlings reached up to 20 % y^{-1} (Okuda et al. 1997).

Functional relationships of mortality and diameter increment are not used in the present applications ($M_\mathrm{I} = 0$).

Falling trees: Gap creation through falling large trees plays an important role in rain forest dynamics and contributes significantly to mortality rates. In a field study in South America 90 % of total mortality was caused by falling trees (van der Meer & Bongers 1996).

Dying trees with a diameter $d \geq 10$ cm can fall over (probability W) and create gaps of different sizes in neighbouring patches. The number of trees N_F destroyed from total number N_p in target patch p is calculated from crown projection area f_F of the falling tree relative to patch size A:

$$N_\mathrm{F} = N_p \frac{f_\mathrm{F}}{A}, \qquad (4.25)$$

Individuals are chosen randomly with the restriction that only trees smaller than the one falling can be destroyed, and contribute with different $N_{\mathrm{F}i}$ to tree losses in the cohorts of target patch.

Self-thinning: In sites with a high tree density, mortality is significantly increased. This phenomenon is called self-thinning. In the model N_T trees in patches with crown closure ($F(z) > 1$) are randomly extracted until crown coverage $F(z)$ decreases below its maximum value of 1.0.

As second main equation covering changes in tree numbers of each cohort we obtain:

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = -(M_i \cdot N_i + N_{\mathrm{T}i} + N_{\mathrm{F}i}). \qquad (4.26)$$

In cohorts with high tree numbers ($N_i \geq 100$) and small individuals (d <10 cm) deterministic mortality takes place. Thus, mortality rate M_i corresponds to the number of trees dying each year. In all other cases ($N_i < 100$, or $d \geq$10 cm) mortality is determined stochastically, and M_i represents the probability of each tree dying.

Recruitment

Recruitment is modelled with a seed pool. For input of new seeds into the pool two different recruitment mechanisms were incorporated in the model.

(1) Scenario **seed pool**: The simplest approach consists of assuming that an intact forest surrounding the simulation area is supporting a constant seed input rate $N_{\mathrm{S}s}$ within the simulated patches.

(2) Scenario **seed tree**: The second approach takes into account the dispersal of

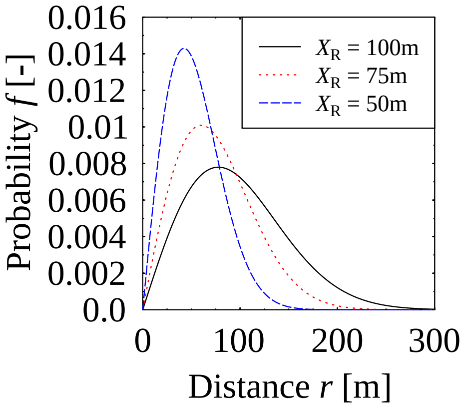

Figure 4.9: Seeds dispersal kernels for a Gaussian distribution with different average dispersal distances X_{R}. Crown diameter was fixed at c_d=20 m.

seeds produced within each patch from local parent trees, which are trees exceeding a certain diameter $D_{\mathrm{R}h}$. Recruitment strategies are highly variable in rain forests, with interspecific differences in the fruiting period, seed sizes varying in a six-fold range (Westoby, 1995), dispersal strategies, dispersal agents, dispersal distances, seed survival, germination probabilities and maturing size of seed dispersers (Denslow 1987; Garwood 1983; Whitmore 1983). Thus, some fundamental assumptions on the most important trends have to be drawn.

Flowering, fruiting and seed production vary in duration and frequency across species, some species fruiting after several years of unfecundity (Garwood 1983). Other species flower and fruit continually throughout the year in Malaysian rain forests (Putz 1979). Seasonal differences in seed production are not taken into consideration.

The rate of seed production $N_{\mathrm{R}s}$ varies widely among species (Whitmore 1998). Various studies have analysed different dispersal strategies and lengths (review in Clark et al. 1999b). A major result is that migration velocity found in paleoecological records can only be explained with a seed dispersal kernel which allows a reasonable amount of seed establishments far away from the mother tree (Clark 1998; Clark et al. 1998a)].

Different dispersal agents (e.g. wind, birds, mammals) are not directly distinguished in our model, but the resulting average dispersal distance $X_{\mathrm{R}s}$ depends upon the tree species and should match with the parameter set. From the dispersal kernels discussed by Clark et al. (1999) we use the Gaussian distribution (as used by Chave 1999b). Assuming rotation symmetry, the probability density f of seeds to be dispersed at the distance r from the mother tree is

$$f(r) = \frac{2r}{(X_{\mathrm{R}} + c_d/2)^2} \exp\left(-\frac{r^2}{(X_{\mathrm{R}} + c_d/2)^2}\right), \tag{4.27}$$

with c_d, the crown diameter (see Fig. 4.9). Thus, 99% of the seeds are dispersed in a distance less than $2.14\times(X_{\mathrm{R}}+c_d/2)$. The actual dispersal distance r is randomly drawn from this probability distribution, and the direction is drawn uniformly. The resulting seed shadow is the product of the rate of seed production and the dispersal kernel (Clark et al. 1999b).

For both recruitment mechanisms, incoming seeds will be added to a seed pool, taking into account the average seed mortality rate $M_{\mathrm{S}s}$ across functional groups (cf. Garwood 1983, 1989). These seeds correspond to the reproductive success and are those which can potentially be established as seedlings at the minimum diameter of 1 cm (Ribbens et al. 1994; Chave 1999b). Seed loss due to predators is implicitly included in relative low seed production rates. The actual seed germination depends upon

- a minimum light intensity at the forest floor $I_{\mathrm{F}} \geq I_{\mathrm{S}s}$ (Whitmore 1998), and
- a not fully closed lowest canopy layer.

If conditions for ingrowth are fulfilled additional cohorts are created. The state variables biomass B_i and tree number N_i are initialised with biomass corresponding to seedlings diameter D_S and number of seeds of PFT available for ingrowth in seed pool of current patch.

Main differential equations

Finally, resulting differential equations are explained in detail:

For each patch $l(l = 1, ..., m)$ a certain number n of time (t) dependent cohorts $i(i = 1, ..., n(l,t))$ exist. For each cohort i, changes in above-ground biomass $B_{i,l}(t)$ of an individual tree and number of trees $N_{i,l}(t)$ belonging to that cohort are calculated.

$$\frac{\mathrm{d}B_i}{\mathrm{d}t} = \tilde{P}_i \cdot q(1 - R_\mathrm{G}) - R_{\mathrm{m}i}$$
$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = -(M_i \cdot N_i + N_{\mathrm{T}i} + N_{\mathrm{F}i})$$

These equations are a system of $2 \times m \times n(l,t)$ coupled ordinary integro-differential equations, which are not solvable with analytic methods. Equations are coupled through the interactions of trees of same and different cohorts and patches. They can be called integro-differential equations, because a differentiation over time and an integration over leaf area (as function of biomass) are incorporated.

For numerical solutions of the system of equations an Euler-Cauchy algorithm is used with time step $\mathrm{d}t$ of one year. The solution of the first equation $(\frac{\mathrm{d}B_i}{\mathrm{d}t})$ is critical for small B_i. Therefore, for small trees $(B_i < 1\ \mathrm{t})$ $\mathrm{d}t$ is reduced to $\mathrm{d}t = 0.01$ y.

The model was coded in C++ using the simulation software XSiSi/SiSi, which was developed in Kassel (http://www.usf.uni-kassel.de/ reinhard/sisi). Simulations were run on a PC (400 MHz, system Linux), taking on average 9 sec to simulate 100 years and 1 ha of rain forest growth.

Improvements to former versions of the model

In comparison to former versions FORMIND1.0 (Köhler & Huth 1998a) and FORMIND1.1 (Köhler et al. 2001) all submodels of the model were revised and improved on the basis of current understanding of the ecological processes in tropical rain forests. *Tree physiology* was formulated in more general functional relationships and parametrised on the basis of new field data available only recently. Assumptions in the *mortality submodel* were simplified and a density dependent self-thinning rule was implemented. The *recruitment submodel* was enlarged with an alternative site-dependent approach, whose development and influence on general model behaviour play a major role in model analysis. *Respiration* was modelled in greater detail, and a concept was developed to validate it on the basis of available field data. *Photosynthesis* was revised slightly. Finally, a simply dependency of tree growth on potential dry periods was implemented and thus the range of applications was enlarged.

In the end, only the concepts of spatial resolution and general formulations of photosynthesis and respiration were taken from previous versions and from the FORMIX3-models, the latter especially from FORMIX3-Q (Ditzer 1999).

The main conceptual difference to FORMIX3 is the individual-oriented approach. FORMIX3 so far works with a simple concept of matrix models incl. transition rates between different size classes, which are difficult to parametrise. With its more general formulation of processes FORMIND2.0 differs from its predecessors also in its basic concept of species grouping, on which the whole parametrisation is based. This allows a relatively fast model application to different forest sites.

Discussion

The modelling approach used in Formind2.0 enables the developer or user to change each submodel and replace it with a currently more practical one. Sometimes research and new available field data for a certain site will suggest such modifications. We discuss each submodel on its own.

The size of the model area in which trees compete with each other is important, as the dynamics of succession processes depend on it. The impact of one dominant tree on the light climate in the patches is too strong in too small areas. Thus, all other plants are repressed more than in reality. Only after the death of the dominant tree does growth in the recruitment take place. In too large simulated areas, leaf area in relation to patch area is too small. Death of even large trees will change the light climate only slightly. In both cases the real dynamic of succession in forest gaps will not be met with acceptable accuracy. From these considerations it emerges that the most appropriate size of a patch used in models should be that of the crown of a typical large-canopy dominant tree of the stand. Typical sizes lie between 400 m^2 and 800 m^2. In forests of the tropical regions patch size can be chosen at the lower end of the range. This may be due to the fact that the steeper sun angles at low latitudes allow light to reach the forest floor in relatively small gaps (Shugart 1998). The patch size of 400 m^2 chosen in Formind2.0 lies in the given range taken from those theoretical considerations.

A large number of forest growth models calculate forest dynamics only in one patch that is why they are called gap models (Liu & Ashton 1995). Most of them emerged from Jabowa (Botkin et al. 1972; Botkin 1993) and use age dependent growth functions. From our point of view a single patch can never be representative of a whole rain forest. Normally, areas in different phase of succession exist beside each other. This is especially the case if secondary succession or external disturbances (e.g. logging of trees) are of interest.

In contrast, the model used in this study is able to simulate an area of any size, restricted only by computing capabilities. This is useful for various reasons. First, the fraction of patches at the border of the simulated area will decrease with increasing size if the shape of area remains quatratic (from 64 % at 1 ha to 15 % at 25 ha). Border areas are sensitive as assumptions on boundary conditions (e.g interactions leaving the simulation area) will affect them strongly. Furthermore, results are more independent of stochasticity, included in mortality and recruitment, the larger the area is.

The individual-oriented cohort-approach is coupled with the chosen spatial resolution of 20 m × 20 m. Only the non-explicit spatial position causes an aggregation of individuals into cohorts. The resolution of available data at the time of the model development was the main reason for that approach. Until now only a few research plots with explicit tree positions for each individual larger than 1 cm in stem diameter have been inventorised (Condit et al. 2000; Smithsonian-Tropical-Research-Institute 2000). In a few cases data are freely available, e.g. for a neo-tropical rain forest in Costa Rica (Clark & Clark 2000). The gap-model approach, used for spatial resolution and calculation of competition situations in single patches, has been proven practical in various case studies (overview in Liu & Ashton 1995). Tropical (Shugart et al. 1980; Doyle 1981; Kürpick et al. 1997) and temperate forests (Botkin et al. 1972; Shugart 1984, 1998; Botkin 1993) have been modelled, and influences of climate and elevation gradients were analysed (Bugmann 1996b, 1997). All gap-models known to the author calculate so-called *potential natural vegetation (PNV)*, which reflects the steady-state of a model at current parametrisation, if simulation was started from a clear-cut area. Thus, tendencies in species composition as a response to assumed changes in environmental conditions can be analysed, but a comparison of simulated dynamics with field data of long term observation areas was missing. This comparison is an important validation method (Vanclay & Skovsgaard 1997), whose results, together with an estimate about the quality of the model, are more important than technical details, e.g. which modelling approach has been chosen.

The few available data sets with explicit tree position raise the question if an application of FORMIND2.0 to those sites is only possible and meaningful after considerable model improvements. In this context only the vertical light competition needs to be discussed. In tests with FORMIND (Köhler 1996) we analysed whether we gain any further information of reducing temporal resolution from steps of one year to months, days or even hours. A case study for French Guiana uses a spatial-explicit forest growth model (Chave 1999b). Complex interactions of individual trees with a three dimensional (3D) field vector of irradiance were calculated. As a result a detailed distribution of irradiance in each part of the canopy can be calculated. This study and our own investigations have shown that computation time mainly depends on calculation of this irradiance field. Thus, Chave was using highly parallel computer systems available only in large research institutes to perform his study in an acceptable time frame. It is questionable if the detailed field vector gets the model closer to the real system, as elevation on the forest floor or daily variations in light climate have not been considered so far. Modelling of sun spots, important for the germination of seeds (Hammond et al. 1999), would be possible with daily variations. Influence of sun spots on growth of seedlings in FORMIND was already analysed (Köhler 1996, p. 31) and can be neglected. As recruitment rates work with the concept of reproductive success covering also seed and seedling predation, a more detailed concept for germination is not needed. For temperate forests detailed models of light climate are available which can be used in spatial-explicit models (Brunner 1998). In this context, an error propagation analysis undertaken in the spatial-explicit model SORTIE has to be discussed (Deutschmann et al. 1999). It was analysed how model dynamics depend on a more detailed resolution of incoming light (in 1, 16, 48, or 216 light rays). It transpires that most results (e.g. succession of tree species) achieved with one ray of light do not significantly differ from those of a more detailed description. Differences between 16 and 216 are always negligible.

Comparisons of model results with diameter increment data from permanent sampling plots without explicit tree positions have proven our light competition model to be of acceptable quality (Köhler et al. 2001).

Formulations concerning tree physiognomy are at the current state of research. The available data sets for South-East Asia verified the used functional relationships between different tree variables (e.g. Forestal-International-Limited 1973; Yamakura et al. 1986; Ashton & Hall 1992; Poker 1993). Currently, research activities in rain forests are concentrated on the neotropics (Condit 1995; Cook 1998; Holl & Kappelle 1999; Peres 1999). Thus, published field data for South America will be improved in the near future. This will enable us to specify some of assumptions, where regional differences were not captured so far (see applications in Chapter 6-8). Site-dependent relationships of several physiognomic variables in South-East Asia has improved parametrisation (Ditzer 1999). The broadening of this approach to the sites in South America was so far not possible because of a lack of field data. In particular, analysis of leaf area or biomass partitioning was only undertaken in a few sites in South-East Asia. A verification of the upper boundary of individual tree's leaf area index LAI_{M} (Eq. 4.7) is of special interest. This boundary is, so far, caused by model comparison with data from photosynthesis production. Self-shading in tree crowns with high values of *LAI* leads to higher production rates of mid successional species compared to early successionals for trees of the same size and for high light intensities. This is inconsistent with observations. In this context parametrisation of the light response curve (Eq. 4.14) does not distinguish different values for the light use efficiency α_s, as differences in field data are statistically weak (Eschenbach 1994; Eschenbach et al. 1998), but results are sensitive to differences in α_s. Other field studies use different regression functions, where α_s is not calculable, or determine only maximum photosynthesis P_{M} (e.g. Bazzaz & Pickett 1980; Oberbauer & Strain 1984; Ellsworth & Reich 1996; Barker et al. 1997). However, the principal differences in photosynthetic characteristics of tropical trees along successional gradients were confirmed (Strauss-Debenedetti & Bazzaz 1996), and were partially correlated with tree height (Davies 1998; Thomas & Bazzaz 1999).

The main improvements of the tree growth submodel were the size-dependent growth limitation and splitting of respiration into maintenance and growth respiration. Limitation of tree growth has been found in field datas (Koch et al. 1994; Maruyama et al. 1997) and was already used in forest grwoth modelling (Valentine 1988 1990; Landsberg & Waring 1997). Thus, growth is limited, even if there is evidence that large emerging trees do not stop growing (Chambers et al. 1998). Species richness is aggregated in PFTs in FORMIND2.0 and only the growth of average trees is modelled. Limitation is a very useful and proper concept.

Respiration in tropical trees is one of the processes of which very little is understood (Kira 1978; Medina & Klinge 1983; Yoda 1983; Oberbauer & Strain 1984; Ryan et al. 1997). The work of Ryan and co-authors mark important progress in this subject. The splitting of respiration and a more detailed description of the processes was only possible with the process-based approach used in the model. Ditzer (1999) has highlighted the importance of these details, which can not be incorporated in simpler approaches, where tree growth is modelled with one diameter growth function based on regressions.

We considered light conditions as most important for determining tree growth, an approach used in other studies before (Bartelink 1998a, 1998b). One obstacle in including below-ground processes is the difficulty in measurement design and implementation. However, there are research activities in this direction in tropical forests (Denslow et al. 1998; Hall & Matson 1999; Chambers et al. 2000) or on a global scale (Jackson et al. 2000). In temperate forest growth models nutrient or water cycles were considered already (Aber et al. 1982; Jansen et al. 1995; Bossel 1996b; Endejan 1997; Friend et al. 1997; Kimmins et al. 1999; Thornley & Cannell 2000). Analysing corelations between soil nuitrients and forest stockings led to corrections factors of tree growth in the rain forest model FORMIX3-Q (Glauner 1999; Ditzer et al. 2000). We are therefore aware of the effects and the dependency of the tree growth on soil matters. Nevertheless, for average site conditions measured diameter growth was matched with simulation results (Chapter 5).

A main improvement of the mortality submodel is to model tree death without growth dependent mortality, which was used in a former version or the FORMIX3 model. Some field data (Swaine & Whitmore 1988) give a hint of that relationship. But as tree size was not considered in their analysis it is difficult to generalise results. Otherwise it would promote higher mortality in large trees, which naturally grow slower than smaller ones. This is in contradiction with observations. Theoretical considerations concerning the product ω of growth rate g, maximum diameter d_{M} and mortality rate M ($\omega = d_{\mathrm{M}}/g \cdot M$) support our thesis. The number of large trees would be over- ($\omega << 1$) or underestimated ($\omega >> 1$) if ω is very different from one (Chave 1999b). Enhanced mortality of young trees is the only effective regulation of ingrowing trees. This effect is well known, but confirmed by only a few studies (Clark & Clark 1992; Kennedy & Swaine 1992; Okuda et al. 1997). Sensitivity analysis of size-dependent mortality and comparison of tree densities with field census make a site-dependent parametrisation possible.

Density regulation through self-thinning is a known phenomenon in forests of different latitude (White 1981; Westoby 1987; Valentine 1988; Clark 1992a, 1992b; Penfold & Lamb 1999; Silva-Matos et al. 1999). Increasing basic mortality rates in dense patches, as done in previous versions (Köhler & Huth 1998a; Ditzer 1999; Huth & Ditzer 2000a) is far less restrictive. In FORMIX3 density regulation might work this way, as transition rates from one layer to the other limit the growth of saplings, and thus, residence times in lower layers are prolonged. Adaptive changes in tree physiognomy (Wirtz 1998), especially crown shape, are not considered in the model. Thus, in self-thinning an instant extraction of trees with overlapping crowns was included in FORMIND.

In experimental ecology, natural regeneration and all processes concerning recruitment as main mechanisms determining future forest compositions were of central interest in the last years. Research can be distinguished in

- seed production (Putz 1979; Garwood 1983, 1989; Charles-Dominique 1993),
- seed dispersal (Fox 1972; Hubbell et al. 1991; Kennedy 1991; Wunderle 1997; Clark 1998; Clark et al. 1998a, 1998b; Higgins & Richardson 1999; Martinez-Garza & González-Montagut 1999; Robinson et al. 1999),
- establishment of seedlings (Lang & Knight 1983; Whitmore 1983; Riéra 1985; Hubbell & Foster 1986a, b; Schupp et al. 1989; Hartshorn 1989; Veblen 1989; Manokaran & Swaine 1994; Milton et al. 1994; Phillips & Gentry 1994; Pinard et al. 1996; Poorter et al. 1996; Sheil & May 1996; Powers et al. 1997; Okuda et al. 1997; Tucker & Murphy 1997; van Gardingen et al. 1998; Diaz et al. 1999; Hammond et al. 1999; Hubbell et al. 1999; Kyereh et al. 1999; Xiong & Nilsson 1999),
- and photosynthesis and growth of seedlings (Chim & On 1973; Enright 1978; Manokaran & Kochummen 1987; Brown 1990, 1993, 1996; Condit et al. 1995a; Lee et al. 1996; Press et al. 1996; Barker et al. 1997; Lee et al. 1997; Zipperlen & Press 1997; Kohyama & Takada 1998; Agyeman et al. 1999; Kobe 1999b; Nicotra et al. 1999; d'Oliveira 2000).

Thus, it is important to incorporate detailed submodels of recruitment in forest growth models. Besides a theoretical verification of field data on recruitment, the simulations of temporal dynamics of forests will be improved.

It is one of the main improvements of the model to be able to model explicit seed dispersal depending on mother trees compared to only constant input of seedlings. However, it is certainly true that the establishment of individual trees of the huge number of tree species in tropical forests follow more complex patterns. A controversial study concerning recruitment on Barro Colorado Island, a nature reserve on an island in the Panama Canal (Hubbell et al. 1999; Chazdon et al. 1999; Hubbell 1999; Kobe 1999a; Brokaw & Busing 2000) found that "*being at the right place at the right time*" is more important for recruitment success than any individual strategy. Hubbell et al. (1999) did not find significant differences in the recruitment of different successional groups in closed forest and canopy gaps. Furthermore, the limiting number of available seedlings determined success more than any other environmental conditions. So far, it is not possible with the model to verify studies which identify tree species diversity as function of different impacts (Cannon et al. 1998, 1999; Sheil et al. 1999). Enhancing FORMIND2.0 in a way that each individual tree is correlated with one specific tree species while still modelling forest growth with a reduced set of plant functional types might address these questions in the future. In particular, recruitment could be coupled to trees of individual species.

A more detailed description of recruitment than done so far does not seem to be useful. Necessary assumptions and data concerning seed predators, wind direction and seed etc. would be highly speculative, and parameters difficult to determine.

Interactions of disturbed animal, bird, or insect populations, which act as seed dispersers and are important for future forest development, are in the focus of current ecological interest (Redford 1992; Curran et al. 1999; Law & Lean 1999; Lynam & Billick 1999; Price et al. 1999; Cullen et al. 2000; da Silva & Tabarelli 2000). As dispersal agents of trees are complex, and mostly not depending on one species, the effects of extinction of a single animal species on plant dynamics is difficult to estimate. However, it is definitely correct that hunting pressure and the collection of seed bearing fruits in now intact forest communities will alter recruitment capabilities of these in the future (Redford 1992). We take this into account through scenario analysis, where those interactions are considered as main effects (Chapter 8).

Chapter 5

Comparison of measured and simulated growth on permanent plots in Sabah's rain forests

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Abstract

In this paper previously unpublished field data from 25 ha of permanent sampling plots (PSPs) in Sabah, Malaysia, in four different forest reserves are analysed for mortality rates and basal area development. Field data of an observation length of nine to 20 years were available. These data then form the basis of several benchmark tests for the evaluation of the individual-oriented tropical rain forest growth model FORMIND. A new version of FORMIND is presented. The model in its version FORMIND1.1 includes enhanced submodels for mortality and tree growth. The model evaluation is focused on the model components for tree growth, competition and mortality. Data for tree recruitment were not available. Results show a good agreement between simulation and field data for the main output variables basal area and stem number indicating a reasonable behaviour of the model components we focused on. Furthermore the results show that differences in site conditions influence tree growth and mortality. Site characteristics should be included in the model in the future.

Keywords: forest growth model; tropical rain forest; dipterocarp forest; mortality; Malaysia; basal area; FORMIND

Forest Ecology and Management (2001) **142**(1–3), in press.

Introduction

Evaluation of forest growth models is an important procedure of model development. Vanclay & Skovsgaard (1997) discussed range and importance of model evaluation. An evaluation of tropical rain forest models is difficult due to a lack of adequate field data. Besides a comparison of model output in a steady state with primary rain forest data (e.g. Bossel & Krieger 1994; Huth et al. 1994; Huth et al. 1998; Köhler & Huth 1998a, 1998b; Kürpick et al. 1997) few permanent sampling plot data exist which are suitable for testing rain forest growth models. The field data used in this paper were not available to the authors at the time of model development and can therefore serve for testing of model results. Because those field data are used here for elaborating parameter values of mortality, they can not be seen as fully independent, but semi-independent.

The data used in the following were collected in the forest reserves Garinono, Gunung Rara, Segaliud Lokan and Sepilok in Sabah, Malaysia by the Forestry Department. Analysis in terms of site and stand characteristics, mortality and recruitment data are unpublished and only available in several research reports (Ong & Kleine 1995; Köhler 1998). Details of the field data used here are therefore documented in this paper. Especially mortality rates are analysed as a function of time and different plant functional types (PFTs).

Comparison of simulation results and field data from permanent sampling plots (PSPs) is important especially when models are used for estimation of long term trends of forest growth with or without anthropogene influences as forest management (Huth et al. 1994, 1998; Riswan & Hartanti 1995) or climate change (Pastor & Post 1988; Overpeck et al. 1990; Shugart 1998).

The simulation model investigated in this study is the tropical rain forest growth model FORMIND. FORMIND was developed following an individual-oriented approach (Huston et al. 1988; Judson 1994; Liu & Ashton 1995; Uchmański & Grimm 1996) and used to validate the approach of the more aggregated process-based model FORMIX3 (Huth et al. 1998). One important feature of both models is the use of species grouping into PFTs. A detailed model description and some results of FORMIND have already been presented in Köhler and Huth (1998a, b). Several submodels (tree growth, competition, mortality) of FORMIND were modified in the meantime due to new available datasets, research activities and model analysis. These improvements are documented in the following.

Area description

The permanent sampling plots (PSPs) investigated in this study were established and inventorised by the Forest Research Centre and Forestry Department Sabah, Malaysia. They are all located in the lowland dipterocarp rain forest of Sabah, Malaysia. The PSPs located in different forest reserves across Sabah sum up to a forest area of 25 ha (see Table 5.1). The data set of Segaliud Lokan is split into two parts because of differing observation times within the forest reserve. The number of PSPs in the different locations varies from one to eleven ha, observation time from nine to 20 years with recordings in intervals between 1 and 5 years. Elevation is below 100 m, only Gunung Rara is located in a higher region (200 m - 600 m). Site quality was analysed by Ong & Kleine (1995) on the basis of landform and parent material. The site quality of Gunung Rara differs significantly from that of the other reserves.

Each PSP covers an area of 100 m × 100 m, subdivided into 25 patches of 20 m × 20 m, which are further split up into 4 sub-patches of 10 m × 10 m. Within these sub-patches no further infor-

Table 5.1: Information about permanent sampling plots (PSPs) located in different forest reserves in Sabah, Malaysia. A: size of PSPs [ha]; B: number of trees at first enumeration; C: time of observation; D: length of observation [y]; E: number of enumerations; F: time between two enumerations [y]; G: time between last logging and first inventory [y]; H: site quality.

Location	A	B	C	D	E	F	G	H	Elevation [m]
Garinono	2	871	1973-1982	9	10	1	45	good	40-80
Gunung Rara	11	4978	1981-1990	9	7	1-2	11-12	poor	200-600
Segaliud Lokan1	7	4258	1982-1992	10	3	5	25	good	40-100
Segaliud Lokan2	1	365	1972-1985	13	8	1-2	8	good	40-100
Sepilok	4	2218	1973-1993	20	5	5	19	good	20-50

mation about tree location were recorded. Trees with a diameter at breast height (dbh) $\geq$ 10 cm are labelled. In regular inventories the dbh of all labelled trees were recorded including ingrowing small trees. Death of labelled trees was also recorded.

Methods

The rain forest growth model FORMIND1.1

The FORMIND model was developed for the simulation of tropical rain forest in Malaysia (see Köhler & Huth 1998a, b for further details). It is a successor of the FORMIX3 model (Appanah et al. 1990; Bossel & Krieger 1991, 1994; Huth et al. 1994, 1998). As main processes the model includes tree growth, competition, mortality and regeneration (last is not included in this version because of a lack of field data). In the following we will explain the approach used in version FORMIND1.1.

Species grouping and spatial structure: Tropical forest stands are usually composed of a large number of species. For the purpose of investigating forest dynamics it is useful to classify species into a small number of plant functional types (PFTs). Different concepts for PFTs were proposed (Swaine & Whitmore 1988; Poker 1993). We use three growth characteristics for grouping (potential height, light demands for growth and regeneration) and derive four PFTs for the dipterocarp lowland rain forests of Malaysia (Table 5.2, for details see Köhler & Huth 1998b). A fifth PFT for bushes and small plants with heights below 1.3 m, which was used in former simulations (Köhler & Huth 1998b) is not necessary here, because PSP inventories were focused on trees with a dbh $\geq$ 10 cm. For simulations a forest stand area of one hectare is divided into smaller patches. The model follows the gap-model approach (Botkin et al. 1972; Shugart 1984; Botkin 1993) to modelling tree competition by describing tree interaction on patches. These patches have the size typical of treefall-gaps as they are naturally created by dying larger trees (20 m × 20 m), which is the same patch size as in the PSP inventories. In contrast to most gap-models (an exception is the ZELIG model by Smith & Urban 1988; Urban et al. 1991) we aim at picturing the shifting forest stand mosaic and we therefore simultaneously simulate several patches explicitly in their neighbouring location within the stand. The patches themselves are pictured as homogeneous.

Table 5.2: Characteristics of the aggregated plant functional types (PFTs) of lowland dipterocarp rain forest of Sabah, Malaysia.

PFT	Maximum heights	Light demand	Species composition
1	>36 m	shade tolerant emerging species	mainly dipterocarps
2	25-36 m	shade tolerant climax species	dipterocarps and non-dipterocarps
3	15-25 m	light demanding pioneer species	mainly *Macaranga spp.* and *Antocephalus chinensis*
4	$\leq$15 m	shade tolerant understorey species	non-dipterocarps

Table 5.3: Parametrisation for a dipterocarp lowland rain forest in Sabah, Malaysia, used by the FORMIND1.1 model. Parameters concerning mortality are depending on the location and can be found in Table 5.4. Names are identical to those used in the detailed model description in Köhler and Huth (1998b). Index j indicates that parameter values differ for different plant functional types.

Name	Description	Unit	Plant functional type 1	2	3	4
a_{0j}	Coefficient of height-diameter relation[a]	[m]	2.94	2.30	1.97	3.11
a_{1j}	Coefficient of height-diameter relation	[m cm^{-1}]	0.42	0.42	0.39	0.30
a_{2j}	Coefficient of height-diameter relation	[m cm^{-2}]	-0.002	-0.002	-0.002	-0.001
ρ_j	Wood density	[t$_{\mathrm{odm}}$ m^{-3}]	0.62	0.57	0.37	0.71
$h_{\mathrm{M}j}$	Maximum potential height	[m]	55	36	25	15
$P_{\mathrm{M}j}$	Maximum photo-productivity	$[\frac{\mathrm{mg}_{\mathrm{CO}_2}}{\mathrm{dm}^2\cdot\mathrm{h}}]$	10.9	11.6	29.1	18.8
α_j	Slope of light response curve total aboveground biomass)	$[\frac{\mathrm{mg}_{\mathrm{CO}_2}\cdot\mathrm{m}^2}{\mathrm{dm}^2\cdot\mathrm{h}\cdot\mathrm{W}}]$	0.36	0.20	0.20	0.30
τ_j	Fraction of stemwood to total biomass	[-]	0.7			
s_j	Crown-to-stem-diameter-ratio	[-]	25			
$\widetilde{LAI}_j$	Leaf area index of single tree	[-]	2			
$R_{\mathrm{P}j}$	Respiration (biomass losses relative to	[y^{-1}]	0.16			
I_0	Light intensity above canopy	[W m^{-2}]	335			
k	Light extinction coefficient	[-]	0.7			
W	Probability for a dying tree to fall	[-]	0.0			

[a] Height-diameter relation: $h = a_{0j} + a_{1j} \cdot d + a_{2j} \cdot d^2$.

Individual tree growth: Within a single patch the model calculates the development of a forest stand based on cohorts of trees of the same PFT. Such a cohort is characterised by the number of trees and by the size of one representative tree. Using allometric relations, the size of a tree can equivalently be expressed in terms of its above-ground biomass, height, or diameter at breast height. The crown projection area is calculated from stem diameter via the proportionality of stem diameter and crown diameter (Rollet 1978; Whitmore 1984; Poker 1993). These relationships between components of tree size (diameter, height and crown dimensions) are based on average field data, and are important simplifications that makes the model tractable, but they may reduce its accuracy. Emergent trees might have a crown projection area bigger than the patch size. Their crowns are then assumed to reach into the neighbouring four patches. Crown length is a function of tree height (Richards 1952; Burgess 1961; Poker 1993). With these relations the distribution of individual tree crowns in the canopy can be calculated. Assuming a fixed leaf area index (LAI) of individual trees the leaf area distribution in the forest can be calculated. The growth of the individual tree is based on a carbon balance. Calculations include photoproduction of the trees and assimilate losses due to respiration and renewal. Photoproduction is calculated from the tree's leaf area and its specific productivity. The latter depends on the local irradiance for each tree (Monsi & Saeki 1953; Thornley 1976). Within a patch light attenuation downwards in the canopy is calculated with respect to the absorption of higher located tree crowns. The dependence of specific photosynthetic productivity on irradiance is modelled using a Michaelis-Menten-type light response curve parametrised for each PFT (Eschenbach et al. 1998). Assimilate losses are estimated in relation to tree biomass (Kira 1978; Yoda 1983). Losses are composed of renewal of roots, above-ground litter fall and of respiration of woody tree organs and of leaves. Respiration is considered a function of tree size and PFT (Ditzer 1999). A water balance is not included in the model. The calculation of tree growth is performed in annual time steps.

Competition: Competition is modelled in terms of competition for light as described above and competition for space as described below concerning *mortality*.

Mortality: Mortality is modelled on an annual basis. In the current version it does not depend on any other processes such as diameter increment. The mortality rates used for the simulations in this study are directly obtained from the analysis of PSP-data. The model includes an additional crowding mortality for trees in dense patches (crowns do not have enough space). In this case trees die to such an extent that crowding does not occur anymore. Because of the short length of simulations (≤ 20 years) we do not include processes of falling trees and the creation of canopy gaps by these trees.

Regeneration: The FORMIND model includes also a submodel for regeneration. Seedling establishment was not measured in

Table 5.4: Average mortality rate m [% y^{-1}] for different plant functional types (PFT) calculated from permanent sampling plot data in different locations and used as parameter values for simulations. For Segaliud Lokan2 we only used the data recorded between 1972-1982 and the parameter values used in simulations therefore differ from the average value.

Location	average	PFT			
		1	2	3	4
Garinono	2.59	2.40	0.62	3.86	2.54
Gunung Rara	0.24	0.31	0.26	0.12	0.16
Segaliud Lokan1	5.10	4.48	2.89	12.03	3.46
Segaliud Lokan2	(6.34)	0.0	0.0	0.0	0.0
Sepilok	5.09	5.49	3.76	5.89	2.58

Table 5.5: Basal area (BA) and stem number of all species (N_{all}) and the different plant functional types (N_1, N_2, N_3, N_4) at the beginning of observation for trees with $d \geq 10$cm in different forest reserves.

Location	BA [m^2 ha^{-1}]	N_{all} [ha^{-1}]	N_1 [ha^{-1}]	N_2 [ha^{-1}]	N_3 [ha^{-1}]	N_4 [ha^{-1}]
Garinono	28.3	435.5	288.0	27.5	95.5	24.5
Gunung Rara	17.4	450.4	205.9	21.6	168.6	56.0
Segaliud Lokan1	31.3	608.3	422.4	41.0	95.1	45.4
Segaliud Lokan2	12.0	365.0	133.0	10.0	199.0	22.0
Sepilok	24.6	554.5	462.0	44.0	16.3	28.5

the PSPs. Estimation of recruitment rates as an alternative to the use of field data is not considered, because uncertainties included in the estimation will lower the quality of the evaluation. Therefore all tests are done without considering regeneration.

Model parametrisation: A detailed description of literature sources of the parameter values used for the lowland dipterocarp rain forests of Sabah, Malaysia, is presented in Köhler & Huth, (1998b). Table 5.3 contains the parametrisation used in the test undertaken for this paper. Values of parameters in Table 5.3 are similar to those used in previous studies (Köhler & Huth 1998a, b) with the exception of mortality rates (see Table 5.4), missing regeneration parameters and the probability W of dying trees to fall.

Initialisation: From the stem-diameter distribution of the first enumeration of each PSP trees are aggregated into different cohorts regarding their PFT, diameter (in diameter classes with a width of 5 cm) and location in the stand (in patches of 20 m × 20 m).

Benchmark tests

As outlined by Vanclay & Skovsgaard (1997) a comparison of simulated data with field data not used for model development is an appropriate method for evaluation of forest growth models. This is called benchmark test. Basal area and stem number were chosen for comparison of simulation results with field data because these variables can directly be derived from the PSP inventory data. For each PSP a simulation with FORMIND1.1 was performed over the same time period for which data were available. In cases where data of more than one hectare were available data were averaged after simulation. Two different kinds of comparison were undertaken. First, basal area and stem number for different PFTs at the end of the simulations were compared with those measured in the PSPs. Second, temporal development of basal area and stem number over simulated/observed time was analysed.

We represent results in the following way:

$$\frac{x_{\mathrm{simulated}}(t_{\mathrm{end}})}{x_{\mathrm{measured}}(t_{\mathrm{end}})} = f(x_{\mathrm{measured}}(t_{\mathrm{end}}), \mathrm{PFT}, \mathrm{FR}) \quad (5.1)$$

and

$$\frac{x_{\mathrm{simulated}}}{x_{\mathrm{measured}}} = f(t, \mathrm{PFT}, \mathrm{FR}), \quad (5.2)$$

with x: basal area or stem number, t_{end}: last year of inventory/simulation, FR: forest reserve, t: time and PFT: plant functional type.

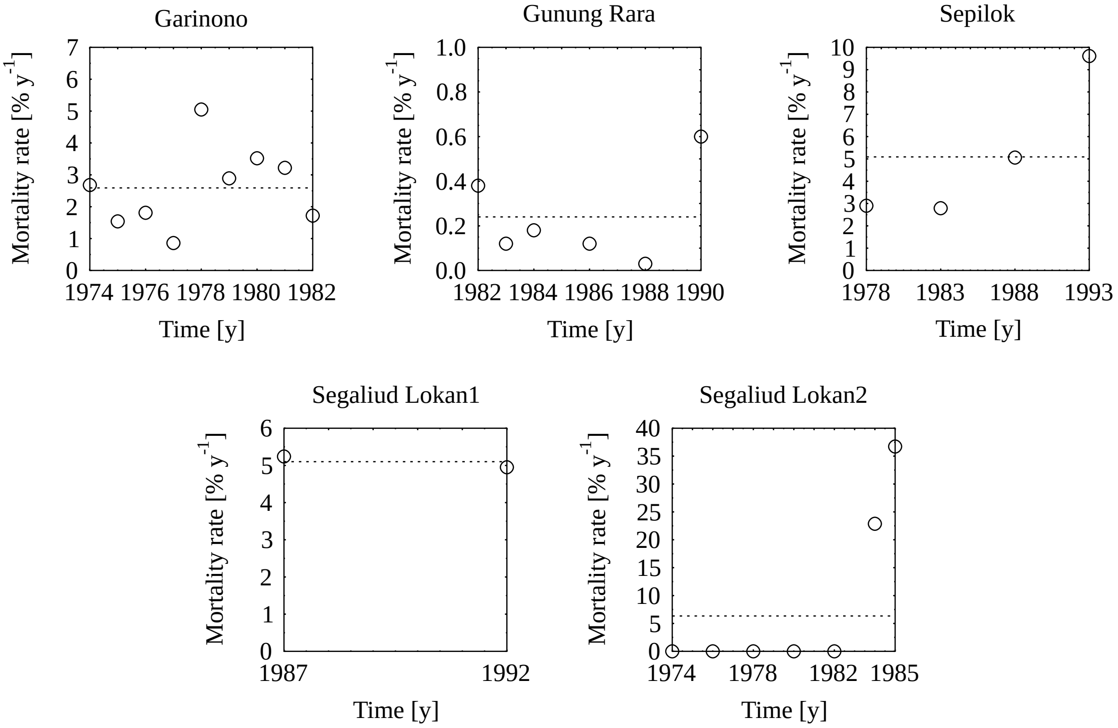

Figure 5.1: Mortality rates as function of time in permanent sampling plots (PSPs) in different locations (Garinono, Gunung Rara, Segaliud Lokan and Sepilok) in Sabah. Detailed information about PSPs in Table 5.1. Dotted Line: Average mortality rate between first and last enumeration. Circles: Mortality rate between actual and previous enumeration. Circles also describe when enumerations took place.

Results

Permanent sampling plot analysis

The structure and stocking of the PSPs varies widely as seen in Table 5.5. Where the stocking of Segaliud Lokan2 and Gunung Rara is very low (basal area (BA) of 12.0 and 17.4 m^2 ha^{-1} respectively) the relative fraction of pioneer species of (PFT 3) is very high indicating that these stands were heavily disturbed by logging. In contrast to that PSPs in Segaliud Lokan1, Garinono and Sepilok are well stocked (BA = 31.3, 28.3 and 24.6 m^2 ha^{-1}, respectively) with a lower fraction of pioneer species. Thus the data represent a wide range of forest stocking.

Annual mortality rates m were calculated in the following way (Manokaran & Swaine 1994): $m = (\log_e n_0 - \log_e n_1)/t$, where n_0 is the number of trees at the first enumeration, n_1 is the number of trees at the second enumeration t years later without considering any new trees growing in between the two enumerations.

Mortality rates differ widely for different forest reserves. Table 5.4 lists average mortality rates for different PFTs over the whole time of observation. Average values range from 0.24 % y^{-1} in Gunung Rara to 6.34 % y^{-1} in Segaliud Lokan2. Mortality rates of pioneer species (PFT 3) are with the exception of Gunung Rara generally higher than of non-pioneer species (e.g. Segaliud Lokan1: m = 5.10 % y^{-1} for PFT 1, m = 12.03 % y^{-1} for PFT 3).

The temporal development of the average mortality rates (Fig. 5.1) shows high fluctuations in most forest reserves. Especially in Gunung Rara, Segaliud Lokan2 and Sepilok there is a constant increase in mortality rate to the end of the observation period. In Segaliud Lokan2 a very high increase of the mortality rate was analysed ($m = 0$ % y^{-1} for eight years, $m = 36$ % y^{-1} in the last year). Trends like this cannot be explained with the present version of the model which is based on constant mortality rates and therefore the last three years of data in Segaliud Lokan2 are not considered in our tests.

Evaluation of FORMIND1.1

In the simulation studies shown in this article we concentrate on the comparison of results with the data from the permanent sampling plots. Other tests like the long term tendency of mature forest stands incl. species composition were performed in Köhler & Huth (1998b).

The results of the benchmark tests following Eq. 5.1 and 5.2 are documented in Fig. 5.2. First we analyse the results for the basal area, then the findings for the stem numbers.

Basal area (Fig. 5.2A&B):

Simulations show good agreement with the field observations. The deviation of simulation results range between 0 % and 30 %, in only one case 50 %. There is no PFT where our simulations show a trend of permanent over- or underestimation. PFT 1 seems to be the most critical PFT with the highest deviation of nearly 50%. The highest deviation was observed for the forest reserve Gunung Rara, which seems not to be simulated accurately with this version of the model. PFTs which have a basal area below 5 m^2 ha^{-1} tend to be simulated with lower values than measured. The total basal areas are matching the measured values more precisely in stands with a higher stand basal area. Again the highest variation is found in the Gunung Rara simulation.

Deviations in total basal area plotted against simulation/observation time show that nearly all forest reserves stabilise within the simulation time at an acceptable error range (± 20%) with the exception of Gunung Rara. Sepilok and Garinono even come closer to measured values the longer we simulate.

Stem number (Fig. 5.2C&D):

Stem number can be simulated more precisely than basal area (maximum deviation: 25 %). This is a result of the mortality rates used in the simulation which were derived from the observations in the PSPs. The deviation of the total stem number after total simulated/observed time is in all forest reserves below 6 %. There is a tendency of underestimating stem number in simulations. Again deviation in plots with a higher stem number is smaller, highest deviation occurs from PFT 3, which represent the pioneer species.

The deviation in total stem number plotted against simulation/observation time indicates always an underestimation of simulated stem number. The deviation is even stabilising with longer simulation time for Sepilok from 10 % to nearly 0 %.

Results in stem number and basal area have to be analysed together. Development of stem number is considered as a result of the simulated mortality processes, but the development of basal area is the product of mortality, growth and competition processes in their interaction in a forest stand.

Discussion

Mortality rates

Typical values of the average tree mortality rates in primary tropical rain forests are 1-2 % of stem number per year (Putz & Milton 1982; Lang & Knight 1983; Swaine et al. 1987a, b; Manokaran & Swaine 1994; Milton et al. 1994; Phillips & Gentry 1994; Condit 1995, 1998; Condit et al. 1995a) with a significant higher mortality rate for pioneer species (Primack & Lee 1991; Manokaran & Swaine 1994). Manokaran & Swaine (1994) analysed mortality rates in

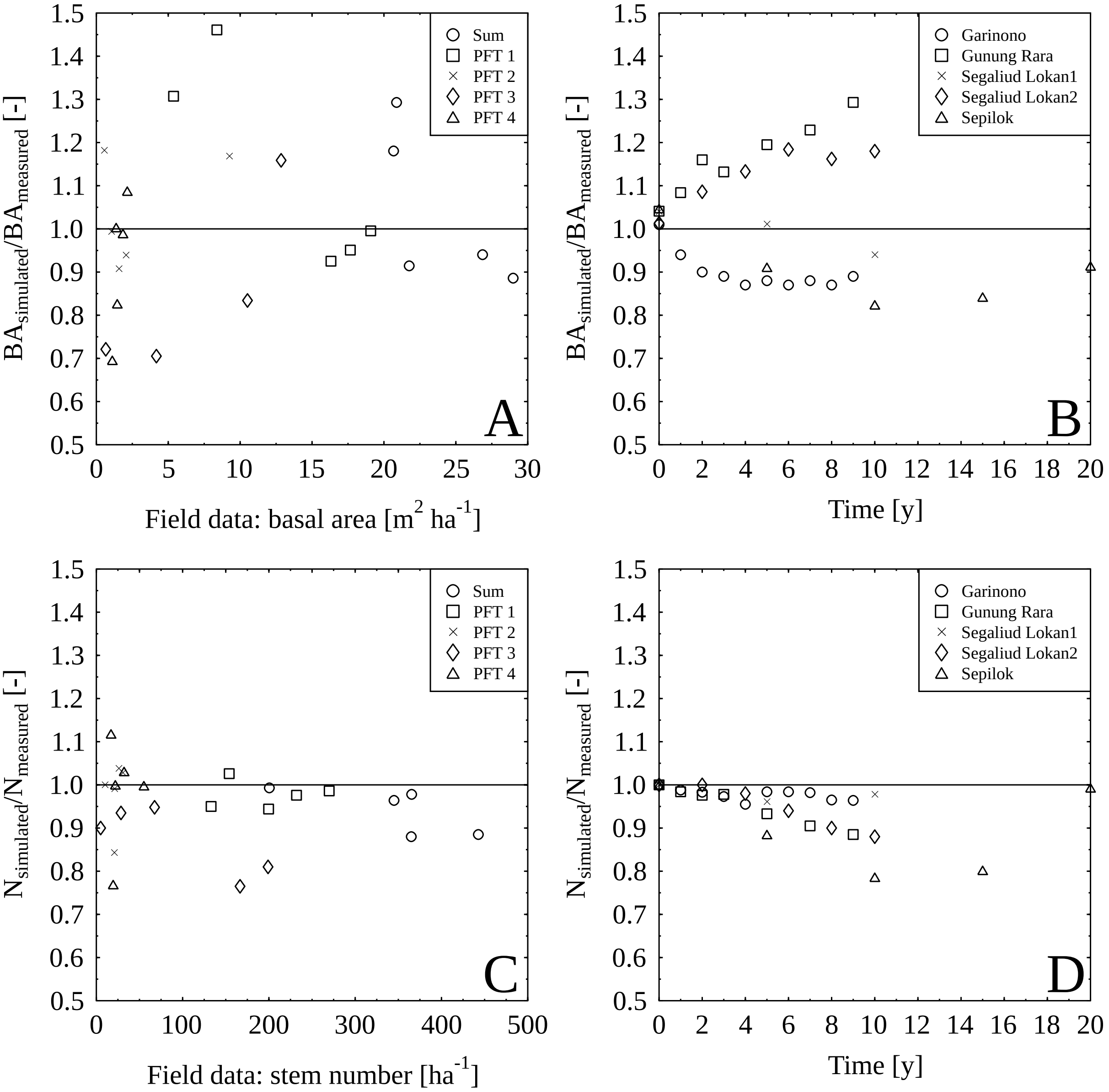

Figure 5.2: Benchmark tests. Relative variation in basal area BA (A, B) and stem number N (C, D) of simulation against field data. A, C: Final variation after maximum simulation time (= length of observation) as a function of field measurement in last enumeration. For each of the permanent sampling plots (PSPs) data for each plant functional type PFT 1-4 and sum are plotted. B, D: Variation as function of simulation/observation time. Plotted are total basal areas and total stem numbers for PSPs in Garinono, Gunung Rara, Segaliud Lokan and Sepilok. For information on PSPs see Table 5.1.

secondary tropical rain forest and find no significant differences. The fact that all our analysed average mortality rates do not fall in this range has to be discussed.

We did not consider ingrowth of trees after the first enumeration for the reason of evaluating our model without recruitment. This was also done assuming that the mortality rate for small trees with a dbh around 10cm does not differ from average mortality. The increasing mortality with time in three forest reserves indicates that older trees might die faster than the average rate. However, the typical fluctuations in mortality as seen in Garinono show no trend at all. Another reason for mortality increase might be an eight month long drought with no rainfall at all in the years 1982/83 in parts of Sabah (Leighton & Wirawan 1986;

Richards 1996).

Gunung Rara's very low mortality of 0.25 % y^{-1} over ten years seems very unrealistic. As mentioned earlier this forest reserve lies on poor sites and in higher elevation, and one might expect a mortality rate even higher than average. It might be that within the process of enumeration tree labels of dying trees were used several times leading to an underestimation of mortality rates. Mortality rate in Segaliud Lokan2, which was zero over ten years, seems reasonable, because of the small area of only 1 ha. On this scale extreme values might occur. Pioneer species show higher mortality rates as expected.

Even if the mortality rates are questionable in comparison with literature, they are a result of the data analysis of the PSPs and it is reasonable to use them as parameter values for simulations performed for benchmark testing.

Model Evaluation

The model in the version documented here is more complex in terms of competition and tree growth processes than any other rain forest growth model known to the authors (e.g. Kohyama 1993; Ong & Kleine 1995; Kürpick et al. 1997; Huth et al. 1998; Liu & Ashton 1998). However one might find models for temperate forests (e.g. Bugmann 1996a) or even monocultures (e.g. Bossel 1996a), which enhance certain features not included in FORMIND (e.g. soil properties, nutrient circles, weather, daily resolution, climate gradients). One might therefore think the model itself is simpler than today's forest growth models. For that reason we like to highlight the general differences in complexity between growth models for temperate and tropical forests and problems arising with a more detailed model structure. Beside the very high number of tree species in the tropics (over 400 per hectare in Sabah) the non existing data on those processes give us very few arguments on how to parametrise them.

The spatial resolution used in the inventories (each PSP plot has an area of 1 ha divided in 25 patches of 20 m × 20 m) and in the model is the same. For that reason competition processes for light and space are simulated as accurately as possible in FORMIND. However nature is not as homogeneous in tree distribution as we assume in the model. Shading processes might therefore have a more significant influence on individual tree growth. The aggregation of field inventory data into diameter classes with a width of 5cm as done in the initialisation results in slight overestimation of basal area at the beginning of the simulations (time = 0 y) as seen in Fig. 5.2.

The deactivation of the recruitment submodel has only a small influence on the simulated stand dynamic, if short time scales are considered as in this paper. With the approximation of an upper diameter increment of 1 cm y^{-1} for non-pioneer species without light competition (Ong & Kleine 1995; Huth et al. 1998) ingrowing trees with a dbh of 10 cm will not exceed a dbh of 30 cm within 20 years. In all competition processes trees are only influencing other trees of approximately the same size or smaller. The ingrowth would, if activated, not effect the growth of the big trees in stand simulation and would therefore lead to only small differences in the simulated stand development. Because PSPs data were analysed without recruitment as well (only trees labelled during first enumeration were considered further), accuracy of the comparison should not be weakened.

Considering mortality without the process of falling trees influences only the spatial distribution of tree mortality. Because mortality effects of gap creating falling trees are implicitly included in the field data, average mortality is parametrised correctly. Locally high mortality rates would effect recruitment pattern in this area, but may be ignored due to inactive recruitment submodel.

Applying the model with four of the five PFT, as indicated in the model description, has no effects on model results. As only trees with a dbh $\geq$ 10 cm are considered in the results, these fifth PFT would not change simulated basal area or stem number directly, trees of the fifth PFT have a maximum diameter of 2 cm. The only consequences might be indirect competition effects on small ingrowing saplings of other PFTs.

The fixed allometric relations between different variables like tree height and crown length in the model do not allow the trees to adapt crown structures to their specific individual environment. Crowns might overlap with those of neighbouring trees in dense patches. Therefore crowding mortality is needed as a regulating process. This is an additional mortality which leads to a constant underestimation of stem numbers. Simulations without this regulation end with higher deviation in basal area from measured data. The process of crowding mortality covers only a small part of the total mortality (0.05-0.25 % out of 2-5 %) but is important for a realistic simulation of basal area.

The simulations for Gunung Rara agree the least with field data. These deviations might be caused by the higher elevation and poor site conditions in Gunung Rara. Conditions found in Gunung Rara fall out of the present application range of FORMIND1.1. However with a more detailed description of individual tree growth as a function of site conditions FORMIND has the potential to simulate stands like Gunung Rara with similar accuracy as the other forest reserves.

To exclude data of the last years in Segaliud Lokan2 from further testing was motivated by the small spatial scale of only 2 ha and the large temporal differences in mortality rates (0.0 % y^{-1} for 10 years and rates between 20 and 40% y^{-1} in the last years). We think errors in field measurements might be one reason for the unexpected data. Additionally, as our main objective in this benchmark testing was to validate our growth model, an assumed average mortality for the whole observation time $\neq$ 0.0 % y^{-1} in Segaliud Lokan2 would largely cover tree growth effects.

The good agreement between simulation and field data are first hints that FORMIND1.1 is an adequate tool for simulating the growth of tropical rain forest not only on a short time scale of some decades but also for long time forest development. Results over simulation periods of 100 years and more were already published in Köhler & Huth (1998a, b).

Given the wide variation in calculated mortality rates, one might ask how safe is it to use an average or published rate to predict forest development. With a sensitivity analysis, which highlights the influences of different parameters, the importance of mortality and the acceptable parameter range can be analysed (Huth et al. 1998). Investigations show that mortality is important for model behaviour, but parameter values might vary reasonably without changing results in general. Thus, using more general independent data for benchmark testing might influence the accuracy only slightly.

Because of the variety of different stockings represented in the PSPs the tests show that FORMIND1.1 is applicable within good site conditions on every possible level of forest degradation. Tests shown in this paper together with results for the simulation of primary forest (Köhler & Huth 1998a, b) evaluate it as an accurate tool for estimating the effects of logging operations on tropical forest ecosystems (future work).

Conclusion

Beside Ong & Kleine (1995) and Liu & Ashton (1998), which all used data from permanent sampling plots to parametrise their models, a detailed comparison of growth data with model results has not been performed so far. A comparison is limited to the quality and observation period of available data sets and therefore the case study in this paper is limited to time periods up to twenty years without consideration of regeneration. However, for the development of models, which estimate long term tendencies in tropical rain forests with and without anthropogeneous influences even those limited data are of importance for model evaluation. Thus, the benchmark test gave us indications as to where the limits of model application are. Only with this knowledge can an application of forest growth models to questions of management practise be viable.

Acknowledgement

We like to thank the Forest Research Centre, the Forestry Department Sabah, Malaysia, and the Malaysian-German Sustainable Forest Management Project and their members, especially M. Kleine. Thanks to R. Glauner for coordinating between Malaysian and German projects. Parts of the work for this paper were supported by the Deutsche Forschungsgemeinschaft (DFG). We also owe thanks to two anonymous reviewers, who gave critical but very useful comments.

Additional remarks and comparison with new grouping - not included in the article

Additionally, it should be mentioned that field measurements of stem diameters might be biased due to the fact that the definition of the height (called *at breast height*) at which measurement took place depended on individual people. This height ranged between 120 cm and 160 cm in a comprehensive literature survey (Brokaw & Thompson 2000). Considering the conical form a trunk this might have also influenced our comparison of modelled and measured tree growth. A comprehensive study, which assesses the growth of tropical rain forest trees and its issues for modelling was published recently (Clark & Clark 1999). The authors highlight the importance of growth models for management questions and possibilities of model evaluation with field data.

The same comparisons of the model results and the field data were repeated with the new grouping concept (Chapter 3) and the current version of the model, FORMIND2.0 (Fig. 5.3). The same concept than in Fig 5.2 was used for the visualisation of results. Now, only total values (A,C,D,F) or of species groups with different successional status (B,E) are plotted. Note difference in y-axes between Fig. 5.2 and 5.3. Overall simulation match field data slightly better, especially for total values (C,F) or stem numbers (D-F). If single PFTs are considered (B,E) differences between modelled and measured growth was highest. The number of individuals per PFT is smaller than in original analysis. Thus, the death of few large trees might lead to relative large errors in estimated biomass.

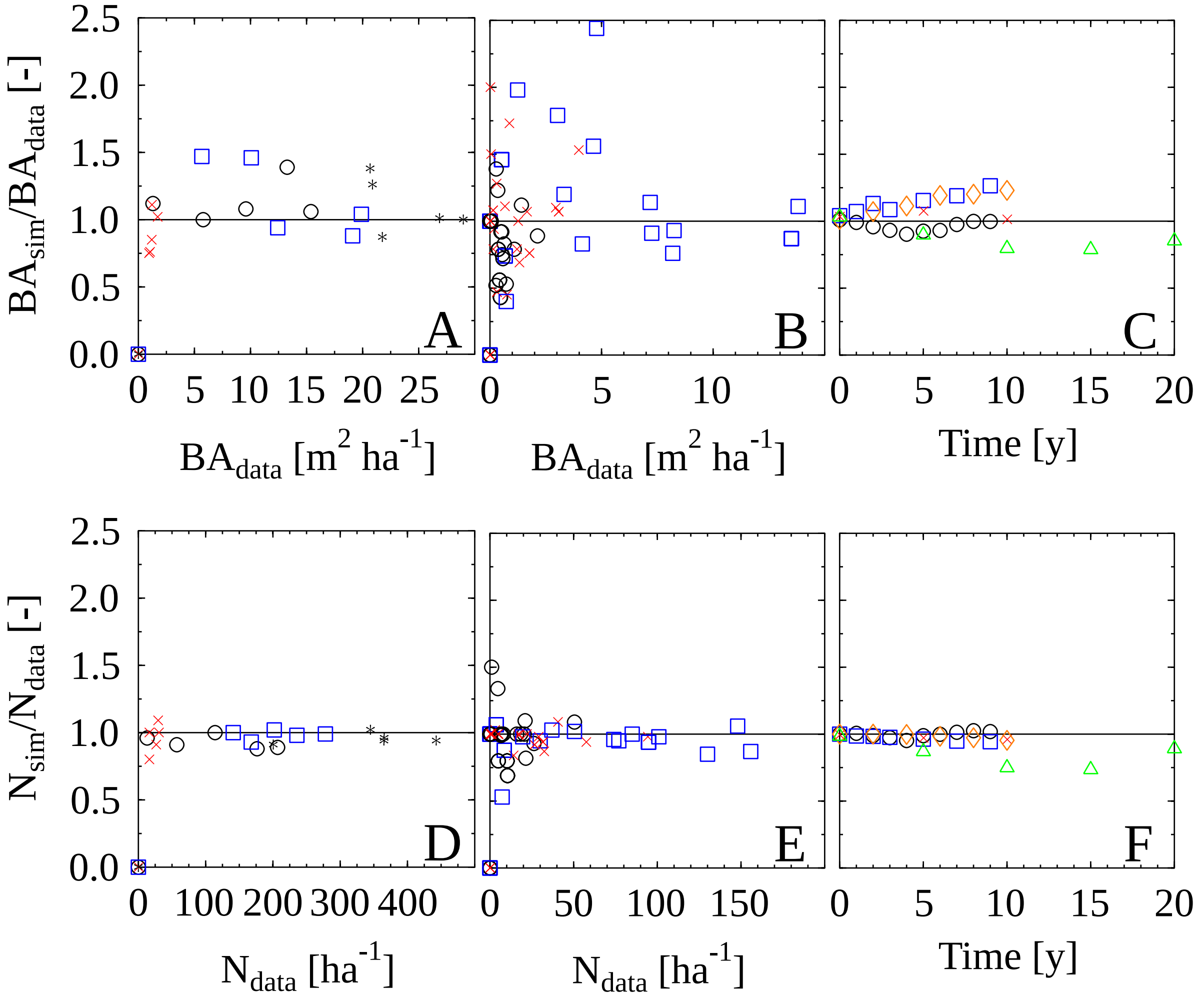

Figure 5.3: Benchmark tests. Relative variation in basal area BA (A-C) and stem number N (D-F) of simulation against field data. A,B,D,E: Final variation after maximum simulation time (= length of observation) as a function of field measurement in last enumeration. For each of the permanent sampling plots (PSPs) data of (A,D) total sum and partial sum of successional groups, (B,E) each PFT, (symbols distinguish only successional status) are plotted (total: ∗; 1: ○; 2: □; 3: ×). C,F: Variation as function of simulation/observation time. Plotted are total basal areas and total stem numbers for PSPs in Garinono (○), Gunung Rara (□), Segaliud Lokan (× and ◇) and Sepilok (△).

Chapter 6

Sustainable timber harvesting in Venezuela: a modelling approach

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Abstract

Reliable data on growth and yield of logged-over forest needed to determine sustainable cutting cycles are widely missing for the tropics. We used the process-based model FORMIND2.0 to analyse growth and yield of logged-over forest in Venezuela under different logging scenarios over a period of 240 years and compared results with unlogged stands. For model evaluation a detailed stability and sensitivity analysis was done. In the absence of further logging, the logged-over stand approached the stand structure of mature forest in terms of bole volume and basal area after about 50-100 years. Thirty year cutting cycles with conventional logging methods and net extraction volumes of 45 and 60 m^3 ha^{-1} $cycle^{-1}$ did not provide sustainable yields under either of two minimum felling diameters (35 or 50 cm) applied. Only the 60 year cutting cycle provided sustainable yields under conventional and reduced-impact logging with the different minimum felling diameters and a range of net volumes extracted (30-60 m^3 ha^{-1} $cycle^{-1}$). With the longest cutting cycle (60 years), bole volume recovered to levels similar to the mature unlogged stand, but the species composition was very different. Scenarios with reduced-impact logging provided a significantly higher timber volume than under conventional logging. The conservation of forest resources will only be possible with long cutting cycles (at least 60 years) in combination with reduced-impact logging.

Keywords: FORMIND2.0, logging scenarios, plant functional types, simulation, tropical forest.

Journal of Applied Ecology (2000), in press.

Introduction

The determination of sustainable cutting cycles and annual allowable cuts is crucial to forestalling further degradation of tropical timber resources. In Latin America, where extensive areas of natural forest have been granted to concession logging in the last few years (FAO 1997), little is known about the long-term dynamics of logged-over stands. The silvicultural system CELOS in Surinam is the only experiment to date giving a fairly comprehensive idea about the management tools needed to sustain timber production in natural forests (de Graaf 1986). However, the suggested cutting cycle of 20 years with a restricted net removal of 20 m^3 ha^{-1} in the CELOS system is based on intensive post-logging treatments. Another long-term study on growth and yield in logged-over and untreated plots in the Brazilian Amazon revealed a low volume increment of timber species, indicating that short cutting cycles are unlikely to be sustainable (Silva et al. 1995, 1996).

Numerous forest models have been developed to bridge the gap between generally short-term empirical data on forest dynamics and the need for reliable long-term yield prediction. Vanclay (1989, 1994), for example, simulated logged-over forest in North-Queensland, Australia, with stand models, based on tree density and basal area. Kürpick et al. (1997) used the gap-model FORMAL to simulate the stand development of logged-over Malayan dipterocarp forest. Process-based models, simulating physiological processes under changing environmental conditions, are another approach to forest modelling (Landsberg & Gower 1997). The FORMIX model and its successor FORMIX3 which were successfully tested in Malayan dipterocarp and peat swamp forest, respectively (Bossel & Krieger 1991; Huth et al. 1994, 1998; Ditzer et al. 2000) combine the advantages of conventional forestry models with process-based models. FORMIX was recently developed into the individual-oriented FORMIND2.0 model which provides more details about forest dynamics compared to its predecessor (cf. Köhler & Huth 1998a; Köhler et al. 2001).

In this paper we test whether prescribed cutting cycles at intervals of 30 years in Venezuela provide sustainable timber yields under the currently uncontrolled logging methods by modelling a logged-over stand with FORMIND2.0. We also test whether controlled logging would allow cutting cycles to be shortened and still allow sustainable timber yields. Finally, we simulate the impact of different cutting cycles, logging methods and extraction volumes on the ingrowth and mortality of commercial species, and species composition. The results are compared with stands that have either never been logged or logged only once.

Material and methods

Study site

The 7000 ha 'Estación experimental' of the Universidad de Los Andes is part of the 'Reserva Forestal de Caparo' located in the western Venezuelan plains (7°30'N, 70°45'W; elevation 100 m). The mean annual rainfall is 1750 mm, with a pronounced dry season from December to March (monthly precipitation < 50 mm). The average annual temperature is 24.6°C. The soils are of alluvial origin and relatively fertile compared to other neotropical lowland areas (Hase & Fölster 1982). Intensive sedimentation by river flooding has resulted in a fine-scaled microrelief, ranging from sandy levee sites to clay-rich depressions. Inundation of depressions lasts up to nine months, depending on soil texture, relief and ground water level (Franco 1979). Levee sites, by contrast, are well-drained throughout the year.

The high-forest of Caparo, naturally distributed on well-drained and poorly drained sites up to an inundation period of six months, is classified as 'moist semi-deciduous' (Lamprecht 1989). On both sites, the palm *Attalea maracaibensis* (Mart.) Burret (Arecaceae) and the large tree *Bombacopsis quinata* (Jacq.) Dugand (Bombacaceae) are the predominant components in terms of basal area share (Franco 1979; Kammesheidt 1994). A total of 53 tree and palm species $\geq$ 10 cm d.b.h. have been recorded and both the well-drained and poorly drained sites are similar in stand structure and species composition (Kammesheidt 1994, unpubl. data). The number of deciduous trees increases from well-drained to poorly drained sites (Franco 1979).

Logging, carried out on both site types, started in the early 1970s. In the beginning, only *B. quinata*, *Swietenia macrophylla* King and *Cedrela odorata* L. (both Meliaceae), and *Cordia thaisiana* Agostini (Boraginaceae) were logged. Currently, more than 20 species are logged (L. Lugo, pers. comm.). The shift from few to many merchantable species and increasingly mechanised logging has resulted in an increase in the level of damage on residual stands compared with stands logged in the 1970s. Although logging is carried out by a local sawmill owner under the supervision of university staff, no efforts have apparently been made to reduce the impact of logging on residual stands. About one-third of the individual logging unit (100 ha) is actually affected by logging; in this third, on average, 10 trees with a standing bole volume of 66.5 m^3 ha^{-1} are removed (Kammesheidt 1998). No post-harvest treatments are carried out.

Data set

The data base for modelling was an inventory of logged (5-, 8-, 19 years after timber harvest) and unlogged stands (hereafter 'mature forest': MF), made in late 1991. The actual logged area was delimited (27-37 ha per 100 ha logging unit). Thereafter, 30 plots of 400 m^2 (1.2 ha in each of the logged stands) were put at systematic distances along transect lines using tape and compass. In MF (total area ca. 30 ha), 25 plots were established in the same way. In all stands, a roughly equal number of plots were laid out on well-drained and poorly drained sites, respectively. Trees and palms $\geq$ 10 cm d.b.h. were measured; seedlings and saplings were sampled in subplots nested in the major sampling unit. Results refer to the stand 5 years after logging (LG5) because it represents a damage level, judged by the proportion of landings in the overall area logged, between those of the other two logged stands (cf. Kammesheidt 1994).

Species grouping

Shrub, tree and palm species (total number: 127 spp., species list available online: http//:www.usf.uni-kassel.de/archiv/dokumente.en.htm, and in Appendix Table B.4) were assigned to 12 different plant functional types based on successional status and maximum height at maturity (Table 6.1), following an approach developed for rain forest in Malaysia (Köhler et al. 2000b). The successional status of species was determined by their gap association at juvenile stage, spatial pattern and ability/inability to persist in closed mature forest as adult individuals (Kammesheidt 2000; unpubl. data). Similar functional groups are defined by Swaine & Whitmore (1988), Manokaran & Swaine (1994) and Thomas & Bazzaz (1999).

Description of the model

FORMIND2.0 is an individual-oriented forest growth model (Köhler & Huth 1998a; Köhler et al. 2001) to simulate stand development under certain scenarios, e.g. different cutting cycles. The model includes tree growth, competition, mortality and regen-

Table 6.1: Autecological characteristics of plant functional types (PFTs) in the Caparo forest, Venezuela. Height and d.b.h. range at maturity. Height group (HG) and successional status (SS). Total number of species (No) in the different PFTs. Relative abundance of trees (>10 cm d.b.h.) in the mature forest (MF) and the stand 5 years after logging (LG5).

Plant functional type	Height (m)	D.b.h. (cm)	PFT index	HG	SS	No	MF (%)	LG5 (%)
Mid successional shrub spp.	1-10	2-10	1	1	2	18	-	-
Late successional shrub spp.	1-10	2-10	2	1	3	7	-	-
Small early successional spp.	10-15	10-25	3	2	1	3	-	2.9
Small mid successional spp.	10-15	10-25	4	2	2	11	3.7	2.7
Small late successional spp.	10-15	10-25	5	2	3	17	0.3	4.6
Medium-sized early successional spp.	15-30	20-70	6	3	1	2	1.0	13.1
Medium-sized mid successional spp.	15-30	20-70	7	3	2	11	6.0	9.9
Medium-sized late successional spp.	15-30	20-70	8	3	3	26	17.4	14.2
Large mid successional spp.	30-40	60-100	9	4	2	16	14.9	8.3
Large late successional spp.	30-40	60-100	10	4	3	12	15.6	9.1
Small palm sp.	1-15	5-10	11	5	4	1	-	-
Medium-sized palm spp.	15-30	10-50	12	6	4	3	41.0	35.1

eration. The main processes including improvements on former versions are described below (functional relationships are found in Table 6.2).

Spatial structure

The model describes tree competition in patches. These patches have the size typical of natural gaps created by the fall of large trees (=400 m^2, van der Meer & Bongers 1996). The model follows the gap-approach (Botkin et al. 1972; Botkin 1993; Shugart 1998) and is therefore spatially non-explicit. Tree positions of falling trees are determined randomly within single patches. In contrast to most gap-models, FORMIND2.0 simulates a shifting stand mosaic. Thus, several contiguous patches (5 × 5 patches per hectare, each a 20 × 20 m^2 in size) are simulated simultaneously (Smith & Urban 1988; Urban et al. 1991).

Tree growth and competition

Within a single patch, the model calculates stand development based on cohorts of trees belonging to the same plant functional type. A cohort i is characterised by the number of trees N_i and by the size of one representative tree. Using allometric relationships, the size of a tree can be expressed in terms of its above-ground biomass B_i, height h_i, or diameter at breast height d_i. A form factor is applied which takes the difference from an idealistic cylindrical stem into account. Tree height is calculated from diameter. The crown projection area f is calculated from the proportionality of stem diameter to crown diameter d_c (Rollet 1978; Poker 1993). Crown length is proportional to tree height (Burgess 1961; Poker 1993), using a constant factor. Leaf area l is a function of diameter but must be corrected to avoid unrealistic high values in leaf area index $LAI = f/l$, which should not exceed a certain value LAI_{M} (Ashton 1978). The bole volume is calculated by the stem wood fraction τ, wood density ρ_s, and the geometrical relation of a truncated cone from biomass B_i. Using these allometric relationships the distribution of individual tree crowns and their leaf area in the canopy are calculated in horizontal canopy layers of 0.5 m.

The growth of an individual tree is based on its carbon balance. Calculations include photoproduction of the trees and assimilate losses due to respiration, litter-fall and fine root decay. Within a patch the light attenuation I_i downwards in the canopy is calculated from light intensity above the canopy I_0 and the light extinction coefficient k with respect to the absorption of tree crowns. The dependence of specific photosynthetic productivity P_i on irradiance is modelled using a Michaelis-Menten-type light response curve. Photoproduction $\tilde{P}_i$ is calculated from the tree's leaf area and its specific productivity P_i by integrating down the canopy of the tree in question (Monsi & Saeki 1953). Differences between wet and dry season y are considered in terms of different light intensity I_{0y}, the different length of daily photoactive period $S_{\mathrm{D}y}$, and the different length of seasons $S_{\mathrm{S}y}$. We assume an increasing limiting effect of water transport deficiencies with increasing tree height. Actual productivity is calculated by applying a size-dependent limitation factor $q(d_i)$ according to $q(d_i) = 1 - (1 - q_{D_{\mathrm{M}}}) \cdot (\frac{d_i}{D_{\mathrm{M}}})^2$, where D_{M} is the maximum diameter of trees and $q_{D_{\mathrm{M}}}$ is the limitation factor at maximum tree height (corresponds to the aging factor c_s of Landsberg & Waring 1997). With the condition of no tree growth at maximum diameter, $q_{D_{\mathrm{M}}}$ can be calculated from the parameter set. Assimilate losses are estimated in relation to tree biomass (Kira 1978; Yoda 1983). Losses are composed of root decay, litter-fall and respiration of tree organs and leaves. We distinguish between a biomass-dependent maintenance respiration $R_{\mathrm{m}}(B)$ and growth respiration R_{G} (Ditzer et al. 2000). This leads to our main growth equation

$$\frac{\mathrm{d}B_i}{\mathrm{d}t} = \tilde{P}_i \cdot q(1 - R_{\mathrm{G}}) - R_{\mathrm{m}}(B_i) \qquad (6.1)$$

Water balance is not included in the model. The calculation of tree growth is performed in annual time steps.

Competition is modelled in terms of competition for light as described above and competition for space as described below concerning *mortality*.

Mortality
Mortality is modelled on an annual basis at a basic mortality rate M_B. To this is added a diameter-dependent mortality M_D, which is zero above a threshold diameter $d_t = M_{\mathrm{D1}}$. Thinning is assumed to occur in dense patches. Mortality is modelled as stochastic event. Senescent trees ($\geq$ 10 cm d.b.h.) die and fall with probability W; they knock down smaller trees in neighbouring patches and create gaps. The number of trees N_{F} destroyed from the total number N_p in the target patch p is calculated from the crown projection area f_{F} of the falling tree relative to patch size A ($N_{\mathrm{F}} = N_p \frac{f_{\mathrm{F}}}{A}$).

Regeneration
Seed germination depends on minimal light intensities I_S on the forest floor. It is assumed that intact forest surrounding the simulation area supports a constant seed input N_{S}. Incoming seeds are added to a seed pool, which takes into account the variance in the length of dormancy (M_{S}) between plant functional types (cf. Garwood 1983, 1989).

Parameters and initial conditions

Table 6.3 contains the parameters used for the simulations. Data on the light environment are drawn from Veillon (1989) and Kammesheidt (unpubl. data). Most allometric relations ($h = f(d), c_{\mathrm{P}}$) are based

Table 6.2: Description of parameters including functional relationships.

Parameter	Description
	Environmental parameters
k	Light extinction coefficient
I_0	Light intensity above canopy
S_{D}	Daylength
S_{S}	Length of wet/dry season
	Establishment parameters
D_{S}	Initial diameter of seedlings
$I_{\mathrm{S}s}$	Minimal light intensity for germination
$N_{\mathrm{S}s}$	Ingrowth rate of seeds into seed pool
	Mortality parameters
M_{B}	Basic mortality rate
M_{S}	Mortality rate of seeds
$M_{\mathrm{D}j}$	Size dependent mortality rate ($M_D = M_{\mathrm{D0}} - M_{\mathrm{D0}}/M_{\mathrm{D1}} \cdot d$)
W	Probability of a dying tree to fall
	Tree physignomic parameters
D_{M}	Maximum diameter
c_{P}	Crown length fraction
τ	Fraction of stemwood biomass to total aboveground biomass
h_{0h} and h_{1h}	Height = f(diameter) ($h = d/(1/h_{0h} + d/h_{1h})$)
γ_{j}	Form factor = f(diameter) ($\gamma = \gamma_0 \cdot exp(\gamma_1 \cdot d^{\gamma_2})$)
f_{j}	Crown diameter = f(diameter) ($d_c = (f_0 + f_1 \cdot d^{f_2}) \cdot d$)
l_{j}	Leaf area = f(diameter) ($l = l_1 \cdot d + l_2 \cdot d^2 + l_3 \cdot d^3$)
LAI_{M}	Maximal leaf area index of single tree
	Biomass production parameters
P_{M}	Photosynthetic capacity in light response curve
α	Photosynthetic efficiency in light response curve
ρ	Stem wood density
r_{0l} and r_{1l}	Respiration = f(biomass) ($R_{\mathrm{m}}(B_i) = r_{0l} \cdot B^{2/3} + r_{1l} \cdot B_i$)
R_{G}	Specific growth respiration rate ss
m	Leaf transmittance
g	Conversation factor g_{CO2} to g_{odm}

on data derived from Kammesheidt (1994, unpubl. data). The form factor γ, leaf and crown area to diameter relations are taken from measurements of Kato, Tadaki & Ogawa (1978) and Kira (1978) in Pasoh, Malaysia. Data on the photosynthetic response of plant functional types to different light levels are given in Oberbauer & Strain (1984). The wood density of species was determined at the Institute of Wood Technol-

Table 6.3: Parameter estimates for the simulation of the Caparo forest, Venezuela. Parameters with subindex vary according to season(y), successional status (s), potential height (h) (corresponding to SS and HG in Table 6.1), or different functional coefficients (j).

Name	Special	Units	Values					
			Environmental parameter					
k		[-]	0.7					
I_{0y}	wet dry	[μmol(p) m^{-2} s^{-1}] ^{a}	816.0	1005.0				
$S_{\mathrm{D}y}$	wet dry	[h]	12.0	12.0				
$S_{\mathrm{S}y}$	wet dry	[-]	0.67	0.33				
			Establishment parameter					
D_{S}		[m]	0.01					
$N_{\mathrm{S}s}$	s=1-4	[ha^{-1} y^{-1})]	500	200	25	50		
$I_{\mathrm{S}s}$	s=1-4	[fraction of I_{0y}]	0.05	0.01	0.01	0.01		
			Mortality parameter					
$M_{\mathrm{B}s,h}$	s=1; h=1-6	[y^{-1}]	0.00	0.12	0.08	0.00	0.00	0.00
$M_{\mathrm{B}s,h}$	s=2; h=1-6	[y^{-1}]	0.06	0.05	0.035	0.03	0.00	0.00
$M_{\mathrm{B}s,h}$	s=3; h=1-6	[y^{-1}]	0.05	0.04	0.03	0.025	0.00	0.00
$M_{\mathrm{B}s,h}$	s=4; h=1-6	[y^{-1}]	0.00	0.00	0.00	0.00	0.01	0.01
$M_{\mathrm{S}s}$	s=1-4	[y^{-1}]	0.1	0.5	1.0	1.0		
$M_{\mathrm{D}j}$	j=0-1	[y^{-1}, m^{-1}]	0.4	0.2				
W		[-]	0.40					
			Tree physignomic parameter					
$D_{\mathrm{M}s,h}$	s≠1; h=1-6	[m]	0.10	0.25	0.70	1.00	0.25	0.40
$D_{\mathrm{M}s,h}$	s=1; h=2-3	[m]		0.13	0.35			
c_{p}		[-]	0.358					
τ		[-]	0.7					
h_{0h}	h=1-6	[cm m^{-1}]	1.63	1.63	1.41	1.50	0.22	0.22
h_{1h}	h=1-6	[m^{-1}]	19.9	19.9	35.7	45.4	325.7	325.7
γ_j	j=0-2	[-, cm^{-1}, -]	2.575	-1.409	0.0358			
f_j	j=0-2	[-, -, -]	0.132	0.933	-0.6615			
l_j	j=1-3	[$\frac{\mathrm{m}}{\mathrm{cm}}$, $\frac{\mathrm{m}}{\mathrm{cm}^2}$, $\frac{\mathrm{m}}{\mathrm{cm}^3}$]	3.197	0.0684	-0.000379			
LAI_{M}		[-]	2					
			Biomass production parameter					
$P_{\mathrm{M}s}$	s=1-4	[μmol(c) m^{-2} s^{-1}] ^{a}	27.7	11.3	6.8	6.8		
α_s	s=1-4	[μmol(c) μmol(p)$^{-1}$] ^{a}	0.043	0.043	0.043	0.043		
ρ_s	s=1-4	[t$_{odm}$ m^{-3}]	0.24	0.69	0.69	0.75		
r_{0s}	s=1-4	[t$_{odm}^{3/2}$]	0.20	0.06	0.05	0.04		
r_{1s}	s=1-4	[-]	0.60	0.02	0.015	0.04		
R_{G}		[-]	0.25					
m		[-]	0.1					
g		[g$_{odm}$ g$_{CO2}^{-1}$]	0.63					

[a] p: photons; c: CO_2

ogy and Wood Biology of Göttingen University. Parameters for respiration processes (r_{0s} and r_{1s}) were investigated using parameter variation to gain realistic diameter increment values for different size classes and light conditions. Mortality and ingrowth rates correspond to typical values found in literature (Swaine 1989; Condit et al. 1992; 1995a, b; Carey et al. 1994; Phillips & Gentry 1994; Silva et al. 1995; van der Meer & Bongers 1996). Mortality M is correlated to the diameter growth rate g_{d} and maximum size $d_{\max}$ such that $\omega = d_{\max}/g_{\mathrm{d}} \cdot M$ is roughly constant. Otherwise the number of large trees would be overestimated ($\omega << 1$) or only small trees would occur ($\omega >> 1$) (Chave 1999b).

From data sets of the two stands chosen for simulations (MF, LG5), 25 patches (of 400 m^2 each) — randomly chosen in the case of LG5 — were clustered to form the initial data set for one hectare. The functional groups were then aggregated into different cohorts regarding their diameter (d.b.h. class of 5 cm). To minimise stochastic effects in tree mortality, each simulation was performed for an area of 25 hectares.

The model was written in the programming language C++. Simulations were run on a PC (400 MHz, system Linux), taking on average 9 sec to simulate the growth of 1 ha of rain forest over 100 years.

Stability and sensitivity analysis

For model evaluation a stability analysis of the long-term model dynamics was performed. It compares field data of the mature stand (MF) with its dynamic variability following the theory of long-term stability in tropical mature forests (Whitmore 1988) without consideration of climate or evolutionary changes. Stability indices were calculated by averaging the values of 28 result variables (leaf area index LAI, succession stages (GAP phase: no trees with $h \geq$ 15m in patch, $BUILDING$ phase: trees with $h \geq$ 15m in patch, and $MATURE$ phase: trees with $h \geq$ 30m in patch), basal area BA, bole volume V of the whole stand, relative basal area of the different plant functional types, successional status, or height groups, total (N) stem number and as function of diameter in four size classes (N_{0-30}, N_{30-60}, N_{60-90}, N_{90}) over the last 100 from 240 simulated years and normalising them with their initial values (cf. Huth & Ditzer 2000a). A stability index of 1.0 corresponds to a stable variable, whose long-term averaged values are identical to field data.

The sensitivity of 28 result variables (same as for stability analysis) to parameter variations was investigated by varying the 60 parameters in Table 6.3 within their realistic range (values found in the literature and within physical boundaries). Seven simulations over 4 hectares and 100 years in the mature stand were performed for each varied parameter, including one simulation with the standard value. Mean values (v) of the chosen result variables were averaged over the seven simulations. The coefficient of variation (CV) from the resulting average (a) was chosen as an indicator to find out whether the individual variable responded sensitively ($CV = \mid v - a \mid / a \times 100$).

Logging scenarios

On the basis of the logging practices in the study area documented by Plonczak (1989) and Kammesheidt (1994) and data from the literature (Hendrison 1990), the following logging scenarios were simulated: (1) during conventional logging one-third of the area was converted into roads and log-landings (complete removal of the residual stand). Beside felling damages which destroyed an area proportional to the crown projection area of the cut tree, 55% of trees in the felling area were killed due to skidding operation. (2) By applying reduced-impact logging, landing areas diminished to 12% and skidding damage was limited to 25%. If possible, trees were felled into existing gaps under both logging scenarios. In the initial phase after logging (year 1-10), mortality was two and three times higher than the normal rate found in mature forest for reduced-impact and conventional logging, respectively. Cutting cycles of 30, 40 and 60 years, respectively, with three net harvest volumes (30, 45 and 60 $\text{m}^3\ \text{ha}^{-1}\ \text{cycle}^{-1}$, respectively), applying a minimum felling diameter (MFD) of 35 and 50 cm, were simulated. The simulation time was 240 years. The simu-

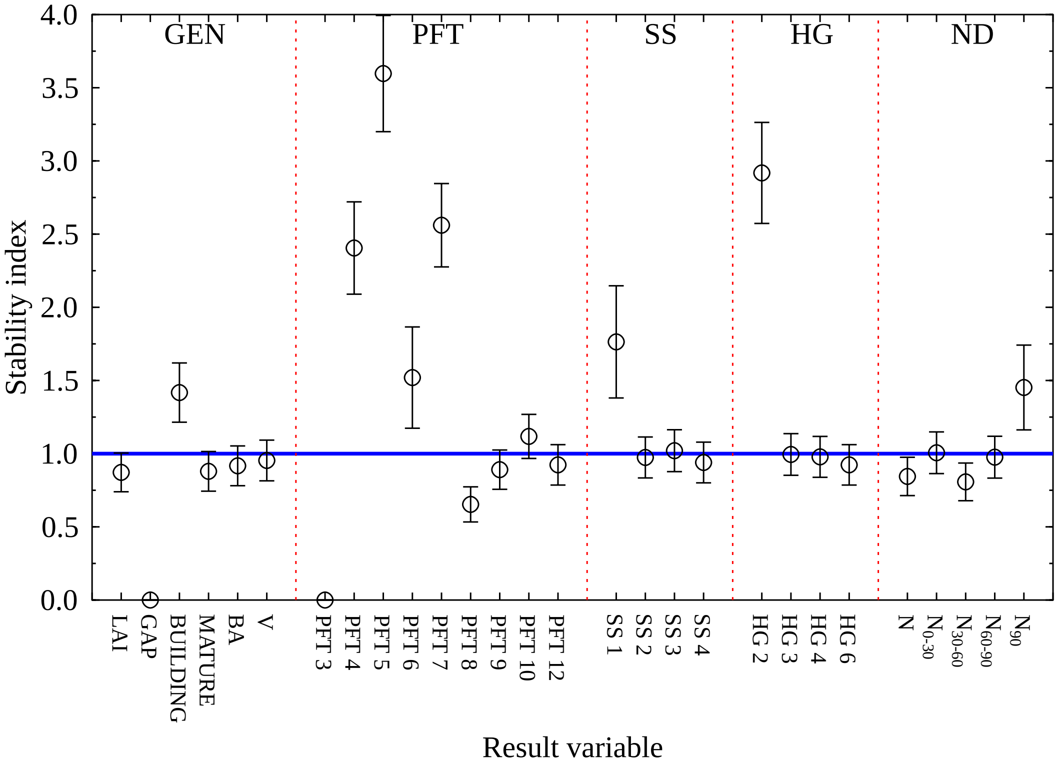

Figure 6.1: Stability index for the simulation of a mature forest stand. A stability index of 1.0 corresponds to a time averaged stable variable. The simulations were run over 240 years in an area of 25 ha, stability was analysed over the last 100 years (mean±SD). Result variables are classified according to their level of information: *GEN:* General information refers to: total leaf area index LAI, succession stages (GAP phase: no trees with $h \geq$ 15m in patch, $BUILDING$ phase: trees with $h \geq$ 15m in patch, and $MATURE$ phase: trees with $h \geq$ 30m in patch), basal area BA and bole volume V of the whole stand. *PFT:* relative basal area of the different plant functional types (cf. Table 6.1). *SS:* relative basal area of the different successional stages (cf. Table 6.1). *HG:* relative basal area of the different height groups (cf. Table 6.1). *ND:* Stem number as function of diameter (N: all trees) for trees between 0 and 30 cm d.b.h. (N_{0-30}), 30 cm and 60 cm d.b.h. (N_{30-60}), 60 cm and 90 cm d.b.h. (N_{60-90}) and above 90 cm d.b.h. (N_{90}). For the stability analysis only trees ≥10 cm d.b.h. are considered. Consequently, $PFT1, PFT2, PFT11, HG1$ and $HG5$ are omitted.

lated area comprised 25 ha. To obtain the given net volume, 30% harvest loss had to be added to the logged volume corresponding to gross volumes of 43, 65 and 86 m^3 ha^{-1} $cycle^{-1}$, respectively. From all medium-sized and large, mid and late successional species at minimum felling diameter, trees were randomly chosen for logging until the target harvest volume was reached. Early successional species are not merchantable and did not attain a diameter $\geq$ 35 cm (Kammesheidt 2000). In case of understocking (if harvestable standing volume is lower than the target gross volume for logging), logging was suspended for one cutting cycle and hence, timber yield was unsustainable.

Data analysis

The G-test was applied to test for differences in the proportion of successional groups in bole volume between logging scenarios. The z-test was used to compare the means of ingrowth and mortality, and bole volume between different logging methods, and the unlogged and once logged stand (Fowler et al. 1998). Two-way ANOVA was employed to test for differences in bole volume prior to logging within and between different logging scenarios.

Results

Model evaluation

The results of the stability analysis of a mature forest are shown in Fig. 6.1. Most general result variables were stable with stability indices between 0.85 and 1.0, except for those relating to the proportion of forest in the gap and building phase. In fact, the initial stand comprised no area in the gap phase, keeping this value at zero and influencing directly the proportion of forest in the building phase. Relative basal areas were stable in PFTs with different successional status and maximum heights. Only $SS1$ and $HG2$ showed values fairly far from stability (1.7 and 2.8, respectively). In the individual PFTs the forest was more stable in PFTs with higher indices, referring to larger trees and higher absolute values in basal area. $PFT3$ was not found in the initial site and therefore its stability index was zero. $PFT4$, $PFT5$ and $PFT7$ were unstable with values between 2.2 and 3.2. In the stem diameter distribution, different diameter classes were stable, total stem number N declined to 80%, while the number of large trees ($N90$) increased by 50%.

In sensitivity analysis, the parameters were grouped according to the different parts of the model they belonged to (Fig. 6.2). Results showed a sensitive behaviour of the forest in gap phase (GAP), relative share of early successional species ($SS1$) and number of trees $\geq$ 90 cm ($N90$). Their values varied throughout nearly the whole parameter range (CV>50%). Relative share of some PFTs ($PFT3 - PFT7$) were medium sensitive over a wide range of parameters. By contrast, the total leaf area index (LAI), forest in mature phase ($MATURE$), total basal area (BA), total stem number (N) and with some exceptions total bole volume (V), and relative share of mid and late successional species ($SS2, SS3$) did not react sensitively. The parameter values for the initial diameter of ingrowing seedlings D_{S}, general and various single mortality rates M_{B} generated sensitive responses over the whole range of result variables. The parameters of the mortality module had a greater influence on simulation results than those of other modules.

Stand development in the absence of logging

The logged stand (LG5) approached the stand structure of mature forest in terms of both basal area and bole volume after about 50-100 years (Fig. 6.3). In the equilibrium phase, mid-successional species dominated over late successional species in both stands. Early successional species disappeared before the equilibrium phase was reached. In both stands, palm species showed a constant high share in basal area. The slight decline of the bole volume and basal area in mature forest over the simulation period indicates that stand structure was crowded at the time of sampling and thinned thereafter.

Figure 6.2: (opposite page): Sensitivity analysis. Analysed were the sensitivity of 28 result variables describing the state of the forest (for abbreviations see Fig. 6.1). The result variables were grouped in five groups: general structure (GEN), abundance of species groups (PFT) and successional groups (SS), abundance of trees in different height classes (HG) and diameter classes (NG). Each parameter was varied within the given range. The grey scale of boxes indicates how sensitive a certain result variable reacts on variations of a model parameter (for abrevations see Table 6.3). Black: high sensitivity ($CV > 50$ %); grey: medium sensitivity (10 % $< CV \leq$ 50 %); white: low sensitivity ($CV \leq 10$ %). The calculation of CV is explained in the text. All simulations werde made for a mature forest of 4 ha (simulation time $t = 100$ y).

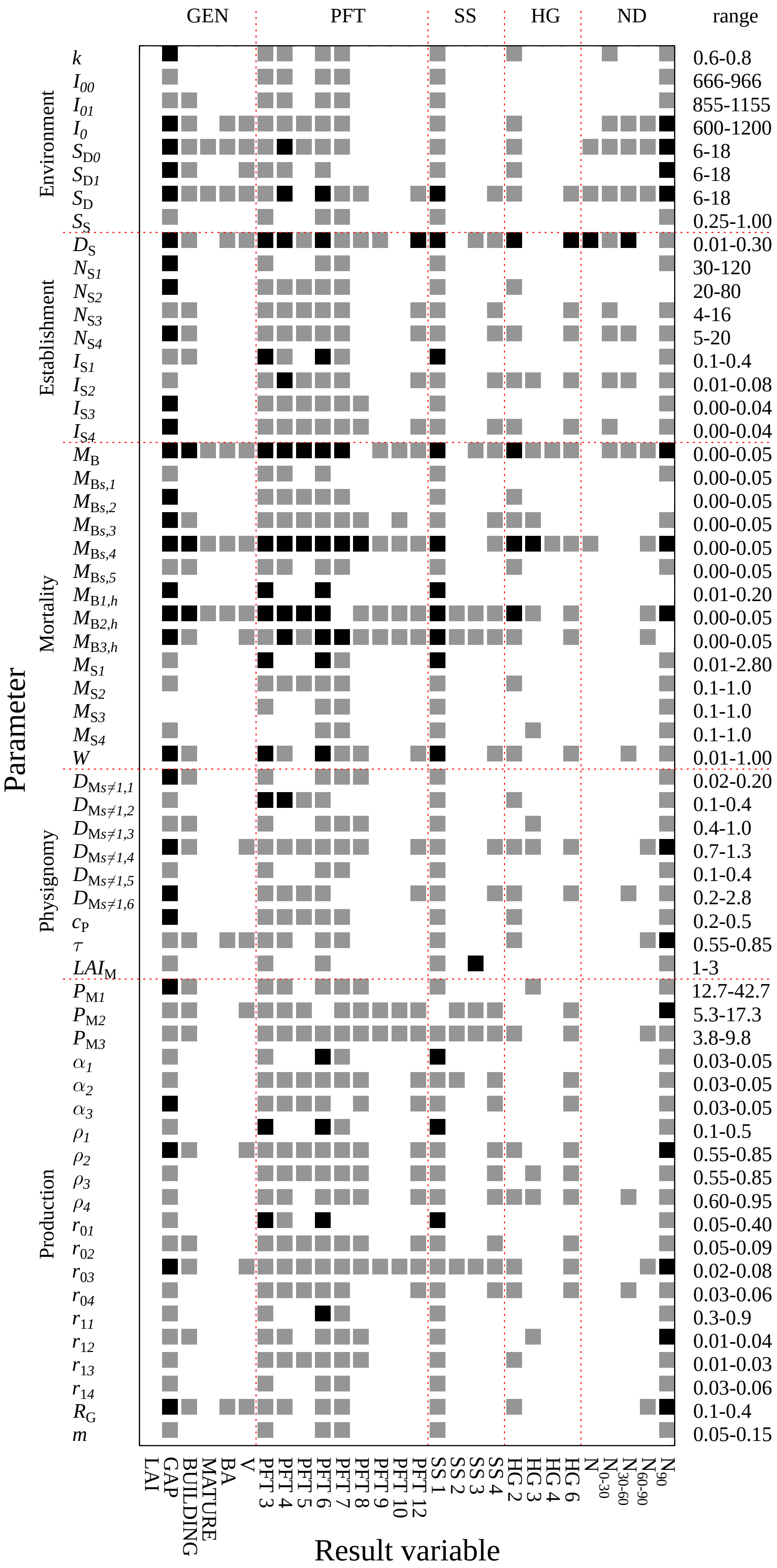

Figure 6.2: Caption are found on opposite page.

Table 6.4: Bole volume of trees ≥ 30 (50) cm d.b.h after and prior to logging applying different logging scenarios (CON = conventional logging, RIL 0 reduced-impact logging) over a simulation period of 240 years. Minimum felling diameter (MFD) either 35 or 50 cm. Values for the mature forest (MF) are given as reference. If the individual gross bole volume was not reached, logging was omitted. Mean values and standard deviation for bole volume after/prior to logging were taken from the different number of logging events (n=4-8). Mean annual bole volume increment was averaged over the simulation period.

Logging method	Cutting cycle (y)	Net volume extracted (m^3 ha^{-1} cycle^{-1})	Bole volume (m^3 ha^{-1}) after logging mean±SD	range	prior to logging mean±SD	range	Times logging omitted	Mean annual bole volume increment (m^3 ha^{-1} y^{-1}) mean±SD
MFD=35cm; trees ≥35 cm d.b.h.								
MF					250±14	231–274		0.0±1.2
CON	30	30	33±16	21–71	77±16	65–116	–	3.5±5.9
CON	30	45	43±34	0–90	109±34	65–157	2	3.2±5.3
CON	30	60	60±17	29–71	147±18	116–159	4	3.2±5.0
RIL	30	30	93±11	71–101	138±11	116–147	–	2.7±2.4
RIL	30	45	54±5	45–61	121±6	112–128	–	3.3±2.4
RIL	30	60	25±5	14–30	112±5	101–117	–	3.8±2.6
CON	40	30	79±12	70–105	125±12	115–151	–	3.0±4.8
CON	40	45	44±18	30–84	111±18	97–151	–	3.5±5.3
CON	40	60	19±20	6–64	106±20	93–151	–	3.6±5.5
RIL	40	30	119±7	105–127	165±7	151–172	–	2.3±2.2
RIL	40	45	89±4	83–94	157±5	150–162	–	2.8±2.3
RIL	40	60	64±3	59–67	151±3	146–155	–	3.2±2.3
CON	60	30	133±9	123–146	178±9	168–191	–	2.2±4.0
CON	60	45	108±9	100–123	176±9	168–191	–	2.6±4.0
CON	60	60	80±13	72–103	169±13	161–191	–	2.9±4.2
RIL	60	30	152±4	146–156	199±5	191–202	–	1.8±2.1
RIL	60	45	128±3	123–131	196±3	191–199	–	2.1±2.0
RIL	60	60	109±4	103–113	196±4	191–202	–	2.4±2.1
MFD=50cm; trees ≥50 cm d.b.h.								
MF					208±12	192–232		0.0±1.3
CON	30	30	5±4	2–16	49±5	44–62	–	1.8±1.9
CON	30	45	70±4	67–77	138±4	135–145	4	2.2±3.1
CON	30	60	45±7	39–57	134±7	127–145	4	2.4±3.4
RIL	30	30	51±16	16–65	96±16	62–111	–	2.1±1.8
RIL	30	45	31±19	17–77	99±19	84–145	1	2.4±1.7
RIL	30	60	42±29	2–72	130±30	88–161	3	2.2±2.2
CON	40	30	27±8	19–45	72±8	64–90	–	1.6±1.8
CON	40	45	58±41	10–104	124±42	75–171	2	2.0±2.8
CON	40	60	52±33	5–77	139±35	90–165	3	1.8±2.9
RIL	40	30	66±10	45–75	112±11	90–121	–	1.7±1.4
RIL	40	45	39±9	23–46	106±9	90–114	–	2.1±1.5
RIL	40	60	27±32	5–91	114±33	90–180	1	2.1±2.0
CON	60	30	98±4	93–104	144±4	138–150	–	1.9±2.9
CON	60	45	71±7	65–82	139±7	133–150	–	2.2±3.2
CON	60	60	45±10	37–62	133±10	126–150	–	2.4±3.4
RIL	60	30	119±10	104–131	165±10	150–177	–	1.6±1.9
RIL	60	45	91±6	82–97	160±6	150–165	–	1.9±2.0
RIL	60	60	69±5	62–74	157±5	150–163	–	2.1±2.1

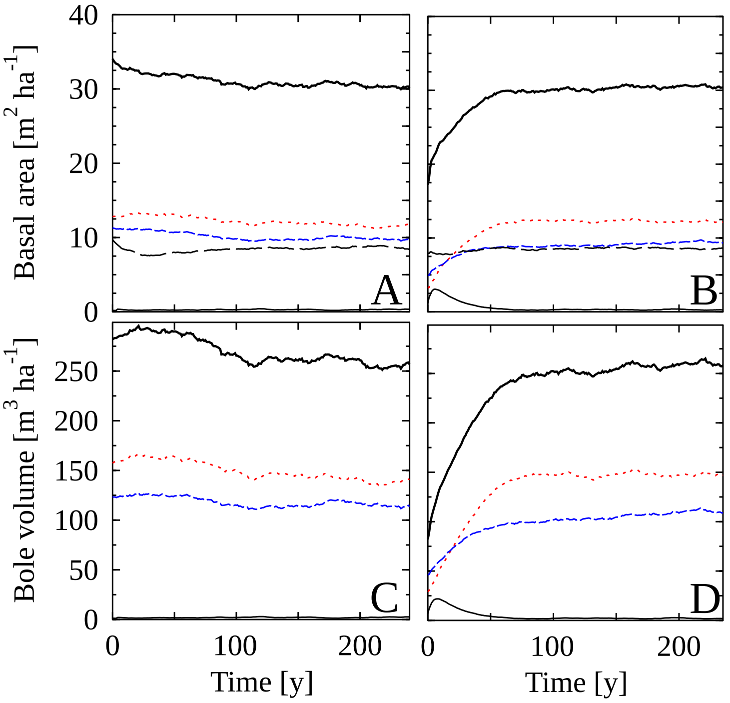

Figure 6.3: Development of the basal area (m^2 ha^{-1}) and bole volume (m^3 ha^{-1}) in unlogged (A, C) and logged stands (B, D) by plant functional type over a simulation period of 240 years in 25 hectares for trees ≥10 cm d.b.h. Total (solid bold line), early successional spp. (solid line), mid-successional spp. (broken dotted line), late successional spp. (broken line), palm spp. (long broken line).

Yield prediction under different logging scenarios

Providing conventional logging with a MFD of 35 cm and 30 year cutting cycles, logging would not take place two and four times, respectively, over a simulation period of 240 years, if the net volume extracted (NVE) were either 45 or 60 m^3 ha^{-1} cycle^{-1} (Table 6.4). All other logging scenarios with a MFD of 35 cm provide a merchantable volume in any of the individual cutting cycles. Conventional logging methods with a MFD of 50 cm and 30 year cutting cycles are unlikely to be sustainable even with low NVEs of 30 m^3 ha^{-1} because the overall volume prior to logging was on average only slightly higher than the minimum level of 43 m^3 ha^{-1} needed as gross volume (Table 6.4, Fig. 6.4). An extension of the length of cutting cycle to 40 years — but otherwise unchanged conditions — led to a significant increase in commercial stock ($z = 37.1, P < 0.01$). By applying reduced-impact logging, timber harvest had to be suspended less often.

In logging scenarios with a sustainable timber supply over the 240 year simulation period differences in bole volume after logging, corresponding to the different NVE diminished until the next cutting cycle (Table 6.4). This trend is largely due to the higher bole volume increment with increasing NVE in most scenarios. However, within-group differences in the 40 year cutting cycle prior to logging remained significant ($F_{2,30} = 8.9, P < 0.01$), while differences were insignificant in the 60 year cutting cycle for both MFDs applied ($F_{2,30} < 1.8, P > 0.05$). Differences between logging methods and NVE prior to logging were significantly different in all scenarios ($F_{1,30} > 31.4, P < 0.01$).

Even under the longest cutting cycle with

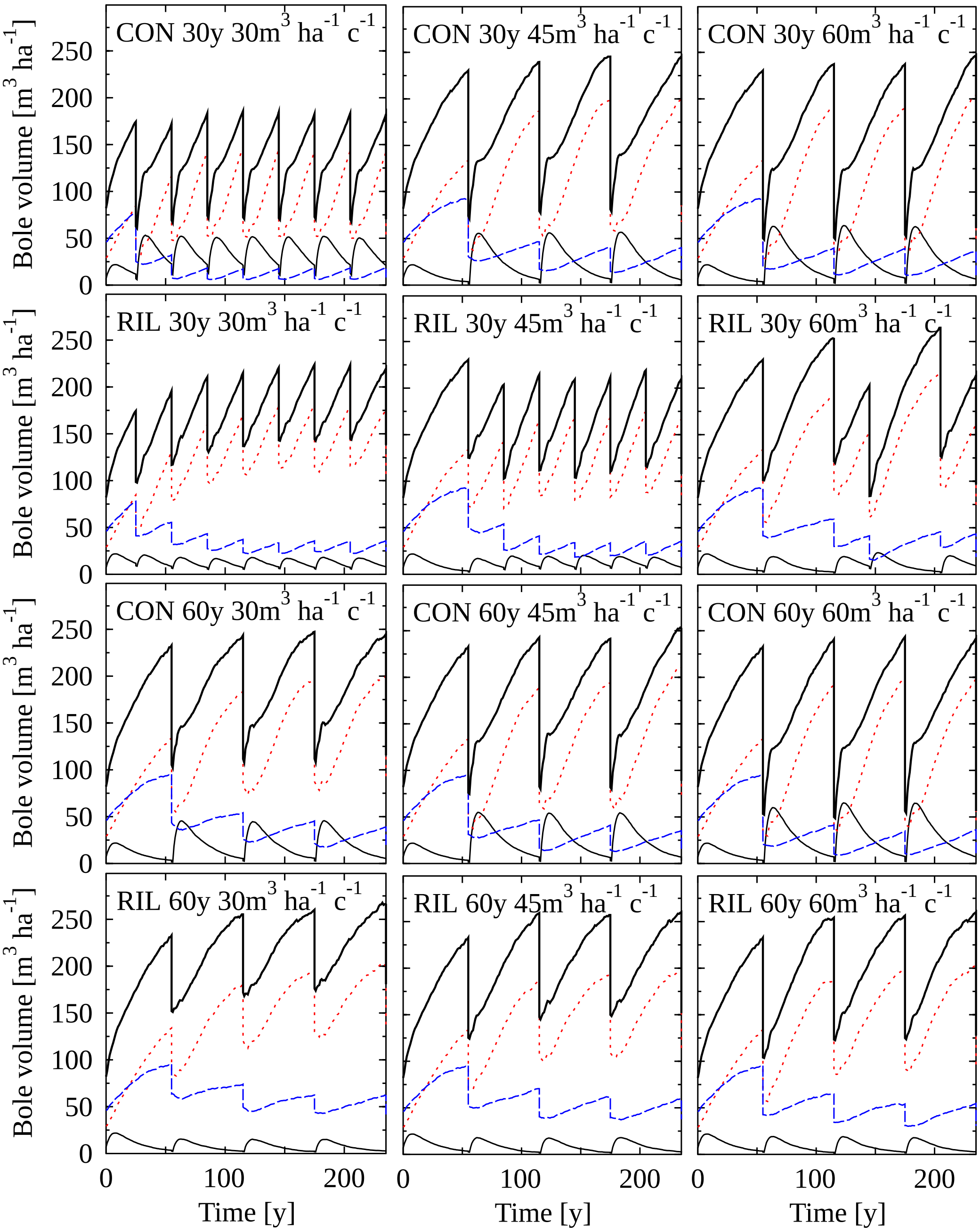

Figure 6.4: Development of bole volume (m^3 ha^{-1}) for a range of logging scenarios by plant functional types over a simulation period of 240 years in 25 heactares for trees ≥10 cm d.b.h. The subheadings indicate logging conditions (method, cycle in years, intensity in m^3 ha^{-1} cycle^{-1}) with RIL: reduced-impact logging; CON: conventional logging. Minimum felling diameter was 50 cm. Total (solid bold line), early successional spp. (solid line), mid-successional spp. (broken dotted line), late successional spp. (broken line).

Table 6.5: Average annual ingrowth and mortality (%) of trees $\geq$ 35 or 50 cm d.b.h., respectively in unlogged (MF), one time (LG5), and several times logged stands under different logging scenarios over a simulation period of 240 years. Minimum felling diameter (MFD) is either 35 or 50 cm. Logging methods are designated as either conventional (CON) or reduced-impact logging (RIL). Data are mean±SD of time averaged values of scenarios with different extraction intensities ($n = 3$).

Logging method	Cutting cycle (y)	Ingrowth	Mortality
MFD=35cm; trees ≥35 cm d.b.h.			
MF		2.7±0.5	2.7±0.3
LG5		3.0±2.5	2.8±2.6
CON	30	6.2±9.7	5.6±9.9
RIL	30	5.1±3.5	4.3±4.5
CON	40	6.0±9.4	5.5±9.8
RIL	40	4.5±2.9	3.9±3.8
CON	60	4.5±7.0	4.4±7.1
RIL	60	3.8±2.6	3.5±2.8
MFD=50cm; trees ≥50 cm d.b.h.			
MF		1.6±0.8	1.6±0.5
LG5		2.3±2.8	1.7±0.6
CON	30	5.7±7.9	3.5±9.1
RIL	30	4.6±4.3	2.6±3.6
CON	40	4.8±7.3	3.1±7.6
RIL	40	4.4±4.8	2.5±3.4
CON	60	4.1±5.1	2.9±6.8
RIL	60	3.3±3.2	2.2±2.5

reduced-impact logging and a low timber extraction of 30 m^3 ha^{-1}, the average bole volume prior to logging was significantly lower compared to mature forest for both diameter limits (z>44.0, P<0.01).

Ingrowth and mortality

Regular logging operations kept the stand under all logging scenarios in a building phase, indicated by the fact that ingrowth dominated over mortality (Table 6.5). Ingrowth was significantly higher than mortality in trees $\geq$ 50 cm d.b.h. under all logging scenarios ($z > 2.6, P < 0.01$), while no significant differences were found in trees $\geq$ 35 cm d.b.h. ($z < 1.4, P > 0.05$). Differences in ingrowth rates between logging methods were insignificant, except for trees $\geq$35 cm d.b.h. in the 40 year cutting cycle ($z = 2.36, P < 0.05$). Although annual ingrowth and mortality was higher under conventional logging, significant differences between logging methods were only found in a few cases. Overall, the rate of ingrowth and mortality declined with longer cutting cycles irrespective of logging methods. However, even under a 60 years cutting cycle and reduced-impact logging, ingrowth and mortality were significantly higher than in both mature forest and LG5 ($z > 2.82, P < 0.01$).

Successional groups of species

Logging methods had a significant influence on the proportion of different successional groups in bole volume ($G > 6.6, P < 0.05$) (Table 6.6). The extension of the length of cutting cycles resulted in a decline of the proportion of early successional species and an increase in late successional species under both conventional and reduced-impact logging. This is also illustrated by the development of these successional groups of species along the 240 years simulation period (Fig. 6.4). Over the whole simulation period, the proportion of successional groups in LG5 differed insignificantly from that of mature forest ($G = 2.4, P > 0.05$), whereas the bole volume was still significantly lower ($z = 13.1, P < 0.01$). Reduced-impact logging kept the standing stock in any of the cutting cycles and MFDs

Table 6.6: Proportion (mean±SD) of plant functional types summarised into successional groups (early (1), mid (2) and late (3) successional spp.; ≥10 cm d.b.h.) in bole volume (m^3 ha^{-1}, mean±SD) in unlogged (MF), one time (LG5) and several times logged stands under different logging scenarios over a simulation period of 240 years. Minimum felling diameter (MFD) is either 35 or 50 cm. Logging methods are desingated as either conventional (CON) or reduced-impact logging (RIL). Bole volume is given as mean annual value out of the average of different net volumes extracted. Data are mean±SD of time averaged values of scenarios with different extraction intensities ($n = 3$).

			Successional groups (%)		
Logging methods	Cutting cycles (y)	m^3 ha^{-1}	1	2	3
MF		270±14	1±0	56±4	44±2
LG5		235±39	3±4	56±6	42±2
MFD≥ 35 cm d.b.h.					
CON	30	144±44	29±18	57±17	14±12
RIL	30	154±36	10±5	70±12	21±10
CON	40	144±39	28±18	56±16	16±14
RIL	40	176±38	7±4	68±12	25±10
CON	60	179±44	15±13	63±15	22±13
RIL	60	201±42	5±4	65±11	30±9
MFD≥ 50 cm d.b.h.					
CON	30	161±45	20±14	61±14	19±13
RIL	30	172±37	8±4	68±12	25±11
CON	40	173±47	16±13	65±15	19±12
RIL	40	181±40	7±4	68±12	25±10
CON	60	179±45	15±13	63±15	23±13
RIL	60	200±42	5±4	65±12	30±9

on a significantly higher level than conventional logging ($z > 1.83, P < 0.05, P < 0.01$). Within the same logging method, the lower MFD applied led to a significantly lower standing stock in short cutting cycles ($z > 3.2, P < 0.01$), except for reduced-impact logging with a 40 year cutting cycle. Only with the longest cutting cycle and reduced-impact logging, differences in species composition to LG5 declined to an insignificant level ($G = 4.0, P > 0.05$). The mean bole volume of all logging scenarios was significantly lower than in both LG5 and mature stand MF ($z > 9.0, P < 0.01$).

Discussion

This study has been a two-step approach to forecast growth and yield of logged-over forest, consisting of testing the model under undisturbed conditions and then simulating logging scenarios. Following this, we discuss the two working steps

Model performance under undisturbed conditions

Although the structure and species composition of mature forest shift continuously on a small scale (Wiens 1999), we think that a stability analysis is worth performing to evaluate model performance. In fact, all forest growth models known to the authors (cf. Liu & Ashton 1995) implicitly accept a so-called ”potential natural vegetation” (PNV), which represents the steady state as a product of model structure and parametrisation. None of them have tested the PNV in detail against field data of mature forest. The critical point of the stability test was whether the site we categorised as mature forest was representative. In a few aspects, the mature forest lacked this representativity. For example, no area was in gap phase and consequently early successional species were rare. We consider these points crucial for the stability analysis. However, a field inventory represents only one condition in space and time. A comparison with the time averaged dynamic as done in this analysis suggests that these points have a minor influence on the quality of the model results. For instance, the time averaged fraction of gap area in mature forest or the proportion of early successional species showed small differences to inital values (cf. Table 6.6). Two further trends need to be discussed: the decrease of most general variables below the 1.0 level (cf. Fig. 6.1), and the increase of most PFTs indices far apart from this level. The latter trend results from the fact that the initial species composition was fairly distinct from the averaged modelled one. Field data of a larger sampling area might be needed to reflect the accuracy of the modelled composition of plant functional types. From our model analysis, we know that recruitment is the most important factor for species composition and needs to be modelled in more detail in future applications. The decline of the values of general variables could be explained by the missing gap phase. The initial data set suggests that the analysed mature forest is a well-structured stand showing high values in basal area, bole volume and leaf area index. The stability index of general variables showed changes below 15%, indicating that the model and its parametrisation is stable and a suitable tool for further analysis of logging scenarios in the Caparo forest.

The sensitivity analysis was undertaken in realistic parameter ranges. This implies that the response in the result variables should not be too sensitive, otherwise a model with that many parameters is not suitable for a sound analysis. The results showed low sensitivity for most parameter variations. The sensitivity of the model to variations in the mortality parameters raises the question of whether these values were chosen properly. However, simulated mortality rates in the mature forest are within the range observed in other neotropical forests (Condit et al. 1992; Carey et al. 1994).

Logging scenarios

Net timber volumes in the range of 30-60 m^3 ha^{-1} $cycle^{-1}$ assumed in the scenarios for the second and subsequent cutting cycles may be perceived as high having in mind the traditionally low intensity of wood removal in Latin America compared to South-East Asia (Plumptre 1996). In fact, the first cutting cycle is selective focusing on the most valuable species i.e. *B. quinata, S. macrophylla* and *C. odorata* in areas where they occur clumped, resulting in low harvest volumes, if referring to the whole logging unit. As individuals of these species are found rarely below the minimum felling diameter MFD (Plonczak 1989; Kammesheidt 1994, 1998), logged-over stands are composed of potential commercial species with a considerably lower market value (cf. Centeno 1995). Further depletion of the most valuable species might result in an increase of log prices of formerly unlogged or rarely logged species. However, even an increase of log prices for less acceptable species would hardly offset the loss of valuable timber species so that a higher volume must be harvested to keep the cost/benefit ratio of the first cutting cycle. To include all species above the legal size in the present logging scenario is reasonable because this is being done already in other concession areas in the western plains (J. Duque, pers. comm.). Also, the currently applied MFD of 50 cm for medium-hardwood species, most of them with a mid-successional status constituting the bulk of commercial volume might be reduced if sawable logs above this size should become scarce. Overall, harvest volume and MFD may vary within the range given in this study depending on the composition of commercial volume in the individual logging unit.

Unlike in other neotropical regions, some empirical data on long-term growth and yield are available to evaluate our results. An average annual bole volume increment of 3.8 m^3 ha^{-1} y^{-1} (SD = 4.2; trees $\geq$ 10 cm d.b.h.) for the 30 years cutting cycle with conventional logging is a conservative growth rate compared with Veillon's (1985) mean figure of 4.4 m^3 ha^{-1} y^{-1} (SD = 0.5) measured in a stand 15-32 years after light logging. The basal area increment in the first 10 years after logging over the simulation period under conventional or reduced-impact logging with 30 years cutting cycles and a removal of 30 and 60 m^3 ha^{-1} $cycle^{-1}$, respectively was 0.3 and 1.1 m^2 ha^{-1} y^{-1}. Lozada (1998) found similar basal area increment rates in the first ten years in experimentally cut stands with a basal area removal of 20-84%. By simulating 240 years, early successional species accounted on average with 83-95% to the basal area increment at any initial phase (1-10 yr) after logging in 30-years intervals, while Lozada (1998) found a mean percentage of 45. This suggests that by shorting cutting cycles over a longer period of time early successional species can become predominant after disturbance.

Ingrowth and mortality declined with increasing length of cutting cycles (cf. Table 6.5). In the 60 year cutting cycle with reduced-impact logging both parameters reached average values in the range of 2.2-3.8% which, is similar to turn-over rates of trees $\geq$ 30 cm d.b.h. in old-growth forest in Panama (Condit et al. 1992). We assumed in our simulation a continuous input of seeds. This might have been too optimistic in case of short cutting cycles. In combination with a low minimum felling diameter at least some commercial species will be harvested before they have attained their reproductive stage. Thus, stand composition will either shift to common species capable of early reproduction or overall regeneration will decline.

We simulated the spatial pattern of disturbance associated with logging. Differences between logging methods in terms of area damaged could be even more pronounced taking into account that cut trees are expected to fall swiftly to the ground if vines are cut well before logging operation as assumed in our model. Conventional logging methods do not consider vine cutting; this results in tree tangles which extend the canopy gap area (cf. Johns et al. 1996). Vine cutting may become an even more important measure in logged-over stands because these areas support a proliferation of lianas (Kammesheidt 1999). With reduced-impact and conventional logging, respectively 23-35% and 50-73% of the simulated area was damaged (i.e. log-landings, felling and skidding areas), corresponding to a basal area removal of 2.5-5 m^2 ha^{-1} $cycle^{-1}$.

By contrast, Hendrison (1990) found in Suriname with a basal area removal of 4 m^2 ha^{-1} $cycle^{-1}$ that 22 and 36%, respectively of the forest area was damaged under controlled and uncontrolled logging. The much higher damage level with conventional logging in Venezuela highlights the careless logging methods in the study area.

The data set for simulation combined well-drained and poorly drained sites. The latter sites might show a slower rate of tree establishment and lower diameter increment rates than the well-drained site owing to different soil water availability in the rainy and dry season. This may result in a different speed of succession. To date, however, no study has tested this hypothesis.

Simulations were made under the assumption of no disturbance other than logging and gap creation owing to tree fall. Fire, for example, is a real hazard because of the considerable increase in fuel mass after logging (cf. Nepstad et al. 1999) which is easily inflammable during the pronounced dry season. Particularly short cutting cycles with conventional logging methods, leaving large tracts of open forest, increase the susceptibility to fire.

Conclusions

Both the stability and sensitivity analysis showed that FORMIND2.0 simulates the stand dynamics of Caparo forest within realistic limits. The model's capability to simulate the spatial heterogeneity of stands with high resolution makes the model useful for simulating growth and yield of logged-over forest. Whether cutting cycles identified as sustainable in terms of timber yield, are economically viable in the long run will strongly depend on species composition and log quality of merchantable trees. Reliable forecasts to this end will offer new challenges to forest modelling.

Acknowledgements

We thank F. Hapla, Göttingen University, who determined the wood density of selected tree species. H. Bossel, J. Chave, A.R. Watkinson, and an anonymous reviewer provided helpful comments on the manuscript. P. Köhler was funded by the Otto-Braun-Foundation of the University of Kassel.

Chapter 7

The effects of logging, fragmentation and recruitment on growth of dipterocarp forest

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Abstract

As deforestation through logging continues, danger to residual stands increases. Overuse of natural resources and a shortage in recruitment rates as indicated in recent research warrant having serious attention to those processes. We contibute to current discussion with a comprehensive simulation study for assessing various impacts on tropical forest dynamics. The effects of different recruitment assumptions, size of observed area, boundary conditions, logging methods and harvesting intervals on growth and yield of two different tropical forest stands in Deramakot (Sabah), Malaysia were analysed. For this purpose, results of simulations of 70 different scenarios with the process-based forest growth model Formind2.0 were analysed. Formind2.0 is based on calculations of the carbon balance of individual trees belonging to 13 different plant functional types. Simulations suggest that natural recruitment acts as a strong buffer in response to disturbances. Thus, especially in fragmented forests, standing bole volume or number of saplings cannot indicate whether recruitment is sufficient to prevent forest degeneration and species loss. Recruitment rates at small diameters (1 cm) must become a focus of observations. From the detailed description of different logging damages, simple regression functions emerge, which enable us to assess logging impacts. Disturbances in fragmented rain forests lead to shifts in abundances of species and to species loss. Reduced-impact logging methods produce up to three times higher yields than conventional methods. In the latter, yield increases with the length of the harvesting intervals, whereas reduced-impact methods produce maximum yield for a cycle period of 40 years. Results are based on optimistic assumptions, but they show that current logging practice in South-East Asia overuses forests to a significant degree.

Keywords: forest growth model; Formind2.0; individual-oriented model; Malaysia; simulation; tropical rain forest;

Journal of Ecology (2000), submitted.

Introduction

Timber harvesting in tropical forests is a widely discussed topic (Pinard & Putz 1996; Whitmore 1998). Damages to the residual forest vary considerably for different logging techniques and cycles. In addition to its function as global carbon sink (Putz & Pinard 1993; Pinard & Putz 1997) a forest logged according to methods of reduced-impact logging is also expected to increase economic profit compared to a conventional logged forest (Barreto et al. 1998, cost/benefit analysis in Korpelainen et al. 1995). Studies show convincingly that only economically sound approaches will lead to conservation and sustainable practices (Plumptre 1996). In this context, criteria for sustainability and ecological certification of timber are subject of much current debate (Johns 1985, 1997; Fölster et al. 1986; Brown & Lugo 1990, 1994; Bruenig 1996; Ong et al. 1996; Putz & Viana 1996; Weidelt 1996; Rice et al. 1997; Bowles et al. 1998). Computerised simulation models aiming to estimate growth and yield of tropical rain forest should become a useful tool to broaden this discussion (Boot & Gullison 1995; Clark & Clark 1999).

This discussion has motivated a lot of recent work on the simulation of tropical forest growth. Chave (1999) simulated the forest dynamics in French Guiana without anthropogeneous influences. Liu & Ashton (1999) concentrated on the consequences of timber harvest on tree species diversity under different seed dispersal assumptions in Malaysia. Ditzer et al. (2000), Huth & Ditzer (2000), and van Gardingen & Phillips (1999) focused on supporting forest management decisions in Malaysian and Indonesian Borneo, while Pinard & Cropper (2000) simulated the effects of logging on carbon storage in dipterocarp forests.

Our aim is to bridge the gap between some of these studies. In our view, the results of Liu & Ashton (1999) need to be generalised to forest management aspects, since many of their assumptions on forest recruitment are relevant in the context of forest management decisions as discussed by Ditzer et al. (2000). Thus, we analyse in this work various logging scenarios for a forest stand in Deramakot (Sabah), Malaysia with a focus on the recruitment pattern. Moreover, as stated by Plumptre (1996), economy plays an important role in making forest management decisions. Thus, timber yield will be analysed as well.

The simulation model used in this study is the process-based forest growth model FORMIND2.0. FORMIND (Köhler & Huth 1998a) was developed following an individual-oriented approach (Huston et al. 1988; Judson 1994; Liu & Ashton 1995; Uchmański & Grimm 1996). It was used to evaluate the approach of the more aggregated model FORMIX3 (Huth et al. 1998). One important feature of both models is grouping of species into plant functional types PFT (Köhler et al. 2000b). A careful comparison of measured and modelled growth with FORMIND for different forest stands in Sabah, Malaysia has been used to validate the growth and competition processes as included in the model (Köhler et al. 2001). A model application to simulate growth and yield in rain forests of Venezuela was performed recently (Kammesheidt et al. 2000).

In this study we want to answer the following questions for a stand of lowland dipterocarp forest in Sabah, Malaysia. (1) How does the size of the area, the boundary conditions and the recruitment pattern influence forest development? (2) Is there a lower threshold of forest fragmentation, below which natural recruitment will fail? (3) How are forest structure and species composition modified by logging as function of the length of cutting cycle, the logging method and assumptions on recruitment? (4) Is there an optimal combination of the logging parameters (method, length of cutting cycle, recruitment assumptions) which maximises yields and minimises changes in the forest structure?

Methods

Area Description

The study area is Deramakot Forest Reserve (DFR) situated in Sabah (North Borneo, Malaysia, 117°30' E, 5°25' N, 130-300 m asl.). Deramakot has a perhumid climate typical for the inner tropics. Mean annual temperature is 27° with little seasonal variations. Average annual precipitation is about 3500 mm, with no pronounced dry season. The geology of Deramakot is characterised by tertiary sediments, mostly sandstones. The soils are nutrient-poor and prone to erosion once left devoid of tree cover. The prevailing forest type is lowland dipterocarp forest (Schlensog 1997). The forest remained essentially undisturbed until this century. Commercial logging started in 1956. The intensity of logging and of logging damages varies widely (Kilou et al. 1993). In 1991 the Sabah Forestry Department carried out a terrestrial inventory. All trees with a diameter $\geq$10 cm in 0.25 ha sample plots regularly distributed in a 1×1 km grid over the whole reserve of 55,000 ha were recorded. Average basal area was 20.9 m^2 ha^{-1} (SD=9.2 m^2 ha^{-1}; range: 1.3-57.8 m^2 ha^{-1}), indicating logged-over forest compositions (Kilou et al. 1993; Köhler 1998).

Within the Deramakot Forest Reserve, eight research plots with different degrees of disturbance were analysed for tree species composition and forest structure (Schlensog 1997). All trees with a diameter at breast height $d \geq 30$ cm were measured in plots of 90×90 m, small trees ($d \geq 10$ cm), saplings (height$\geq$1.5 m and $d<10$ cm) and seedlings (height<1.5 m) in nested plots of 30×30 m, 30×5 m, and 59 plots of 1×1 m, respectively. Out of the eight plots, three were primary forest stands possibly never logged, four were logged-over stands (two with few pioneers, two dominated by pioneers) and the last one was a recently (one year prior) logged stand using methods of reduced-impact logging.

For the purpose of our simulations, we choose the recently logged stand (plot 4 in the work of Schlensog, labelled L1 in Huth et al. 1998 and here) as an example of forest structure after logging, which also corresponds to most of the forests in DFR, and one of the primary forest stands (plot 1, referred to as P1 here) for reference.

Species grouping

Shrub and tree species (total number: 468 species) were assigned to 13 different plant functional types (PFT) based on their successional status and maximum height at maturity (Table 7.1). The successional status (early, mid, or late) was determined by their growth rates under various light regimes, as well as through a survey of wood densities, which are good indicators of growth rates for most species. Species list including grouping is available online (http://www.usf.uni-kassel.de/usf/archiv/dokumente.en.htm, Appendix of thesis, Table B.2). A detailed description and validation of the grouping concept and its application to Sabah was published elsewhere (Köhler et al. 2000b). Similar grouping concepts are found in Swaine and Whitmore (1988), Manokaran & Swaine (1994), Thomas & Bazzaz (1999), and Kammesheidt (2000). In addition, a subgrouping into commercial and non-commercial species is performed for all mid and late successional species. Since detailed information of the commercial status was not available at the individual tree level, 80 % of mid and late successional species are considered as commercial timber (Sabah-Forestry-Department 1994). A sufficient number of PFTs is essential for the accuracy of the output in the simulation of highly diverse rain forests. However, in the analysis and for the sake of simplicity, we

Table 7.1: Autecological characteristics of 13 plant functional types (PFTs) of Sabah's lowland tree species. H: Height at maturity. SS: successional status. HG: height group. COM: fraction of commercial species in PFT. No: Number of species per PFT (total 468 spp.). P1, L1: Abundance of trees with diameter >10 cm in plot P1 and L1, respectively. Sum of abundances might not match 100 % due to rounding errors. (Modified from Köhler et al. 2000b.)

Plant functional type	H [m]	PFT	SS	HG	COM [%]	No	P1 [%]	L1 [%]
Shrub mid succ. spp.	0-5	1	2	1	0	15	0.0	0.0
Understorey early succ. spp.	5-15	2	1	2	0	5	0.0	4.6
Understorey mid succ. spp.	5-15	3	2	2	80	28	6.9	1.3
Understorey late succ. spp.	5-15	4	3	2	80	65	6.4	0.8
Lower canopy early succ. spp.	15-25	5	1	3	0	14	0.7	65.8
Lower canopy mid succ. spp.	15-25	6	2	3	80	92	18.8	2.1
Lower canopy late succ. spp.	15-25	7	3	3	80	13	0.2	0.8
Upper canopy early succ. spp.	25-36	8	1	4	0	10	0.0	4.6
Upper canopy mid succ. spp.	25-36	9	2	4	80	89	6.6	4.6
Upper canopy late succ. spp.	25-36	10	3	4	80	18	3.6	2.5
Emergent early succ. spp.	>36	11	1	5	0	3	0.0	0.4
Emergent mid succ. spp.	>36	12	2	5	80	93	37.0	11.7
Emergent late succ. spp.	>36	13	3	5	80	24	19.5	0.0

distinguish results only between the three different successional status (early, mid, and late).

Description of the model

FORMIND2.0 is an individual-oriented process-based forest growth model (Köhler & Huth 1998a; Köhler et al. 2001) to simulate spatial and temporal development of uneven-aged mixed forest stands. A complete description including all the relevant functional relationships of the model version FORMIND2.0 was published elsewhere (Kammesheidt et al. 2000). We concentrate in the following after a short general description on the recruitment submodel. Basic functions are shown in the Appendix (of article).

The model describes forest dynamics as a mosaic of interacting forest patches of 20 m^2×20 m^2 in size. Within these patches trees are not spatially explicit distributed, and thus all compete for light and space following the gap model approach (Botkin 1993; Shugart 1998). Allometric relationships connect above-ground biomass, stem diameter, tree height, stem volume and crown dimensions. Using these allometric relationships, the distribution of individual tree crowns and their leaf area in the canopy is calculated in horizontal canopy layers with a depth of 0.5 m.

The growth of an individual tree is based on a carbon balance. Calculations include photoproduction of the trees and assimilate losses due to respiration, litter-fall and fine root decay. Within a patch, vertical light attenuation in the canopy is calculated from light intensity above the canopy with respect to the absorption of tree crowns. The dependence of specific photosynthetic productivity on irradiance is modelled using a Michaelis-Menten-type light response curve. Photoproduction $\tilde{P}$ is calculated from the tree's leaf area (Monsi & Saeki 1953). We assume an increasing limitation effect of water transport deficiencies with growing tree height (Ryan et al. 1997). Thus, actual productivity is calculated by applying a size-dependent limitation factor $q(d)$ (according to the aging factor of Landsberg & Waring 1997). Assimilate losses are estimated in relation to tree biomass B (Kira 1978; Yoda 1983). We distinguish between a biomass-dependent maintenance respiration R_{m} and growth respiration R_{G} (Ditzer et al. 2000). Our main time-dependent growth equation for one tree i is

$$\frac{\mathrm{d}B_i}{\mathrm{d}t} = \tilde{P}_i \cdot q(d_i)(1 - R_{\mathrm{G}}) - R_{\mathrm{m}}(B_i) \quad (7.1)$$

Tree growth is calculated in annual time steps.

Competition is modelled in terms of competition for light and space, the latter resulting in self-thinning.

For small trees (diameter < 10 cm a diameter-dependent mortality is added to a basic mortality rate. Trees resulting in crown closure are eliminated to avoid crowding (self-thinning). Mortality is modelled as stochastic event. Senescent trees ($\geq$ 10 cm d.b.h.) die and collapse with a certain probability, knocking down smaller trees in neighbouring patches thereby creating gaps of a size that depends upon their crown size.

Two different recruitment mechanisms were incorporated in the model. The simplest approach consists in assuming that an intact forest is supporting a constant seed input rate. The second takes into account the dispersal of seeds produced from local mother trees, i.e. trees exceeding a certain diameter D_{R}. As recruitment strategies are highly variable in rain forests, with interspecific differences in fruiting period, number of seeds, seed sizes (Leishman et al. 1995), dispersal strategies, agents, and distances, seed survival, germination probabilities and maturing size of seed disperser (Garwood 1983; Whitmore 1983; Denslow 1987) some fundamental assumptions on the most important trends have to be made.

Flowering, fruiting and seed production vary in duration and frequency across species, some species fruiting after several years of unfecundity (Garwood 1983; Curran & Leighton 2000). Other species flower and fruit continually throughout the year in Malaysian rain forests (Putz 1979). Seasonal differences in seed production are not taken into consideration. The rate of seed production varies widely among species (Whitmore 1998). Various studies have analysed different dispersal strategies and lengths (review in Clark et al. 1999b). Different dispersal agents (e.g. wind, birds, mammals) are not directly distinguished in our model, but the resulting average dispersal distance X_{R} depends upon the species and should match with the parameter set. From the dispersal kernels discussed by Clark et al. (1999) we use the Gaussian distribution (as used by Chave 1999b). Assuming rotation symmetry, the probability density f of seeds to be dispersed at the distance r from the mother tree is

$$f(r) = \frac{2r}{(X_{\mathrm{R}} + \frac{c_d}{2})^2} \exp\left(-\frac{r^2}{(X_{\mathrm{R}} + \frac{c_d}{2})^2}\right), \quad (7.2)$$

with c_d, the crown diameter (see Fig. 7.1). Thus, 99% of the seeds are dispersed in a distance less than $2.14 \times (X_{\mathrm{R}} + c_d/2)$. The actual dispersal distance r is randomly drawn from this probability distribution, and the direction is drawn uniformly. The resulting seed shadow is the product of the rate of seed production and the dispersal kernel (Clark et al. 1999b).

For both recruitment mechanisms, incoming seeds update a seed pool, taking into account the dormancy variability across functional groups (cf. Garwood 1983,

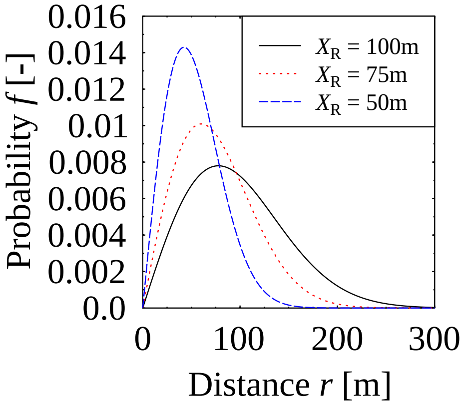

Figure 7.1: Seeds dispersal kernels for a Gaussian distribution with different average dispersal distances X_R. Crown diameter was fixed at c_d=20 m.

1989). These seeds correspond to the reproductive success and are those which can potentially be established at the minimum diameter of 1 cm (Ribbens et al. 1994; Chave 1999b). Seed loss due to predators is implicitly included in relative low seed production rates. The actual seed germination depends upon understorey light intensities.

Parameters and initialisation

Parametrisation used in our simulations is found in the Appendix (of article). Data on light environment are taken from Schlensog (1997). Allometric relations of tree crowns were found in Rollet (1978), Poker (1993), and Schlensog (1997). The form factor, leaf and crown area to diameter relations are taken from measurements of Kato et al. (1978) and Kira (1978) in Pasoh, Malaysia. Height-to-diameter relations are obtained from an inventory of Sabah's forests (Forestal-International-Limited 1973). Data on photosynthetic response of functional groups to different light intensities are given in Eschenbach et al. (1998). The wood density of species was determined from various sources (Meijer & Wood 1964; Burgess 1966; Fox 1970; Cockburn 1980; Keating & Bolza 1982; PROSEA 1994). Parameter values for respiration processes were estimated by sensitivity analysis to obtain realistic diameter increment values for different size classes and different light conditions. Mortality rates correspond to typical values found in the literature (Manokaran & Kochummen 1987; Swaine 1989; Condit et al. 1992, 1995a, 1995b; Carey et al. 1994; Manokaran & Swaine 1994; Phillips & Gentry 1994; Silva et al. 1995; van der Meer & Bongers 1996). Seed production rate N_R per mother tree and constant seed input rate N_S were estimated from a sensitivity analysis of long-term runs of the mature stand P1, assuming a dynamic equilibrium of the forest structure and a given species composition.

In both stands (P1, L1), trees were distributed randomly to the 5×5=25 patches of one hectare. P1 contained nearly no early successional species, abundance was highest in PFT 12, 13 and 6 with 37, 19.5, and 18.8 % respectively. Site L1 was dominated by medium-size pioneers (PFT 5: 65.8 %), and contained nearly no late successional species (Table 7.1). The seed pool was filled with average seed numbers from long term simulations.

Model evaluation

One of the main results of a previous analysis with FORMIND2.0 applied to a Venezuelan rain forest was that the mortality parameters contributed to most of the variance in the simulation outputs (Kammesheidt et al. 2000). While the bole volume, basal area and total leaf area index were quite insensitive, the density of early successional species was highly sensitive to most parameter changes. The present application for rain forests in Sabah differed only in the value of the parameters, the sensitivity analysis was expected to yield the same results as the previous study.

In the present work, we mainly focus on the influence of the recruitment parameters on the results. Sensitivity of

28 output quantities to variations of parameter values was investigated in 231 simulations (cf. Vanclay & Skovsgaard 1997). Each of the twelve parameters for the seed pool submodel and each of the 21 parameters for the within-patch fecundity module (see parameters in Appendix) was varied seven times, from the standard value (StV), using an identical scheme spanning two orders of magnitude (0.1×StV; 0.5×StV; 0.9×StV; StV; 1.1×StV; 2×StV; 10×StV). In a few cases physical boundaries restricted the range of the parameter values, thus slightly reducing the total number of simulations performed (e.g. mortality rates cannot exceed values of 1.0). Simulations over 4 hectares and 1000 years in the mature stand (P1) were performed for each varied parameter. Mean values of the chosen result variables were averaged over the seven simulations. The coefficient of variation (CV) from this average was chosen as an indicator to find whether a result variable was sensitive to parameter changes or not. More details on variations are found in caption of Fig. 7.2.

Simulation scenarios

Once our model is validated, we designed 70 different simulation scenarios for this study. The scenarios differ in at least one factor: recruitment pattern, size, boundary conditions, logging cycle, and logging method.

Recruitment pattern. - In former studies using FORMIND, recruitment was modelled on the basis of constant input of seeds over the whole simulation area. This was justified assuming an intact forest structure surrounding the simulated area. As forest fragmentation has increased in the tropics (Laurance et al. 1997; Gascon et al. 2000) these assumption might be too simplistic for the future. Explicit seed dispersal was modelled in an alternative recruitment model. Our simulation areas were still small (up to 25 ha). Thus, a mixture of explicit seed dispersal from the simulated stand in addition to a constant seed shadow seems to be the most realistic situation. Five scenarios with different recruitment pattern were defined from strict local seed dispersal to a constant seed input without local influences (seed tree, mixed seeds 1-3, seed pool). The number of dispersed seeds per mother tree N_{Rs} and constant seedling input N_{Ss} are modified from standard values using the factors given in Table 7.2. An extreme scenario was the forest development without any recruitment, which was simulated for both stands P1 and L1.

Table 7.2: Contribution of constant seeds input and local recruitment to different recruitment scenarios [%]. ST: Seed trees only, MS: mixed seeds, and SP: seed pool.

	Recruitment scenarios[a]				
Input process	ST	MS1	MS2	MS3	SP
Constant input	0	2	10	50	100
Local recruitment	100	98	90	50	0

[a] As number of seeds dispersed from each mother tree must not be a fraction, seed numbers are rounded up to natural numbers.

Size of the simulated area. - To analyse the effects of size we ran simulations on three different scales: 1 ha, 9 ha, 25 ha, all square in shape. After an analysis of size effects on forest development without timber harvest, logging was performed on a medium size of 9 ha.

Boundary conditions. - By simulating relative small areas of a few hectares, boundary effects are worth considering. In an 1 ha area with 25 patches 64% of them are at an outer border. This is reduced to 15% in an area of 25 ha. Especially when explicit seed dispersal is modelled, boundary conditions are important for forest development. Two different conditions were examined: toroidal (or periodic) boundaries and open boundaries. With the toroidal boundary conditions it was assumed that the right boundary is connected to the left boundary, and the top to the bottom. Thus, falling trees or seeds leaving the simulation area reenter at the opposite site. With open boundaries, everything leaving the simulated area is lost and nothing enters the system. Open boundary scenarios can be understood as a strongly fragmented landscape without any interactions as immigration between different forest islands. In contrast, with toroidal boundaries the simulated area can be understood as nested in a larger forest of a similar structure. Logging scenarios are performed with toroidal boundary conditions.

Logging method and cycle length. - Our modelling of logging practices was motivated by several studies (Hendrison 1990; Crome et al. 1992;Cannon et al. 1994; Johns et al. 1996; Pinard & Putz 1996; Johns 1997; Bertault & Sist 1997; Sist et al. 1998; Ditzer et al. 2000; Kammesheidt et al. 2000). Two methods were distinguished: highly damaging conventional logging (CON) which generally makes use of heavy machinery, unskilled workers and little planning effort, and reduced-impact logging (RIL), where substantial planning for road construction, felling directions etc. was performed. In RIL, tree removal usually implies the use of winching cables or airborne cable systems. Modelled differences of the two methods were damages to the residual stand. We distinguished (1) damages through tree felling, (2) skidding damages in the patch of a felled tree, (3) area loss due to road construction and log landings, and (4) increased mortality rates for ten years after logging (Table 7.3). Tree-fell damage was proportional to crown size and method-independent. The felling direction was random in CON, but directed towards neighbouring gaps in RIL, whenever possible. In the patches where felled trees were situated, 25% and 55% of the stems were killed through skidding in RIL and CON, respectively. Area loss was simulated by complete removal of the residual stand in 12% (RIL) and 33% (CON) of randomly chosen patches. Mortality in the years after logging was twice (RIL) and three times (CON) higher than normally, counting for damaged but not instantly destroyed trees. The time between two harvesting operations was varied in steps of 20 y between 20 y and 80 y. Stand L1 was recorded directly after a logging operation, therefore the first logging starts right after one cycle length. All commercial trees of the mid and late successional species with a minimum diameter of 60 cm were removed in a logging operation.

Table 7.3: Different logging impacts to residual stand if reduced-impact logging (RIL) or conventional logging (CON) is applied. Skidding damages were percentages of stem numbers, area losses were percentages of simulation area.

Impact	RIL	CON
Felling damage	~ crown size	
Felling direction	to gaps	random
Skidding damage	25%	55%
Area loss	12%	33%
Mortality 10 y after logging	× 2	× 3

Results

Model evaluation

We used the analysis of variance (ANOVA) to detect significant differences in our simulation results (Graf et al. 1987; Sachs 1997; Fowler et al. 1998). Across scenarios the standard error is generally small, it is normally not shown in the figures. Furthermore, tests of statistical differences at a 1% level were performed as t-test for matched pairs (Fowler et al. 1998), but cannot be

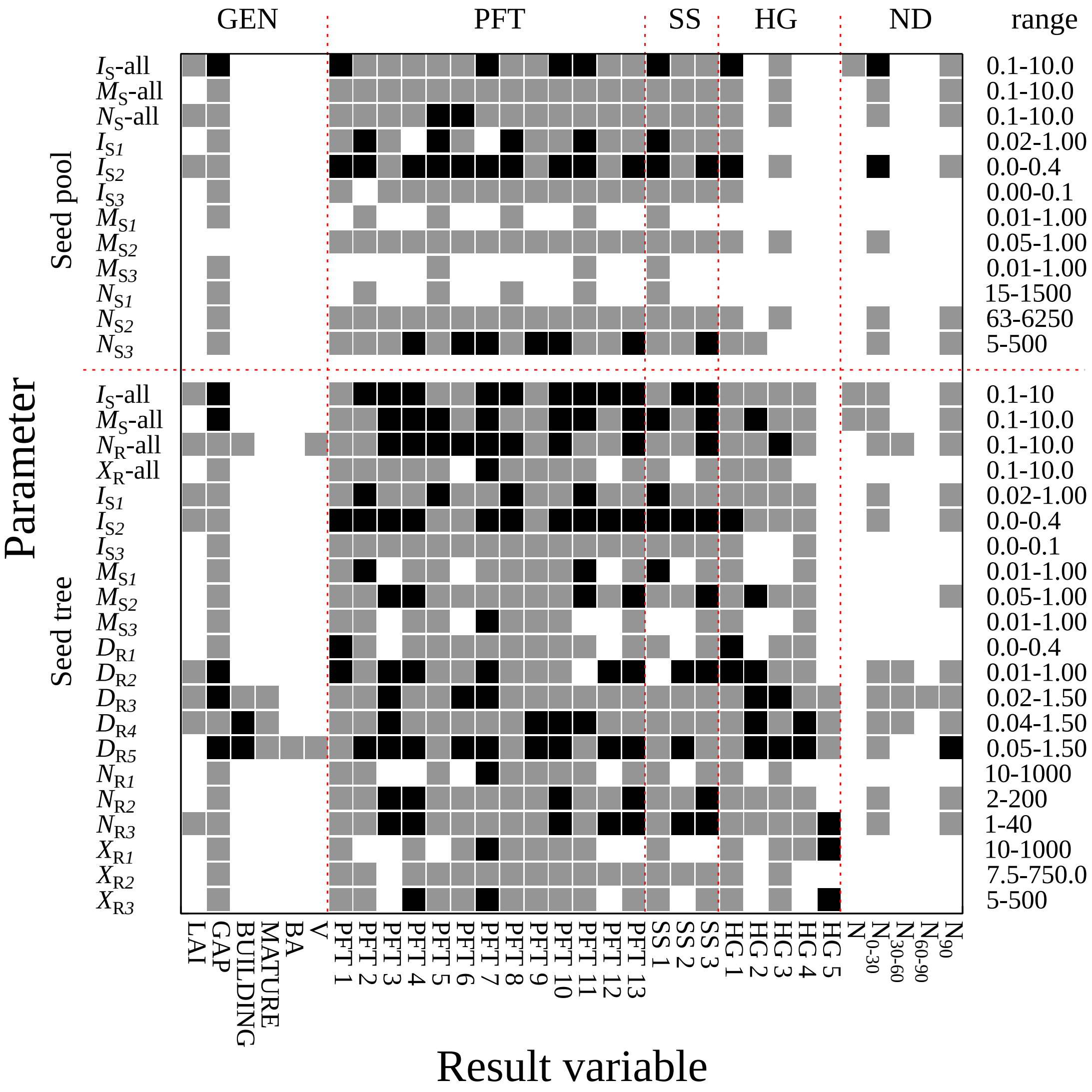

Figure 7.2: Sensitivity analysis. Each parameter of the recruitment module (different approaches *Seed pool* and *Seed tree* are distinguished) was varied seven times in the given range (one simulation with standard parameter value). Range stretched from 1/10 to 10× standard parameter value. Simulations were made for 4 ha over 1000 years of mature forest (P1). Description of labels and units is found in Appendix (of article). Time averaged values (v) vary from average (a) with coefficient of variation ($CV =\mid v - a \mid /a \times 100$). White: low sensitivity ($CV \leq 10$ %); grey: medium sensitivity (10 % $< CV \leq 50$ %); black: high sensitivity ($CV > 50$ %). Parameters varied for all groups, where indicated (e.g. I_S-all). Result variables are: *GEN:* General information refers to (LAI) total leaf area index, succession stages ((GAP) gap phase: no trees with h≥15 m in patch, ($BUIDLING$) building phase: trees with h≥15 m in patch, and ($MATURE$) mature phase: trees with h≥30 m in patch), (BA) basal area, and (V) bole volume of the whole stand. *PFT, SS, HG:* relative bole volume of the 13 PFTs, 3 successional status groups, or 5 height groups, respectivly (cf. Tab. 7.1). *ND:* Stem number as function of diameter (N: all trees) for trees between 0 and 30 cm dbh (N_{0-30}), 30 cm and 60 cm dbh (N_{30-60}), 60 cm and 90 cm dbh (N_{60-90}) and above 90 cm dbh (N_{90}).

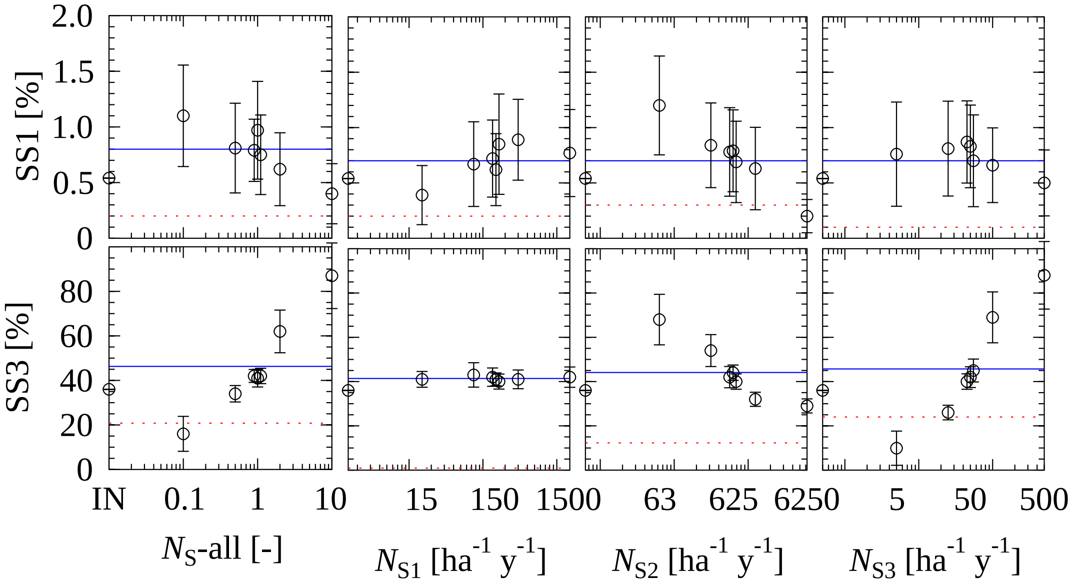

Figure 7.3: Sensitivity analysis of constant seeds input rate N_{Sx} (x=all, or s=1,2,3: successional status, Table 7.1) on abundance of early (SS1) and late (SS3) successional species. Further description see Fig.7.4.

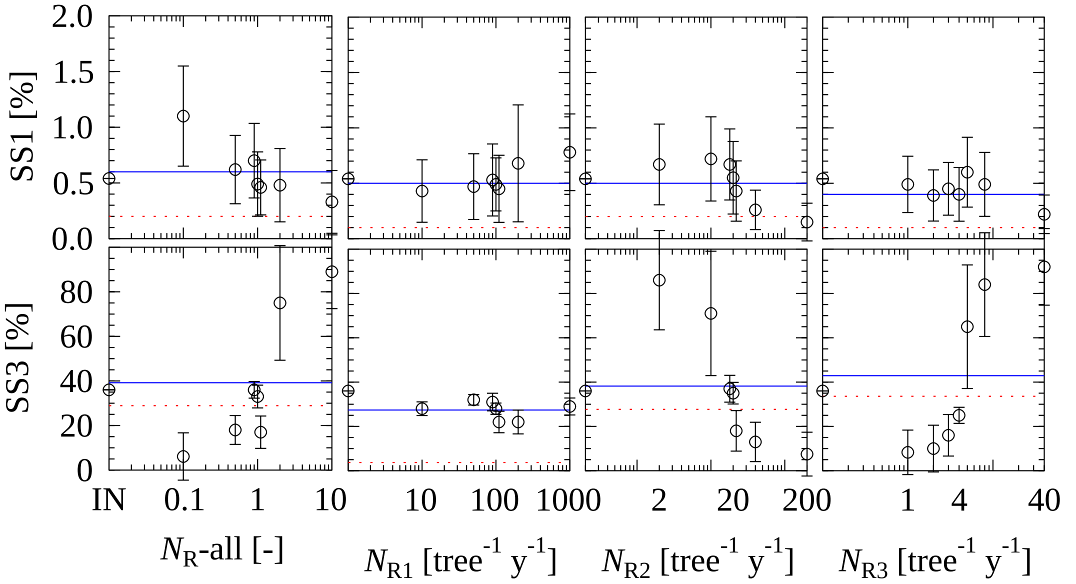

Figure 7.4: Sensitivity analysis of seed production rates N_{Rx} (x=all, or s=1,2,3: successional status, Table 7.1) on abundance of early (SS1) and late (SS3) successional species. Circles mark time averaged values ± SD. Parameters were varied over two orders of magnitude with standard value inbetween. Simulations were made for 4 ha over 1000 years of mature forest (P1) with toroidal boundaries. Solid line: average of all variations. Doted line: coefficient of variation (CV) of single values to average. Values on the y-axes (labeled *IN* in lower left subfigure) correspond to inventory of P1. Note logarithmic scale of x-axis. Further information in Fig. 7.2 and text.

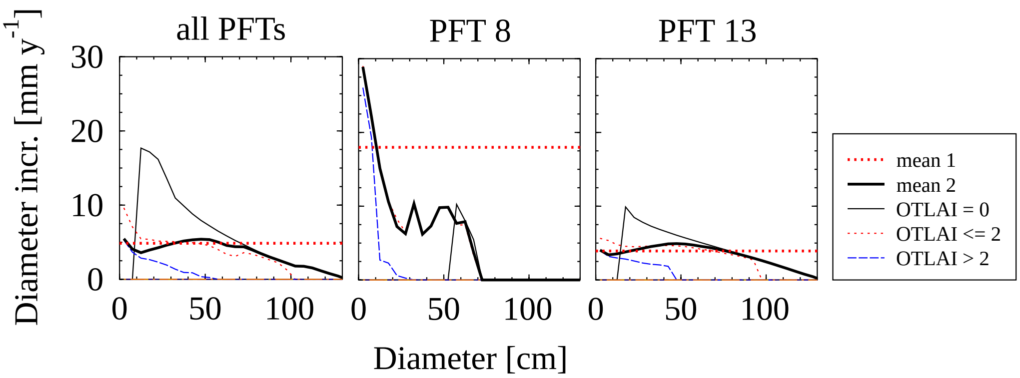

Figure 7.5: Diameter increment as function of diameter, light competition and plant functional type (PFT). Analysis of annual increments of all trees in simulations of 4 ha and 1000 y of mature forest (P1). Left: Average over different plant functional types; middle: PFT 8 as an example for early successional species; right: PFT 13 as an example of late successional species. Light competition in overtopping leaf area index (OTLAI) from OTLAI=0: no competition to OTLAI$\geq$2: strong competition. Mean 1: average over both diameter and OTLAI; mean 2: average over different OTLAI.

shown in the figures, where up to 40 different scenarios were compared. They were reported in the Figure captions.

Diameter increment rates as function of tree diameter, PFT, and light intensity were analysed in average and for PFTs (Fig. 7.5). The overall increment is about 5 mm y^{-1}, mainly caused by late successional species, as abundance of early succ. spp. is low in mature stands. There are obvious differences between early (e.g. PFT 8: mean 18 mm y^{-1}) and late (e.g. PFT 13: 4 mm y^{-1}) successional species. Light competition reduced both the maximum reachable diameter, and diameter increment rates. Small (d<20 cm) trees of PFT 13 were never found in unshaded position, whereas most of PFT 8 are exposed to full or near to full light.

An overview of the sensitivity analysis concerning the two recruitment scenarios seed pool (SP) and seed tree (ST) is shown in Fig. 7.2. Results in ST were more sensitive than in SP. While minimum light intensity for germination I_S produces sensitive behaviour in SP and ST, similar strong response were achieved by varying minimum diameter of seed producing trees D_R in ST. Total bole volume, basal area and leaf area index were insensitive to most parameter changes, while species composition varied widely. Size structure of the forest remained insensitive as well. For the most uncertain parameters seed input rate N_S in SP and seed production rate N_R in ST more detailed analysis of species composition were undertaken (Fig. 7.3, 7.4).

Influence of area size, boundary conditions and recruitment pattern on forest structure

There were no significant effects of the area size on the total bole volume. Though ANOVA indicates significant differences of boundary conditions or recruitment assumptions (Table 7.4A), those were hardly seen when the total bole volume (469-499 m^3 ha^{-1}) was plotted for all the scenarios (Fig. 7.6). However, species composition varied significantly when the boundary conditions, recruitment assumptions (early and late succ. spp.), or area size (only early succ. spp.) (Table 7.4B,C) were changed. Abundance of early successional species were below 2 % (0.5-1.3 %), while fraction of late successional species increased from about 25 % in the ST scenario to 37 %

Table 7.4: ANOVA for the main and interactive effects of area size (1 ha, 9 ha, 25 ha), boundary conditions (open, closed), and recruitment assumptions (scenarios SP, MS3, MS2, MS1, ST) on (A) total bole volume, (B) relative share of early successional species, (C) relative share of late successional species. No logging was performed. Simulation of primary forest at site P1, simulation time was 1000 y (n = 5). SS: sum of squares; df: degree of freedom; MS: mean of squares; P: probability (details in Fowler et al. 1998).

Effects	SS	df	MS	F ratio	P
A) Total bole volume					
Size	357.68	2	178.84	4.66	>0.01
Boundary	810.02	1	810.02	21.10	<0.001
Recruitment	1010.48	4	252.62	6.58	<0.001
Size × boundary	60.52	2	30.26	0.79	>0.1
Size × recruitment	834.65	8	104.33	2.72	<0.01
Boundary × recruitment	1143.01	4	285.75	7.44	<0.001
Size × boundary × recruitment	1013.93	8	126.74	3.30	<0.005
Error	4606.69	120	38.39		
B) Share of early successional species					
Size	2.063	2	1.032	41.11	<0.001
Boundary	2.137	1	2.137	85.18	<0.001
Recruitment	2.602	4	0.651	25.93	<0.001
Size × boundary	0.690	2	0.345	13.75	<0.001
Size × recruitment	0.087	8	0.011	0.43	>0.5
Boundary × recruitment	0.113	4	0.028	1.13	>0.1
Size × boundary × recruitment	0.399	8	0.050	1.99	>0.05
Error	3.011	120	0.025		
C) Share of late successional species					
Size	67.64	2	33.82	2.51	>0.05
Boundary	190.83	1	190.83	14.19	<0.001
Recruitment	3704.63	4	926.16	68.86	<0.001
Size × boundary	41.63	2	20.81	1.55	>0.1
Size × recruitment	213.16	8	26.64	1.98	>0.05
Boundary × recruitment	36.66	4	9.16	0.68	>0.5
Size × boundary × recruitment	40.89	8	5.11	0.38	>0.5
Error	1614.03	120	13.45		

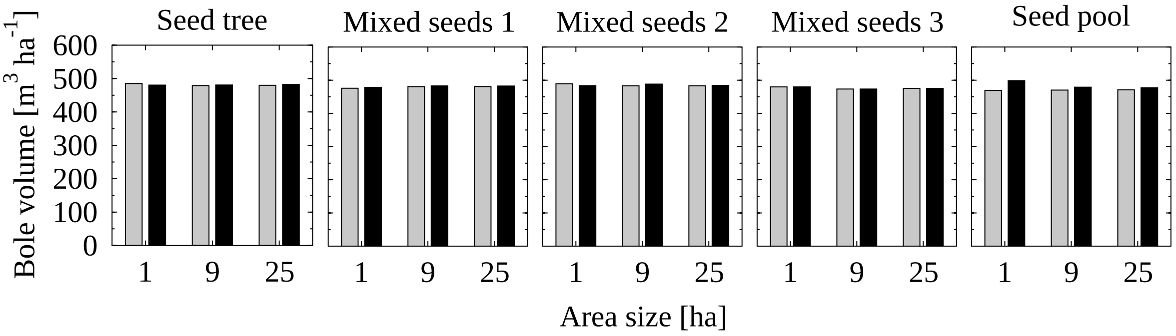

Figure 7.6: Effects of area size (1 ha, 9 ha, 25 ha), boundary conditions (toroidal (left, grey), open (right, black)) and recruitment scenarios (seed tree; mixed seeds 1-3; seed pool) on standing bole volume. Simulations of primary forest at site P1 without logging. Results are means (n=5) of 1000 simulated years. SE was always <6 m^3 ha^{-1} and thus not shown. T-test for matched pairs found significant differences at 1 % level for 20% of tested pairs.

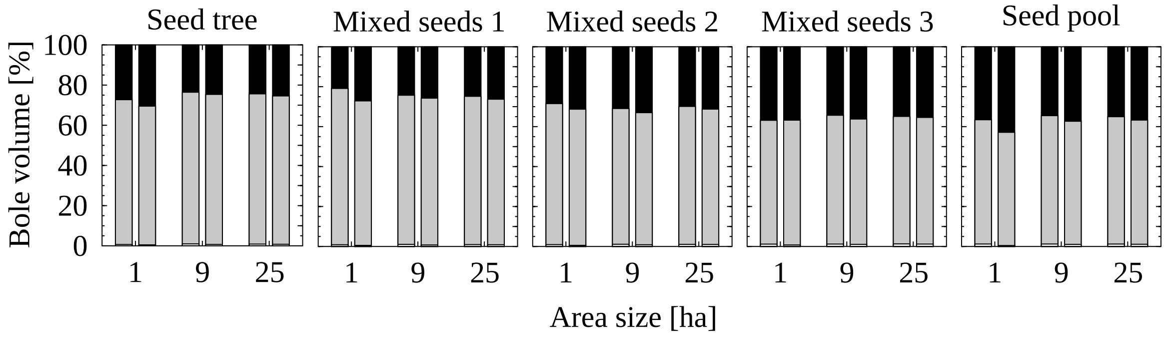

Figure 7.7: Effects of area size (1 ha, 9 ha, 25 ha), boundary conditions (toroidal (left), open (right)) and recruitment scenarios (seed tree; mixed seeds 1-3; seed pool) on species composition (early (white), mid (grey) and late (black) successional species). Simulations of primary forest at site P1 without logging. Results are means (n=5) of 1000 simulated years. SE not shown for technical reasons (SE: early succ spp.<0.13 m^3 ha^{-1}; late succ spp.<3.38 m^3 ha^{-1}). T-test for matched pairs found significant differences at 1 % level for 34% and 35 % of tested pairs of abundance early and late successional species, respectively.

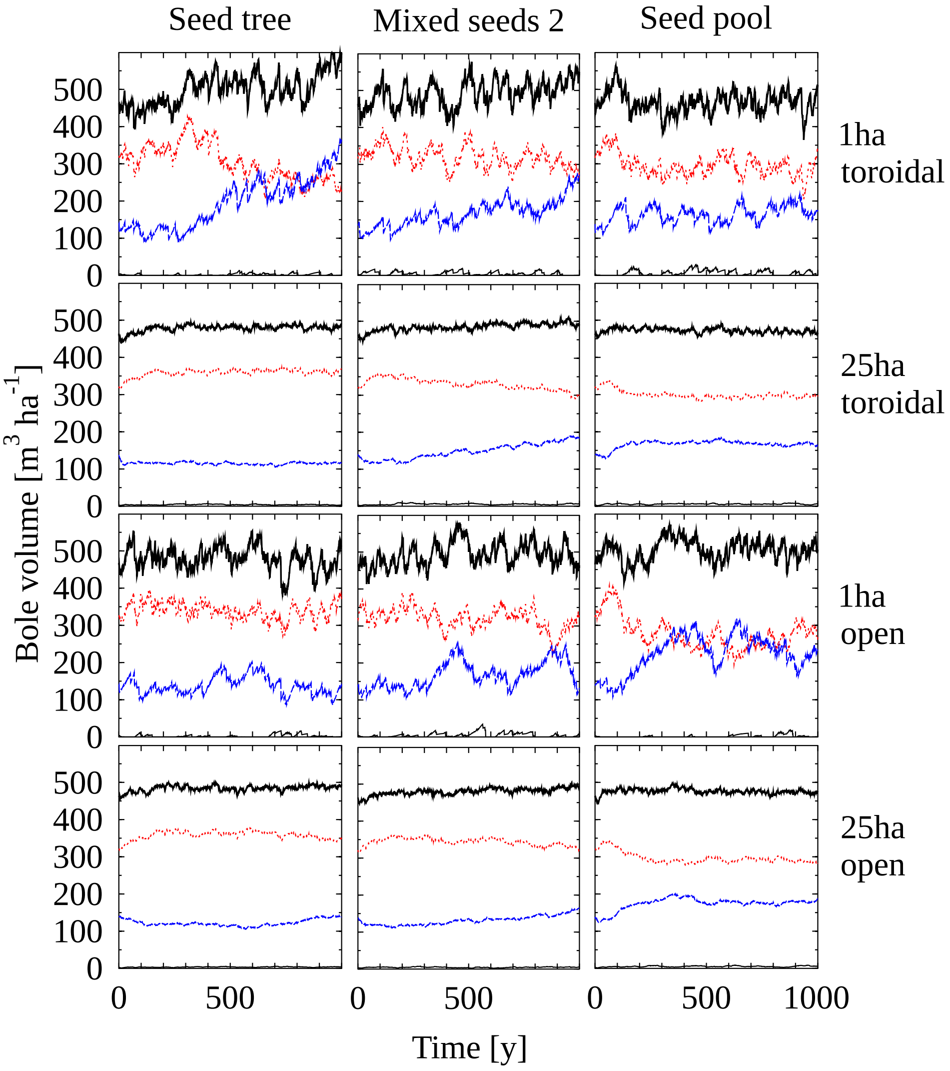

Figure 7.8: Development of bole volume ($m^3\ ha^{-1}$) for different scenarios. Simulation of 1000 y of mature forest at site P1, not averaged over n=5 runs to show dependency on stochastics. Variation of area size (1 ha, 25 ha), boundary conditions (toroidal, open) and recruitment scenarios (seed tree; mixed seeds 2; seed pool). Total (solid bold line), early successional spp. (solid line), mid successional spp. (broken dotted line), late successional spp. (broken line).

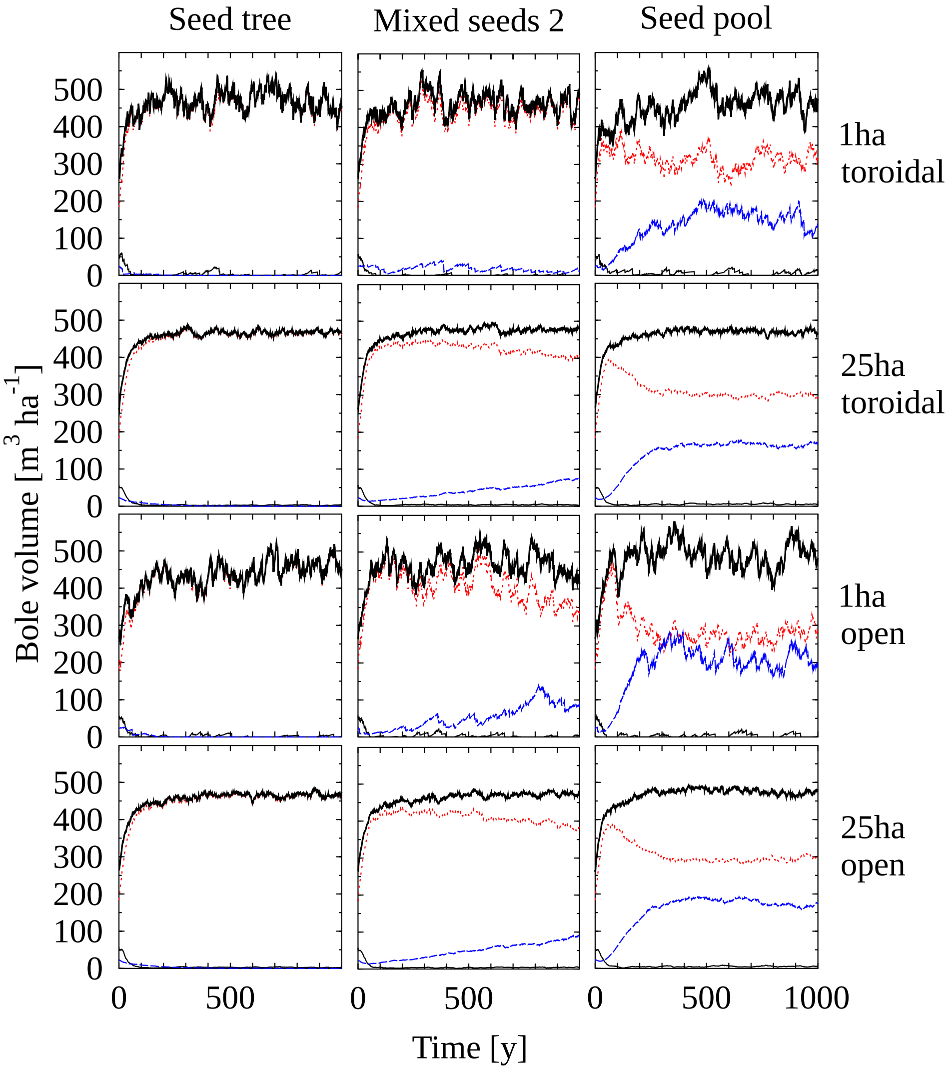

Figure 7.9: Development of bole volume (m^3 ha^{-1}) for different scenarios. Simulation of 1000 y of logged forest at site L1, not averaged over n=5 runs to show dependency on stochastics. Variation of area size (1 ha, 25 ha), boundary conditions (toroidal, open) and recruitment scenarios (seed tree; mixed seeds 2; seed pool). Total (solid bold line), early successional spp. (solid line), mid successional spp. (broken dotted line), late successional spp. (broken line).

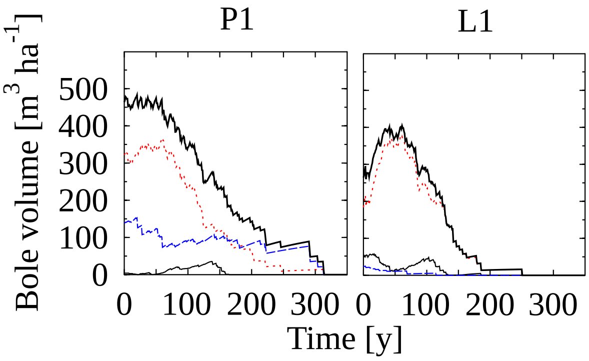

Figure 7.10: Development of bole volume (m^3 ha^{-1}) without seed supply. Simulation of 1 ha and 350 y of mature (P1) and logged forest (L1) under open boundary conditions. Total (solid bold line), early successional spp. (solid line), mid successional spp. (broken dotted line), late successional spp. (broken line).

in SP (Fig. 7.7). This fraction was always higher in scenarios with open than with toroidal boundary conditions, which is a result of lower average seed dispersal distance in late compared to early and mid successional species. The temporal development of the bole volume (total and for different successional types) showed high fluctuations in simulations of small areas (Fig. 7.8). To visualise the temporal dependence of forest structure on initial stand composition, the same dynamics are shown for simulations with logged stand L1. (Fig. 7.9). Here, few and only small trees of late successional species persist in the inventory, which led to an extinction of those species in scenario ST, but substantial regeneration in scenario SP.

Forest fragmentation

Following the above analysis, open boundary conditions (forest islands with no immigration) favoured species with lower seed dispersal distance (e.g. late vs. mid successional species), as less seeds are lost in the surrounding. Furthermore, in border patches, the number of gap creating tree fall events, which favour early successional species, was reduced in open boundary conditions. However, as a most realistic recruitment scenario, local supply with seeds (SP) will be insufficient in logged small forests and will lead to a loss of tree species, even if the standing bole volume remains at a comparable high level of about 500 m^3 ha^{-1}. In dramatic events, e.g. a total loss of seed supply, possible through enhanced seed predation coupled with low seed production (Curran & Leighton 2000), forest fragmentation will lead to a collapse of the forest structure, but only after about 300 and 200 y for stand P1 and L1, respectively (Fig. 7.10). In the latter case the bole volume increased first from 280 to 400 m^3 ha^{-1} before volume eventually decreased.

Modification of forest structure and species composition through logging

The total bole volume was significantly affected (ANOVA) by all logging cycles, methods, and recruitment assumptions (Table 7.5A). Average total bole volume varied from 226 to 395 m^3 ha^{-1}. Short logging cycles always resulted in lower bole volume than longer cycles, and likewise conventional logging had greater impacts than reduced-impact logging, if all other parameters were held constant (Fig. 7.11). Differences between recruitment scenarios were small. Logging damage was correlated to harvesting intensities. Thus, basal area of residual, logged, and damaged trees were plotted as function of removed basal area (Fig. 7.12). The percentage of residual standing basal area (denoted y_{rs}) and of damaged trees (y_{dt}) were linear functions the basal area x. In the RIL scenario we found: $y_{rs} = 83.3 - 3.2x$ and $y_{dt} = 15.9 + 0.7x$, while in the CON scenario: $y_{rs} = 70.7 - 5.1x$ and $y_{dt} = 28.0 + 2.6x$. Higher damages in conventional method are clearly seen.

Changes of abundance of early and late

Table 7.5: ANOVA for the main and interactive effects of logging cycle (20 y, 40 y, 60 y, 80 y), logging method (conventional (CON), reduced-impact (RIL)) and recruitment assumptions (scenarios ST, MS1, MS2, MS3, SP) on (A) Total bole volume, (B) relative share of early successional species, (C) relative share of late successional species, and (D) harvest yield. Simulation of logged forest at site L1 covering 9 ha for 240 y (n = 5) with toroidal boundaries. Columns are explained further in Table 7.4.

Effects	SS	df	MS	F ratio	P
A) Total bole volume					
Cycle	297993.34	3	99331.11	9485.88	<0.001
Method	40431.62	1	40431.62	3861.12	<0.001
Recruitment	19639.96	4	4909.99	468.89	<0.001
Cycle × method	3317.78	3	1105.93	105.61	<0.001
Cycle × recruitment	11383.34	12	948.61	90.59	<0.001
Method × recruitment	1615.02	4	403.75	38.56	<0.001
Cycle × method × recruitment	1166.07	12	97.17	9.28	<0.001
Error	1675.44	160	10.47		
B) Share of early successional species					
Cycle	2628.66	3	876.22	2118.25	<0.001
Method	7740.53	1	7740.53	18712.66	<0.001
Recruitment	210.22	4	52.56	127.05	<0.001
Cycle × method	272.94	3	90.98	219.94	<0.001
Cycle × recruitment	147.61	12	12.30	29.74	<0.001
Method × recruitment	73.93	4	18.48	44.68	<0.001
Cycle × method × recruitment	46.46	12	3.87	9.36	<0.001
Error	66.18	160	0.41		
C) Share of late successional species					
Cycle	60.39	3	20.13	233.69	<0.001
Method	86.87	1	86.87	1008.44	<0.001
Recruitment	2427.15	4	606.79	7044.16	<0.001
Cycle × method	1.46	3	0.49	5.63	<0.005
Cycle × recruitment	88.57	12	7.38	85.68	<0.001
Method × recruitment	82.52	4	20.63	239.51	<0.001
Cycle × method × recruitment	1.40	12	0.12	1.36	>0.1
Error	13.78	160	0.09		
D) Harvest yield					
Cycle	189696.41	3	63232.14	233.67	<0.001
Method	475111.67	1	475111.67	1755.73	<0.001
Recruitment	1047346.36	4	261836.59	967.59	<0.001
Cycle × method	85767.21	3	28589.07	105.65	<0.001
Cycle × recruitment	20074.29	12	1672.86	6.18	<0.001
Method × recruitment	67639.75	4	16909.94	62.49	<0.001
Cycle × method × recruitment	19516.92	12	1626.41	6.01	<0.001
Error	43297.14	160	270.61		

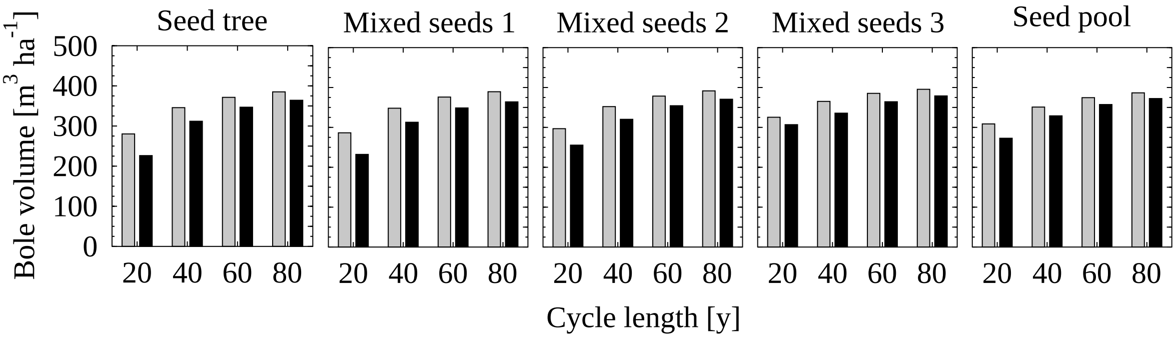

Figure 7.11: Effects of logging cycle (20 y, 40 y, 60 y, 80 y), method (reduced-impact (grey), conventional (black)) and recruitment scenarios (seed tree; mixed seeds 1-3; seed pool) on standing bole volume. Simulations of 9 ha with toroidal boundaries. Results are means (n=5) of 240 simulated years. SE was always <2 m^3 ha^{-1} and thus not shown. T-test for matched pairs found significant differences at 1 % level for 89% of tested pairs.

successional species in relation to logging cycles, methods, and recruitment assumptions were significant (Table 7.5B,C). Abundance of early successional species varied between 4.9 % and 29.2 %, late successional species between 1.3 % and 13.9 % (Fig. 7.13). The more the recruitment depended on local seed production (ST), the rarer the late successional species were. Conventional logging favoured abundance of early successional species and suppressed development of late successional species. Temporal forest development showed drastic increases of early successionals after conventional logging, and short logging cycles did not give the forest the possibility to recover (Fig. 7.14). Furthermore, in scenario ST and conventional logging, a constant decline of total bole volume resulting from a missing seed supply was detectable. In conventional logging with short cycles and local seed production, an increase in the number of suspended logging operations was observed, because of a total lack of marketable timber. Conventional logging with long cycles led to increasing fraction of early successional species. Extinction of late successionals was detectable in all ST scenarios with CON after 100 simulated years, in RIL a very small fraction <1 % survived.

Optimising harvest results

Timber harvest varied significantly across the three scenario parameters (Table 7.5D). Gross yield ranged from 0.8 to 2.2 m^3 ha^{-1} y^{-1}. Net yield, covering an additional 30 % loss due to hollow stems and skidding damages (Pulkki 1997), varied between 0.6 to 1.4 m^3 ha^{-1} y^{-1} (Fig. 7.15). While differences between recruitment scenarios were again negligible, the species origin of timber might be worth considering, as yield in ST scenarios was mostly achieved from mid successional species. SP scenarios sustained a higher share of late successional species. Reduced-impact logging achieved more than double yield compared to conventional scenarios in short cycles. Yield was maximised in cycles of 40 y in RIL, where conventional logging achieved higher timber yields in long logging cycles. In cycles length of 80 y timber yields converged towards similar yields independent of the logging method (Fig. 7.15).

Discussion

A comparison of simulated forest growth with data from permanent plots was performed with a former version of the model, including a different parameter set (Köhler et al. 2001). The same tests were under-

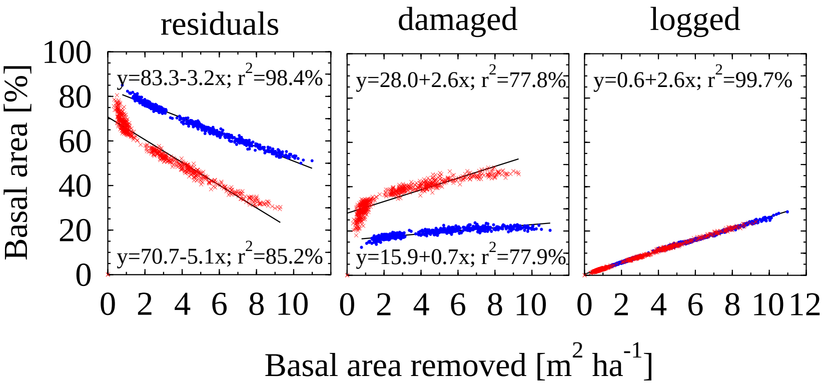

Figure 7.12: Impacts of different logging methods (reduced-impact (dots), conventional (crosses)) and intensity on the forest structure. Basal area (residuals, damaged, logged) is plotted as function of removed basal area.

taken with the current version (not shown). Thus, growth data and the simulation results of 25 ha for 9 to 20 y in four different forest reserves in Sabah with different site and stocking conditions were compared. The ratio of simulated data to field data of total basal area lay in the range of 0.9 to 1.25. The accuracy of these results is therefore slightly better than in previous simulations.

The present knowledge of recruitment and recruitment rates in tropical forests is still limited (ter Steege et al. 1995; Clark et al. 1999b; Duncan & Chapman 1999; Nicotra et al. 1999; Webb & Peart 1999). Sensitivity analyses of simulation models offer the possibility to evaluate the importance of different processes on forest development.

Analysis of the effects of different parameters of the recruitment modules highlights the fact that the influence of average seed dispersal distances X_{R} on results is weaker than that of absolute seed production rates N_{S} and N_{R} (Fig. 7.2). In addition, the sensitivity analysis of the recruitment rates suggests that mid successional species have a key role in the recruitment process, as their recruitment strongly influences the specific composition of the forest.

Recent research highlights the importance of mast-fruiting for recruitment success in dipterocarp forests (Curran et al. 1999; Curran & Leighton 2000; Curran & Webb 2000). In tests (not shown in the present study) we have compared the sensitivity of model output on regular mast-fruiting events. Populations of seed predators were not modelled explicitly, thus results did not depend on mast-fruitings. The dynamics of stem numbers of small trees (d<10 cm) is affected, but effects were smoothed out for larger trees through self-thinning. There were only minor fluctuations in stem volume and species composition. We therefore relied on the approach without mast-fruiting, but are aware that seed predation might be the crucial bottleneck of current recruitment scenarios. New findings in seed dispersal limitations through extinction of key dispersal bird species in Brazil (da Silva & Tabarelli 2000) are another example of how important fauna-flora interactions in tropical forests are. But seeds in dipterocarp forests are mostly wind dispersed, and those limitations might not be important in South-East Asia.

Different assumptions on recruitment led to changes in species composition (Fig. 7.7), as analysed in greater details by Liu & Ashton (1999). However, the level of total bole volume was reasonably constant (Fig. 7.6, 7.8, and 7.9). As a consequence it was important to isolate the effect of regeneration on forest development, e.g. by simulations

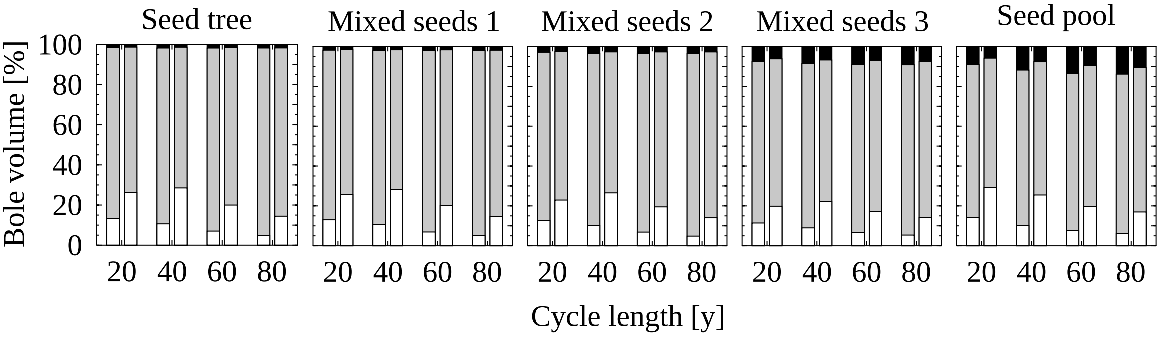

Figure 7.13: Effects of logging cycle (20 y, 40 y, 60 y, 80 y), method (reduced-impact (left), conventional (right)) and recruitment scenarios (seed tree; mixed seeds 1-3; seed pool) on species composition (early (white), mid (grey) and late (black) successional species). Simulations of 9 ha with toroidal boundaries. Results are means (n=5) of 240 simulated years. SE was always < 0.5 m^3 ha^{-1} and thus not shown. T-test for matched pairs found significant differences at 1 % level for 86% and 80 % of tested pairs of abundance early and late successional species, respectively.

without recruitment input (Fig 7.10). It turned out that changes in the recruitment rates will affect standing volume only with a time-lag. Thus, standing bole volume, numbers of saplings or mother trees are no appropriate indicators to detect early stages of forest dieback. Important variables are the recruitment and mortality rates. Natural recruitment thus acts as a buffer system for the stand development (Holling 1973; Warner & Chesson 1985). Changes in seed production rates are buffered over several orders of magnitude. It is not obvious whether a threshold of seed production rates exists below which the forest collapses or degenerates to a large degree. Analysis of data from long-term research plots (Condit 1998) might disentangle this issue, and indicate for which values recruitment rates are low enough to draw our attention to a possible dieback in a given tropical forest. To study long-term trends in future forest inventories we suggest paying more attention to recruitment rates, and recording not only standing volume and estimating recruitment potential not through existing young trees and saplings. In this context the work of Curran and colleagues on seed predation is remarkable and important (Curran & Leighton 2000; Curran & Webb 2000).

The size of the simulated forest area plays a minor role in determining future forest composition, if undisturbed forest development was considered. Even in small simulation areas the forest stand was able to supply itself with sufficient recruitment. This conclusion has to be seen in the context of the assumptions used. We are aware that field studies indicate dramatic changes in mortality and recruitment rates in fragmented forests (Benitez-Malvido 1998; Laurance et al. 1997; Mesquita et al. 1999), which was not considered in our studies so far. However, disturbances resulted in a loss of species within a short time-period, if an external seed supply was missing, as seen in the development of logged-over forest (Fig. 7.9). Liu & Ashton (1999) found similar effects. They propose the establishment of a seed zone around logging areas, which enables natural recruitment of the disturbed forest.

We found that the detailed description of logging damages was important for a realistic simulation of logging impacts. Logging damages were depending upon logging intensity and were non-uniform in space. It seemed important to distinguish different types of logging damages, including one damage class which is proportional to the size of the felled tree. Other forest models

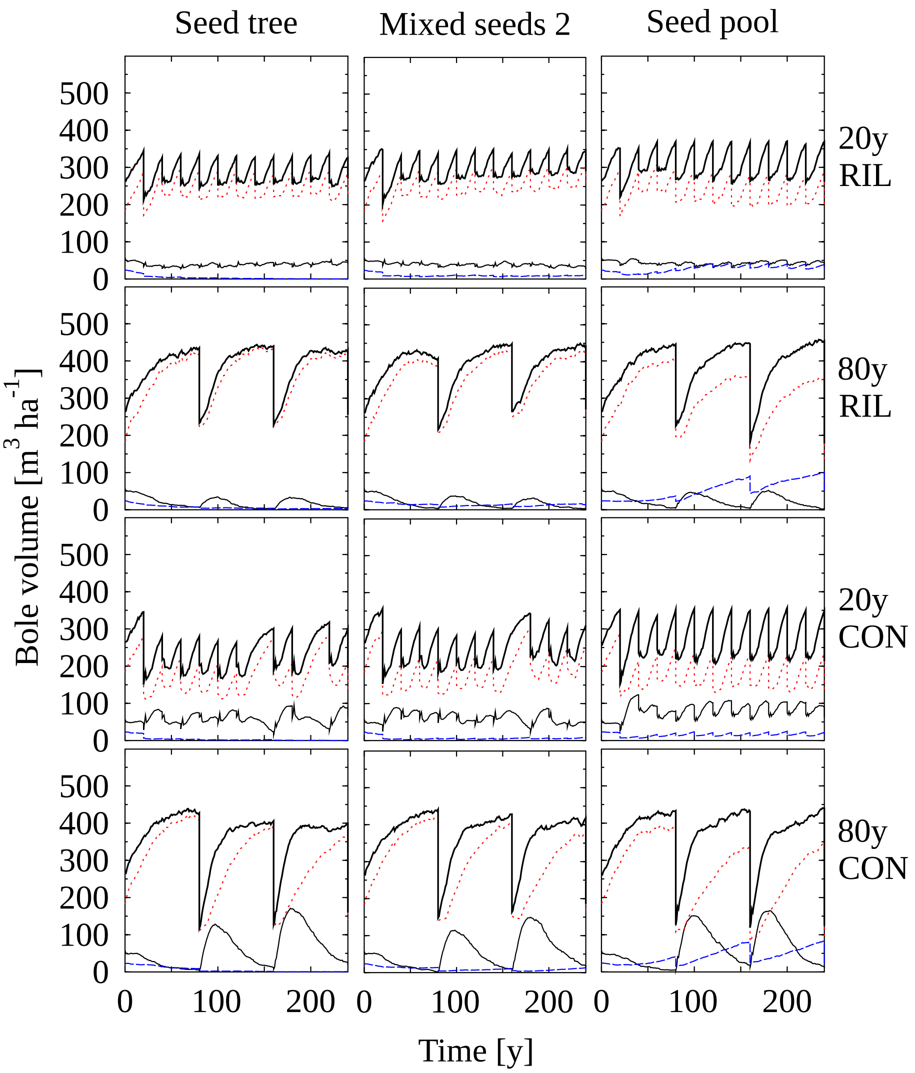

Figure 7.14: Development of bole volume (m^3 ha^{-1}) for different scenarios. Simulation of 9 ha over 240 y (n=5) of logged forest at site L1 with toroidal boundaries. Variation of logging cycle (20 y; 80 y), method (RIL: reduced-impact; CON: conventional) and recruitment scenarios (seed tree; mixed seeds 2; seed pool). Total (solid bold line), early successional spp. (solid line), mid successional spp. (broken dotted line), late successional spp. (broken line).

assume only one type of damage (Boscolo et al. 1997; Liu & Ashton 1999; Huth & Ditzer 2000a) or use regression equations (Howard & Valerio 1992; Vanclay 1995). Resulting light climate in our logging simulations was more realistic and growth of early successional species in canopy gaps benefit from spatial differences in damages. As emerging property of the modelled logging methods the resulting linear relationships between logging damages and logging intensity (Fig 7.15) was achieved. They correspond well to field measurements (Jonkers 1987; Hendrison 1990; Cannon et al. 1994; Pinard & Putz 1996; van der Meer & Bongers 1996; Weidelt 1996; Johns et al. 1996; Bertault & Sist 1997; Pulkki 1997; Brown 1998). For example, in a study in Kalimantan (Indonesian Borneo) damages to the residual stand varied from 30 % in reduced-impact logging to 48 % in conventional logging at an extraction intensity of 87 m^3 ha^{-1} (Bertault & Sist 1997).

For conventional logging the highest yields were obtained by a logging cycle of 80 y. In logging scenarios with short cycles the forest was overused, and had not enough

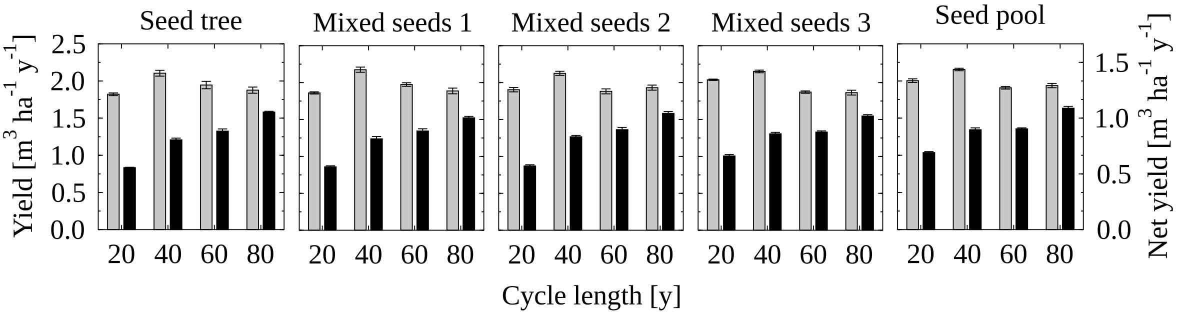

Figure 7.15: Effects of logging cycle (20 y, 40 y, 60 y, 80 y), method (reduced-impact (grey bars), conventional (black bars)) and recruitment scenarios (seed tree; mixed seeds 1-3; seed pool) on harvest yields. Yield (left scale) was reduced to net yield (right scale) by 30 % losses due to skidding etc. Simulations of 9 ha with toroidal boundaries. Results are means ± 1 SE (n=5) of 240 simulated years. T-test for matched pairs found significant differences at 1 % level for 74% of tested pairs.

time to regenerate. For reduced-impact logging the highest yields were observed for a cycle of 40 y. The yield obtained with RIL methods were always higher than those obtained with conventional methods. For short logging cycles the yield was doubled in RIL compared to CON. Many of the currently practised selective logging systems in South-East Asia are based on logging cycles between 20 and 40 years and conventional logging methods (Whitmore 1998). Thus, our results suggest that these systems are not appropriate for the recruitment capabilities of the forests and will lead to resource depletion.

Yields obtained in the present study are similar to previous studies on the same area (Kürpick et al. 1997; Ditzer et al. 2000; Huth & Ditzer 2000a). Maximal net extracted volumes ranged between 0.8-1.5 m^3 ha^{-1} y^{-1}. Huth & Ditzer (2000) obtain similar results for reduced-impact and conventional logging in cycles of 60 years and longer. Differences between the studies result from different assumptions on logging damages and different logging intensities. In the present study, lower yields were obtained than in the previous ones, especially in conventional logging. This is an important result, all the more so because local recruitment was considered for the first time here.

Yield losses were mainly caused by high abundance of early successional species after each logging event. Reducing light conditions which favour those species can be achieved by reducing the numbers and the sizes of log landings and roads. Switching from the use of heavy and destructive machinery as caterpillars to skyline yarding or cable supported systems will also reduce damages and thus make shorter cycles more economical.

Recruitment assumptions have only little impact on yield, but strongly influence the species composition. In fragmented forests without external seed input, the late successional species have nearly disappeared after the first logging operation. With an external seed input it takes more than 200 years before these species recover to their natural abundance. Thus, disturbances such as logging in fragmented forests change species composition drastically.

These findings correspond to observations in forest fragments. Growth of trees at the edge of fragmented forests is highly disturbed due to microclimatic changes and elevated wind turbulence (Laurance et al. 1997). Regeneration rates are biased towards families of early successional species (Laurance et al. 1998). Liu & Ashton (1999) showed in simulations that logging in fragmented forests will also reduce the number of tree species. Nevertheless, undisturbed forest fragments show also shifts in species composition (Turner 1996; Turner & Corlett 1996). As consequence of species groupings, our simulations suggest that these shifts occur inside the early, mid and late successional species groups, a hypothesis which should be tested.

The simulation results in this study may be optimistic regarding harvesting impact, because the model assumed that the soil in the logged forest provided suitable conditions for seeds to germinate and establish. In reality, soil in parts of the logged forest may be compacted and, therefore establishment and germination of seeds reduced (Cannon et al. 1994; Pinard & Putz 1996; Johns 1997; Frederickson & Mostacedo 2000; Guariguata 2000; Pinard et al. 2000). Heavily compacted soils may loose also their nutrients due to erosion processes (Malmer 1996). Another problem might be the extraction of nutrient due to harvesting. In logged dipterocarp forest it will take 20 to 60 years to restore the normal nutrient amount in the ecosystem (Ruhiyat 1989; Bruijnzeel 1992; Glauner 1999). In other regions nutrient input due to precipitation or rock decomposing may be much lower (Golley 1983; Bruijnzeel 1991). Moreover, we have no knowledge yet which nutrient level trees need (Whitmore 1998). In other words, logging impacts might be more serious than those shown in the simulations. Nevertheless, the model provides a first assessment of impacts of different harvest regimes. Even if we might have underestimated the impacts of timber harvesting on recruitment capabilities, simulated impacts are still large enough to warrant attention to present tropical forest management.

Acknowledgement

Thanks to H. Bossel, J. Chave, R. Glauner and L. Kammesheidt for very helpful comments and improving suggestions on former versions of the manuscript. P. Köhler was funded by the Otto-Braun-Foundation of the University of Kassel, Germany.

Appendix

Table 7.6: Short description of parameters incl. functional relationships (modified from Kammesheidt et al. 2000).

Parameter	Description
	Environmental parameters
k	Light extinction coefficient
I_0	Light intensity above canopy
S_{D}	Day length
	Establishment parameters
D_{S}	Initial diameter of seedlings
I_{S}	Minimal light intensity for germination
N_{S}	Ingrowth rate of seeds into seed pool
N_{R}	Seed dispersal rate of mother trees
X_{R}	Average seed dispersal distance
D_{R}	Minimum diameter of mother trees
	Mortality parameters
M_{B}	Basic mortality rate
M_{S}	Mortality rate of seeds
M_{D}	Size dependent mortality rate ($M_D = M_{\mathrm{D0}} - M_{\mathrm{D0}}/M_{\mathrm{D1}} \cdot d$)
W	Probability of a dying tree (d>10 cm) to fall
	Tree physiognomic parameters
H_{M}	Maximum height
c_{p}	Crown length fraction
τ_j	Site dependent fraction of stemwood biomass to total above-ground biomass ($\tau = \tau_1 + \tau_2 \cdot h(d = 120\mathrm{cm})$)
h_0 and h_1	Height = f(diameter) ($h = d/(1/h_1 + d/h_2)$)
γ_{j}	Form factor = f(diameter) ($\gamma = \gamma_0 \cdot exp(\gamma_1 \cdot d^{\gamma_2})$)
f_{j}	Crown diameter = f(diameter) ($d_c = (f_0 + f_1 \cdot d^{f_2}) \cdot d$)
l_{j}	Leaf area = f(diameter) ($l = l_1 \cdot d + l_2 \cdot d^2 + l_3 \cdot d^3$)
LAI_{M}	Maximum leaf area index of single tree
	Biomass production parameters
P_{M}, α	Photosynthetic capacity and efficiency in light response curve ($P_i(I_i) = \alpha \cdot I_i/(1 + \frac{\alpha}{P_{\mathrm{M}}} I_i)$)
ρ	Stem wood density
r_1	Maintenance respiration = f(biomass) ($R_{\mathrm{m}}(B_i) = r_1 \cdot B_i$)
R_{G}	Growth respiration as part of biomass
m	Leaf transmittance
g	Conversation factor $\mathrm{g}_{\mathrm{CO2}}$ to $\mathrm{g}_{\mathrm{odm}}$

Table 7.7: Parametrisation for Sabah (Malaysia). Short description of parameters found found in Table 7.6. Parameters with subindex vary with successional status (s), potential height (h) (corresponding to SS and HG in Table 7.1, respectively), or different functional coefficients (j).

Parameter	Subindex	Units	Values				
			Environmental parameters				
k		[-]	0.7				
I_0		$[\frac{\mu\text{mol(photons)}}{\text{m}^2\text{s}}]$	642.0				
S_D		[h]	12.0				
			Recruitment parameters				
D_S		[m]	0.01				
$I_{\text{S}s}$	s=1-3	[fraction of I_0]	0.20	0.04	0.01		
$N_{\text{S}s}$	s=1-3	[ha^{-1} y^{-1}]	150	625	50		
$N_{\text{R}s}$	s=1-3	[tree^{-1} y^{-1}]	100	20	4		
$X_{\text{R}s}$	s=1-3	[m]	100	75	50		
$D_{\text{R}h}$	h=1-5	[m]	0.04	0.10	0.18	0.40	0.50
			Mortality parameters				
$M_{\text{B}s,h}$	s=1; h=1-5	[y^{-1}]	0.00	0.12	0.10	0.08	0.06
$M_{\text{B}s,h}$	s=2; h=1-5	[y^{-1}]	0.06	0.05	0.04	0.03	0.025
$M_{\text{B}s,h}$	s=3; h=1-5	[y^{-1}]	0.00	0.04	0.03	0.02	0.015
$M_{\text{S}s}$	s=1-3	[y^{-1}]	0.1	0.5	1.0		
$M_{\text{D}j}$	j=0-1	[y^{-1}, m^{-1}]	0.2	0.1			
W		[-]	0.40				
			Tree physiognomic parameters				
$H_{\text{M}h}$	h=1-5	[m]	5	15	25	36	50
c_p		[-]	0.358				
τ_j	j=0-1	[-, m^{-1}]	-0.035	0.0139			
h_{0h}	h=1-5	[cm m^{-1}]	1.24	1.18	0.97	1.08	1.33
h_{1h}	h=1-5	[m^{-1}]	38.5	43.6	88.6	57.3	70.5
γ_j	j=0-2	[-, cm^{-1}, -]	2.575	-1.409	0.0358		
f_j	j=0-2	[-, -, -]	0.132	0.933	-0.6615		
l_j	j=1-3	$[\frac{\text{m}}{\text{cm}}, \frac{\text{m}}{\text{cm}^2}, \frac{\text{m}}{\text{cm}^3}]$	3.197	0.0684	-0.000379		
LAI_M		[-]	2				
			Biomass production parameters				
$P_{\text{M}s}$	s=1-3	$[\frac{\mu\text{mol(CO}_2)}{\text{m}^2\text{s}}]$	19.4	9.3	6.8		
α_s	s=1-3	$[\frac{\mu\text{mol(CO}_2)}{\mu\text{mol(photons)}}]$	0.043	0.043	0.043		
ρ_s	s=1-3	[t$_\text{odm}$ m^{-3}]	0.37	0.55	0.75		
r_{1s}	s=1-3	[-]	0.12	0.05	0.02		
R_G		[-]	0.25				
m		[-]	0.1				
g		[g$_\text{odm}$ g$_\text{CO2}^{-1}$]	0.63				

Chapter 8

Long-term response of tropical rain forests to the effects of fragmentation: a simulation study

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Abstract

The impacts of forest fragmentation on the residual stands have only recently come to attention. We combined the current knowledge of a higher tree mortality rate at the forest edges and a lower recruitment capability of tree species in forest fragments in a comprehensive simulation study for a rain forest site in French Guiana using the individual-oriented and process-based forest growth model FORMIND2.0. Simulations were based on the aggregation of the tree species into 19 different plant functional types. Specially, we investigated the spatial and temporal effects of the fragment size (1–100 ha) on forest dynamics, species composition, and future recruitment potentials in terms of the number of seed producing trees. Biomass in small scale forest fragments declined after 300 years below 10 % of the primary forest level in the most extreme scenario. In particular, the decreasing recruitment capability limited forest growth. Furthermore, different intensities and pattern of forest clearing were analysed in the simulation of a forest/non-forest landscape of 1 km^2 over several centuries. The cleared areas were abandoned after 300 simulated years. Thus, the regrowth of a secondary succession as function of size and shape of forest fragments was also investigated.

Keywords: fragmentation; modelling; rain forest; secondary succession; simulation.

To be submitted.

Introduction

The fraction of forested area being clearcut is still high around 1 % per year on average (FAO 1997; Whitmore 1998; Malhi & Grace 2000). Tropical forests may soon have shrunk to quite small patches of isolated remnants. Indeed, from the small-scale slash-and-burn agriculture, to large-scale clearing for monocultures (sugar cane, oil palm, ecalyptus or hevea) the overall impact on the ecosystems should be very different. There has been a strong effort in trying to understand the ecology of these fragmented forests (for a review, see Saunders et al. 1991; Murcia 1995; Laurance 1999a). Observations in Australia (e.g. Crome 1991; Law & Lean 1999), Thailand (e.g. Lynam 1997; Lynam & Billick 1999), French Guiana (e.g. Thiollay 1989; Thiollay 1992; Cosson et al. 1999), the Brazilian Atlantic forest (e.g. da Fonseca 1985; Tabarelli et al. 1999) and central Amazon (e.g. Lovejoy et al. 1984; Gascon et al. 1999) have enriched our current knowledge of processes in animal and plant communities within forest fragments and with respect to scale. These studies have shown that a forest community, when restricted to small disconnected fragments, shows dramatic changes in its dynamics. For example, the mortality in emergent mature trees increases, establishment of light demanding pioneer plants and potentially invading plants is promoted, local microclimatic conditions are changed, leading to higher daily transpiration (Nepstad et al. 1999). Likewise, the age structure of animal populations is altered (Woodroffe & Ginsberg 1998; Curran et al. 1999; da Silva & Tabarelli 2000). These factors result in a significant diminuition of species diversity and a modification of the species composition (Laurance & Bierregaard 1997; Tabarelli et al. 1999). The disturbed landscapes have a potential to recover from clearings, but abandoned pastures are rapidly invaded by regrowing secondary forests (Saldarriaga et al. 1988; Brown & Lugo 1990). Existing field studies show clear differences in secondary vegetation dynamics depending on disturbance type (Uhl et al. 1988; Aide et al. 1995). However, direct data on secondary regrowth are rarely older than 50 years (Finegan 1996).

While long-term assessements are obviously required, our current knowledge can be gathered into an integrative modelling approach, in order to relate the recent findings of field ecology to conservation issues (Kremen et al. 2000). Recently, simple models on forest fragmentation have been published. However, they only take into account global, spatially-implicit variables, such as the core area of a forest fragment left undisturbed (Laurance & Yensen 1991), or persistence probability of plant species within a land clearing (Laurance et al. 1999). Moreover, the long term consequences of fragmentation over large scale patterns in tropical ecosystems are still poorly understood at the community-level (Brown et al. 1995, Chave et al. 2000c). In the temperate zone, a modelling approach has been used to analyse the effects of fragmentation on tree species diversity (Malanson 1996; Malanson & Armstrong 1996). In the present paper, we provide a more detailed analysis for the tropical zone. Our approach combines the current knowledge of mortality and recruitment patterns in fragmented rain forests in the framework of the individual-oriented and process-based forest growth model FORMIND (Köhler & Huth 1998a). This model describes the spatio-temporal dynamics of a mixed forest stand for an area up to several km^2 based on a carbon cycle model for different plant functional types. The model was applied to the rain forests of Malaysia (Köhler & Huth 1998a; Köhler et al. 2001) and the neotropical moist forests of Venezuela (Kammesheidt et al. 2000) to address forest management issues such as the long-term impacts of logging on the forest dynamics. Here, we address the issue of fragmentation with a new parameterization of our model, for the rain forest of French Guiana.

We shall assess the generality of our results with respect to the forest type.

We shall here focus on the influence of the scale and of the shape of the disturbed area, a topic that has quite a long history in the context of plant ecology (Levin & Paine 1974). However, our aim is not only theoretical, and we aim to come up with reasonable suggestions for land-use and landscape-scale management of wet tropical areas. Specially, we want to address the following questions: (1) How do the size and the shape of a fragmented forest influence both forest dynamics and species composition? (2) Do different patterns of fragmentation in a landscape influence spatio-temporal dynamics? (3) What is the forest structure after clear-cut areas, such as pastures, are abandoned?

Methods

Study area

Our study focuses on the French Guiana rain forest. This forest is reminiscent of the 'Wallaba' forest type (Richards 1996). Dominant families are Lecythidaceae and Caesalpiniaceae (Mori 1990; Poncy et al. 1998).

The forest in French Guiana is one of the best protected in South America, due to low anthropogenic pressure and high labor cost, having made this forest unattractive for logging companies, for the last 60 years at least. French Guiana lies between 2°10' North and 5°45' North and 51°40' West and 54°30' West in Northeastern South America. Of the region, 97 % is covered by a pristine lowland wet tropical forest, which extends, northwards, to the Surinam, Guyana and western Venezuela, and, southwards, to Brazil. Annual rainfall is between 1650 and 4000 mm, with a decreasing gradient from the coastal area southwards. A pronounced dry season of 2 months is recorded from September to November and a short dry season in March. The average temperature is 25.8 °C with an annual amplitude of 2 °C and daily amplitudes of 7 °C in the rainy season (10 °C during the dry season). Geology is typical of the Guiana Shield with a central pediplain and sparse rugged mountains of Precambrian metamorphic and granitic rocks. The altitude is less than 500 m above sea level.

The observed forest of La Piste de Saint-Elie (5°30' N, 53°00' W) is located 16 km south of Sinnamary and has been much studied since 1976 (Lescure et al. 1983, Lescure & Boulet 1985, Puig et al. 1990, Pelissier & Riéra 1993, Roggy et al. 1999). Annual rainfall is slightly above 3 000 mm y^{-1}. The forest mostly grows on a schist mantle covered by a sandy clayey soil (Lescure & Boulet 1985).

A 5 ha forest inventory where all the 2740 trees $\geq$ 10 cm in dbh have been tagged, measured and mapped has been used for this study. 261 species (or morphospecies) have been found in a sample of 2475 individuals (Tab. 8.1). Fisher's α diversity parameter gives $\alpha = 73.3$ which is quite large (Gentry 1988; Valencia et al. 1994; Leigh-Jr. & de Lao 2000). The forest is dominated by Lecythidaceae (22 spp., 30.0 % of the trees, 22.4 % of the basal area), Caesalpiniaceae (19 spp., 18.4 % of the trees, 31.4 % of the basal area) and Chrysobalanaceae (24 spp., 9.3 % of the trees, 10.1 % of the basal area). The average basal area is 30.2 m^2 ha^{-1}.

The model

FORMIND2.0 is an individual-oriented and process-based forest growth model which simulates the spatial and temporal dynamics of uneven-aged mixed forest stands. A complete model description has been published in previous papers (Köhler & Huth 1998a; Kammesheidt et al. 2000; Köhler et al. 2000c). Nonetheless, since we

Table 8.1: Density and basal area of the major tree species at the Piste de Saint Elie Research Station. Of 2740 trees $\geq$ 10 cm dbh in the 5 ha plot, 2475 (90.3 %) were identified to the species. The actual number of species recorded was 261, and the total diversity extrapolated using Fisher's α is 267 species.

Rank	Species	No. trees	%	Basal area (m^2 ha^{-1})	%
1	Lecythis idatimon Aubl. (Lecyth.)	241	9.7	1.78	6.3
2	Eperua falcata Aubl. (Caesalp.)	204	8.2	1.07	3.8
3	Lecythis persistens Sagot (Lecyth.)	133	5.4	0.79	2.6
4	Eschweilera micrantha (Berg) Miers (Lecyth.)	119	4.8	0.8	3.0
5	Eschweilera sagotiana Miers (Lecyth.)	81	3.3	1.2	4.3
6	Licania alba (Bernoulli) Cuatrec. (Chryso.)	77	3.1	1.1	4.0
...					
11	Eperua grandiflora (Aubl.) Benth. (Caesalp.)	52	2.1	1.1	3.7
...					
15	Dicorynia guianensis Amsh. (Caesalp.)	40	1.6	0.8	3.0
Total		947	38.3	8.7	30.6
Grand total		2475	100	28.4	100

have parametrized our model specifically for the Guiana rain forest, basic informations about the model and the species groups can be found in the Appendix.

The model describes a forest stand as a mosaic of interacting patches of 20 m × 20 m in size. Within these patches trees are not spatially-explicit distributed, and thus compete for light and space following the gap model approach (Botkin 1993; Liu & Ashton 1995; Shugart 1998; Bugmann & Solomon 2000). The carbon balance of each individual tree is modelled explicitly including as main processes photosynthesis and respiration. Allometric relationships relate the above-ground biomass, the stem diameter, the tree height and the crown diameter with each other. Growth process equations and physiological parameters are taken from a related model Formix3-Q (Ditzer et al. 2000). Beside normal mortality, death of trees can occur either through self-thinning in dense patches or through falling of large trees (gap formation). The dispersal of seeds produced by mature trees is, beside gap formation, the other major cause of spatial correlation in the model. The seed production rates of mature trees correspond to the reproductive success at dbh 1 cm. Thus, the rates include fecundity, seed survival, germination and possible predation upon young seedlings (Chave 1999b).

Species grouping, parametrisation and initialisation

A species list covering 1022 tree and shrub species found in French Guiana was constructed (Chave 1999a), extending the work of Favrichon (1995), using the data of van Roosmalen (1985) and some new information (Chave & Riéra, in preparation). Nine-

Table 8.2: Autecological characteristics of 19 plant functional types (PFT) of French Guiana's tropical rain forest tree species. Height at maturity. SS: successional status. HG: height group. No: Number of species per PFT. Ab: Abundance of trees with dbh $\geq$ 10 cm in research plots in Nouragues (from the AUBLET database), Piste de Saint-Elie, and Paracou (from Favrichon 1995).

Plant Functional Type	Height [m]	PFT	SS	HG	No	Ab [%]
Shrub savanna spp.	0-5	1	0	1	7	0.0
Shrub early successional spp.	0-5	2	1	1	17	0.1
Shrub mid successional spp.	0-5	3	2	1	29	1.0
Shrub late successional spp.	0-5	4	3	1	83	2.0
Understorey savanna spp.	5-15	5	0	2	31	0.0
Understorey early successional spp.	5-15	6	1	2	74	1.4
Understorey mid successional spp.	5-15	7	2	2	76	3.5
Understorey late successional spp.	5-15	8	3	2	152	5.4
Lower canopy savanna spp.	15-25	9	0	3	7	0.0
Lower canopy early successional spp.	15-25	10	1	3	48	2.8
Lower canopy mid successional spp.	15-25	11	2	3	84	11.4
Lower canopy late successional spp.	15-25	12	3	3	122	18.1
Upper canopy savanna spp.	25-36	13	0	4	2	0.0
Upper canopy early successional spp.	25-36	14	1	4	38	1.6
Upper canopy mid successional spp.	25-36	15	2	4	67	22.2
Upper canopy late successional spp.	25-36	16	3	4	103	21.0
Emergent early successional spp.	>36	17	1	5	12	0.9
Emergent mid successional spp.	>36	18	2	5	38	6.4
Emergent late successional spp.	>36	19	3	5	32	2.2

teen different plant functional types (PFT) based on successional status and maximum tree height at maturity were assigned (Table 8.2). The grouping of tree species uses an approach already described for a rain forest community in Sabah, Malaysia (Köhler et al. 2000b). The species list (available from the authors) contains savanna species, which are considered as extreme pioneers. In addition, we consider three classes of successional behaviour for forest species (early, mid and late successional species), and five classes of maximum tree height. We classify the species into shrubs (0–5 m), understorey (5–15 m), lower canopy (15–25 m), upper canopy (25–36 m), and emergents (more than 36 m) similarly to Sabah's rain forest species grouping (Köhler et al. 2000b).

Parameter values (see Appendix) were gathered from a former case study in French Guiana (Chave 1999b), and from parameter variations and sensitivity analysis to match typical diameter increment pattern (Gourlet-Fleury 1997; Gourlet-Fleury & Houllier 2000). Model structure and its sensitivity to parameter variations were inves-

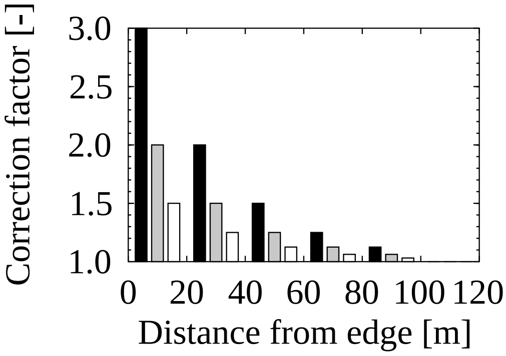

Figure 8.1: Correction factor of tree mortality rates at forest edges. Black: correction factor for large trees with $d \geq 60$ cm in the neighbourhood of cultivated lands; grey: correction factor for trees with d<60 cm in the neighbourhood of cultivated lands; white: correction factor for trees in the neighbourhood of secondary succession for the first 20 y. Mortality in patches more than 100 m inwards is not affected. All distances between patches were computed between patch centers.

tigated in detail and reported in previous reports (Kammesheidt et al. 2000; Köhler et al. 2000c).

By simulating the long-term dynamics of the 5 ha inventory (only trees with dbh $\geq$ 10 cm) with constant recruitment input, we generate a stem-dbh distribution of an undisturbed forest. It reflects for trees with dbh $\geq$10 cm the characteristics of field data. This generated forest stand at equilibrium is then used as the initial stand for our simulations.

Fundamental mechanisms in forest fragments

The dynamics of the forest relies strongly upon any fragmentation. Tree mortality was observed to increase at the edge of the fragmented remnants. Fragmentation results in microclimatic changes as well as enhanced wind disturbances (Laurance et al. 1997; Laurance et al. 1998). Trees affected by edge effects were found up to 100 m inwards, and the nature of surrounding ecosystems also had a great impact on the type of edge effect (Mesquita et al. 1999). Overall, emergent trees (d$\geq$60 cm) are most sensitive to edge effects both because of a larger impact of winds and because of changes in microclimatic conditions (Laurance et al. 2000). We have included these mechanisms into a correction factor for mortality rates. Tree mortality rates are explicit functions of the distance to the nearest forest edge, of the type of surrounding vegetation and of tree size (Fig. 8.1).

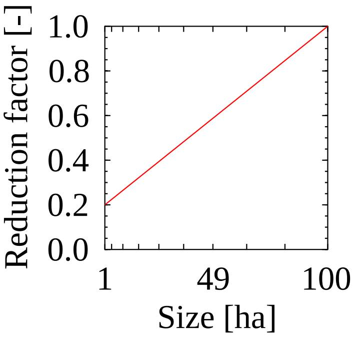

Figure 8.2: Reduction factor of recruitment rates in small forest fragments as function of the system size. In fragments larger than 100 ha recruitment is not altered.

Fragmentation also leads to a drastic alteration of the recruitment. Once the forest matrix has been sufficiently fragmented, the density of various animal and bird populations, the main seed dispersers of neotropical plants, was found to decrease significantly, resulting in a reduction of the seed dispersal, as well as on the predation rates on seedlings (Laurance et al. 1998; Lawton et al. 1998; Law & Lean 1999; Lynam & Billick 1999; Price et al. 1999; da Silva & Tabarelli 2000). Thus, the number of ingrowing seedlings per year (at a 1 cm dbh) depends critically upon the size of forest fragments. We have therefore introduced a hypothetical reduction factor on seed production rate as function of fragment size (Benitez-Malvido 1998) and we have assumed that areas larger than 1 km^2 were unaffected by these effects (Fig. 8.2).

Table 8.3: Description of different fragmentation scenarios. Mortality is only altered in a border zone of 100 m (Fig. 8.1), and, if switched on, affect all size classes (^{a}) or can depend on the size-class (^{b}). In scenario *fragmented 3*, the recruitment is affected over the whole area (Fig. 8.2).

Scenario	Boundary condition	Increase in mortality	Reduction in recruitment (global)
periodic	periodic	no	no
open 1	open	yes^a	no
open 2	open	yes^b	no
open 3	open	yes^a	yes

Scenarios

To address the issue of scale and shape using our model, we have performed several computer experiments.

Scale: Seven different fragment sizes — from 1 to 100 ha —, and four different fragmentation assumptions (scenarios *non-fragmented*, *fragmented 1* to *fragmented 3*) were matched, which resulted in possible $7 \times 4 = 28$ scenarios. The assumptions on fragmentation included boundary conditions and alterations of mortality and recruitment rates (Table 8.3). We have used two types of boundary conditions: periodic, or toroidal condition (opposite ends are wrapped), and open boundaries (free flow of seeds outwards). The former assumes that the simulated area is embedded in a larger forest with a similar structure. With the latter, the landscape outside the simulated area is different from a mixed tropical rain forest (agriculture, pasture, monocultural forests). The sensitivity of forest dynamics to boundary conditions was investigated recently (Köhler et al. 2000c). For all sizes the runs contained of 300 simulated years and were replicated ($n = 5$).

Shape: Moreover, we have studied the spatio-temporal dynamics of fragmented landscapes to assess the long-term impact of fragmentation on the forest dynamics. Within a landscape of 1 km^2 $CF = 0$ % to 90 % of the total area was cleared and converted into non-forest areas (values of CF every 10 %). Different pattern of fragmentation were investigated. The null-model of fragmentation (Fahrig 1992), which consists in removing patches at random (scenario *random*), was compared with simulations with some spatial correlation in the fragmentation process. Weakly, medium and highly clustered fragmentation scenarios were investigated (scenarios *clustered 1* to *clustered 3*, respectively), giving $9 \times 4 = 36$ scenarios. A mathematical interpretation of this spatial correlation can be found in Moloney & Levin (1996). The regrowth of a secondary succession after the cleared landscape has been abandoned at year 300 was analysed for another 300 years. Seed dispersal was made possible throughout the landscape. For this set of scenarios, the edge correction of mortality rate was not depending on tree size, and assumed reduced edge effects in the first 20 y of secondary succession (Fig. 8.1, Mesquita et al. 1999). The nutrient budgets of the abandoned areas were kept constant. These scenarios included periodic boundary conditions.

The analysis of variance (ANOVA) was restricted to the special case with $n = 1$ (Graf et al. 1987).

In our analysis we have used four different indicators to keep track of the various effects of a fragmentation experiment on a control pristine forest. We have monitored (i) the standing above-ground biomass, (ii) the abundance of early and late successional species, as indicator for species composition, (iii) the number of large trees, capable for seeds production (for the height groups upper canopy and emergents), as an indicator of size distribution and potential recruitment limitation, (iv) the spatial distribution of dominant trees in fragmented landscapes. Successional status and height of dominant trees in each patch is shown in those figures. As simulations were undertaken with 19 PFTs, aggregation of results is necessary for interpreting them.

Results

Influence of fragmentation intensity and of system size on forest dynamics

Fragmentation affected the simulated area in various ways. For example, mortality was increased in the border zone, whereas recruitment decreased over the whole area. Therefore, nontrivial correlations might be unveiled when the size of the simulated area and fragmentation assumptions were changed.

We found that the influence of both system size and fragmentation method had a significant influence on the total biomass and on the fraction of early successional species (ANOVA: $P < 0.001$, see Table 8.4). Late successional species were significantly affected by size ($P < 0.01$), but not by the fragmentation type ($P > 0.1$). The number of seed trees was significantly affected by all scenarios ($P < 0.001$).

In the control run (scenario *non-fragmented*), size influenced the variance of diagnostics, but time averaged values were only slightly affected (Fig. 8.3). The total above ground biomass was almost unaffected by the system size in the non-fragmented scenario; it fluctuated around 445 ± 15 Mg ha^{-1}. The biomass fraction of early successional species was negligible (around 4 %), while that of late successional species was 54 ± 2 % of the total biomass. Finally, the density of mature trees was slightly less than 20 ha^{-1} (upper canopy) and 17 ha^{-1} (emergents).

The forest dynamics of selected scenarios are plotted in Fig. 8.4. The three scenarios of fragmented forest situations raised the same global pattern, albeit a stronger influence of finite size effects. Below a system size of about 50 ha, the total above ground biomass was below 300 Mg ha^{-1}. At maximum it reached 400 Mg ha^{-1} for the largest simulated fragment (100 ha). Early successional species took advantage of edge disturbances and reached values around 10 % of the total biomass. The density of mature trees was also slightly reduced (21 % decrease for upper canopy species, and 6 – 19 % decrease for emergents). For the 1 ha runs, standing above-ground biomass was reduced to 30 % compared with the control run after 300 y (scenario *fragmented 1*), 25 % (scenario *fragmented 2*), and 7 % (scenario *fragmented 3*). Mature trees completely disappeared from the 1 ha plot in scenario *fragmented 3*. Thus, species composition and size structure in small scale fragments were altered dramatically. When recruitment is altered through fragmentation (*fragmented 3*) the community was still not in a steady state after 300 y, and abundance of early successional species was still increasing for all sizes <100 ha. As abundance of savanna species was always below 1 %, each shift in species composition strongly influences mid-successional species as well.

Fragmentation mostly influences forest edges. Overall, the fraction of patches containing trees larger than 30 m in height declined between the control run (from 91 –

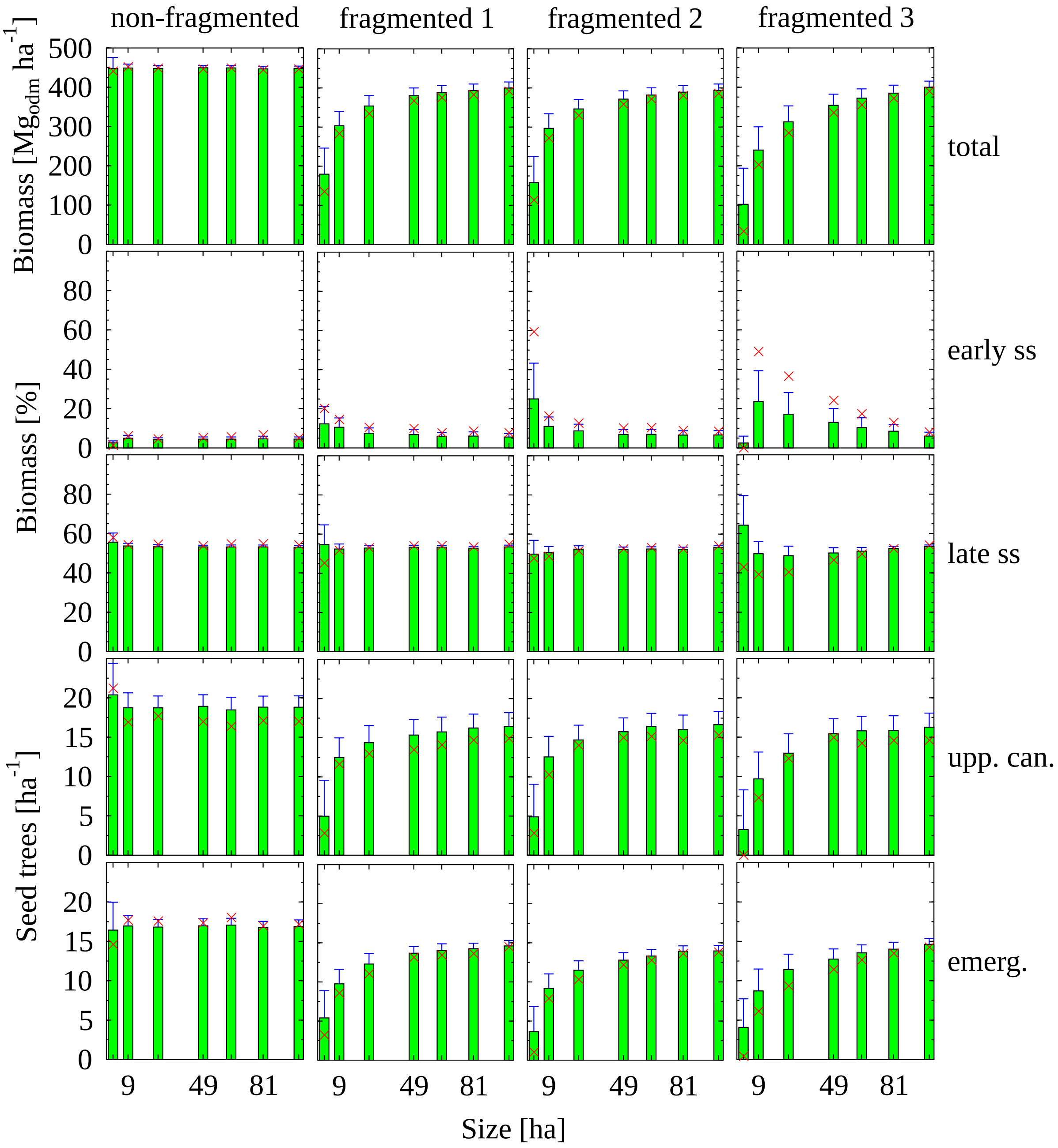

Figure 8.3: Above-ground biomass (row 1-3) and number of seed trees (row 4-5) as function of different fragmentation scenarios (non-fragmented and fragmented 1–3, see Table 8.3 for details) and spatial scale (1–100 ha). Row 1: total biomass; row 2: fraction of early successional species; row 3: fraction of late successional species; row 4: number of seed producing trees of upper canopy species; row 5: number of seed producing trees of emergent species. Bars show the time averaged values, including standard deviation. Crosses correspond to values at $t = 300$ y. Data are averages over $n = 5$ runs.

Table 8.4: Forest dynamics in a single forest fragment. ANOVA for the main and interactive effects of size (1 ha to 100 ha) and fragmentation assumptions (boundary conditions, increased edge mortality and reduced recruitment) on the following monitored quantities: (A) total above-ground biomass, (B) fraction of early successional species on biomass, and (C) fraction of late successional species on biomass. Simulation time was 300 y ($n = 5$).

Effects	SS	df	MS	F ratio	P
A) Biomass					
Size	544801.02	6	90800.17	3699.61	<0.001
Fragmentation	397447.43	3	132482.48	5397.94	<0.001
Size × fragmentation	196128.34	18	10896.02	443.95	<0.001
Error	2748.83	112	24.54		
B) Early successional species					
Size	1024.70	6	170.78	11.05	<0.001
Fragmentation	1381.77	3	460.59	29.80	<0.001
Size × fragmentation	776.51	18	43.14	2.79	<0.01
Error	1730.97	112	15.46		
C) Late successional species					
Size	275.66	6	45.94	3.06	<0.01
Fragmentation	62.48	3	20.83	1.39	>0.1
Size × fragmentation	645.10	18	35.84	2.39	<0.01
Error	1682.04	112	15.02		

93 % for all system sizes) and fragmented regimes. Again, the impact was quite limited in large areas (100 ha), which were only slightly altered, while in 1 ha simulations in most extreme scenarios few to no plots were dominated by large trees (32 %, 16 %, and 0 % for *fragmented 1*, *fragmented 2*, and *fragmented 3*, respectively).

Influence of the fragmentation shape at the landscape scale

The total biomass and the abundance of early successional species were both significantly affected by the clearing fraction and by the fragmentation shape ($P < 0.001$). However, the abundance of late successional species was not significantly influenced by the shape of the forest fragments ($P > 0.1$, Table 8.5). The biomass per ha, as well as the fraction of this biomass corresponding to early successional species was compareable with the control run.

When the clearing fraction (CF) increased close to 50 %, the abundance of early successional species saturated at 33 % for the case of fragmentation without clustering (null-model). The total biomass loss also reached a maximum around $CF = 0.5$. Differences in the shape of the fragmentation procedure only led to slight changes in

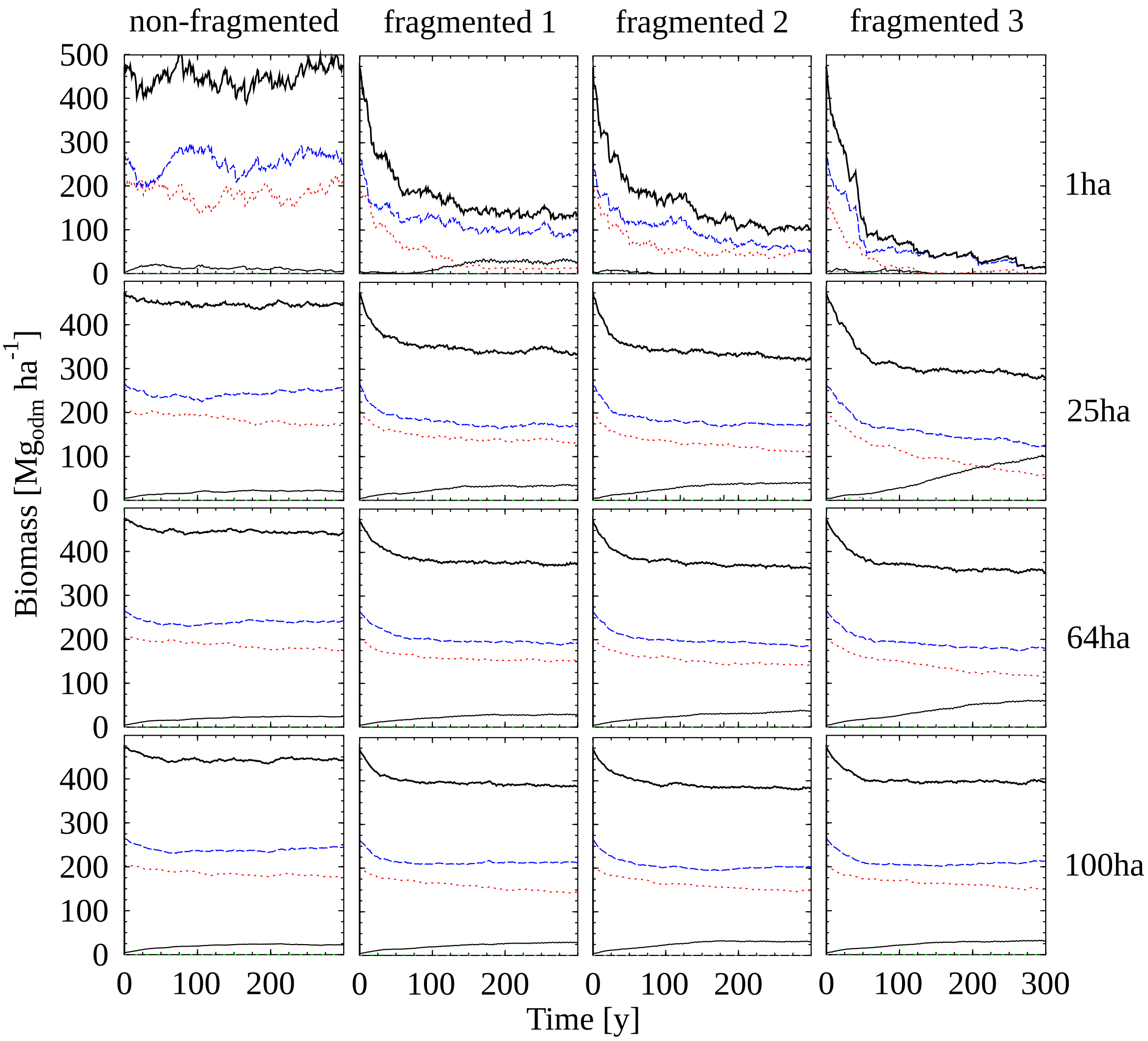

Figure 8.4: Time variation of the above-ground biomass for selected fragmentation scenarios (non-fragmented and fragmented 1–3, see Table 8.3 for details) and spatial scale (1-100 ha). Total biomass (solid bold line), biomass for early successional species (solid line), for mid-successional species (broken dotted line), and for late successional species (broken line). Savanna species are always below 1 Mg ha^{-1} and are not shown.

the dynamics. At maximum fragmentation ($CF = 90$ %) scenario *clustered 3* achieved highest value in total biomass (51 % of reference case compared to $32 - 37$ % in other scenarios). Abundance of early successional species increased from 4 ± 1 % in the control run, to $27 - 33$ % at $CF = 90$ %. Late successional species were relatively unaffected in all scenarios ($43 - 56$ %) (Figs. 8.5, 8.7).

Undisturbed forest remnants persisted in the center of forest fragments (Fig. 8.8 top). The fraction of patches dominated by trees > 30 m decreased from 91 % (control run) to $28 - 34$ % at year 300 and with $CF = 90$ %. Large dominant trees were most sensitive to fragmentation patterns in clearing scenarios of medium intensity (e.g. $CF = 50$ %, dominance varied between $39 - 70$ %).

Regeneration and secondary succession in abandoned lands

Besides the short-term impact of framentation upon the ecology of the forest rem-

Table 8.5: Forest dynamics in partially fragmented landscape. ANOVA for the main effects of clearing fraction ($CF = 0 - 90$ %) and shape of the fragmentation pattern (random, three types of clustering) on the following monitored quantities: (A) total above-ground biomass, (B) fraction of early successional species on biomass, and (C) fraction of late successional species on biomass. Simulation time was 300 y, simulated area was 1 km^2. Sample size $n = 1$ and no cross-correlation.

Effects	SS	df	MS	F ratio	P
A) Biomass					
Clearing	185746.38	9	20638.49	36.86	<0.001
Pattern	30521.83	3	10173.94	18.17	<0.001
Error	15118.98	27	559.96		
B) Early successional species					
Clearing	545.04	9	60.56	15.97	<0.001
Pattern	164.62	3	54.87	14.47	<0.001
Error	102.37	27	3.79		
C) Late successional species					
Clearing	64.91	9	7.21	3.75	<0.005
Pattern	6.00	3	2.00	1.04	>0.1
Error	51.94	27	1.92		

nants, our model allowed us to investigate long-term trends. Of central interest is the question of how previously clear-cut areas regenerate once they are abandoned by human exploitation.

In the time-averaged pattern of secondary succession, all monitored variables — total biomass, abundance of early and of late successionals — were significantly affected by the fraction of clear-cut land, CF (ANOVA: $P < 0.001$). None of the monitored quantities was sensitive to the shape of the disturbed area ($P > 0.01$, $P > 0.5$, $P > 0.01$, Tab. 8.6), but the dominance of early successional species lasted longer in highly clustered landscapes (200 y in scenario *clustered 3* versus only 100 y in scenario *random*, both for $CF = 90$ %, cf. Fig. 8.7). In all scenarios a steady state was not reached after 300 simulated years, but the abundance of early successional species declined to closed forest levels (around 5 %) in all cases except for $CF \geq 80$ % and *clustered 3*, were this fraction ranged between $7 - 12$ %.

In the final years of the simulation, the important aspects of the dynamics were the height growth of established long living trees and species shift between mid to late successional species. Abundance of late successionals ranged between $15 - 56$ % at year 300 (Fig. 8.6). The total standing biomass reached 264-306 Mg ha^{-1} or $59 - 68$ % of the closed forest level reached in the control simulation (448 t ha^{-1}), for $CF = 90$ %. Even at medium clearing intensity ($CF =$

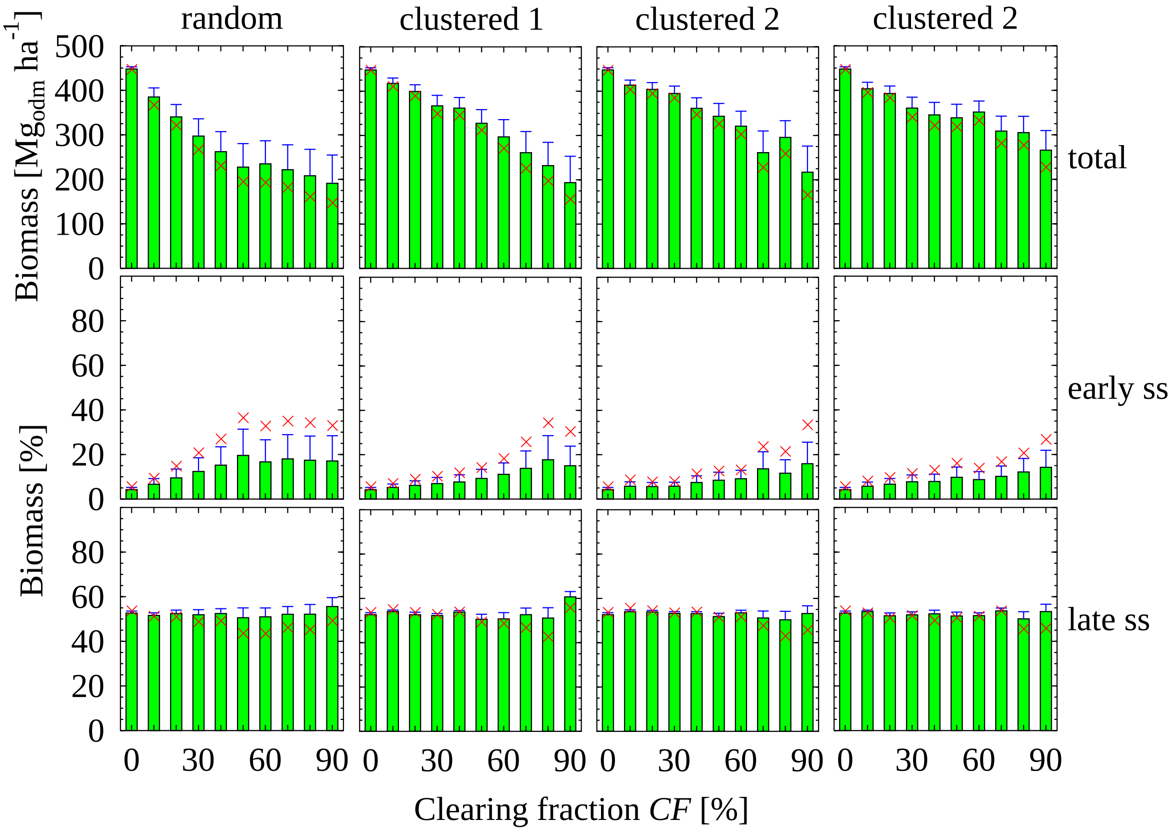

Figure 8.5: Patterns with a fraction of landscape being cleared ($t = 0 - 300$ y). Above-ground biomass as function of cleared fraction (CF) and pattern formation (random, clustered $1 - 3$). Bars show time averages, (including SD), crosses correspond to values at $t = 300$ y. Total biomass (1st row), and fraction of early and late successional species (2nd and 3rd row).

50 %) the final biomass was not totally recovered after 300 years (82 – 84 % of the control run).

A landscape with one intact forest remnant (*clustered 3*, $CF = 90$ %), will not regrow as quickly as forests with other spatial distribution of forest fragments. Indeed, long distance seed dispersal favour early successional species in the latter case (Fig. 8.8 bottom). Large tree (height > 30 m) dominating patches in the final year were fewer in scenario *clustered 3* (42 %), compared with others scenarios (49 – 60 %, all scenarios with $CF = 90$ %). Again, in medium clearing intensity ($CF = 50$ %) differences across patterns are negligible (78 – 79 %).

Discussion

The simplifications of the modelled regeneration processes might need further discussion. While usual pollinators and seed-dispersers of the species found in the pristine forest have disappeared, they are often replaced by invasive animals of the neighboring areas which might over-predate the relict flora (Curran et al. 1999; Curran & Leighton 2000; Curran & Webb 2000). There is also evidence that large carnivores which prey upon herbivores, and which may stabilize the food web by preventing the over-grazing are threatened with extinction even inside large protection areas (Woodroffe & Ginsberg 1998). Animal species are further threatened with extinction if wildlife harvest is taken into account (Redford 1992; Robinson et al. 1999; Cullen

Table 8.6: Regeneration and secondary succession in abandoned lands. ANOVA for the main effects of clearing fraction ($CF = 0 - 90$ %) and shape of the fragmentation pattern (random, three types of clustering) on the following monitored quantities: (A) total above-ground biomass, (B) fraction of early successional species on biomass, and (C) fraction of late successional species on biomass. Simulation time was 300 y, simulated area was 1 km^2. Sample size $n = 1$ and no cross-correlation.

Effects	SS	df	MS	F ratio	P
A) Biomass					
Clearing	211957.38	9	23550.82	474.47	<0.001
Pattern	705.84	3	235.28	4.74	>0.01
Error	1340.18	27	49.64		
B) Early successional species					
Clearing	4666.19	9	518.47	55.86	<0.001
Pattern	74.49	3	24.83	2.68	>0.5
Error	250.62	27	9.28		
C) Late successional species					
Clearing	6490.55	9	721.17	211.60	<0.001
Pattern	48.57	3	16.19	4.75	>0.01
Error	92.02	27	3.41		

et al. 2000). All these effects are obviously too complex to be taken into account explicitely into our model. However, the approach of the reproductive success in the regeneration rates as used in the model is well established and was used before (Ribbens et al. 1994; Chave 1999b).

The multiple consequences of forest deforestation

The simulation of forest fragments of different sizes showed three different directions in which forest remnants might develop (examples for size were taken from results of scenario *fragmented 3*): (i) collaps of the forest structure (1 ha); (ii): a forest with a high fraction of early successional species (9–64 ha); (iii): rain forest with a species composition of an undisturbed forest (81–100 ha). A size of at least 80 ha is necessary for maintaining a total biomass and species composition, which is similar to a primary forest. It might be that even in these large scale areas a shift in the species composition within the different species groups occurs. Turner & Corlett (1996) found in a rain forest fragment of 100 ha in Southeast-Asia no change in standing biomass over 50 years, but strong shifts in the species composition.

So far, little modelling effort has been focused towards attempting to understand the interplay between fragmentation processes and natural regeneration of the forest. A probable explanation for this is that

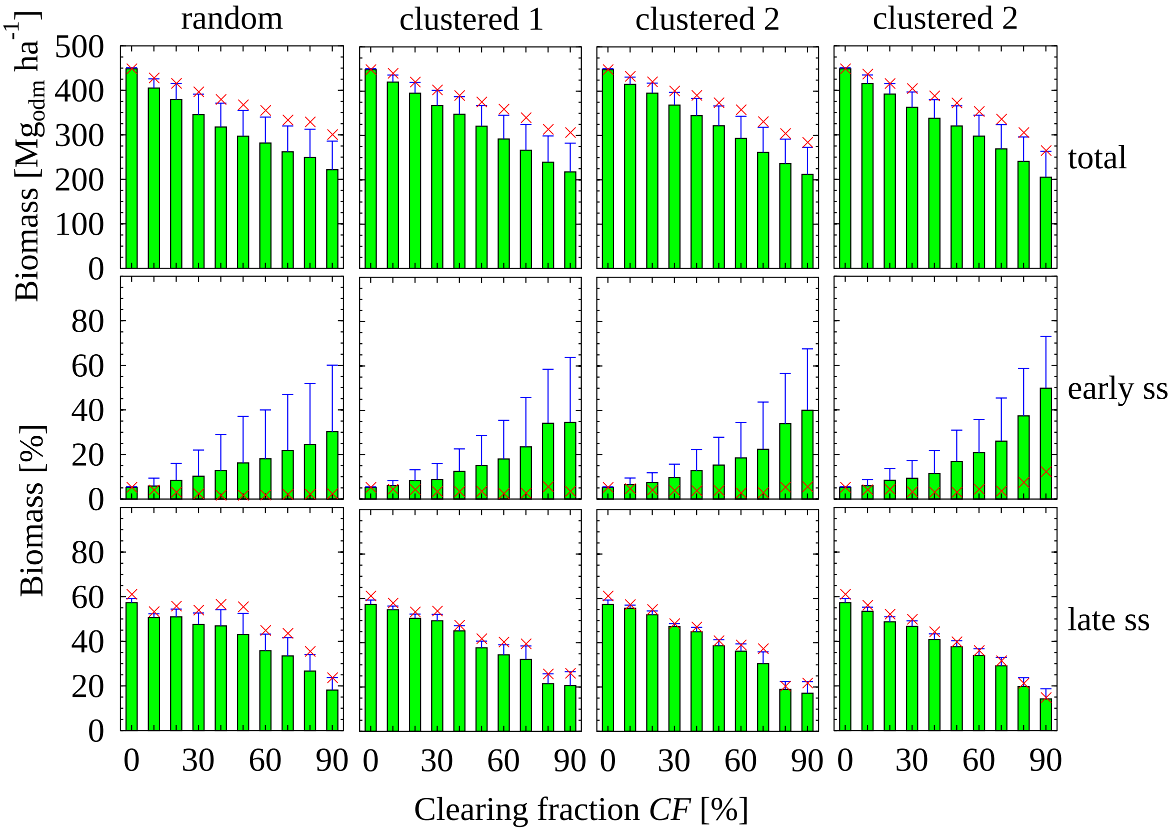

Figure 8.6: Patterns with a fraction of the landscape being regrowed with secondary succession after abandoned of cleared ares (same scenarios as Fig. 8.5 but $t = 301 - 600$ y). Above-ground biomass as function of cleared fraction (CF) and pattern formation (random, clustered $1 - 3$). Bars show time averages (including SD), crosses correspond to values at $t = 600$ y. Total biomass (1$^{\text{st}}$ row), and fraction of early- and late-successional species (2$^{\text{nd}}$ and 3$^{\text{rd}}$ row).

the problem of fragmentation is spatially explicit. Laurance et al. (1998) estimated with the model of Laurance & Yensen (1991) when forest fragments were dominated by edge effects. According to their analyses strong and moderate effects should rise once the fragment size falls below 90–500 ha. After our simulations strong effects on standing biomass and species composition are only seen at the lower end of this range. Ferreira & Laurance (1997) stated that even in forest fragments of 1000 ha a substantial impact of fragmentation will be expected, because $22 - 42$ % of the border area was influenced by edges. With our simulations the structural characteristics of the forest are not expected to change substantial for that large areas. The estimate of impacts of fragmentation over the ratio of the border area seems to overestimate the effects largely.

Therefore, it requires forest growth simulators able to describe the spatial structure of the landscape. Such quantitative models have only recently become available (Bossel & Krieger 1994, Pacala et al. 1996, Köhler & Huth 1998a, Chave 1999b).

The structure of the forest matrix has been repeatedly shown to be an important indicator of the faunal diversity (Gascon et al. 1999; Hanski & Ovaskainen 2000; Jordan 2000). Indeed, the three-dimensional spatial heterogeneity of forest communities is the main mechanism which allows for the observed diversity of heterotrophic species. The species composition is strongly affected by the invasion of ecotonal species, which

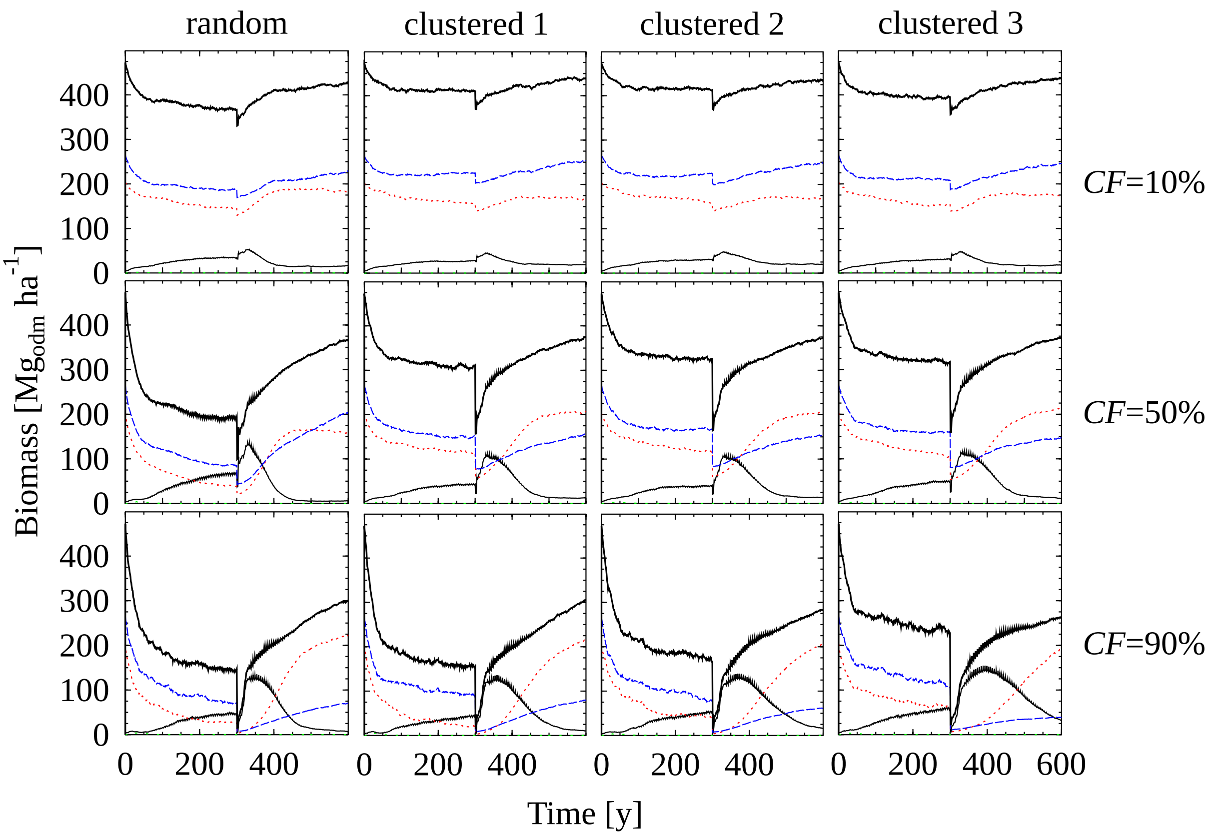

Figure 8.7: Time variation of the above-ground biomass for selected fragmentation scenarios (random, clustered $1-3$) and cleared fraction ($CF = 0-90$ %). Total biomass (solid bold line), biomass for early successional species (solid line), for mid-successional species (broken dotted line), and for late successional species (broken line). Savanna species are always below 1 Mg ha^{-1} and are not shown. Land-uses were abandoned at year 300. The biomass was computed only within the forest plots from $t = 0$ y to $t = 300$ y, and over the whole landscape after $t = 300$ y, whence the apparent discontinuity in the biomass curve.

might outcompete the species of the closed rain forest. Our simulations show that the indicators of forest structure such as the within-plot maximal canopy height are indeed strongly affected by fragmentation. The underlying mechanism in our simulations is the increased mortality rate for large edge trees. Since the ecotone area increases quickly with fragmented fraction, the strong positive correlation between canopy height and fragmented fraction is unsurprising.

Above-ground biomass estimates for neotropical forests still rely upon scarce data, and the models used to relate the dbh with the tree biomass (e.g. Brown 1997; Higuchi et al. 1998) have a limited predictive power (Brown et al. 1995; Chave et al. 2000c). At the Piste de Saint Elie 5 ha dataset, Brown's (1997) allometric equation gave an estimate of 210.7 Mg ha^{-1}, Higuchi-Santos's (1998) equation yielded a high 358.9 Mg ha^{-1}, and the fit proposed in Chave et al. (2000) gave

Figure 8.8: (opposite page): Spatial distribution of dominant trees as function of clearing fraction (CF) and of spatial clustering (random, clustered $1-3$) of selected scenarios for different times. Top: time $t = 300$ y, just before meadows are abandoned; bottom: $t = 600$ y. Simulation area was 1 km^2, each pixel corresponds to one patch (20 m × 20 m). Pixels inform about size and successional group of the dominat tree of the patches according to legend.

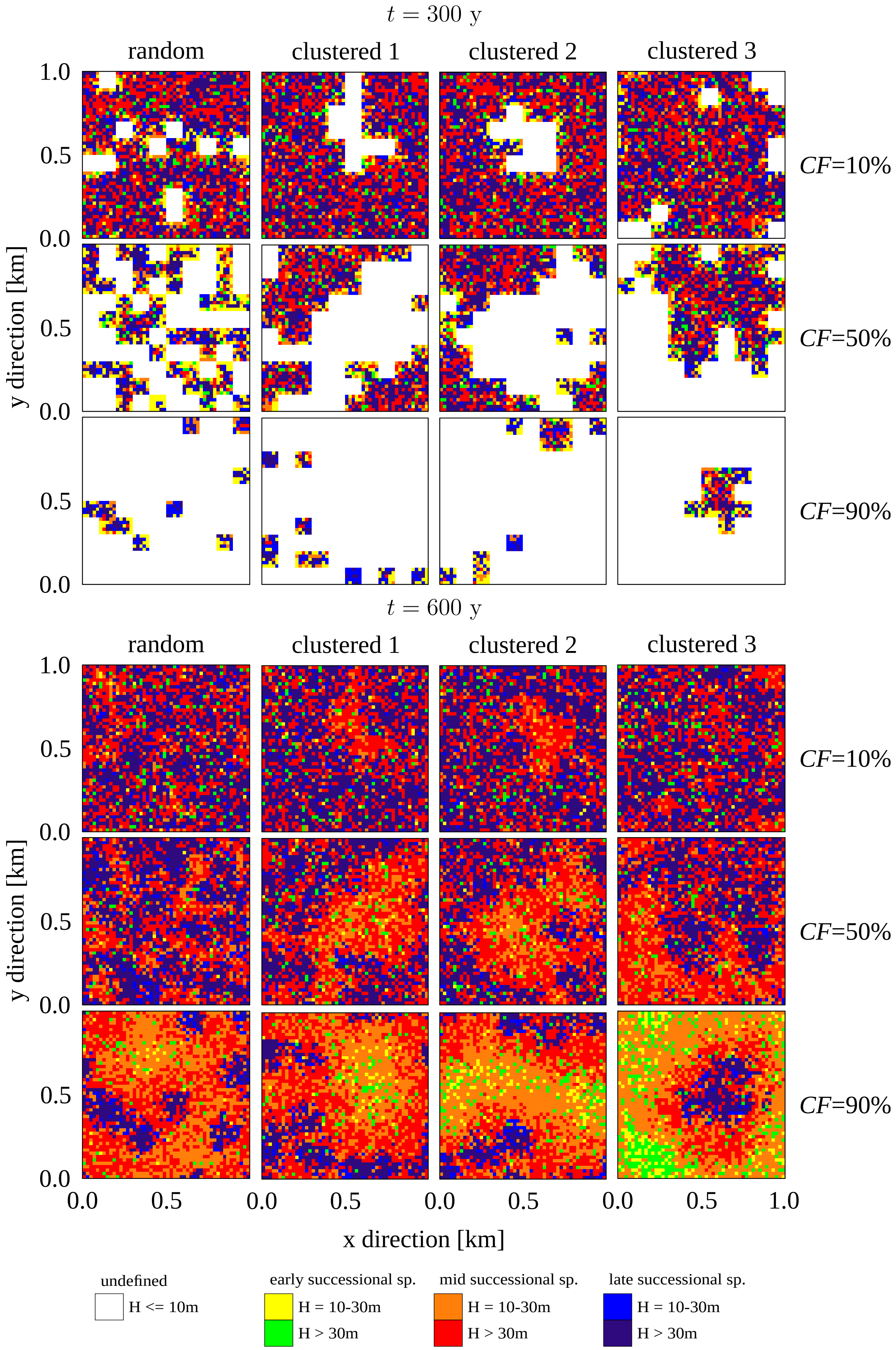

Figure 8.8: Captions are found on opposite page.

245.2 ± 30 Mg ha^{-1}. An in situ biomass experiment (0.25 ha plot where all trees were felled and weighed) predicted values above 400 Mg ha^{-1} more consistent with Higuchi-Santos's predictions, but probably skewed by the choice for the experiment plot. Therefore, although it is quite difficult to assess the quality of the values predicted by our model (445 ± 15 Mg ha^{-1} in the control run), it is probable that the real number is smaller. We have found that after 300 years the regenerating forest reached significantly smaller figures than in the control run (59 – 68 %). This suggests a long-lasting effect of disturbances upon the carbon pool of forests, as observed in field experiments (Saldarriaga et al. 1988). Another explanation is that natural disturbances operating over large areas (such as large treefalls) maintain the system below its expected biomass capacity.

Plant functional diversity was strongly affected by fragmentation in all the simulations. The fraction of early successional species which were maintained was significantly larger over the whole landscape, which had to be expected because of the increased area available for this PFT. However, the increase was also significant within the forest fragments (up to 30 % for $CF = 90$ %). Regeneration after land use change showed that the forest recovered only after 100 years. In clustered fragmentation scenarios, this transient regime was longer ($>$ 200 y), which is a consequence of seed-dispersal limitation for late successional species. A recent study has found that species composition took even longer to recover (Ferreira & Prance 1999). Undisturbed forest had 147 species per ha while the secondary forest had a mere 89 species per ha, but the estimated biomass was comparable. This picture constrasts with that of Saldarriaga et al. (1988), in part because the disturbance type were clearly different in the two forests, but also because of an unsufficient taxonomic effort in the latter survey (only 75 % of the trees were identified to the species level).

Which strategy is best?

Our results show that the extent of forest boundaries should be minimized within a fragmented landscape. However, scenarios which minimize the edge-to-area ratio (clustered scenarios) also lead to a longer regeneration.

In the random model of fragmentation, the forest structure is only weakly affected by the cleared fraction up to about $CF =$ 50 %. Below this level, clear-cut plots are surrounded by an intact matrix which provides favorable microenvironmental conditions and seeds as for treefall gaps. However, above this level most of the fragments are isolated and seed dispersal becomes the major issue for the regeneration. A possible strategy would be to preserve large mature trees in a sufficient density to favour a subsequent regeneration of the forest. This strategy is however quite difficult to apply in practice because large trees are usually valuable timber species.

Limitations of the present modelling approach

Our study provides a first attempt to assess the long-term impact of fragmentation on tropical rain forest, and our results are consistent with available field studies in South America. We believe that the modelling approach is an efficient tool to address landscape-scale issues. Moreover, it makes it possible to relate our findings with satellite imagery information.

For example, data at 1 km^2 spatial resolution are available, with a percentage of forest cover from 0 % to 100 % (DeFries et al. 2000). Using this dataset, it is easy to compute the fraction of rain forest edge pixels in South America (1 km^2 plots of rain forest at the edge of the population). Overall, these sites represent

0.60 million km^2, out of 8.37 million km^2 of rain forest (7.17 %). Of this edge area, 0.219 million km^2 (37 %) is a boundary between forest and agriculture/grasslands.

We may want to address the generality of these patterns across forest types. Our model was validated for two other forests, in Venezuela and in Sabah, Malaysia. Nevertheless, we think that the model application to the French Guiana rain forest was more appropriate than to Venezuela or Malaysia. Most field data on fragmentation were collected in different research plots in South America. Moreover, the current knowledge on forest growth and published data was wider for the French Guiana site than for that of Venezuela. Furthermore, available satellite imagery data sets already mentioned allow us to validate our approach for forests in French Guiana (future project). However, even if this case study was restricted to a rain foret in French Guiana, we think that the general pattern of how fragmentation will influence forest dynamics will be similar in different sites.

We have investigated scenarios assuming that the major mechanisms were the increased mortality of trees near edges ($\leq$ 100 m) and a reduced recruitment rate. Although these assumptions are realistic they compound several distinct mechanisms, such as, for the mortality gradient, microclimate changes (higher temperature and lower moisture), higher probablity of tree uprooting, and explicit competition with ecotone species. It would be difficult, yet valuable, to construct a model which would take these as separate mechanisms.

A similar comment should be made for land-used areas. The soil properties are usually radically modified by agricultural activities, with a rapid loss of nutrients (Saldarriaga 1986; Uhl et al. 1988; Buschbacher et al. 1988; Mackensen & Fölster 2000), that might considerably slow down the forest regeneration pace. Also, possibly invasive species can take over abandoned pastures, as for the palm babaçu (*Orbignya phalerata* Mart.) in Brazil, which impedes the succession.

Our analysis was restricted to forest sizes up to 100 ha. Recent studies identify indirect edge effects of fragmentation on larger scales up to several thousands of hectars (Curran & Leighton 2000). Fauna-flora interactions on recruitment in terms of seed dispersal and predation might be far more important for the long-term forest dynamics as assumed today. Animals migrate to the remnant forests, if land clearing destroys their old habitats. Thus, even large forest fragments will be affected by anthopogeneous impacts. A size above which fragmentation effects are negliglible might not exist on scales still found in tropical rain forests.

Acknowledgements

We thank Paul Moorecroft for giving us ref. Moorecroft et al. (2000) prior to publication. J. Chave was supported by grants to S.A. Levin, from the Andrew W. Mellon Foundation and from the David and Lucille Packard Foundation (grant 99-8307). P. Köhler was funded by the Otto-Braun-Foundation at the University of Kassel. H. Bossel provided helpful comments to the manuscript.

Appendix

Table 8.7: Short description of parameters including functional relationships (modified from Köhler et al. 2000c).

Parameter	Description
	Environmental parameters
k	Light extinction coefficient
I_0	Light intensity above canopy
S_D	Day length
	Establishment parameters
D_S	Initial diameter of seedlings
$I_{\mathrm{S}s}$	Minimal light intensity for germination
$N_{\mathrm{S}s}$	Ingrowth rate of seeds into seed pool
$N_{\mathrm{R}s}$	Seed dispersal rate of mother trees
$X_{\mathrm{R}s}$	Average seed dispersal distance
$D_{\mathrm{R}h}$	Minimal diameter of mother trees
	Mortality parameters
$M_{\mathrm{B}s,h}$	Basic mortality rate
$M_{\mathrm{S}s}$	Mortality rate of seeds
$M_{\mathrm{D}j}$	Size dependent mortality rate ($M_D = M_{\mathrm{D0}} - M_{\mathrm{D0}}/M_{\mathrm{D1}} \cdot d$)
W	Probability of a dying tree to fall
	Tree physiognomic parameters
H_M	Maximum height
c_p	Crown length fraction
τ_j	Site dependent fraction of stemwood biomass to total aboveground biomass ($\tau = \tau_1 + \tau_2 \cdot h(d = 120cm)$)
h_0 and h_1	Height = f(diameter) ($h = d/(1/h_0 + d/h_1)$)
γ_j	Form factor = f(diameter) ($\gamma = \gamma_0 \cdot exp(\gamma_1 \cdot d^{\gamma_2})$)
f_j	Crown diameter = f(diameter) ($d_c = (f_0 + f_1 \cdot d^{f_2}) \cdot d$)
l_j	Leaf area = f(diameter) ($l = l_1 \cdot d + l_2 \cdot d^2 + l_3 \cdot d^3$)
LAI_M	Maximal leaf area index of single tree
	Biomass production parameters
P_M, α	Photosynthetic capacity and efficiency in light response curve ($P_i(I_i) = \frac{\alpha_s \cdot I_i}{1+\frac{\alpha_s}{P_{\mathrm{M}s}} I_i}$)
ρ	Stem wood density
r_{1l}	Maintenance respiration = f(biomass) ($R_\mathrm{m}(B_i) = r_{1l} \cdot B_i$)
R_G	Growth respiration as part of biomass
m	Leaf transmittance
g	Conversation factor $\mathrm{g_{CO2}}$ to $\mathrm{g_{odm}}$

Table 8.8: Parametrisation for French Guiana. Short description of parameters in Table 8.7. Parameters with subindex vary with successional status (s), potential height (h) (corresponding to SS and HG in Table 8.2, respectively), or different functional coefficients (j).

Name	Special	Units	Values				
			Environmental parameters				
k		[-]	0.7				
I_{0y}	wet dry	[μmol(p) m^{-2} s^{-1}] ^{a}	642.0	694.0			
$S_{\mathrm{D}y}$	wet dry	[h]	12.0	8.0			
$S_{\mathrm{S}y}$	wet dry	[-]	0.75	0.25			
			Establishment parameters				
D_{S}		[m]	0.01				
$I_{\mathrm{S}s}$	s=0-3	[fraction of I_{0y}]	0.2	0.1	0.04	0.01	
$N_{\mathrm{S}s}$	s=0-3	[ha^{-1} y^{-1})]	25	125	500	100	
$N_{\mathrm{R}s}$	s=0-3	[ha^{-1} y^{-1})]	50	100	15	10	
$X_{\mathrm{R}s}$	s=0-3	[m]	100	50	40	20	
$D_{\mathrm{R}h}$	h=1-5	[m]	0.028	0.103	0.20	0.35	0.56
			Mortality parameters				
$M_{\mathrm{B}s,h}$	s=0; h=1-5	[y^{-1}]	0.18	0.16	0.12	0.10	0.00
$M_{\mathrm{B}s,h}$	s=1; h=1-5	[y^{-1}]	0.16	0.12	0.10	0.08	0.06
$M_{\mathrm{B}s,h}$	s=2; h=1-5	[y^{-1}]	0.07	0.06	0.05	0.04	0.03
$M_{\mathrm{B}s,h}$	s=3; h=1-5	[y^{-1}]	0.06	0.05	0.04	0.03	0.02
$M_{\mathrm{S}s}$	s=0-3	[y^{-1}]	0.01	0.1	0.5	1.0	
$M_{\mathrm{D}j}$	j=0-1	[y^{-1}, cm]	0.2	0.1			
W		[-]	0.40				
			Tree physignomic parameters				
$H_{\mathrm{M}s,h}$	h=1-5	[m]	5.0	15.0	25.0	36.0	40.0
c_{p}		[-]	0.358				
τ		[-]	0.7				
h_0		[cm m^{-1}]	1.96				
h_1		[m^{-1}]	49.0				
γ_j	j=0-2	[-, cm^{-1}, -]	2.575	-1.409	0.0358		
f_j	j=0-2	[m cm^{-1}, m cm^{-2}, -]	0.132	0.933	-0.6615		
l_j	j=1-3	[m cm^{-1}, m cm^{-2}, m cm^{-3}]	3.197	0.0684	-0.000379		
LAI_{M}		[-]	2				
			Biomass production parameters				
$P_{\mathrm{M}s}$	s=1-4	[μmol(c) m^{-2} s^{-1}]$^{\mathrm{a}}$	27.7	27.7	11.3	6.8	
α_s	s=1-4	[μmol(c) μmol(p)$^{-1}$]$^{\mathrm{a}}$	0.043	0.043	0.043	0.043	
ρ_s	s=1-4	[t$_{odm}$ m^{-3}]	0.83	0.62	0.75	0.81	
r_{1s}	s=1-4	[-]	0.08	0.08	0.04	0.03	
R_{G}		[-]	0.25				
m		[-]	0.1				
g		[g$_{odm}$ g$_{CO2}^{-1}$]	0.63				

[a] p: photons; c: CO_2

Summary

Background

Deforestation and degradation of tropical rain forests threaten these ecosystems all over the world. Rain forests, which were heavily disturbed through timber extraction or fragmentation, are endangered further if exposed to hurricanes or forest fires.

Currently, these human impacts on tropical forests are unsustainable and will certainly continue for the near future. Field studies in various research activities try to analyse short term impacts on forests, but cannot address questions of forest development and the threat of species loss in the long term.

Research goals and objectives

The research objective was to analyse the effects of timber logging and forest fragmentation as two important anthropogenic impacts on growth and yield of tropical rain forests, using a newly developed process-based forest growth model. Current practices were analysed for their sustainability, and suggestions concerning possible management improvement were stated, where possible. The following research questions were defined:

1. Is there a general approach for classifing several hundred tree species in different rain forest sites into a few groups?
2. Does simulated tree growth match measured data sets with acceptable accuracy?
3. Which logging method and rotation length can be called sustainable depending on the forest site?
4. How does recruitment determine forest growth and yield?
5. Can tropical rain forests buffer the effects of ongoing fragmentation?

Modelling framework

The process-based and individual-oriented forest growth model Formind2.0 was developed to answer these questions. It simulates the spatio-temporal dynamics of uneven-aged mixed forest stands in areas of one hectare to several km^2. The model describes forest dynamics as a mosaic of interacting forest patches of 20 m^2×20 m^2 in size. Within these patches trees are not spatially-explicit distributed, and thus all compete for light and space following the gap model approach. A concept for aggregating tree species diversity into 10-20 plant functional types (PFT) on the basis of species maximum tree height and successional status was developed and applied to all study sites. The carbon balance of each individual tree including photosynthesis and respiration is modelled explicitly. Thus, we can model measured diameter increment for different PFT, size and light conditions accurately. Allometric relationships connect above-ground biomass, stem diameter, tree height and crown dimensions. Besides increasing mortality through self-thinning in dense patches, one of the main processes of mortality is gap creation by the falling of large trees. This process, as well as seed dispersal from mature trees, interlinks neighbouring patches with each other. The modelling approach was discussed in detail and compared with several others. Comparison of modelled and measured growth data were used to validate model performance and accuracy.

Study sites

One of the key aspects was model applications to several different rain forest areas. Thus, data from three study sites were used for further analysis. They are:

- Capara Forest Reserve (Venezuela, 7°30'N, 70°45'W; elevation 100 m). The mean annual rainfall is 1750 mm, with a pronounced dry season from December to March (monthly precipitation < 50 mm). The average annual temperature is 24.6°C. 127 tree and palm species were grouped into 12 PFTs. Data of a mature forest and a forest logged five year prior to enumeration (each 1 ha in size) were used for model applications.
- Deramakot Forest Reserve, (Sabah, Malaysia, 117°30'E, 5°25'N, 130-300 m asl.). Mean annual temperature is 27° with little seasonal variations. Average annual precipitation is about 3500 mm, with no pronounced dry season. A tree species list of 468 species was aggregated into 13 PFTs. Inventory data for a mature and a recently logged-over forest (each 0.81 ha in size) were taken for model initialisation.
- Piste de Saint-Elie (French Guiana, 5°30'N, 53°00'W; elevation < 500 m). Annual rainfall is slightly above 3 000 mm y^{-1}. A pronounced dry season of 2 months is recorded from September to November and a short dry season in March. The average temperature is 25.8 °C with an annual amplitude of 2 °C and daily amplitudes of 7 °C in the rainy season (10 °C during the dry season). A species list covering 1022 tree and shrub species was aggregated into 19 PFTs. Inventories of five hectares of mature forest was used for simulations.

Growth & yield of forest in Venezuela

Stability and sensitivity analysis of the model behaviour was tested in detail for the application in Venezuela. Mortality rates were the most crucial for model dynamics. The stability of primary forest was analysed. Most result variables were stable. Only biomass of small growing tree species showed higher fluctuations.

Typical logging practices in Venezuela were analysed for their sustainability and impact on further forest dynamics. Thus, logging methods (conventional, or reduced-impact logging), length of cutting cycles (30, 40, or 60 years), and logging intensities in terms of extracted net bole volume (30, 45, 60 m^3 ha^{-1} $cycles^{-1}$), under two different minimum felling diameters (35, 50 cm) were analysed.

Conventional logging methods did not provide sustainable timber yields under most logging concepts. Only with the longest (60 years) cutting cycles, standing bole volume recovers similarly to mature unlogged stands. However, species composition varies significantly from mature forest for all logging impacts. Abundance of fast growing early successional species increased up to 29 % (mature forest: 1 %), while late successional species declined remarkably (down to 14 % compared to 44 %).

Scenarios with reduced-impact logging provided a significantly higher timber volume than under conventional logging. If long logging cycles were provided they could be called sustainable with respect to achievable timber yields, but impact on species composition was still large.

Forest growth in Sabah

In ongoing forest fragmentation seed dispersal will be one of the most important factors determining forest dynamics. Thus, model assumptions on recruitment were enhanced. Five alternative recruitment scenarios, which cover the range of possible fragmentation effects from single island to a closed forest, were analysed. Additionally, impacts of boundary effects and fragment size on forest dynamics were investigated.

Sensitivity analyses of all parameters of recruitment processes show that seed production rates influenced forest dynamics and species composition the most. Others, like average seed dispersal distances, were of minor importance.

To isolate the effects of recruitment from other parts of the model, scenarios without any recruits were computed, showing the buffer capacity of standing forests. Only after 50 simulated years did the standing biomass begin to decline. This shows the importance of field studies on ingrowth rates of saplings at about 1 cm in diameter.

The impacts of logging (reduced-impact and conventional methods, cycle length of 20-80 years) as one main disturbance in Sabah were analysed. In fragmented forests these impacts led to immediate shifts in species composition and species loss. Yields did not depend on recruitment assumptions, and thus fragmentation status. But the fraction of late successional species in logged timber was declining in forest fragments. Timber was highest with reduced-impact methods and medium cutting cycles of 40 years. In short cycles the timber gain depend strongly on logging methods.

Further impacts of logging on forest floor and nutrient content were omitted, and thus the results were optimistic. But with respect to current logging cycles of 10-40 years and conventional methods, the simulations demenstrate the unsustainability of common practices.

Forest fragmentation in French Guiana

The number of field studies in forest fragments has increased greatly in the last years. It has been shown that mortality rates are increased at forest edges, and that recruitment rates in fragments will differ from the ones in undisturbed forests.

These findings were incorporated in four different scenarios to analyse the effects of fragmentation and future forest dynamics. The size of fragmented forest was a second variable. Biomass was reduced to 7 % of the mature forest level after 300 y in the most extreme scenario (forest fragment of one hectare, alteration of mortality and recruitment rate through fragmentation). Species composition was shifted towards light demanding early successional species.

In a second study, forest clearing and regrowth of secondary vegetation in a landscape context was analysed. Clearings were clustered at different degrees, and the fraction of cleared area varied between 0 % (no clearing) and 90 %. Stable and unchanged forest structures in large forest islands were easy to identify. However, in the process of secondary succession distribution of seed-producing mother trees was important for the succession process. Thus, in landscapes with highly clustered forest fragments, secondary succession of abandoned areas took longest. The danger of species loss was high. Immigration was not considered and species composition and recruits depend solely on local abundance.

Conclusions

The following conclusions are drawn in relation to the five research questions stated in Chapter 1:

Tree species grouping:
A general approach for the aggregation

of several hundred tree species into a few (10-20) plant functional types was developed. Grouping was based on the two independent criteria successional status and maximum tree height. Application of the approach was discussed in detail for the rain forest in Sabah, and was applied additionally to the two other sites (Venezuela, French Guiana).

Simulated vs. measured tree growth:
Simulated tree growth was compared with measurements from permanent sampling plot data in Sabah (25 ha, observation period 9-20 y). The current application was limited to good site conditions. For single species groups stochasticity in mortality influenced results widely. The total basal area and stem number agreed with good accuracy.

Sustainability of logging methods:
Dependent on forest site, criteria for sustainability changed. However, current logging practices in Sabah and Venezuela overuse forests to a great degree. This is all the more important as results were based on optimistic assumptions concerning recruitment capabilities. Reduced-impact logging methods produced higher timber yields than conventional methods. Yield was also higher in longer logging cycles.

Assumptions on recruitment:
A detailed description of recruitment processes was necessary in fragmented or highly disturbed forests. Species composition depended on a detailed description of recruitment, while total biomass did not.

Forest fragmentation:
The species composition in fragmented forests was changed. If regrowth of former human-use areas was a possibility for forest conservation, species loss was limited, but depended on the length of the human impacts. Even in large forest fragments (∼ 100 ha) standing biomass was reduced compared to closed forest structures. Thus, the potential of tropical forests for carbon sequestration declined as well.

Recommendations concerning the modelling approach

For further applications, FORMIND2.0 could be improved and extended in several ways:

- In the context of climate change research, tropical rain forests act as global carbon sink of different potentials depending on anthropogenic impacts. Analysing these potentials is important for questions concerning carbon sequestration and might be possible with a simulation study using FORMIND.
- Various site dependent factors (slope, soil) might be incorporated, as done in FORMIX3-Q (Ditzer 1999).
- Testing of the current version with spatially-explicit forest inventory data may suggest improvements for modeling the light competition process.
- The coupling of recruitment with a model for animal diversity (Reinhard 1999) would be a first step to model seed dispersal and predation more accurately.
- Modelling of individual tree species might be of interest for further model applications. Using the current approach of plant functional types to derive parameter sets, but relating each individual tree to one specific species would improve complexity significantly. In particular, recruitment processes would depend on a single

species and thus analysis of species composition would be possible. This might contribute to answering the question, of what is the key process in determining high species diversity in tropical rain forests (Cook 1998; Hubbell et al. 1999).

Zusammenfassung

Hintergrund

Entwaldung und Degradierung bestehender tropischer Regenwälder bedrohen diese Ökosystem weltweit. Die durch Holzentnahme oder Fragmentierung stark gestörten Regenwälder sind noch tiefgreifender gefährdet, wenn Wirbelstürme oder Waldbrände über sie herziehen.

Momentan sind menschliche Eingriffe in tropische Wälder weit entfernt von einem nachhaltigem Konzept, und werden es sicher auch in der nahen Zukunft sein. Felduntersuchungen in unterschiedlichen Forschungsaktivitäten versuchen die kurzfristigen Störungen auf die Wälder zu untersuchen. Es wird jedoch nicht möglich sein, Fragen der langfristigen Waldentwicklung und die Gefahr des Aussterbens etlicher Spezies zu beantworten.

Forschungsziel und Fragestellungen

Ziel der Forschungsarbeit war es, die Auswirkungen der Holzentnahme und der Waldfragmentierung - zwei Beispiele anthropogener Einflüsse auf die Wuchsdynamik tropischer Regenwälder - mit Hilfe eines neu entwickelten prozess-basierten Waldwachstumsmodells zu analysieren. Momentane Nutzungspraktiken wurden auf ihre Nachhaltigkeit hin untersucht, und Vorschläge zu einer möglichen Verbesserung des heutigen Managements gemacht, soweit möglich. Die folgenden Fragestellungen wurden definiert:

1. Gibt es einen generellen Ansatz, um mehrere hundert Baumarten an unterschiedlichen Standorten in wenige Gruppen zusammenzufassen?
2. Stimmen simuliertes und gemessenes Baumwachstum mit akzeptabler Genauigkeit überein?
3. Welche Managementmethoden und Nutzungszyklen können, abhängig vom jeweiligen Standort, nachhaltig genannt werden?
4. Inwieweit bestimmt die Naturverjüngung Waldwachstum und Erntekapazität?
5. Kann tropischer Regenwald die Auswirkungen der voranschreitenden Waldfragmentierung abpuffern?

Modellierungskonzept

Das prozess-basierte und individuenorientierte Waldwachstumsmodell Formind2.0 wurde entwickelt, um diese Fragen zu beantworten. Es simuliert die raumzeitliche Dynamik eines ungleichaltrigen gemischten Waldbestandes auf Flächen zwischen einem Hektar und mehreren Quadratkilometern. Das Modell beschreibt die Walddynamik als ein Mosaik interagierender Waldflächen von 20 $\mathrm{m}^2 \times 20$ m^2. Die Bäume sind innerhalb dieser Teilflächen nicht räumlich-explizit verteilt und konkurrieren somit nach dem Ansatz für Gap-Modelle allesamt um Licht und Raum.

Ein Konzept zur Aggregation der Baumartenvielfalt in 10-20 pflanzenfunktionale Typen (PFT) wurde entwickelt. Es basiert auf maximaler Baumhöhe und dem

Sukzessionsstatus einzelner Baumarten und wurde in allen Untersuchungsgebieten angewendet.

Die Kohlenstoffbilanz jedes Einzelbaumes, einschließlich Photosynthese und Respiration, wird explizit modelliert. Somit kann der Durchmesserzuwachs in Abhängigkeit des PFT, der Baumgröße und der Lichtbedingungen genau modelliert werden. Allometrische Zusammenhänge verknüpfen oberirdische Biomasse, Stammdurchmesser, Baumhöhe und Kronendimensionen. Neben einer erhöhten Mortalität durch Ausdünnungsprozesse in dichtstehenden Flächen ist die Lückenbildung durch umfallende große Bäume ein wichtiger Mortalitätsprozess. Diese Lückenbildung sowie Samenverbreitung ausgehend von Mutterbäumen verknüpfen benachbarte Teilflächen miteinander.

Der Modellierungsansatz wurde detailiert diskutiert und mit verschiedenen anderen verglichen. Mittels eines Vergleichs von modellierten und gemessenen Wuchsdaten wurden Modellverhalten und Genauigkeit validiert.

Untersuchungsgebiete

Eine der Grundideen dieser Arbeit war die Modellanwendung in unterschiedlichen Regenwaldgebieten. Es wurden Daten aus drei Untersuchungsgebieten für die weiteren Analysen verwendet. Im einzelnen sind dies:

- Capara Forest Reserve (Venezuela, 7°30'N, 70°45'W; Erhebung 100 m). Der durchschnittliche jährliche Niederschlag beträgt 1750 mm, mit einer ausgeprägten Trockenperiode von Dezember bis März (monatlicher Niederschlag < 50 mm). Die durchschnittliche mittlere Jahrestemperatur ist 24.6°C. 127 Baum- und Palmenarten wurden in 12 PFT zusammengefasst. Daten eines ausgewachsenen Waldes und eines Waldes fünf Jahre nach einem Holzernteeingriff (jeweils 1 ha groß) wurden für die Modellanwendung benutzt.
- Deramakot Forest Reserve, (Sabah, Malaysia, 117°30' E, 5°25' N, 130-300 m über NN). Die mittlere jährliche Temperatur beträgt 27° mit geringen saisonalen Unterschieden. Mittlerer jährlicher Niederschlag ohne nennenswerte Trockenperiode beläuft sich auf 3500 mm. Eine Baumartenliste mit 468 Arten wurde in 13 PFT zusammengefasst. Inventurdaten eines ausgewachsenen und eines kurz zuvor genutzten Bestandes (jeweils 0.81 ha) wurden für die Modellinitialisierung verwendet.
- Piste de Saint-Elie (Französisch Guayana, 5°30'N, 53°00'W; Erhebungen < 500 m). Der jährliche Niederschlag liegt etwas über 3000 mm. Eine ausgeprägte zweimonatige Trockenperiode wird zwischen September und November registriert sowie eine weitere kurze im März. Die durchschnittliche Temperatur liegt bei 25.8 °C mit jährlichen Amplituden von 2 °C und täglichen Amplituden von 7 °C in der Regenzeit (10 °C in der trockenen Jahreszeit). Eine Artenliste mit 1022 Baum- und Straucharten wurde aggregiert zu 19 PFT. Inventuren von fünf Hektar ausgewachsenem Regenwald wurden für die durchgeführten Simulationen verwendet.

Wuchs und Ernte von venezuelanischem Wald

Das Modellverhalten wurde in der Anwendung in Venezuela detailliert in Stabilitäts- und Sensitivitätsuntersuchungen getestet. Die Modelldynamik wurde am meisten durch die Mortalitätsraten beeinflusst. Die Stabilität eines Primärwaldes wurde analysiert, wobei die meisten Ergebnisgrößen stabiles Verhalten zeigten. Nur die Biomasse kleinwüchsiger Baumarten unterlag hohen Fluktuationen.

Typische Holzentnahmepraktiken in Venezuela wurden auf ihre Nachhaltigkeit und ihre Auswirkungen auf die weitere Waldentwicklung hin untersucht. Die Analyse erstreckte sich auf Erntemethoden (konventionelle oder schadensreduzierte Nutzung), Länge der Nutzungszyklen (30, 40, oder 60 Jahre), Nutzungsintensitäten in Form von entnommenem Nettostammvolumen (30, 45, 60 m^3 ha^{-1} $Zyklus^{-1}$) und unterschiedlichen minimalen Entnahmegrößen (Durchmesser=35, 50 cm).

Konventionelle Nutzungsmethoden ergaben keinen nachhaltigen Ernteertrag unter den meisten Nutzungskonzepten. Nur bei den längsten (60 Jahre) Nutzungszyklen erholt sich das stehende Stammvolumen zu einem Niveau vergleichbar mit ungenutzten Beständen. Doch auch dort wie bei allen anderen Nutzungen verändert sich die Artenzusammensetzung signifikant im Vergleich zum ausgewachsenen Wald. Die Abundanz der schnell wachsenden Frühsukzessionsarten stieg auf bis zu 29 % an (ausgewachsener Wald: 1 %), während das Vorkommen der Spätsukzessionsarten merklich zurückging (auf 14 % im Vergleich zu 44 % im ausgewachsenen Wald).

Szenarios mit schadensreduzierter Nutzung ergaben signifikant höhere Volumenerträge als konventionelle Verfahren. Unter langen Nutzungszyklen können sie im Bezug auf erreichbare Ernteerträge hin nachhaltig genannt werden. Doch auch hier sind die Störungen der Artenzusammensetzung noch immer groß.

Waldwuchs in Sabah

In der immer weiter fortschreitenden Waldfragmentierung wird die Samenverbreitung einer der wichtigsten Faktoren für die Bestimmung zukünftiger Walddynamiken sein. Daher wurden die Modellannahmen zur Naturverjüngung erweitert. Fünf alternative Verjüngungsszenarien wurden analysiert, die das gesamte Spektrum möglicher Fragmentierung abdecken, von einzelnen Bauminseln bis hin zu einem geschlossenen Wald. Zusätzlich wurden die Auswirkungen von Randbedingungen und Fragmentierungsgröße auf die Walddynamik hin untersucht.

Eine Sensitivitätsanalyse aller Parameter der Verjüngungsprozesse verdeutlichte, dass Samenproduktionsraten die Waldentwicklung und Artenzusammensetzung am meisten beeinflussen. Andere Parameter, wie z.B. durchschnittliche Distanzen der Samenverbreitung, waren von geringerer Bedeutung.

Um die Auswirkungen der Verjüngung von den anderen Modellteilen zu trennen, wurden Szenarien ohne jeglichen Jungwuchs durchgeführt, die die Pufferkapazität des bestehenden Waldes verdeutlichen. Erst nach 50 simulierten Jahren gab es einen Rückgang in der stehenden Biomasse. Die Bedeutung von Feldstudien zu Einwuchsraten von kleinen Bäumen von etwa 1 cm Stammdurchmesser wird hierdurch unterstrichen.

Die Auswirkungen von Holznutzung (schadensreduzierte und konventionelle Methoden, Zykluslängen von 20 bis 80 Jahren) als eine der bedeutensten Eingriffe in Sabah's Regenwäldern wurden analysiert. In fragmentierten Wäldern führten diese Eingriffe zu sofortigen Verschiebungen in der Artenzusammensetzung und zu einem Verlust etlicher Baumarten. Ernteerträge hingen nicht von den Annahmen zur Verjüngung und somit dem Fragmentierungsgrad ab. Die Erträge waren am höchsten mit schadensreduzierten Methoden und einem Nutzungszyklus von 40 Jahren. In kurzen Zyklen hing die Ernte maßgeblich von der gewählten Erntemethode ab.

Weitere Auswirkungen der Holznutzung auf den Waldboden und den Nährstoffhaushalt wurden nicht berücksichtigt, weshalb die Ergebnisse als optimistisch eingeschätzt werden können. Die Simulationen zeigten dennoch die fehlende Nachhaltigkeit heutiger Erntezyklen von 10-40 Jahren unter konventionellen Methoden.

Waldfragmentierung in Französisch Guayana

Die Anzahl von Feldstudien zur Waldfragmentierung hat in den vergangenen Jahren deutlich zugenommen. Anhand dieser Studien wurde gezeigt, dass die Mortalitätsrate an Waldrändern erhöht ist und dass die Verjüngungsraten in Waldfragmenten sich von denen in ungestörten Wäldern unterscheiden.

Diese Ergebnisse wurden in vier unterschiedlichen Szenarien integriert, um die Auswirkungen der Fragmentierung auf zukünftige Walddynamiken hin zu untersuchen. Die Größe der Waldfragmente war eine zweite Variable. Die stehende Biomasse wurde in dem extremsten Szenario (Waldfragment von einem Hektar und einer Veränderung von Mortalitäts- und Verjüngungsraten) nach 300 Jahren auf 7 % eines ausgewachsenen Waldes reduziert. Die Artenzusammensetzung verschob sich zugunsten lichtliebender Frühsukzessionsarten.

In einer zweiten Studie wurden Waldrodung und der Wuchs einer Sukundärvegetation untersucht. Rodungsflächen wurden in unterschiedlichem Maße geclustert, der Anteil der gerodeten Fläche variierte zwischen 0 % (keine Rodung) und 90 %. Stabile und unveränderte Waldstrukturen konnten in großen Waldinseln identifiziert werden. Da jedoch im Zuge der Sekundärsukzession die Verteilung samenproduzierender Mutterbäume von Bedeutung war, dauerte die Sukzession in brachliegenden Flächen der hochgradig geclusterten Landschaft am längsten. Die Gefahr der Extinktion einzelner Arten war hoch. Immigration wurde nicht betrachtet, so dass die Artenzusammensetzung nur von der lokalen Verjüngung abhing.

Schlussfolgerungen

Die folgenden Schlüsse können als Antworten auf die im Kap. 1 gestellten Fragen gezogen werden:

Baumartengruppierung:
Ein genereller Ansatz zur Aggregation mehrerer hundert Baumarten in wenige (10-20) pflanzenfunktionale Typen wurde entwickelt. Die Gruppierung basierte auf den beiden unabhängigen Kriterien Sukzessionstatus und maximale Baumhöhe. Dieser Ansatz wurde für einen Regenwald in Sabah ausführlich diskutiert, und zusätzlich in den beiden anderen Untersuchungsflächen angewendet (Venezuela, Französisch Guayana).

Simuliertes vs. gemessenes Baumwachstum:
Simuliertes Baumwachstum wurde mit Messungen aus permanenten Aufnahmeflächen in Sabah verglichen (25 ha, Beobachtungszeitraum 9-20 Jahre). Die momentane Modellanwendung war beschränkt auf Standorte mit guten Bedingungen. Für einzelne Artengruppen beeinflussten stochastische Prozesse des Mortalitätsmodells die Ergebnisse deutlich. Die Gesamtstammgrundfläche und die Gesamtstammzahl wurden jedoch mit guter Genauigkeit wiedergegeben.

Nachhaltigkeit von Holznutzungsmethoden:
In Abhängigkeit von der Untersuchungsfläche veränderten sich die Kriterien einer nachhaltigen Holznutzung. Unabhängig davon übernutzen momentane Praktiken in Sabah und Venezuela den Wald zu großen Teilen.

Dies ist umso besorgniserregender, da unsere Ergebnisse auf optimistischen Annahmen zum Verjüngungspotential basierten. Schadenreduzierende Nutzungsmethoden erzielten höhere Ernteerträge als konventionelle Methoden. Die Ernte war weiterhin in längeren Zyklen am größten.

Annahmen zur Verjüngung:
In fragmentierten oder hochgradig gestörten Wäldern war eine detaillierte Beschreibung der Verjüngungsprozesse notwendig. Die Artenzusammensetzung hing maßgeblich hiervon ab, während die Gesamtbiomasse unabhängig davon blieb.

Waldfragmentierung:
Die Artenzusammensetzung in fragmentierten Wäldern änderte sich. Durch den Wuchs einer Sekundärvegetation in ehemals genutzten Flächen konnte der Verlust einzelner Arten eingeschränkt werden. Dieser Verlust hing jedoch von der Länge der Nutzung ab. Selbst in großen Waldfragmenten (~ 100 ha) reduzierte sich die stehende Biomasse im Vergleich zu geschlossenen ungestörten Waldstrukturen. Somit verringert sich auch das Potential tropischer Wälder zur Bindung von Kohlenstoff.

Erweiterungen des Modellierungsansatzes

Für weitere Anwendung kann FORMIND2.0 in unterschiedlichen Aspekten verbessert und erweitert werden:

- Im Zusammenhang der Klimafolgenforschung werden tropische Regenwälder als globale Kohlenstoffsenken diskutiert. Ihr Senkenpotential hängt hierbei vom Grad anthropogener Störungen ab. Die Analyse dieses Potentials ist wichtig für die Fragen der Bindung des atmosphärischen Kohlenstoffes und mag durch Simulationsstudien mit FORMIND möglich sein.
- Mehrere standortabhängige Faktoren (Hangneigung, Fertilität des Bodens) können in das Modell eingebaut werden, wie bereits in FORMIX3-Q (Ditzer 1999).
- Ein Test der momentanen Modellversion mit räumlich-expliziten Waldinventurdaten mag ergeben, inwieweit der Mechanismus zur Beschreibung der Lichtkonkurrenz verbessert werden kann.
- Eine Kopplung des Verjüngungsmodelles an ein Modell zur Beschreibung der Tierartenvielfalt (Reinhard 1999) wäre ein erster Schritt, um Samenverbreitung und Samenverlust genauer zu beschreiben.
- Die Modellierung einzelner Baumarten wäre für weitere Untersuchungen von Interesse. Hierbei könnten mit dem momentanen Ansatz der pflanzenfunktionalen Typen die notwendigen Parametersätze erzeugt werden. Jedem Einzelbaum wird jedoch eine spezifische Baumart zugeordnet werden. Insbesondere die Verjüngungsprozesse könnten somit auf der Ebene einzelner Baumarten modelliert werden. Somit mag ein Beitrag zur Lösung der Frage gegeben werden, welches die entscheidenden Prozesse sind, die die hohen Artenvielfalt in tropischen Regenwäldern bestimmen (Cook 1998; Hubbell et al. 1999).

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Appendix A

Inventory data

Typical inventory data of field measurements are distributions of stem numbers over diameter, total and for single species or species groups. Most inventories used in the applications discussed in this thesis are compliled in the following Appendix. In detail they are:

- Sabah:
  - Chapter 5: Data of permanent sampling plots in Garinono, Gunung Rara, Segaliud Lokan, and Sepilok are taken from forest management inventories (Chai et al. 1991; Kilou et al. 1993; Ong, unpublished data), consist of 25 hectares and are therefore not plotted here.
  - Chapter 7: mature forest (P1, Table A.1) and recently logged over forest (L1, Table A.2) in Deramakot Forest Reserve, Sabah. They were complied from the data sets A1-A4 (P1) and D5-D8 (L1) in the appendix of Schlensog (1997).
- Venezuela: mature forest (MF, Table A.3) and logged over forest 5 years prior (LG5, Table A.4) in Caparo Forest Reserve, Venezuela, taken from work of Kammesheidt (Kammesheidt 1994, 1998).
- French Guiana: mature forest (Table A.5) at Piste de Saint Elie, French Guiana (B. Riera, unpublished data).

Table A.1: Inventory data for site P1 in Deramakot, Sabah. Stem Number [ha^{-1}] in diameter classes D, total and per plant functional type PFT. (A1-A4 in Schlensog 1997).

D [cm]	Total	PFT												
		1	2	3	4	5	6	7	8	9	10	11	12	13
0-10	4149	0	0	600	800	0	200	0	0	0	0	0	2082	467
10-20	322	0	0	33	33	0	66	0	0	22	0	0	89	79
20-30	110	0	0	0	0	0	22	0	0	0	11	0	55	22
30-40	53	0	0	1	1	4	12	0	0	5	3	0	25	2
40-50	28	1	0	0	0	0	3	1	0	5	5	0	13	0
50-60	16	0	0	4	1	0	0	0	0	1	0	0	10	0
60-70	5	0	0	0	0	0	0	0	0	1	1	0	3	0
70-80	5	0	0	0	0	0	0	0	0	0	0	0	5	0
80-90	1	0	0	0	0	0	0	0	0	0	0	0	1	0
90-100	3	0	0	0	0	0	0	0	0	1	0	0	2	0
100-110	2	0	0	0	0	0	0	0	0	1	0	0	0	1
110-120	1	0	0	0	0	0	0	0	0	0	0	0	0	1
120-130	1	0	0	0	0	0	0	0	0	0	0	0	0	1
130-140	1	0	0	0	0	0	0	0	0	0	0	0	0	1
140-150	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	4697	1	0	638	835	4	303	1	0	36	20	0	2285	574

Table A.2: Inventory data for site L1 in Deramakot, Sabah. Stem Number [ha^{-1}] in diameter classes D, total and per plant functional type PFT. (D5-D8 in Schlensog 1997)

D [cm]	Total	PFT 1	2	3	4	5	6	7	8	9	10	11	12	13
0-10	3600	333	67	0	267	0	0	0	67	2333	0	0	533	0
10-20	88	0	11	0	0	66	0	0	11	0	0	0	0	0
20-30	78	0	0	0	0	78	0	0	0	0	0	0	0	0
30-40	33	1	0	1	1	10	3	0	0	3	3	1	10	0
40-50	22	0	0	2	0	3	1	2	0	5	1	0	8	0
50-60	5	0	0	0	1	1	0	0	0	0	1	0	2	0
60-70	6	0	0	0	0	0	1	0	0	2	0	0	3	0
70-80	3	0	0	0	0	0	0	0	0	1	0	0	2	0
80-90	3	1	0	0	0	0	0	0	0	0	1	0	1	0
90-100	0	0	0	0	0	0	0	0	0	0	0	0	0	0
100-110	0	0	0	0	0	0	0	0	0	0	0	0	0	0
110-120	0	0	0	0	0	0	0	0	0	0	0	0	0	0
120-130	1	0	0	0	0	0	0	0	0	0	0	0	1	0
130-140	0	0	0	0	0	0	0	0	0	0	0	0	0	0
140-150	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	3840	335	78	3	269	158	5	2	78	2344	6	1	561	0

Table A.3: Inventory data for site MF in Caparo, Venezuela. Stem Number [ha^{-1}] in diameter classes D, total and per plant functional type PFT. (PW or MF in Kammesheidt 1994, 1998).

D [cm]	Total	PFT											
		1	2	3	4	5	6	7	8	9	10	11	12
0-10	2400	176	644	0	80	136	4	124	256	36	160	476	308
10-20	161	0	0	0	15	0	1	15	35	15	21	0	59
20-30	102	0	0	0	0	1	3	7	23	4	17	0	47
30-40	76	0	0	0	0	0	0	2	6	14	6	0	48
40-50	22	0	0	0	0	0	0	0	3	3	5	0	11
50-60	16	0	0	0	0	0	0	0	2	8	6	0	0
60-70	9	0	0	0	0	0	0	0	1	6	2	0	0
70-80	8	0	0	0	0	0	0	0	0	6	2	0	0
80-90	6	0	0	0	0	0	0	0	0	2	4	0	0
90-100	1	0	0	0	0	0	0	0	0	1	0	0	0
100-110	0	0	0	0	0	0	0	0	0	0	0	0	0
110-120	0	0	0	0	0	0	0	0	0	0	0	0	0
120-130	1	0	0	0	0	0	0	0	0	1	0	0	0
130-140	0	0	0	0	0	0	0	0	0	0	0	0	0
140-150	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	2802	176	644	0	95	137	8	148	326	96	223	476	473

Table A.4: Inventory data for site LG5 in Caparo, Venezuela. Stem Number [ha^{-1}] in diameter classes D, total and per plant functional type PFT. (EW87 or LG5 in Kammesheidt 1994, 1998).

D[cm]	Total	PFT 1	2	3	4	5	6	7	8	9	10	11	12
0-10	3568	1304	272	112	288	360	136	176	188	152	48	248	284
10-20	220	0	0	11	9	16	43	21	31	21	17	0	51
20-30	74	0	0	0	1	1	6	11	16	4	4	0	31
30-40	49	0	0	0	0	0	0	4	3	4	5	0	33
40-50	22	0	0	0	0	0	0	1	1	0	5	0	15
50-60	6	0	0	0	0	0	0	0	2	1	2	0	1
60-70	1	0	0	0	0	0	0	0	0	0	1	0	0
70-80	1	0	0	0	0	0	0	0	0	1	0	0	0
80-90	0	0	0	0	0	0	0	0	0	0	0	0	0
90-100	0	0	0	0	0	0	0	0	0	0	0	0	0
100-110	0	0	0	0	0	0	0	0	0	0	0	0	0
110-120	0	0	0	0	0	0	0	0	0	0	0	0	0
120-130	0	0	0	0	0	0	0	0	0	0	0	0	0
130-140	0	0	0	0	0	0	0	0	0	0	0	0	0
140-150	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	3941	1304	272	123	298	377	185	213	241	183	82	248	415

Table A.5: Inventory data for 19 PFTs at site Piste de Saint Elie, French Guiana. Stem Number [ha^{-1}] in diameter classes D, total and per plant functional type PFT. (B. Riera, unpublished data).

D [cm]	Total	PFT																		
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
0-10	2	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
10-20	322	0	1	4	15	4	4	48	31	0	5	38	64	0	8	29	48	1	20	2
20-30	104	0	1	1	6	1	1	6	5	0	2	7	23	0	2	12	28	0	7	2
30-40	56	0	0	0	2	1	0	3	1	0	2	3	9	0	1	13	17	0	3	1
40-50	29	0	0	0	1	0	0	1	0	0	1	2	2	0	1	11	7	0	3	0
50-60	14	0	0	0	1	0	0	0	1	0	0	1	1	0	0	7	1	0	2	0
60-70	10	0	0	0	0	1	0	0	0	0	0	1	0	0	0	3	2	0	2	1
70-80	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1	0	0	0
80-90	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
90-100	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
100-110	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
110-120	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
120-130	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
130-140	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
140-150	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	546	0	2	5	25	7	5	61	38	0	10	53	99	0	12	79	105	1	38	6

Appendix B

Lists of tree species

Model application in each site is based on a species grouping following the concept discussed in Chapter 3. All available and relevant information on single tree species is found in the following three species list. Informations differ for each site, so labelling of columns is explained in legends before each species list.

The species list for Sabah (Table B.2) is based on a compilation by Ong & Kleine (1995), updated with own informations (Köhler 1998). Venezuela's species list (Table B.4) is based on work of Kammesheidt (1994, 2000), the one of French Guiana's rain forest (Table B.6) was compiled by Chave (1999; Chave and Riéra, unpublished manuscript), use of both with kind permission of the authors.

A compressed version of species lists is available online (http://www.usf.uni-kassel.de/usf/archiv/dokumente.en.htm).

Table B.1: Legend of tree species lists of Sabah (Table B.2).

Column	Description
Botanical name	Genus and species name
Local name	Local name
PFT	Plant functional type according to Table 7.1
SS	Successional status according to Table 7.1
HG	Height group according to Table 7.1
CFRC	Species code for identification of Forest Research Center, Sepilok
CHQ	Species code for identification of Head Quarter, Sandakan
TGRP	Timber group after Ong & Kleine (1995)
IGRP	Diameter ingrowth group after Ong & Kleine (1995)
F3	Plant functional type used by FORMIX3
GGRP	Glauner group out of Canadian inventory, used for height calculations
Height	Maximum height at maturity [m] out of literature. Special symbols (s: small; m: middle; l: large; b: bush; t: tree).
Dia	Maximum diameter at maturity [cm] out of literature
H=f(d)	Maximum height calculated out of Diameter
Den	wood density [$\mathrm{kg_{ODM}\ m^{-3}}$]
SPHQ	Number of species per C-HQ
NDer	Number of trees (diameter≥10cm) in Deramakot inventory
NFMU	Number of trees (diameter≥10cm) in inventories in Deramakot, Lingkabau, Kalabakan and Ulu Segama
F	Qualitative abundance according to literature (1: rare; 2: medium; 3: common)

Table B.2: Tree species list of Sabah (modified from Ong & Kleine 1995; Köhler 1998).

Botanical name	Local name	PFT	SS	HG	CFRC	CHQ	TGRP	IGRP	F3	GGRP	Height	Dia	H=f(d)	Den	SPHQ	NDer	NFMU	F
Acronychia sp.	Limau hutan	6	2	3	ACRO	OTH	OTHR	14	1	15	-	44.6	20.75	-	89	245	999	-
Actinodaphne glomerata	Medang serai	6	2	3	ACGL	MDS	NDLH	19	1	9	18	-	-	-	2	0	66.5	-
Adenanthera pavonia	Saga	9	2	4	SAGA	OTH	OTHR	14	1	15	30.5	-	-	960	89	245	999	-
Adina trichotoma	Mengkeniab	6	2	3	ADTR	MGB	NDLH	14	1	15	20	-	-	897.1	1	0	0	-
Adinandra dumosa	Bawing	5	1	3	BAWI	BW	NDLH	16	2	15	20	-	-	610	1	3350	5482	3
Afzelia borneensis	Ipil darat	7	3	3	IDRT	IPD	NDMH	19	1	15	25	76.4	26.06	880	1	0	0	2
Agathis dammara	Mengilan	12	2	5	AGDA	MGL	NDLH	15	1	14	48.8	165.5	-	465	2	2	14.5	2
Aglaia argentea	Koping-koping	6	2	3	AGAR	KOP	NDLH	14	1	15	30	35	18.26	853	1	0	0	3
Aglaia cordata	Kalambio	4	3	2	AGCO	OTH	OTHR	14	1	15	10	9.5	9.59	-	89	245	999	-
Aglaia elliptica	Lantupak jambu	3	2	2	AGEL	OTH	OTHR	14	1	15	20	4.8	7.64	-	89	245	999	-
Aglaia sp.	Langsat-langsat	3	2	2	AGOD	LLS	NDLH	14	1	15	s	22.3	14.3	800	1	300	1004	-
Ailanthus integrifolia	Tree of heaven	6	2	3	AIIN	TOH	OTHR	14	1	15	24	0	-	370	1	0	0	-
Alangium sp.	Kondolon	3	2	2	KOND	KON	NDLH	14	1	15	12.2	38.2	19.14	752.9	1	329	945	1
Albizzia sp.	Batai	3	2	2	BTAI	BTI	NDLH	15	1	15	s-m	-	-	480	1	37	95	-
Aleurites moluccana	Kamiri	1	2	1	KMRI	KMR	NDLH	14	1	15	1.2	-	-	309.9	2	14.5	116.5	3
Alphitonia incana	Pakudita	6	2	3	PAKU	PAK	OTHR	14	1	15	m	-	-	-	1	0	29	-
Alstonia macrophylla	Pulai daun besar	8	1	4	ALMA	OTH	NDLH	13	3	8	30	66.8	38.23	-	89	245	999	3
Alstonia sp.	Pulai	12	2	5	PULA	PUL	NDLH	13	3	8	-	76.4	40.31	432.5	1	632	1714	2
Amoora rubiginosa	Lantupak paya	9	2	4	AMRU	OTH	OTHR	14	1	15	35	-	-	928	89	245	999	-
Anacardiaceae family	Rengas	12	2	5	RENG	RGS	NDMH	19	1	8	-	-	-	801	1	2263	7649	1
Angelesia splendens	Tampaluan	4	3	2	TAMP	OTH	OTHR	14	1	15	15	-	-	-	89	245	999	3
Anisophyllea disticha	Payung-payung	4	3	2	ANDI	OTH	OTHR	14	1	15	7	-	-	-	89	245	999	3
Anisoptera costata	Pengiran kesat	12	2	5	PKST	PS	DLH	2	1	2	60	143.2	-	624	1	8	12	2
Anisoptera grossivenia	Pengiran kunyit	12	2	5	PKUN	PY	DLH	2	1	2	45	-	-	729	1	0	0	-
Anisoptera laevis	Pengiran durian	12	2	5	PDUR	PD	DLH	2	1	2	60	-	-	600	1	0	0	-
Anisoptera marginata	Pengiran kerangas	12	2	5	PKER	PK	DLH	2	1	2	30-50	-	-	640	1	0	0	1
Anisoptera reticulata	Pengiran gajah	12	2	5	PGAJ	PJ	DLH	2	1	2	l	-	-	-	1	0	0	-
Anisoptera sp.	Pengiran	12	2	5	PENG	PG	DLH	2	1	2	l	-	-	-	1	8	119	-
Anonaceae family	Karai	8	1	4	PGPG	KRY	NDLH	14	1	8	30	57.3	35.39	600	1	233	1003	3
Anonaceae family	Pisang-pisang	8	1	4	PGPG	PIS	NDMH	14	1	8	-	-	-	-	1	2852	18335	-
Anthocephalus chinensis	Laran	8	1	4	LARA	LRN	PION	13	3	14	-	47.7	35.49	416	1	3410	0	3
Anthoshorea group of Shorea	Melapi	12	2	5	MELA	MP	DLH	2	1	2	50-60	95.5	36.51	-	1	1156	2440	3
Antidesma ghasemblica	Tandoropis	3	2	2	ANGH	OTH	NDLH	14	1	15	6	28.6	16.37	672	89	245	999	3
Antidesma sp.	Gerusih	4	3	2	ANTI	OTH	OTHR	14	1	15	6	-	-	600	89	245	999	-
Apocynaneae family	Jelutong	11	1	5	JELU	JLT	NDLH	15	1	8	1.5-30	-	-	440	1	8	260	3
Aporusa grandistipulata	Galang-galang	4	3	2	APGR	GLG	OTHR	14	1	15	s	-	-	-	1	0	200	-
Aporusa nitida	Bagil	4	3	2	APOL	BGL	OTHR	14	1	15	7	-	-	-	1	300	300	-
Aporusa sp.	Penatan	6	2	3	APEL	PTN	OTHR	14	1	15	20	-	-	-	1	479	2366	-
Aquilaria malaccensis	Gaharu	6	2	3	GAHA	GH	NDLH	12	4	15	36	57.3	23.43	-	1	112	507	3
Archidendron	Patai keryong	9	2	4	PATA	PATA	OTHR	14	1	15	-	0	-	-	1	0	0	-
Ardisia sp.	Serusop	4	3	2	ARDI	OTH	OTHR	14	1	15	8	31.8	17.34	-	89	245	999	-
...																		

Botanical name	Local name	PFT	SS	HG	CFRC	CHQ	TGRP	IGRP	F3	GGRP	Height	Dia	H=f(d)	Den	SPHQ	NDer	NFMU	F
...																		
Aromadendron sp.	Kepayang ambok	6	2	3	ARNU	KAP	DMH	14	1	15	20	-	-	-	1	4	4	-
Artocarpus anisophyllus	Terap ikal	6	2	3	ARAN	TRI	OTHR	14	1	15	30	57.3	23.43	739	1	25	2341	1
Artocarpus elasticus	Terap togop	5	1	3	AREL	TRO	NDLH	15	1	15	45	66.8	24.95	490	1	29	2162	3
Artocarpus sp.	Terap	5	1	3	TRAP	TRP	NDLH	15	1	15	24	47.7	21.49	612	1	964	3295	-
Artocarpus sp.	Terap timadang	3	2	2	AROD	TRT	NDLH	15	1	15	15	9.5	9.59	-	1	0	362	-
Artocarpus tamaran	Timbangan	6	2	3	ARTA	TIMD	NDLH	15	1	15	m	-	-	-	1	0	0	-
Azadirachta excelsa	Limpaga	12	2	5	LIMP	LM	NDLH	17	1	8	50	127.3	-	600	1	4	29	-
Baccaurea angulata	Belimbing hutan	4	3	2	BAAN	BBH	OTHR	14	1	15	15	14.3	11.44	-	1	150	233	-
Baccaurea lanceolata	Limpaung	4	3	2	BALA	OTH	OTHR	14	1	15	7	-	-	-	89	245	999	3
Baccaurea sp.	Kunau-kunau	4	3	2	BACC	KNU	NDLH	14	1	15	s-m	-	-	-	1	750	4575	-
Baccaurea sp.	Tampoi	4	3	2	BACC	TMP	NDLH	14	1	15	-	-	-	-	1	1165	3106	-
Barringtonia sp.	Tampalang	3	2	2	TMPL	TNG	NDLH	14	1	15	7	-	-	600	1	1466	5205	-
Berrya cordifolia	Mengkapang darat	4	3	2	BECO	OTH	OTHR	14	1	15	7	-	-	960	89	245	999	1
Bischofia javanica	Tungou	9	2	4	TUAI	TUN	NDMH	19	1	15	45	143.2	-	768	1	0	0	3
Blumeodendron tokbrai	Gangulang	6	2	3	BLUM	CG	NDLH	14	1	15	21	28.6	16.37	678	1	4	129	3
Borneodendron enigmaticum	Bangkau-bangkau	6	2	3	BKAU	BB	NDMH	19	1	15	27	57.3	23.43	860	1	0	200	3
Breynia patens	Kubamban-kubamban	4	3	2	BRPA	OTH	OTHR	14	1	15	s	-	-	-	89	245	999	-
Bridelia glauca	Manik-manik/kutang	4	3	2	BRGL	OTH	OTHR	14	1	15	s	-	-	-	89	245	999	-
Bridelia stipularis	Balatotan	6	2	3	BRST	OTH	OTHR	14	1	15	6	-	-	-	89	245	999	2
Brownlowia peltata	Pingau-pingau	6	2	3	BRPE	OTH	OTHR	14	1	15	m	-	-	-	89	245	999	-
Bruinsmia stracoides	Tingo-tingo	6	2	3	BRST	OTH	OTHR	14	1	15	m	-	-	-	89	245	999	-
Buchanania sp.	Kepala tundang	6	2	3	BUSE	KET	NDLH	14	1	15	27	38.2	19.14	559	1	0	125	3
Buchanania sp.	Kepala tundang t. pendek	6	2	3	BUAR	KPLT	NDLH	16	2	15	27	38.2	19.14	559	1	100	108	3
Burseraceae family	Kedondong	6	2	3	KDDG	KD	NDLH	16	2	10	25	0	-	-	1	2511	10479	3
Callophyllum sp.	Bintangor	5	1	3	BINT	BIN	NDLH	13	3	9	32	38.2	19.31	682	1	1214	3908	3
Calophyllum inophyllum	Penaga laut	6	2	3	CAIN	PGI	NDMH	18	4	15	35	63.7	24.49	690	1	0	0	2
Campnosperma auriculta	Terentang	5	1	3	TERA	TRG	NDLH	15	1	15	33	38.2	19.14	432	1	104	670	3
Cananga odorata	Bunga gadong	9	2	4	CADD	BUG	OTHR	14	1	15	31	-	-	382	1	0	0	3
Canarium decumanum	Pomotodon	9	2	4	POMO	POT	NDLH	15	1	15	55	146.4	-	512	1	25	79	1
Canarium odontophyllum	Kembayu	6	2	3	KBYU	KMY	NDLH	18	4	15	25	57.3	23.43	608	1	0	50	-
Carallia sp.	Meransi	6	2	3	MRSI	MRSI	NDLH	14	1	15	30	66.8	24.95	848	1	12	162	2
Cassia nodosa	Busuk-busuk	6	2	3	CANO	BSK	NDLH	14	1	15	25	57.3	23.43	-	1	4	8	3
Castanopsis	Berangan	6	2	3	BERA	BER	NDMH	20	1	9	25	50.9	22.82	688	1	290	2502	-
Casuarina equisetifolia	Aru	13	3	5	ARUX	ARU	NDHH	19	1	14	50	95.5	-	1010	1	0	0	3
Celastraceae family	Perupok	9	2	4	PERU	PEP	NDLH	20	1	8	27	47.7	31.8	801	1	678	1285	3
Cerbera odollom	Burung gagak	4	3	2	CEOD	OTH	OTHR	14	1	15	7	-	-	-	89	245	999	-
Chaetocarpus castanocarpus	Kayu dusun	4	3	2	CHAE	KAY	NDMH	20	1	15	12	19.1	13.19	1000	1	0	166	3
Chisocheton beccarianus	Lisi-lisi	6	2	3	CHBE	OTH	OTHR	14	1	15	-	28.6	16.37	560	89	245	999	-
Chisocheton glomeratus	Berindu	6	2	3	CHGL	BDU	OTHR	14	1	15	-	28.6	16.37	560	1	100	100	-
Cleistanthus paxii	Garu-garu	4	3	2	CLPA	OTH	OTHR	14	1	15	s	-	-	-	89	245	999	-
Cleistanthus sp.	Baubo	9	2	4	CLEI	BBO	OTHR	14	1	15	-	-	-	-	1	54	454	-
Combretocarpus rotundatus	Perapat paya	6	2	3	CORO	PPP	NDMH	18	4	15	25	76.4	26.06	750	1	54	54	1.2
Cordia dichotoma	Guma	4	3	2	CODI	OTH	OTHR	14	1	15	13	60.5	23.98	479	89	245	999	1
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Botanical name	Local name	PFT	SS	HG	CFRC	CHQ	TGRP	IGRP	F3	GGRP	Height	Dia	H=f(d)	Den	SPHQ	NDer	NFMU	F
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Cordia subcordata	Agutud	4	3	2	COSU	OTH	OTHR	14	1	15	15	47.7	21.49	560	89	245	999	2
Cotylelobium melanoxylon	Resak temporong	13	3	5	RETP	RBG	DHH	7	2	3	38	-	-	987	1	0	0	3
Crateva religiosa	Pangos	4	3	2	CRRE	OTH	OTHR	14	1	15	6	-	-	-	89	245	999	1
Cratoxylon arborescens	Serungan	2	1	2	SERU	SERU	NDLH	13	3	9	42	6.4	7.88	469	1	0	0	3
Cratoxylon sp.	Geronggang	3	2	2	GERO	SG	NDLH	18	4	9	10	-	-	480	1	125	1062	
Croton caudatus	Angguk-angguk	4	3	2	CRCA	OTH	OTHR	14	1	15	9	-	-	-	89	245	999	2
Croton heterocarpus	Bendak	4	3	2	CRHE	OTH	OTHR	14	1	15	12	-	-	-	89	245	999	2
Croton oblongus	Lokon	4	3	2	CROT	OTH	OTHR	14	1	15	s	-	-	-	89	245	999	-
Croton sp.	Croton	4	3	2	CROT	OTH	OTHR	14	1	15	s	-	-	-	89	245	999	-
Crudia reticulata	Anggar-anggar	3	2	2	CRUD	OTH	NDLH	14	1	15	s	-	-	-	89	245	999	-
Crypteronia griffithii	Rambai-rambai	9	2	4	CRGR	KAM	DMH	14	1	15	45	85.9	26.75	-	1	4	4	2
Crypteronia griffithii	Rambai-rambai	9	2	4	CRGR	RAM	OTHR	14	1	15	45	85.9	26.75	-	1	0	0	2
Ctenolophon parvifolius	Besi-besi	6	2	3	CTPA	BSI	NDLH	14	1	15	s-l	-	-	-	1	0	0	-
Cynometra sp.	Katong-katong	4	3	2	KATO	KAT	NDHH	14	1	8	s-m	-	-	1075	1	187	1665	-
Dacrydium elatum	Sempilor	12	2	5	SPLR	SPL	NDMH	14	1	14	37	76.4	42.68	570	1	0	237	3
Dactylocladus stenostachys	Jongkong	8	1	4	JONG	J	NDLH	18	4	15	-	117.8	-	528	1	0	529	1
Dehassia incrassata	Medang sisek	3	2	2	DEIN	MDK	NDLH	19	1	9	24	4.8	7.21	612	1	0	25	2
Dialium sp.	Keranji	10	3	4	KRNJ	KJ	NDHH	10	1	9	l	-	-	1020	1	380	1144	-
Dillenia borneensis	Simpor gajah	5	1	3	SIMG	SIG	NDMH	19	1	15	36.5	66.8	24.95	-	1	108	649	-
Dillenia sp.	Simpor	9	2	4	SIMP	SIM	NDLH	19	1	15	20-38	-	-	725	1	1528	6453	3
Dimocarpus longan	Mata kuching	6	2	3	MKUC	MAT	DMH	14	1	9	m	-	-	960	1	483	545	-
Dimorphocalyx muriana	Obah puteh	4	3	2	DIMU	DIMU	OTHR	14	1	9	12	-	-	-	1	0	0	-
Diospyros durionoides	Sabah ebony	10	3	4	SEBY	SEB	NDHH	19	1	15	-	85.9	26.75	958	1	4	4	3
Diospyros sp.	Kayu malam	3	2	2	KMLM	KMM	NDMH	19	1	8	s-m	-	-	650	1	4256	19607	2
Dipterocarpus applanatus	Keruing daun besar	9	2	4	KDBR	KDB	DMH	4	1	5	31	-	-	675	1	344	501	3
Dipterocarpus caudatus	Keruing gasing	12	2	5	KGAS	KGS	DMH	4	1	5	l	-	-	-	1	0	0	-
Dipterocarpus confertus	Keruing kobis	12	2	5	KKOB	KKO	DMH	4	1	5	46	175.1	-	802	1	132	193	3
Dipterocarpus conformis	Keruing beludu kuning	12	2	5	KBKU	KBK	DMH	4	1	5	l	-	-	-	1	100	100	-
Dipterocarpus costulatus	Keruing kipas	12	2	5	KKIP	KEK	DMH	4	1	5	37	-	-	-	1	4	37	
Dipterocarpus coudiferus	Keruing putih	12	2	5	KPUT	KPT	DMH	4	1	5	l	-	-	670	1	1343	2900	3
Dipterocarpus crinitus	Keruing mempelas	12	2	5	KMEM	KMP	DMH	4	1	5	l	-	-	925	1	0	0	2
Dipterocarpus exalatus	Keruing rapak	12	2	5	KRAP	KRP	DMH	4	1	5	37	89.1	41.2	666	1	8	233	3
Dipterocarpus geniculatus	Keruing tangkai panjang	6	2	3	KTPJ	KTP	DMH	4	1	5	m	-	-	758	1	0	45	3
Dipterocarpus globosus	Keruing buah bulat	12	2	5	KBBT	KBB	DMH	4	1	5	37	-	-	872	1	100	125	1
Dipterocarpus gracilis	Keruing kesat	12	2	5	KKES	KKS	DMH	4	1	5	l	-	-	755	1	36	364	2
Dipterocarpus grandiflorus	Keruing belimbing	12	2	5	KBEL	KB	DMH	4	1	5	42	136.9	-	790	1	57	65	-
Dipterocarpus hasseltii	Keruing kerukap kecil	12	2	5	KKKL	KKK	DMH	4	1	5	l	-	-	790	1	0	0	2
Dipterocarpus humeratus	Keruing kerukup	12	2	5	KKUK	KKU	DMH	4	1	5	46	87.5	41.14	765	1	74	74	3
Dipterocarpus kerri	Keruing gondol	12	2	5	KGON	KGD	DMH	4	1	5	l	-	-	735	1	89	93	1
Dipterocarpus lamellatus	Keruing jarang	12	2	5	KJAR	KEJ	DMH	4	1	5	55	-	-	925	1	0	0	1
Dipterocarpus lowii	Keruing shol	12	2	5	KSHO	KS	DMH	4	1	5	55	98.7	-	866	1	0	507	3
Dipterocarpus oblongifolius	Keruing neram	3	2	2	KNER	KN	DMH	4	1	5	s	-	-	654	1	0	0	3
Dipterocarpus ochranceus	Keruing ranau	6	2	3	KRAN	KRN	DMH	4	1	5	m	-	-	766	1	25	25	3
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Botanical name	Local name	PFT	SS	HG	CFRC	CHQ	TGRP	IGRP	F3	GGRP	Height	Dia	H=f(d)	Den	SPHQ	NDer	NFMU	F
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Dipterocarpus palembanicus	Keruing palembang	12	2	5	KPAL	KPD	DMH	4	1	5	42	-	-	678	1	4	4	2
Dipterocarpus sp	Keruing	12	2	5	KERU	KR	DMH	4	1	5	m-l	-	-	815	1	2571	12145	-
Dipterocarpus stellatus	Keruing bulu	12	2	5	KBUL	KBU	DMH	4	1	5	l	-	-	817	1	112	224	2
Dipterocarpus tempehes	Keruing asam	9	2	4	KASM	KA	DMH	4	1	5	36	-	-	642	1	8	8	2
Dipterocarpus verrucosus	Keruing merah	12	2	5	KMRH	KMR	DMH	4	1	5	61	117.8	-	731	2	14.5	116.5	2
Dipterocarpus warburgii	Keruing kasugoi	9	2	4	KKAS	KK	DMH	4	1	5	31	-	-	658	1	0	0	2
Dolichandrone spathacea	Tui	6	2	3	TUIX	OTH	OTHR	14	1	15	24	-	-	-	89	245	999	-
Dracrontomelon sp.	Sengkuang/soronsob	6	2	3	SENG	SGK	NDLH	18	4	15	36	47.7	21.49	600	1	0	8	3
Dryobalaonops beccarii	Kapur merah (minyak)	12	2	5	KPMH	KPM	DMH	5	1	4	61	95.5	49.29	731	1	1467	2826	1
Dryobalaonops keithii	Kapur gumpait	12	2	5	KPGM	KG	DMH	5	1	4	36.6	66.8	43.74	778	1	767	9992	1
Dryobalaonops lanceolata	Kapur paji	12	2	5	KPJI	KPG	DMH	5	1	4	76	146.4	-	736	2	1280.5	8963	2
Dryobalaonops rapa	Kapur paya	12	2	5	KPYA	KY	DMH	5	1	4	37	66.8	43.74	752	1	0	129	1
Drypetes microphylla	Odopan putih	3	2	2	DRMA	ODP	NDLH	14	1	15	s-m	-	-	-	1	454	1433	1
Duabanga moluccana	Magas	11	1	5	MAGA	MAG	PION	13	3	14	-	66.8	41.73	400	1	623	6968	-
Durio graveolens	Durian merah	12	2	5	DUGR	DUGR	NDLH	17	1	8	46	98.7	-		1	0	0	-
Durio sp.	Durian	12	2	5	DURI	DRN	NDLH	17	1	8	21-46	-	-	640	1	347	2137	1
Dyera costulata	Jelutong bukit	12	2	5	DYCO	JLB	NDLH	15	1	8	60	248.3	-	465	1	4	33	2
Dyera polyphylla	Jelutong paya	6	2	3	DYPO	JLP	NDLH	15	1	8	m	-	-	-	1	0	25	-
Elaeocarpus sp.	Tonop	9	2	4	ELST	KUK	NDLH	16	2	15	-	-	-	-	1	308	1735	-
Elaeocarpus sp.	Kungkurad	3	2	2	ELAE	KUL	NDMH	16	2	15	s-m	-	-	625	1	200	200	1
Elaeocarpus sp.	Kulibobok	3	2	2	ELAE	TNP	NDLH	14	1	15	-	-	-	382	1	0	0	-
Elateriospermum tapos	Perah ikan	6	2	3	ELAT	PEI	NDLH	14	1	15	-	57.3	23.43	840	1	0	200	1
Endospermum sp.	Sendok-sendok	8	1	4	SEND	SSB	NDLH	16	2	15	40	-	-	-	1	1177	4234	3
Ervatamia sp.	Burut-burut	9	2	4	ERMA	OTH	NDLH	14	1	15	-	-	-	-	89	245	999	1
Erythrina variegata	Dadap	3	2	2	ERVA	DDP	NDLH	14	1	15	15	-	-	-	1	0	0	3
Erythroxylum cuneatum	Perepat burung	6	2	3	PEBR	PB	NDMH	19	1	15	46	50.9	22.18	848	1	0	104	-
Eugenia sp.	Obah	9	2	4	OBAH	OB	NDMH	12	4	9	27	-	-	800	1	6081	40588	3
Euodia sp.	Pau-pau	6	2	3	OTHR	PAU	OTHR	14	1	15	31	57.3	23.43	-	1	1957	7740	2
Eurycoma longifolia	Pahit-pahit (tongkat ali)	4	3	2	EULO	OTH	OTHR	14	1	15	10	-	-	-	89	245	999	-
Eusideroxilon zwageri	Belian	10	3	4	BELI	B	NDHH	12	4	13	-	117.8	-	1038	1	985	3401	3
Eusideroxylon malagangai	Malangangai	7	3	3	MGAI	MA	NDHH	12	4	13	m-l	57.3	24.21	685	1	0	0	-
Fagraea racemosa	Tadapon puak	4	3	2	FARA	OTH	OTHR	14	1	15	s	-	-	-	89	245	999	3
Fagraea sp.	Tadapon putih	7	3	3	TEMB	TM	NDHH	14	1	15	s	-	-	-	1	0	448	-
Fagraea sp.	Tambusu	7	3	3	TEMB	TPP	NDHH	14	1	15	m	-	-	-	1	4	104	-
Ficus fulva	Togung korop	6	2	3	TAND	OTH	OTHR	14	1	15	18	-	-	-	89	245	999	3
Ficus sp.	Jiwit	9	2	4	KRAH	ARA	OTHR	14	1	15	m-l	-	-	-	1	0	1045	-
Ficus sp.	Ara	9	2	4	JIWT	OTH	OTHR	14	1	15	l	-	-	-	89	245	999	-
Flacourtia rukam	Rukam	4	3	2	RUKA	OTH	OTHR	14	1	15	12	-	-	-	89	245	999	2
Ganua motleyana	Nyatoh katiau	9	2	4	GAMO	GAMO	OTHR	14	1	9	40	82.8	28.96	560	1	0	0	3
Garcinia forbesii	Bebata	3	2	2	GAFO	BBA	NDMH	19	1	15	18	9.5	9.59	-	1	0	0	2
Garcinia mangostana	Manggis	4	3	2	GAMA	GAMA	NDMH	19	1	15	s	-	-	998	1	0	0	-
Garcinia nervosa	Kandis daun besar	6	2	3	GARC	KAN	NDMH	20	1	15	21	9.5	9.59	960	1	0	0	2
Garcinia parvifolia	Kandis	3	2	2	KNDS	KNDS	NDMH	20	1	15	30	22.3	14.3	688	1	325	2736	3
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Botanical name	Local name	PFT	SS	HG	CFRC	CHQ	TGRP	IGRP	F3	GGRP	Height	Dia	H=f(d)	Den	SPHQ	NDer	NFMU	F
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Geunsia pentandra	Tambung	5	1	3	TAMB	TAMB	OTHR	14	1	15	18	-	-	-	1	1016	3948	-
Gironniera sp.	Ampas tebu	4	3	2	GINE	OTH	OTHR	14	1	15	s	-	-	-	89	245	999	-
Glochidion litorale	Saka-saka	1	2	1	GLLI	OTH	OTHR	14	1	15	Busch	-	-	-	89	245	999	2
Glochidion sp.	Oba nasi	1	2	1	OBNA	ONA	NDLH	14	1	15	Bsche	-	-	-	1	2649	5877	2
Glochidion superbum	Gerumong jantan	6	2	3	GLSU	OTH	OTHR	14	1	15	18	38.2	19.14	-	89	245	999	3
Gonystylus bancanus	Ramin	6	2	3	RAMN	R	NDLH	18	4	15	27	66.8	24.95	675	1	220	1228	3
Gordonia sp.	Melulok	1	2	1	GORD	OTH	OTHR	14	1	15	b & t	-	-	-	89	245	999	-
Guioa sp.	Tanggir manuk	4	3	2	GUIO	OTH	OTHR	14	1	15	s	-	-	-	89	245	999	-
Gymnacranthera contracta	Lunau	6	2	3	GYCO	OTH	OTHR	14	1	15	18	25.5	15.36	-	89	245	999	1
Helicia sp.	Kurunggu	1	2	1	KGGU	KRGU	NDLH	14	1	15	b & t	-	-	-	1	8	108	2
Heritiera littoralis	Dungun	4	3	2	HELI	DUGN	NDHH	19	1	9	15	76.4	28.03	795	1	100	650	2
Heritiera simplicifolia	Kembang/ mengkulang	9	2	4	KEMB	KM	NDMH	19	1	9	45	133.7	-	749	1	410	4078	3
Hibiscus tiliceus	Baru	4	3	2	HITI	BRU	OTHR	14	1	15	12	19.1	13.19	-	1	4	4	3
Homalium caryophyllaceum	Takaliu	7	3	3	TLIU	TKU	NDHH	14	1	15	6	31.8	17.34	928	2	266.5	360	3
Homalium sp.	Takaliu	7	3	3	TLIU	TKU	OTHR	14	1	15	s-l	-	-	1000	2	266.5	360	-
Hopea aequalis	Selangan sama	13	3	5	SSAM	SLS	DMH	7	2	2	-	-	-	-	1	0	0	-
Hopea argentea	Selangan urat	6	2	3	SURT	SLT	DMH	7	2	2	m	-	-	-	1	0	0	2
Hopea beccariana	Selangan penak	13	3	5	SPEN	SLE	DMH	7	2	2	37	95.5	36.51	786	1	29	41	2
Hopea dryobalanoides	Selangan daun kapur	4	3	2	SDKP	SLK	DMH	7	2	2	s	-	-	718	1	0	0	-
Hopea dyeri	Selangan daun halus	4	3	2	SDHS	SDH	DMH	7	2	2	s	-	-	766	1	33	66	1
Hopea ferruginea	Selangan mata kucing	7	3	3	SMKC	SMC	DMH	7	2	2	m	-	-	699	1	0	0	2
Hopea latifolia	Selangan jongkong	13	3	5	SJON	SJK	DMH	7	2	2	-	-	-	-	1	316	54	-
Hopea mengerawan	Selangan hitam	13	3	5	SHTM	SH	DMH	7	2	2	-	-	-	715	1	0	0	-
Hopea micrantha	Selangan lunas	13	3	5	SLUN	SLN	DMH	7	2	2	-	-	-	787	1	0	0	1
Hopea montana	Selangan bukit	13	3	5	SBUK	SUK	DMH	7	2	2	-	-	-	851	1	0	8	1
Hopea myrtifolia	Selangan beludu	13	3	5	SBDU	SU	DMH	7	2	2	-	-	-	-	2	0	0	-
Hopea nervosa	Selangan jangkang	9	2	4	SJKG	SJ	DMH	7	2	2	31	47.7	26.2	704	1	1210	4417	3
Hopea nutans	Giam	10	3	4	GIAM	G	DHH	7	2	15	l	-	-	1056	1	8	8	3
Hopea pentanervia	Selangan lima urat	10	3	4	SLUR	SLU	DHH	7	2	2	30	57.3	29.17	1104	1	114	114	-
Hopea sangal	Gagil	13	3	5	GAGL	GL	DMH	7	2	4	46	117.8	-	699	1	8	0	3
Hopea semicuneata	Giam kulit merah	10	3	4	HOSE	GK	DHH	7	2	15	-	108.2	-	1008	1	0	124	2
Hopea sp.	Selangan	13	3	5	SELA	S	DMH	7	2	2	m-l	-	-	1080	1	182	4239	-
Hopea tenuinervula	Selangan daun serong	13	3	5	SDSG	SDS	DMH	7	2	2	-	-	-	-	1	0	0	-
Hopea vaccinifolia	Selangan ribu	4	3	2	SRIB	SLR	DMH	7	2	2	s	-	-	-	2	0	0	-
Hopea wyatt-smithii	Selangan daun bulat	6	2	3	SDBL	SLB	DMH	7	2	2	m	-	-	-	1	0	0	-
Hydnocarpus sp.	Karpus	6	2	3	KARP	KAR	NDMH	18	4	15	15-30	57.3	23.43	700	1	2417	4952	-
Ilex cissoidea.	Morogis	6	2	3	MORO	MGS	OTHR	14	1	15	m	-	-	-	2	4	218.5	-
Ilex cymosa	Bangkulatan	4	3	2	BKLT	BGN	OTHR	14	1	15	s-m	-	-	-	1	0	125	3
Intsia bijuga	Ipil laut	7	3	3	ILAT	IPL	NDHH	14	1	15	24	57.3	23.43	838	1	0	0	3
Intsia palembanica	Merbau	10	3	4	MERB	MER	NDHH	12	4	9	55	146.4	-	793	1	165	813	2
Irvingia malayana	Pauh kijang	10	3	4	PAUH	PKI	NDHH	10	1	15	40	146.4	-	992	1	118	421	3
Itea macrophylla	Marapid/kaintuhan	4	3	2	ITMA	OTH	OTHR	14	1	15	s	-	-	-	89	245	999	1
Ixonanthes reticulata	Inggir burung	4	3	2	IXON	IB	NDMH	14	1	15	s	-	-	-	1	100	300	-
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Botanical name	Local name	PFT	SS	HG	CFRC	CHQ	TGRP	IGRP	F3	GGRP	Height	Dia	H=f(d)	Den	SPHQ	NDer	NFMU	F
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Jackia ornata	Selumar	7	3	3	JAOR	SLR	NDHH	20	1	15	35	57.3	23.43	912	2	0	0	2
Kleinhovia hospita	Timahar	6	2	3	KLHO	OTH	OTHR	14	1	15	20	28.6	16.37	480	89	245	999	2
Koilodepus sp.	Kilas	4	3	2	KILA	KLS	NDHH	14	1	15	7	9.5	9.59	-	1	525	8050	1
Koompassia excelsa	Mengaris	12	2	5	MENG	MEN	NDMH	10	1	12	80	222.8	-	827	1	273	981	2
Koompassia malaccensis	Kempas	13	3	5	IMPS	IMP	NDHH	10	1	12	55	95.5	38.7	1114	1	153	573	2
Koordersiodendron pinnatum	Ranggu	9	2	4	RGGU	RGU	NDMH	18	4	8	30	47.7	31.8	801	1	607	1509	2
Lagerstroemia speciosa	Bungor	6	2	3	OTHR	OTH	OTHR	14	1	15	30.5	47.7	21.49	674	89	245	999	3
Lansium domesticum	Langsat	4	3	2	LADO	LADO	OTHR	14	1	15	15	19.1	13.19	-	1	0	0	3
Lapisanthes sp.	Lapisanthes	9	2	4	LAPI	OTH	OTHR	14	1	15	-	-	-	-	89	245	999	-
Lasianthus sp.	Kopi-kopi	1	2	1	KOPI	OTH	OTHR	14	1	15	b & t	-	-	-	89	245	999	-
Lauraceae family	Medang	1	2	1	MEDA	MD	NDLH	19	1	9	b & t	-	-	615	1	7394	32885	2
Leea sp.	Mali-mali	1	2	1	LEEA	OTH	OTHR	14	1	15	b & t	-	-	-	89	245	999	3
Leptospermum sp.	Gelam bukit	4	3	2	LEPT	OTH	OTHR	14	1	15	12	-	-	-	89	245	999	-
Linociera sp.	Bangkulat	6	2	3	LIPL	BGT	OTHR	14	1	15	oft m	-	-	-	1	154	154	-
Lithocarpus sp.	Mempening	12	2	5	MEMP	MEM	NDMH	20	1	2	-	-	-	-	1	2672	23659	3
Litsea cubeba	Lindos/railos	9	2	4	LICB	LDS	NDLH	19	1	15	-	-	-	-	1	0	100	-
Litsea graciea	Pengulobon	6	2	3	LIGA	PGN	NDLH	19	1	9	m	38.2	19.31	-	1	0	8	1
Litsea odorifera	Medang pawas	6	2	3	LIOD	MDP	NDLH	19	1	9	m	47.7	22	509	1	0	25	-
Litsea odorifera	Medang pawas	6	2	3	LIOD	TWD	NDLH	19	1	9	m	47.7	22	509	1	0	0	-
Macaranga conifera	Ludai	5	1	3	LUDA	LUDA	NDLH	13	3	14	24	47.7	35.49	400	2	1033	1562	1
Macaranga hosei	Lopokon	8	1	4	MAHO	OTH	OTHR	14	1	15	-	-	-	-	89	245	999	-
Macaranga sp.	Kubin	5	1	3	MAGI	OTH	MACA	13	3	14	s-m	-	-	400	89	245	999	-
Macaranga sp.	Sedaman	5	1	3	MACA	SEDA	MACA	13	3	14	s-m	-	-	400	2	18555.5	64049.5	-
Macaranga sp.	Sedaman	5	1	3	SEDA	SEDA	MACA	14	1	14	s-m	-	-	400	2	18555.5	64049.5	-
Macaranga tanarius	Lingkabong	5	1	3	MATA	OTH	OTHR	14	1	15	21	-	-	500	89	245	999	-
Magnoliaceae family	Cempaka	1	2	1	MAGN	CP	NDMH	20	1	15	b & t	-	-	-	1	629	1008	-
Mallotus mollissimus	Dahu	4	3	2	MAMO	OTH	OTHR	14	1	15	s	-	-	-	89	245	999	3
Mallotus muticus	Mallotus paya	6	2	3	MAMU	MAMU	OTHR	14	1	15	24	44.6	20.75	432	1	0	0	3
Mallotus philipinensis	Mallotus philipine	4	3	2	MAPH	OTH	OTHR	14	1	15	10	9.5	9.59	749	89	245	999	2
Mallotus sp.	Melutos	4	3	2	MALL	MTS	NDLH	14	1	15	s-m	-	-	-	1	3970	12803	-
Mangifera pajang	Bambangan	9	2	4	MGPA	BBG	NDLH	17	1	15	-	-	-	-	1	4	4	-
Mangifera sp.	Bachang	6	2	3	ASAM	BC	NDLH	19	1	15	s-l	-	-	600	1	429	433	-
Mangifera sp.	Dumpiring	6	2	3	ASAM	DUM	NDLH	19	1	15	s-l	-	-	600	1	0	0	-
Mangifera sp.	Pahu	6	2	3	ASAM	PHU	NDLH	19	1	15	s-l	-	-	600	1	0	404	-
Mangitera sp.	Assam	6	2	3	ASAM	ASS	NDLH	19	1	15	s-l	-	-	600	1	258	307	-
Mangostana sp.	Manggis	6	2	3	GARC	MGS	NDMH	19	1	15	-	-	-	-	2	4	218.5	-
Meliaceae family	Lantupak	6	2	3	LANT	LA	OTHR	14	1	8	m	-	-	-	1	7473	21692	3
Meliosma sumatrana	Gapas-gapas	6	2	3	GPAS	GP	NDMH	14	1	15	m	-	-	-	1	0	100	-
Memecylon sp.	Nipis kulit	1	2	1	MLAE	OTH	OTHR	14	1	15	b & t	-	-	-	89	245	999	-
Mesua macrantha	Bintangor batu	4	3	2	MEMA	BIB	NDMH	19	1	9	s	-	-	-	1	158	283	-
Microcos sp.	Korodong	1	2	1	KRDG	DAMA	OTHR	15	1	15	b & t	-	-	600	1	875	975	-
Microcos sp.	Korodong/damak-damak	1	2	1	KRDG	KDG	OTHR	14	1	15	b & t	-	-	600	1	741	2236	-
Milletia sp.	Taroi-taroi	4	3	2	MILL	OTH	OTHR	14	1	15	s-m	-	-	-	89	245	999	3
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Botanical name	Local name	PFT	SS	HG	CFRC	CHQ	TGRP	IGRP	F3	GGRP	Height	Dia	H=f(d)	Den	SPHQ	NDer	NFMU	F
Myristicaceae family	Darah-darah	6	2	3	DARA	DRA	NDLH	16	2	15	s-l	-	-	591	1	3985	18355	3
Nauclea sp.	Bangkal	8	1	4	BKAL	BKL	NDLH	14	1	15	m-l	-	-	720	1	3027	10070	-
Neesia sp.	Durian monyet	12	2	5	DMYT	DRM	NDLH	17	1	8	m-l	-	-	-	1	312	1032	2
Nephelium glabrum	Satu inchi	4	3	2	NEGL	NEGL	OTHR	14	1	15	s-m	-	-	-	1	0	0	-
Nephelium maingayi	Kelamondoi	6	2	3	NEPH	KDI	OTHR	14	1	15	35	50.9	22.18	-	1	0	0	-
Nephelium mutabile	Maritam	9	2	4	MERI	MTM	NDLH	14	1	15	35	19.1	13.19	-	2	386.5	1067.5	-
Nephelium sp.	Meritam	9	2	4	MERI	MTM	NDLH	14	1	15	45	127.3	-	-	2	386.5	1067.5	-
Nephelium sp.	Rambutan	9	2	4	RBTN	RBTN	OTHR	14	1	15	45	127.3	-	-	1	158	570	-
Notaphoebe obovata	Lamau-lamau	9	2	4	NOOB	LMU	NDLH	18	4	15	m	-	-	-	1	0	13432	-
Ochanostachys amentacea	Petaling	7	3	3	TGGL	PET	NDMH	19	1	15	30	57.3	23.43	880	1	381	1092	2
Octomeles sumatrana	Binuang	11	1	5	BINU	BN	PION	13	3	11	55	194.2	-	400	1	259	3457	3
Omalanthus sp.	Ludai	5	1	3	LUDA	LUDA	NDLH	16	2	15	s	-	-	-	2	1033	1562	-
Osbornia octodonta	Gelam laut	9	2	4	OSOC	OTH	OTHR	14	1	15	-	-	-	-	89	245	999	-
Ostodes sp.	Pait-pait	6	2	3	PAIT	PAIT	OTHR	14	1	15	m	-	-	-	1	0	0	-
Otophora fruticosa	Balingasan	4	3	2	OTFR	OTH	OTHR	14	1	15	6	-	-	-	89	245	999	-
Pangium edule	Pangi	9	2	4	KEPA	PAN	NDLH	14	1	15	38	85.9	26.75	660	1	0	0	-
Paranephelium sp.	Membuakat	4	3	2	MEMB	OTH	OTHR	14	1	15	s-m	-	-	-	89	245	999	-
Parashorea malaanonan	Urat mata daun licin	12	2	5	UMDL	UML	DLH	1	1	3	61	194.2	-	531	1	1432	7890	3
Parashorea parvifolia	Urat mata daun kecil	12	2	5	UMDK	UMK	DLH	5	1	3	43	85.9	46.43	665	1	0	25	1
Parashorea smythiesii	Urat mata batu	12	2	5	UMBT	UMB	DMH	5	1	3	43	194.2	-	678	1	1123	2566	2
Parashorea sp.	Urat mata	12	2	5	WHSY	WS	DLH	1	1	3	l	-	-	-	1	94	10725	-
Parashorea tomentella	Urat mata beludu	12	2	5	UMBL	UMU	DLH	1	1	3	61	194.2	-	506	1	4859	13103	2
Parastemon urophyllum	Mandailas	9	2	4	PAUR	MDS	NDLH	18	4	15	36	-	-	1075	2	0	66.5	3
Parinari	Bangkawang	9	2	4	BKWG	NAN	NDLH	12	4	15	48	-	-	810	1	0	0	3
Parinari oblongifolia	Merbatu	9	2	4	PAOD	MEB	NDMH	12	4	15	40	82.8	26.56	739	1	543	1670	3
Parishia insignis	Layang-layang	9	2	4	LAYA	LAY	NDMH	20	1	15	60	60.5	23.98	560	2	0	359.5	2
Parishia sp.	Layang-layang	9	2	4	LAYA	LAY	OTHR	20	1	15	60	105	-	-	2	0	359.5	3
Parkia javanica	Kupang	9	2	4	KUPA	KNG	NDLH	14	1	8	30	-	-	-	1	100	100	3
Parkia sp.	Petai	9	2	4	PTAI	PTI	NDMH	14	1	8	30	79.6	40.84	600	1	315	1303	3
Peltophorum racemosum	Timbarayong	9	2	4	TIMB	OTH	OTHR	14	1	15	l	-	-	640	89	245	999	-
Pentace adenophora	Takalis daun bulat	10	3	4	PEAD	PEAD	NDHH	17	1	9	30	66.8	26.36	-	1	0	0	-
Pentace laxiflora	Takalis daun halus	3	2	2	PELA	TKH	NDLH	16	2	9	s	315.1	-	360	1	1274	2011	3
Pentace sp.	Takalis	9	2	4	TAKA	TKS	NDLH	17	1	9	m-l	-	-	750	1	2663	7985	2
Pentaspodon motleyii	Pelajau	6	2	3	PELJ	PEL	NDLH	19	1	15	36	42	20.13	722	1	0	0	1
Pericopsis mooniana	Ipil air	6	2	3	IAYR	IPA	NDMH	19	1	15	30	47.7	21.49	800	1	0	0	2
Phaleria perrottetetiana	Alig pagi	2	1	2	ALIG	OTH	OTHR	14	1	15	s	-	-	-	89	245	999	-
Phyllanthus emblica	Laka	6	2	3	PYEM	OTH	OTHR	14	1	15	36	47.7	21.49	600	89	245	999	2
Pithecellobium sp.	Jering	1	2	1	JARG	OTH	OTHR	14	1	15	b & t	-	-	-	89	245	999	-
Planchonia valida	Putat paya	9	2	4	PUTP	PUT	NDLH	18	4	8	30	95.5	42.2	792	1	66	865	1
Plectronia confertum	Grubai	4	3	2	PLCO	OTH	OTHR	14	1	15	s	-	-	-	89	245	999	-
Pleiocarpidia sandakanensis	Buloh-buloh	3	2	2	PLSA	BLH	NDLH	14	1	15	s	-	-	-	1	0	0	-
Podocarpus blumeii	Lampias	12	2	5	POBL	LPS	NDLH	17	1	14	37	95.5	-	619	1	0	0	2
Podocarpus imbricatus	Lompoyou	9	2	4	POIM	LOM	NDLH	17	1	14	35	76.4	42.68	520	1	0	0	2

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Botanical name	Local name	PFT	SS	HG	CFRC	CHQ	TGRP	IGRP	F3	GGRP	Height	Dia	H=f(d)	Den	SPHQ	NDer	NFMU	F
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Podocarpus rumphii	Kayu china	6	2	3	PORU	KCN	NDMH	17	1	14	m	-	-	-	1	0	4	-
Polyosma integrifolia	Bedaru	4	3	2	BEDA	BED	OTHR	14	1	15	14	-	-	-	1	0	0	-
Pometia pinnata	Kasai	9	2	4	KASA	KAS	NDMH	19	1	15	40	76.4	26.06	832	1	33	111	3
Pongomia pinnata	Marabahai	6	2	3	MHAI	MHI	NDMH	18	4	15		47.7	21.49	800	1	0	0	-
Prunus javanica	Kelanus	6	2	3	PRJA	KNS	NDLH	14	1	15	30	66.8	24.95	-	1	0	0	1
Pternandra coerulescens	Sirih-sirih	6	2	3	SIRE	OTH	OTHR	14	1	15	20	85.9	26.75	1000	89	245	999	3
Pterocarpus indicus	Angsana	9	2	4	ANGS	ANG	NDLH	17	1	8	31	76.4	40.31	624	1	0	0	-
Pterocymbium tinctorium	Teluto	6	2	3	TELU	TTO	NDMH	14	1	9	-	57.3	24.35	672	1	0	87	1
Pterospermum sp.	Bayor	5	1	3	BAYO	BY	NDLH	14	1	9	m	-	-	400	1	1990	12526	3
Quassia borneensis	Manunggal	6	2	3	QUBO	MGL	OTHR	14	1	15	m	-	-	-	2	2	14.5	-
Randia anisophylla	Bembalor	4	3	2	RAAN	OTH	OTHR	14	1	15	12	-	-	600	89	245	999	2
Ryparosa sp.	Giwie	6	2	3	GIEW	GWI	OTHR	14	1	15	21	-	-	-	1	650	2733	-
Sandoricum maingayi	Sentul hutan	9	2	4	SAMA	STH	NDLH	19	1	15	45	76.4	26.06	-	1	0	0	2
Sandoricum mangyi	Sentol hutan	9	2	4	SAMA	STL	NDLH	15	1	15	45	76.4	26.06	-	1	0	0	2
Sapium indicum	Apid-apid	6	2	3	APID	OTH	OTHR	14	1	15	18	38.2	19.14	448	89	245	999	2
Sapotaceae family	Nyatoh	9	2	4	NYAT	NT	NDMH	21	2	9	s - l	-	-	-	1	4217	17451	2
Saracca sp.	Gapis	3	2	2	GAPI	GAPI	NDLH	14	1	15	14	-	-	-	1	137	241	2
Sarcotheca diversifolia	Tabarus	4	3	2	SADI	OTH	OTHR	14	1	15	s	-	-	-	89	245	999	-
Saurauia sp.	Sokong-sokong	4	3	2	SAUR	OTH	OTHR	14	1	15	s	-	-	-	89	245	999	-
Scaphium affine	Kembang semangkok	9	2	4	KSMK	KEM	NDLH	17	1	15	45	76.4	26.06	560	1	1250	2194	3
Schima wallichii	Gatal-gatal	9	2	4	GTAL	GT	NDLH	14	1	15	45	76.4	26.06	672	1	0	150	3
Scorodocarpus borneensis	Bawang hutan	9	2	4	BWHN	BWH	NDMH	19	1	8	36	76.4	40.31	905	1	445	851	2
Serialbizzia splendens	Kungkur	9	2	4	KKUR	KUR	NDLH	20	1	15	30	95.5	27.03	720	1	4	4	2
Serianthes dilmyi	Batai laut	3	2	2	SEDI	BLT	NDLH	14	1	15	s-m	-	-	-	1	0	0	2
Shorea acuminatissima	Seraya kuning runcing	12	2	5	SKRG	SPC	DLH	6	2	6	l	-	-	-	1	638	1188	-
Shorea agami	Melapi agama	12	2	5	MEAG	MPA	DLH	2	1	2	60	143.2	-	665	1	33	62	2
Shorea almon	Seraya kerukup	12	2	5	SKER	SKE	DLH	2	1	2	61	117.8	-	527	1	98	729	2
Shorea andulensis	Seraya daun merah	12	2	5	SDME	SDR	DLH	3	1	2	38	-	-	-	1	0	258	1
Shorea angentifolia	Seraya daun mas	12	2	5	SDMS	SDM	DLH	8	1	2	53	117.8	-	829	1	709	2127	2
Shorea angustifolia	Seraya kuning bukit	3	2	2	SKBT	SKT	DLH	6	2	6	15	31.8	21.42	853	1	0	325	1
Shorea atrinervosaq	Selangan batu hitam	13	3	5	SBHM	SBX	DHH	10	1	7	60	127.3	-	997	1	0	4	2
Shorea beccariana	Seraya langgai	12	2	5	SLGG	SLG	DLH	11	1	2	55	98.7	36.8	597	1	278	781	3
Shorea biawak	Selangan batu biawak	10	3	4	SBBK	SBW	DHH	10	1	7	31	-	-	930	1	0	0	3
Shorea bracteolata	Malapi pang	12	2	5	MEPG	MPP	DLH	2	1	2	m-l	-	-	647	1	4	4	1
Shorea coriacea	Seraya tangkai panjang	12	2	5	STKP	STP	DLH	7	2	2	43	-	-	699	1	0	0	1
Shorea cristata	Kawang daun merah	12	2	5	KWDM	KWM	DLH	11	1	2	-	-	-	828	1	0	33	1
Shorea curtissii	Seraya betul	12	2	5	SBET	SRU	DLH	8	1	2	61	146.4	-	656	1	0	0	1
Shorea dasyphylla	Seraya batu	12	2	5	SBAT	SRB	DLH	9	1	2	l	-	-	520	1	0	54	2
Shorea domatiosa	Selangan batu mata-mata	13	3	5	SBMM	SMM	DHH	10	1	7	60	143.2	-	1022	1	0	0	1
Shorea exeliptica	Selangan batu tembaga	13	3	5	SBTM	SBZ	DHH	10	1	7	60	143.2	-	944	1	0	0	3
Shorea faguetiana	Seraya kuning siput	12	2	5	SKSP	SSP	DLH	6	2	6	63	146.4	45.71	634	1	1050	1392	2
Shorea falciferoides	Selangan batu laut	12	2	5	SBLT	SBP	DMH	10	1	7	-	-	-	-	1	86	86	-
Shorea fallax	Seraya daun kasar	3	2	2	SEDK	SDK	DLH	3	1	2	7	-	-	-	1	0	0	1
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Botanical name	Local name	PFT	SS	HG	CFRC	CHQ	TGRP	IGRP	F3	GGRP	Height	Dia	H=f(d)	Den	SPHQ	NDer	NFMU	F
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Shorea ferruginea	Seraya melantai kecil	12	2	5	SMKL	SMK	DLH	11	1	2	-	-	-	-	1	0	233	2
Shorea flaviflora	Seraya daun besar	6	2	3	SDBR	SDB	DLH	11	1	2	m	-	-	-	1	0	220	-
Shorea foxworthyii	Selangan batu bersisek	13	3	5	SBBS	SBB	DHH	10	1	7	60	143.2	-	992	1	8	16	2
Shorea gibbosa	Seraya kuning gajah	12	2	5	SKGH	SGT	DLH	6	2	6	70	146.4	45.71	509	1	20	95	2
Shorea glaucescens	Selangan batu laut	10	3	4	SBLX	SBL	DMH	10	1	7	35	79.6	45.86	838	1	70	236	-
Shorea gratissima	Melapi laut	12	2	5	MELT	MPU	DLH	2	1	2	53	98.7	36.8	620	1	0	0	2
Shorea havilandii	Selangan batu pinang	4	3	2	SBPG	SPG	DHH	10	1	7	15	31.8	26.06	1088	1	0	0	1
Shorea hopeifolia	Seraya kuning jantan	12	2	5	SKJN	SJT	DLH	6	2	6	61	98.7	40.71	570	1	0	428	1
Shorea hypoleuca	Selangan batu kelabu	10	3	4	SBKB	SBG	DHH	10	1	7	35	79.6	45.86	938	1	124	136	2
Shorea johorensis	Seraya majau	12	2	5	SMAJ	SM	DLH	2	1	1	69	117.8	-	499	1	2244	10955	3
Shorea kudatensis	Seraya kuning kudat	12	2	5	SKKU	SDD	DLH	6	2	6	46	-	-	638	1	0	0	2
Shorea kunstleri	Seraya sirap	9	2	4	SSIR	SSR	DHH	10	1	2	55	76.4	33.74	848	1	0	0	1
Shorea lamentella	Melapi lapis	12	2	5	MELP	MPL	DLH	2	1	2	46	-	-	728	1	0	0	1
Shorea laxa	Seraya kuning keladi	3	2	2	SKKL	SLI	DLH	6	2	6	s	-	-	-	1	0	129	1
Shorea leprosula	Seraya tembaga	12	2	5	STEM	ST	DLH	3	1	2	61	98.7	36.8	575	1	917	6453	3
Shorea leptoderma	Selangan batu biabas	10	3	4	SBBI	SBI	DHH	10	1	7	31	-	-	930	1	70	194	2
Shorea macrophylla	Kawang jantung	12	2	5	KWJT	KWJ	DLH	11	1	2	46	98.7	36.8	350	1	464	770	2
Shorea macroptera	Seraya melantai	12	2	5	SMEL	SML	DLH	11	1	2	61	98.7	36.8	540	1	3519	7132	2
Shorea mecistopteryx	Kawang burung	9	2	4	KWBR	KWR	DLH	11	1	2	39	76.4	33.74	550	1	942	2776	1
Shorea multiflora	Banjutan	3	2	2	BANJ	BJ	DMH	7	2	6	15	76.4	35.87	659	1	122	413	2
Shorea myrionerva	Seraya urat banyak	9	2	4	SUBK	SBK	DLH	11	1	2	38	85.9	35.36	610	1	0	0	1
Shorea nebulosa	Seraya kabut	12	2	5	SKAB	SKB	DLH	9	1	2	55	127.3	-	604	1	174	174	2
Shorea obscura	Selangan batu tanduk	9	2	4	SBTA	SBT	DHH	10	1	7	35	79.6	45.86	922	1	137	137	-
Shorea ochracea	Melapi daun besar	12	2	5	MEDB	MPB	DLH	2	1	2	l	-	-	539	1	100	112	2
Shorea oleosa	Seraya minyak	12	2	5	SMIN	SMY	DLH	3	1	2	61	-	-	478	1	1951	10303	-
Shorea ovalis	Seraya kepong	12	2	5	SKEP	SKP	DLH	11	1	2	61	117.8	-	509	1	840	4072	3
Shorea ovata	Seraya punai bukit	6	2	3	SPBT	SNB	DLH	7	2	2	m	-	-	784	1	0	2017	2
Shorea parvifolia	Seraya punai	12	2	5	SPUN	SNI	DLH	3	1	2	61	98.7	36.8	468	1	3385	12993	3
Shorea parvistipulata	Seraya lupah	9	2	4	SLUP	SLA	DLH	8	1	2	35	63.7	30.89	499	1	0	0	2
Shorea patoiensis	Seraya kuning pinang	12	2	5	SKPG	PN	DLH	6	2	6	38	-	-	-	1	0	4	1
Shorea pauciflora	Oba suluk	12	2	5	OSUL	OS	DLH	5	1	2	69	146.4	-	675	1	358	674	3
Shorea pilosa	Kawang bulu	12	2	5	KWBL	KWB	DLH	11	1	2	-	-	-	409	1	609	621	1
Shorea pinanga	Kawang pinang	9	2	4	KWPG	KWP	DLH	11	1	2	30	79.6	34.33	419	1	1635	1643	2
Shorea platycarpa	Seraya paya	9	2	4	SPAY	SYA	DLH	7	2	2	46	57.3	29.17	709	1	0	29	-
Shorea platyclodos	Seraya bukit	12	2	5	SBKT	SRI	DLH	5	1	2	55	175.1	-	736	1	25	503	2
Shorea polyandra	Seraya kuning quion	12	2	5	SKQN	SPQ	DLH	6	2	6	-	-	-	-	1	0	0	1
Shorea quandrinervis	Seraya sudu	12	2	5	SSUD	SSU	DLH	9	1	2	38	-	-	569	1	0	0	2
Shorea quiso	Selangan batu merah	13	3	5	SBMH	SBM	DHH	10	1	7	-	-	-	-	1	33	33	-
Shorea retusa	Seraya daun tumpul	9	2	4	SDTU	SDU	DLH	3	1	2	30	54.1	28.23	-	1	0	0	1
Shorea revoluta	Seraya daun tajam	9	2	4	SBTA	SRT	DLH	7	2	2	32	63.7	30.89	-	1	0	0	1
Shorea rubra	Seraya bingkai	12	2	5	SBIN	SRK	DLH	8	1	2	l	-	-	668	1	25	29	1
Shorea rugosa	Seraya buaya hantu	12	2	5	SBHA	SRH	DLH	7	2	2	-	-	-	649	1	0	0	1
Shorea scaberrima	Seraya mempelas	9	2	4	SMMP	SMP	DLH	11	1	2	35	63.7	30.89	549	1	0	0	2
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Botanical name	Local name	PFT	SS	HG	CFRC	CHQ	TGRP	IGRP	F3	GGRP	Height	Dia	H=f(d)	Den	SPHQ	NDer	NFMU	F
...																		
Shorea scabrida	Seraya lop	9	2	4	SLOP	SLP	DLH	3	1	2	31	47.7	26.2	558	1	0	0	2
Shorea scrobiculata	Selangan batu kurap	13	3	5	SBKP	SBS	DHH	10	1	7	-	-	-	-	1	0	4	-
Shorea seminis	Selangan batu terandak	13	3	5	SBTK	SBY	DHH	10	1	7	55	117.8	-	921	1	16	20	2
Shorea slooteni	Seraya kepong kasar	9	2	4	SKEK	SKG	DLH	11	1	2	40	79.6	34.33	-	1	125	250	1
Shorea smithiana	Seraya timbau	12	2	5	STIM	SBU	DLH	1	1	2	53	146.4	-	499	1	1532	5488	3
Shorea sp.	Kawang	12	2	5	KWNG	KW	DLH	11	1	2	m-l	-	-	-	1	702	1988	-
Shorea sp. (Eushorea group)	Selangan batu	13	3	5	SBTU	SB	DHH	10	1	7	m-l	-	-	-	1	1454	8149	-
Shorea sp. (Richetia group)	Seraya kuning s.d. besar	12	2	5	SKUN	DLH	DLH	6	2	6	-	-	-	-	1	0	0	-
Shorea sp. (Rubroshorea group)	Seraya	12	2	5	SRYA	SR	DLH	3	1	2	l	-	-	-	1	792	19282	1
Shorea superba	Selangan b. daun halus	13	3	5	SBDH	SBH	DHH	10	1	7	63	146.4	-	581	1	194	210	2
Shorea symingtonii	Melapi kuning (bunga)	12	2	5	MEBG	MPK	DLH	2	1	2	61	146.4	-	520	1	4	20	2
Shorea teysmanniana	Seraya bunga	9	2	4	SBGA	SRG	DLH	7	2	2	l	79.6	34.33	589	1	0	25	2
Shorea venulosa	Seraya kerangas	12	2	5	SKGS	SKA	DLH	5	1	2	60	-	-	803	1	0	8	-
Shorea virescens	Melapi sulang salig	12	2	5	MSSG	MPS	DLH	2	1	2	64	175.1	-	499	1	8	8	2
Shorea waltonii	Seraya kelabu	12	2	5	SKBU	SKK	DLH	9	1	2	60	-	-	428	1	262	578	-
Shorea xanthophylla	Seraya kuning barun	9	2	4	SKBA	SKU	DLH	6	2	6	26	-	-	654	1	1274	3466	2
Sindora irpicina	Sepetir	9	2	4	SEPT	SPT	NDLH	14	1	9	30	79.6	28.52	598	1	369	1249	1
Stemonurus corniculata	Samala	6	2	3	STCO	OTH	OTHR	14	1	15	39	57.3	23.43	1130	89	245	999	2
Stemonurus scorpioides	Katok	6	2	3	KTOK	KTK	OTHR	14	1	15	33	47.7	21.49	1000	1	450	725	-
Sterculia macrophylla	Kelumpang	6	2	3	KLPG	KPG	NDMH	16	2	9	36	47.7	22	560	2	1280.5	8963	-
Sympetalandra borneensis	Merbau lalat	6	2	3	MLAL	MBL	NDMH	19	1	15	22	76.4	26.06	680	1	412	511	2
Symplocos fasciculata	Jiak	2	1	2	JIAK	JAK	OTHR	14	1	15	15	12.7	10.84	-	1	600	725	3
Symplocos lateviridis	Poroi untu	6	2	3	SYMP	OTH	OTHR	14	1	15	21	-	-	-	89	245	999	1
Symplocos polyandra	Mogkulat	6	2	3	SYMP	OTH	OTHR	14	1	15	-	-	-	-	89	245	999	-
Symplocos sp.	Kemenyan	1	2	1	LOBO	LOBO	OTHR	14	1	15	b & t	-	-	-	1	0	0	3
Symplocos sp.	Lobo	1	2	1	KEME	OTH	OTHR	14	1	15	b & t	-	-	-	89	245	999	3
Tectona grandis	Jati	9	2	4	JATI	JTI	NDMH	18	4	15	l	-	-	625	1	0	0	-
Teijsmanniodendron sp.	Buak-buak	3	2	2	BUAK	BU	NDMH	16	2	15	s	-	-	-	1	791	2586	1
Teijsmanniodendron sp.	Buak-buak jarietek	4	3	2	TEPT	BUJ	NDMH	16	2	15	s	-	-	-	1	0	0	1
Terminalia copelandii	Talisai paya	12	2	5	TECO	TLP	NDLH	15	1	8	l	79.6	40.84	430	1	0	0	3
Terminalia sp.	Talisai	12	2	5	TALI	TLI	NDMH	18	4	8	l	95.5	42.2	730	1	174	368	2
Tetramerista glabra	Tuyut	6	2	3	TUYT	TUY	NDLH	16	2	15	-	57.3	23.43	720	1	0	0	2
Thespesia populnea	Baru laut	6	2	3	THPO	BRL	OTHR	14	1	15	18	-	-	-	1	0	0	-
Timonius flavescens	Tapai-tapai	4	3	2	TIFL	OTH	OTHR	14	1	15	10	-	-	-	89	245	999	1
Toona sp.	Surian	6	2	3	TOON	SU	NDLH	18	4	15	30	66.8	24.95	368	2	0	0	3
Trema orientalis	Randagong	9	2	4	RAND	RAND	OTHR	14	1	14	27	66.8	41.73	-	1	4	2433	2
Trigonopleura malayana	Gambir hutan	6	2	3	TRMA	GRH	NDLH	14	1	15	27	38.2	19.14	600	1	0	125	-
Tristania clementis	Pelawan-pelawan	6	2	3	PLWN	PP	NDMH	19	1	15	m	38.2	19.14	-	1	191	2867	-
Unknown	Unknown	9	2	4	UNKN	OTH	OTHR	14	1	15		-	-	-	89	245	999	-
Upuna borneensis	Upun	13	3	5	UPUN	UP	DLH	2	1	3	46	-	-	995	1	0	0	1
Vatica albiramis	Resak putih	4	3	2	REPU	RBT	DHH	7	2	3	8	25.5	22.66	893	1	25	50	-
Vatica bancana	Resak banka	7	3	3	REBA	REBA	DHH	7	2	3	24	-	-	768	1	0	0	2
Vatica dulitensis	Resak bukit	10	3	4	REBU	RBK	DHH	7	2	3	27	38.2	30.09	824	1	0	82	2
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Botanical name	Local name	PFT	SS	HG	CFRC	CHQ	TGRP	IGRP	F3	GGRP	Height	Dia	H=f(d)	Den	SPHQ	NDer	NFMU	F
...																		
Vatica maritima	Resak laut	7	3	3	RELT	RBU	DHH	7	2	3	19	-	-	-	1	0	0	1
Vatica oblongifolia	Resak daun panjang	10	3	4	REDP	RBP	DHH	7	2	3	31	-	-	858	1	4	129	2
Vatica odorata	Resak biabas	13	3	5	REBI	RBS	DHH	7	2	3	-	50.9	36.22	-	1	0	25	1
Vatica sarawakensis	Resak sarawak	7	3	3	RESK	RBW	DHH	7	2	3	15.3	-	-	-	1	0	0	1
Vatica sp.	Resak degong	10	3	4	RESA	RBD	DHH	7	2	3	s-l	-	-	-	1	0	0	-
Vatica/cotylelobium sp.	Resak	10	3	4	RESA	RB	DHH	7	2	3	-	-	-	-	1	2060	8934	-
Viburnum amplificatum	Ranuk	4	3	2	VIAM	OTH	OTHR	14	1	15	s	-	-	-	89	245	999	-
Vitex pubescens	Kulimpapa	2	1	2	KULI	KULI	NDHH	14	1	15	9.5	-	-	800	1	1448	2177	3
Weinmannia blumei	Sumu-silan	4	3	2	WEBL	OTH	OTHR	14	1	15	12.2	19.1	13.19	-	89	245	999	-
Wendlandia dasythyrsa	Malitap bukit	4	3	2	WEDA	OTH	OTHR	14	1	15	s	-	-	-	89	245	999	-
Wetria macrophylla	Rambai hutan	4	3	2	WEMA	OTH	OTHR	14	1	15	s	-	-	-	89	245	999	-
Wikstroemia tenuiramis	Tindot	4	3	2	TIND	OTH	OTHR	14	1	15	s	-	-	-	89	245	999	-
Xanthophyllum sp.	Minyak beruk	6	2	3	XANT	MNY	NDMH	20	1	15	s-l	-	-	-	1	1424	6838	-
Xanthophyllum sp.	Minyak beruk	6	2	3	XAEL	XAEL	OTHR	14	1	15	s-l	-	-	-	1	0	0	-
Xerospermum sp.	Gurulau	6	2	3	OTHR	GU	NDMH	14	1	15	s-m	-	-	-	1	0	0	-
Xylosma sumatrana	Linau	6	2	3	XYSU	OTH	OTHR	14	1	15	18	-	-	-	89	245	999	-
Zizyphus angustifolius	Monsit	3	2	2	MSIT	MST	NDLH	14	1	15	s	-	-	-	1	0	100	-
N.N.	Buah-buah	6	2	3	OTHR	BHN	OTHR	14	1	15	-	-	-	-	1	125	125	-
N.N.	N.N.	9	2	4	CEMP	CEMP	OTHR	14	1	15	-	-	-	-	1	0	0	-
N.N.	N.N.	10	3	4	DHHX	DHHX	DHH	10	1	15	-	-	-	-	1	0	0	-
N.N.	N.N.	9	2	4	DLHX	DLHX	DLH	3	1	15	-	-	-	-	1	0	0	-
N.N.	N.N.	9	2	4	DMHX	DMHX	DMH	5	1	15	-	-	-	-	1	0	0	-
N.N.	N.N.	9	2	4	DURM	DURM	OTHR	14	1	15	-	-	-	-	1	0	0	-
N.N.	N.N.	9	2	4	EURO	EURO	OTHR	14	1	15	-	-	-	-	1	0	0	-
N.N.	N.N.	9	2	4	KARA	KARA	OTHR	14	1	15	-	-	-	-	1	0	0	-
N.N.	N.N.	9	2	4	KTUN	KTUN	OTHR	14	1	15	-	-	-	-	1	0	0	-
N.N.	N.N.	9	2	4	KURI	KURI	OTHR	14	1	15	-	-	-	-	1	0	0	-
N.N.	N.N.	8	1	4	MACX	MACX	MACA	14	1	15	-	-	-	-	1	0	0	-
N.N.	N.N.	9	2	4	MEDP	MEDP	OTHR	14	1	15	-	-	-	-	1	0	0	-
N.N.	N.N.	9	2	4	NDX	NDX	NDLH	14	1	15	-	-	-	-	1	0	0	-
N.N.	Adarah	9	2	4	ADAR	OTH	OTHR	14	1	15	-	-	-	-	89	245	999	-
N.N.	N.N.	9	2	4	ANJA	OTH	OTHR	14	1	15	-	-	-	-	89	245	999	-
N.N.	N.N.	9	2	4	BNKL	OTH	OTHR	14	1	15	-	-	-	-	89	245	999	-
N.N.	N.N.	9	2	4	BRUN	OTH	OTHR	14	1	15	-	-	-	-	89	245	999	-
N.N.	N.N.	9	2	4	DARU	OTH	OTHR	14	1	15	-	-	-	-	89	245	999	-
N.N.	Dryepetes	9	2	4	DRYP	OTH	OTHR	14	1	15	-	-	-	-	89	245	999	-
N.N.	N.N.	9	2	4	KUWG	OTH	OTHR	14	1	15	-	-	-	-	89	245	999	-
N.N.	N.N.	9	2	4	LPDA	OTH	OTHR	14	1	15	-	-	-	-	89	245	999	-
N.N.	N.N.	9	2	4	OTHX	OTHX	OTHR	14	1	15	-	-	-	-	1	0	0	-
N.N.	N.N.	8	1	4	PIOX	PIOX	PION	14	1	15	-	-	-	-	1	0	0	-

Table B.3: Legend of tree species lists of Venezuela (Table B.4).

Column	Description
Family	Family name
Species	Species name
PFT	Plant functional type after Table 6.1
SS	Successional status after Table 6.1
HG	Height group after Table 6.1
Code	Species code for identification
Abund.	Qualitative abundance in compartment in which species mature (VR: very rare; R: rare; C: common; VC: very common)
Phen.	Different phenologies (EV: evergreen; SD: semi-decidous; DE: deciduous)
Dispersal a.	Different dipersal agents (ZO: zoochor; ZB: zoochor or barochor; AN: anemochor; AB: anemochor or barochor)
N-Trees	Number of trees (diameter$\geq$10cm) in 4.6 ha in Caparo
N-Sapl.	Number of saplings (height$\geq$130 cm; diameter$<$10cm) in 1.15 ha in Caparo
N-Seedl.	Number of seedlings (30cm$\leq <$height$<$130 cm) in 0.368 ha in Caparo
Density	wood density [$\mathrm{kg_{ODM}\ m^{-3}}$]

Table B.4: Tree species list of Venezuela (taken from Kammesheidt 1994, 2000, used with kind permission).

Family	Species	PFT	SS	HG	Code	Abund.	Phenol.	Dispersal a.	N-Trees	N-Sapl.	N-Seedl.	Density
Acanthaceae	Trichantera gigantea	5	3	2	Yatag	C	SD	ZB	20	76	6	-
Anacardiaceae	Astronium graveolens	9	2	4	Gatea	VR	SD	AN	1	22	61	822
Anacardiaceae	Spondias mombin	9	2	4	Joboo	C	DE	ZO	38	9	11	-
Annonaceae	Annona sp.	8	3	3	Guana	R	EV	ZO	3	5	3	-
Apocynaceae	Tabernaemontana psychotrifolia	8	3	3	Cojbe	R	SD	ZB	5	12	9	-
Areaceae	Bactris mayor	11	4	5	Palcu	VC	EV	ZO	-	356	44	-
Areaceae	Roystonia sp.	12	4	6	Mapor	R	EV	ZO	3	-	-	-
Arecaceae	Attalea maraicabensis	12	4	6	Palag	VC	EV	ZO	576	403	496	-
Arecaceae	Syagrus sancona	12	4	6	Palsa	C	EV	ZO	68	13	2	-
Asteraceae	N.N.	1	2	1	Tabaq	VR	-	AN	-	1	-	-
Bignoniaceae	Jacaranda rhombifolia	7	2	3	Sanro	VR	EV	AN	2	9	24	-
Bignoniaceae	Tabebuia rosea	9	2	4	Apama	VR	-	AN	-	4	-	-
Bixaceae	Bixa orellana	4	2	2	Onoto	C	SD	ZB	33	40	20	-
Bombacaceae	Bombacopsis quinata	9	2	4	Saqui	C	DE	AN	16	5	2	-
Bombacaceae	Ceiba pentandra	9	2	4	Ceiba	VR	SD	AN	1	-	-	-
Bombacaceae	Ochroma lagopus	6	1	3	Balso	VC	SD	AN	111	15	-	222
Boraginaceae	Cordia apurensis	10	3	4	Parne	C	SD	AN	29	26	43	-
Burseraceae	Protium crenatum	10	3	4	Triac	C	EV	ZO	20	12	6	-
Caesalpinaceae	Bauhinia sp.	1	2	1	Patav	VR	EV	ZB	-	-	1	-
Caesalpinaceae	Caesalpinia granadillo	8	3	3	Grana	VR	DE	ZB	-	-	6	-
Caesalpinaceae	Cassia grandis	9	2	4	Canfi	VR	SD	ZO	-	1	1	-
Caesalpinaceae	Swartzia leptopetala	10	3	4	Orura	VR	EV	ZB	2	3	-	-
Capparidaceae	Capparis badocea	2	3	1	Zalre	VC	SD	ZB	-	161	190	-
Capparidaceae	Crataeva tapia	5	3	2	Zorro	VR	SD	ZB	2	7	5	-
Caricaceae	Carica sp.	1	2	1	Lecho	VR	DE	ZO	-	2	-	-
Chrysobalanaceae	Hirtella americana	8	3	3	Guaja	R	EV	ZB	11	16	27	-
Chrysobalanaceae	Licania sp.	7	2	3	Toson	R	EV	ZO	6	3	2	-
Clusiaceae	Rheedia madrono	8	3	3	Madro	VR	SD	ZO	2	19	18	-
Cochlospermaceae	Cochlospermum vitifolium	3	1	2	Botot	R	DE	AN	12	27	-	254
Combretaceae	Terminalia guianensis	10	3	4	Guaya	C	SD	AN	38	17	67	-
Elaeocarpaceae	Muntingia calabura	1	2	1	Nigui	VR	SD	ZO	-	-	1	-
...												

Family	Species	PFT	SS	HG	Code	Abund.	Phenol.	Dispersal a.	N-Trees	N-Sapl.	N-Seedl.	Density
...												
Eleaocarpaceae	Sloenea terniflora	8	3	3	Picap	C	SD	ZO	27	2	-	-
Euphorbiaceae	Acalypha diversifolia	1	2	1	Palne	VC	EV	AB	-	910	1757	-
Euphorbiaceae	Adelia recinella	4	2	2	Clane	VR	SD	ZB	2	7	4	-
Euphorbiaceae	Phyllantus suripaensis	5	3	2	Cirlo	VR	SD	ZO	1	-	-	-
Euphorbiaceae	Sapium stylare	9	2	4	Leche	C	DE	ZO	38	43	2	-
Flacourtiaceae	Banara sp.	1	2	1	Pelud	R	SD	ZO	-	3	6	-
Flacourtiaceae	Casearia nitida	4	2	2	Frupa	R	SD	ZO	7	49	18	713
Flacourtiaceae	Laetia americana	5	3	2	Ranch	VR	SD	-	1	-	-	-
Flacourtiaceae	Xylosma sp.	8	3	3	Barti	VR	SD	-	1	-	-	-
Flacourticaceae	Casearia sp.	4	2	2	Clabl	R	SD	AB	11	71	69	-
Hypericaceae	Vismia macrophylla	4	2	2	Guapa	VR	SD	ZO	2	31	21	-
Lauraceae	Ocotea glomerata	8	3	3	Laune	VR	SD	ZO	-	2	-	-
Lauraceae	Pleurothryrium aff. reflexum	10	3	4	Lauam	C	SD	ZO	18	24	70	614
Lecythidaceae	Coroupita guianensis	8	3	3	Cocmo	R	SD	ZO	6	5	-	-
Lecythidaceae	Gustavea angustifolia	5	3	2	Radef	R	EV	ZO	7	20	34	-
Malvaceae	Malachra sp.	1	2	1	Cardi	R	DE	ZO	-	15	5	-
Melastomaceae	Micania sp.	1	2	1	Benao	R	EV	ZO	-	2	11	-
Melastomaceae	Micania sp.	1	2	1	Melas	R	EV	ZO	-	3	-	-
Melastomaceae	Mouriri barinensis	8	3	3	Perhu	R	SD	ZO	9	1	-	-
Meliaceae	Cedrela odorata	9	2	4	Cedro	VR	DE	AN	1	1	-	-
Meliaceae	Guarea trichiloides	8	3	3	Tromp	R	EV	ZB	7	5	13	-
Meliaceae	Swietenia macrophylla	9	2	4	Caoba	VR	EV	AN	2	1	-	-
Meliaceae	Trichilia maynasiana	5	3	2	Guram	R	EV	-	6	59	78	-
Meliaceae	Trichilia pallida	5	3	2	Cafec	VR	EV	ZB	-	7	1	-
Meliaceae	Trichilia palmerorum	8	3	3	Cedri	C	EV	ZO	28	30	7	-
Meliaceae	Trichilia unifoliata	8	3	3	Rejit	C	DE	ZB	24	93	54	-
Mimosaceae	Albizia caribaea	9	2	4	Carab	VR	SD	AB	1	3	4	-
Mimosaceae	Cassia alata	4	2	2	Mucut	VR	SD	ZB	2	-	-	-
Mimosaceae	Inga marginata	4	2	2	Guamo	VR	SD	ZO	1	4	3	-
Mimosaceae	Inga sp.	5	3	2	Gudec	VR	SD	ZO	-	1	1	-
Mimosaceae	Inga sp.	5	3	2	Gublo	VR	SD	ZO	1	22	42	-
Mimosaceae	Inga sp.	5	3	2	Gucar	VR	SD	ZO	1	-	-	-
Mimosaceae	Inga sp.	8	3	3	Guarm	R	SD	ZO	6	23	118	-
...												

Family	Species	PFT	SS	HG	Code	Abund.	Phenol.	Dispersal a.	N-Trees	N-Sapl.	N-Seedl.	Density
...												
Mimosaceae	Inga sp.	8	3	3	Guano	VR	SD	ZO	2	2	22	-
Mimosaceae	Inga sp.	8	3	3	Guane	C	SD	ZO	31	31	57	-
Mimosaceae	Inga sp.	8	3	3	Guamc	VR	SD	ZO	-	-	2	-
Mimosaceae	Piptadenia peregrina	10	3	4	Yopio	VR	DE	ZB	1	-	-	-
Mimosaceae	Pithecellobium guachapele	9	2	4	Masag	VR	SD	ZB	-	1	-	-
Mimosaceae	Pithecellobium sp.	8	3	3	Cazab	VR	EV	ZB	2	5	8	-
Moraceae	Brosimum alicastrum	10	3	4	Chaam	C	EV	ZB	48	84	93	-
Moraceae	Cecropia peltata	6	1	3	Yagru	VC	SD	ZO	127	101	-	-
Moraceae	Chlorophora tinctora	8	3	3	Moraa	VR	SD	ZO	1	4	-	-
Moraceae	Clarisia biflora	10	3	4	Chane	R	EV	ZB	5	8	25	-
Moraceae	Ficus insipida	10	3	4	Higue	R	EV	ZB	4	1	4	-
Moraceae	Trophis racemosa	10	3	4	Chabl	VR	EV	ZB	1	1	-	-
Myrsinaceae	Rapanea sp.	5	3	2	Cucha	VR	IM	-	-	1	-	-
Myrsinaceae	Stylogene venezolana	5	3	2	Morti	R	SD	ZO	3	27	15	-
Myrtaceae	N.N.	7	2	3	Paujo	R	EV	ZO	4	2	-	-
Myrtaceae	Myrcia sp.	5	3	2	Guato	VR	SD	ZB	1	42	52	-
Nyctaginaceae	Torrubia olfersiana	5	3	2	Casav	VR	SD	ZB	2	7	30	-
Papilionaceae	Fissicalyx fendleri	9	2	4	Tasac	C	SD	ZB	27	38	32	-
Papilionaceae	Lonchocarpus pictus	9	2	4	Cuesa	C	DE	ZB	23	12	33	-
Papilionaceae	Lonchocarpus sericeus	10	3	4	Zapca	R	DE	ZB	14	8	30	-
Papilionaceae	Lonchocarpus sp.	8	3	3	Laubl	R	SD	ZB	9	2	-	-
Papilionaceae	Lonchocarpus sp.	8	3	3	Jebec	R	SD	ZB	-	2	12	-
Papilionaceae	Ormosia macrocalyx	7	2	3	Pioni	VR	EV	ZB	1	-	-	-
Papilionaceae	Platymyscium pinnatum	9	2	4	Roble	R	SD	AN	4	3	4	-
Papilionaceae	Poeppigia procera	1	2	1	Frijo	VR	-	ZB	-	1	1	-
Papilionaceae	Pterocarpus acapulensis	7	2	3	Sadra	VR	SD	AN	2	-	-	-
Piperaceae	Piper aduncum	2	3	1	Corne	VC	EV	ZB	-	13	1028	-
Piperaceae	Piper sp.	1	2	1	Cobla	R	EV	ZB	-	-	5	-
Piperaceae	Piper sp.	1	2	1	Pixxx	R	EV	ZB	-	-	3	-
Piperaceae	Piper sp.	1	2	1	Pipxx	VR	EV	ZB	-	-	1	-
Piperaceae	Piper sp.	1	2	1	Pipex	VR	EV	ZB	-	-	2	-
Piperaceae	Piper sp.	4	2	2	Pxxxx	VR	EV	ZB	2	-	-	-
Polygonaceae	Coccoloba fallax	5	3	2	Uvero	R	SD	ZO	5	16	9	-
...												

Family	Species	PFT	SS	HG	Code	Abund.	Phenol.	Dispersal a.	N-Trees	N-Sapl.	N-Seedl.	Density
...												
Polygonaceae	Coccoloba padiformis	8	3	3	Cacai	C	EV	AB	37	55	57	751
Polygonaceae	Symmeria paniculata	9	2	4	Palua	R	SD	AN	7	1	1	-
Polygonaceae	Triplaris caracasana	7	2	3	Palma	C	EV	AN	38	92	203	576
Rubiaceae	N.N.	1	2	1	Manza	VR	SD	-	-	1	1	-
Rubiaceae	Chomelia poliantha	1	2	1	Garba	VR	SD	ZO	-	1	-	-
Rubiaceae	Genipa americana	8	3	3	Carau	VR	SD	ZO	-	1	-	-
Rubiaceae	Hamelia patens	2	3	1	Coral	C	SD	ZO	-	21	4	-
Rubiaceae	Psychotria carthagensis	2	3	1	Hierr	VC	EV	ZO	-	47	1025	-
Rutaceae	Zanthoxylum sp.	4	2	2	Mapon	VR	SD	ZB	1	1	1	-
Rutaceae	Zanthoxylum sp.	7	2	3	Tachu	C	SD	AN	24	39	29	725
Sapindaceae	Cupanea americana	5	3	2	Rpava	VR	SD	ZB	-	11	9	-
Sapotaceae	Chrysophyllum auratum	8	3	3	Caimi	C	SD	ZO	19	24	1	-
Sapotaceae	Pouteria anibaefolia	10	3	4	Churo	C	EV	ZO	59	11	53	-
Sapotaceae	Serjania sp.	8	3	3	Chubl	R	EV	ZO	3	-	-	-
Sterculiaceae	Guazuma tomentosa	7	2	3	Guabl	C	SD	AN	32	39	25	497
Sterculiaceae	Herranea sp.	2	3	1	Cacao	C	SD	ZO	-	20	3	-
Theophrastaceae	Clavija longifolia	2	3	1	Sancr	C	EV	ZO	-	77	37	-
Tiliaceae	Goethalsia meiantha	7	2	3	Guaco	VR	SD	AN	-	3	-	-
Tiliaceae	Heliocarpus popayanensis	3	1	2	Majag	C	DE	AN	42	10	-	-
Tiliaceae	Luecea cymulosa	7	2	3	Guaci	C	SD	ZO	28	56	26	831
Ulmaceae	Trema micrantha	3	1	2	Bocho	VR	EV	ZO	2	-	-	-
Urticaceae	Urera caracasana	4	2	2	Ortig	R	DE	AN	5	46	2	-
Urticaceae	Urera sp.	1	2	1	Pring	R	DE	ZO	-	12	-	-
Verbenaceae	Vitex orinocensis	7	2	3	Guaro	R	SD	ZB	7	3	13	-
Violaceae	Hybanthus prunifolius	2	3	1	Campa	VC	DE	ZB	-	399	373	-
Vochysiaceae	Vochysia lehmanii	9	2	4	Murci	VR	DE	ZB	1	-	14	-
N.N.	Cordia sp.	8	3	3	Candi	VR	SD	ZO	-	3	1	-
N.N.	N.N.	1	2	1	Limon	R	SD	-	-	3	1	-
N.N.	N.N.	4	2	2	Fruto	VR	-	-	1	4	-	-
N.N.	N.N.	5	3	2	Caven	R	SD	ZB	4	25	51	-

Table B.5: Legend of tree species lists of French Guiana (Table B.6).

Column	Description
Family	Family name
Genus	Genus name
Species	Species name
PFT	Plant functional type after Table 8.2
SS	Successional status after Table 8.2
HG	Height group after Table 8.2
Code	Species code for identification
NNOU	Number of trees with diameter >10cm in Nouragues
NPSE	Number of trees with diameter >10cm in Piste de Saint-Elie
NPAR	Number of trees with diameter >10cm in Paracou
NTOT	Total number of trees with diameter >10cm in Nouragues, Piste de Saint-Elie and Paracou
VRI	Van Roosmalen index of adundance (0: very rare; 1: rare; 2: fairly rare; 3: not common; 4: fairly common; 5: common; 6: very common). The average number of individuals per species should roughly follow $N\ exp(-a \cdot VRI)$
Height	Maximum height at maturity [m]
Disp.	Dispersion strategies (AN: anemochorous; HY: hydrochorous; Z: zoochorous; EZ: endozoochorous (seed eaten, then defecated); SZ: synzoochorous (seed transported)) by different processes (B: birds; M: monkeys; bat: bats; R: rodents; T:tortoises). Generally, the dispersing capacity of each of these modes can be roughly estimated in terms of distance HY<SZR<SZM∼EZT<SZbat∼EZM<EZB<AN
Density	wood density [t_{ODM} m^{-3}]
Architecture	Crown architecture type after Halle, Oldeman and Tomlinson

Table B.6: Tree species list of French Guiana (taken from Chave 1999a; Chave & Riera, unpublished manuscript, used with kind permission).

Family	Genus	Species	PFT	SG	HG	Code	NNOU	NPSE	NPAR	NTOT	VRI	Height	Disp.	Density	Architecture
Anacardiaceae	Anacardium	giganteum	15	2	4	ANAG	0	0	0	0	2	30	SZM	0.55	Scarrone
Anacardiaceae	Anacardium	spruceanum	16	3	4	ANAS	0	2	25	27	1	35	SZ	0.55	Scarrone
Anacardiaceae	Astronium	ulei	19	3	5	ASNU	1	0	0	1	4	40	EZB	-	-
Anacardiaceae	Loxopterygium	sagotii	14	1	4	LOXO	0	0	0	0	5	30	AN	-	-
Anacardiaceae	Spondias	mombin	16	3	4	SPON	0	0	0	0	5	35	EZMB	-	-
Anacardiaceae	Tapirira	bethanniana	2	1	1	TAPB	1	0	0	1	-	-	EZ	0.5	Scarrone
Anacardiaceae	Tapirira	guianensis	17	1	5	TAPG	0	0	15	15	5	45	EZ	0.5	Scarrone
Anacardiaceae	Tapirira	obtusa	11	2	3	TAPO	0	1	1	2	2	20	EZ	0.5	Scarrone
Anacardiaceae	Thyrsodium	guianense	16	3	4	THYG	0	4	14	18	3	30	EZ	0.8	-
Anacardiaceae	Thyrsodium	spruceanum	12	3	3	THYS	1	1	0	2	1	25	EZ	0.8	-
Annonaceae	Anaxagorea	acuminata	8	3	2	ANCA	0	0	0	0	4	7	AUT	0.67	Troll
Annonaceae	Anaxagorea	dolichocarpa	8	3	2	ANCD	0	1	42	43	5	15	AU	0.67	Troll
Annonaceae	Anaxagorea	phaeocarpa	8	3	2	ANCP	0	0	0	0	1	10	AUT	0.67	Troll
Annonaceae	Anaxagorea	prinoides	4	3	1	ANCQ	0	0	0	0	1	5	AUT	0.67	Troll
Annonaceae	Annona	ambotay	12	3	3	ANNA	0	1	0	1	1	20	SZMR	-	-
Annonaceae	Annona	densicoma	8	3	2	ANND	0	1	0	1	3	12	SZMR	-	-
Annonaceae	Annona	echinata	8	3	2	ANNE	0	0	0	0	1	8	SZMR	-	-
Annonaceae	Annona	foetida	8	3	2	ANNF	0	0	0	0	1	15	SZMR	-	-
Annonaceae	Annona	glabra	8	3	2	ANNG	0	0	0	0	5	10	SZMR	-	-
Annonaceae	Annona	hypoglauca	8	3	2	ANNH	0	0	0	0	4	13	SZMR	-	-
Annonaceae	Annona	montana	8	3	2	ANNM	0	0	0	0	4	8	SZMR	-	-
Annonaceae	Annona	paludosa	5	0	2	ANNP	0	0	0	0	1	7	SZMR	-	-
Annonaceae	Annona	sericea	6	1	2	ANNS	0	0	0	0	5	10	SZMR	-	-
Annonaceae	Crematosperma	brevipes	4	3	1	CREB	0	0	0	0	1	5	EZ	-	-
Annonaceae	Cymbopetalum	brasiliense	6	1	2	CYMB	0	0	0	0	4	15	EZ	-	-
Annonaceae	Duguetia	cadaverica	4	3	1	DUGC	2	0	0	2	4	5	SZMR	-	-
Annonaceae	Duguetia	calycina	7	2	2	DUGD	0	20	0	20	5	12	SZMR	-	-
Annonaceae	Duguetia	eximia	8	3	2	DUGE	0	0	0	0	2	8	SZMR	-	-
Annonaceae	Duguetia	inconspicua	4	3	1	DUGI	0	0	0	0	3	5	SZMR	-	-
Annonaceae	Duguetia	pycnastera	8	3	2	DUGP	0	0	0	0	3	15	SZMR	-	-
Annonaceae	Duguetia	surinamensis	12	3	3	DUGS	17	27	0	44	4	20	SZMR	-	-
Annonaceae	Fusaea	longifolia	12	3	3	FUSA	0	0	0	0	4	20	EZM	-	-
Annonaceae	Guatteria	guianensis	8	3	2	GUAS	0	0	0	0	1	15	EZ	-	-
Annonaceae	Guatteria	ouregou	7	2	2	GUAT	0	0	0	0	3	7	EZ	-	-
Annonaceae	Guatteria	punctuata	16	3	4	GUAU	0	0	0	0	5	28	EZM	-	-
Annonaceae	Guatteria	wachenheim	8	3	2	GUAW	0	0	0	0	1	15	EZ	-	-
Annonaceae	Oxandra	asbeckii	11	2	3	OXAN	0	53	334	387	5	20	EZ	0.9	Troll
Annonaceae	Rollinia	exsucca	6	1	2	ROLL	1	1	0	2	5	15	EZBM	-	-
Annonaceae	Rollinia	mucosa	7	2	2	ROLM	0	0	0	0	1	10	EZBM	-	-
Annonaceae	Unonopsis	guatterioides	8	3	2	UNOG	0	0	0	0	5	15	EZBM	-	-
Annonaceae	Unonopsis	perrottetii	12	3	3	UNOP	0	0	0	0	1	18	EZBM	0.72	-

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Family	Genus	Species	PFT	SG	HG	Code	NNOU	NPSE	NPAR	NTOT	VRI	Height	Disp.	Density	Architecture
...															
Annonaceae	Unonopsis	rufescens	8	3	2	UNOR	0	16	17	33	5	12	EZBM	0.72	-
Annonaceae	Unonopsis	stipitata	8	3	2	UNOS	2	1	0	3	3	10	EZBM	0.72	-
Annonaceae	Xylopia	aromatica	10	1	3	XYLA	0	2	0	2	5	25	EZBM	-	Roux
Annonaceae	Xylopia	cayennensis	11	2	3	XYLB	0	0	0	0	3	20	EZBM	-	-
Annonaceae	Xylopia	crinita	7	2	2	XYLC	0	3	0	3	-	15	EZBM	-	Roux
Annonaceae	Xylopia	frutescens	10	1	3	XYLF	0	0	0	0	5	20	EZBM	-	-
Annonaceae	Xylopia	nitida	15	2	4	XYLN	17	2	10	29	3	35	EZBM	0.6	Roux
Annonaceae	Xylopia	sericea	14	1	4	XYLS	0	7	0	7	-	30	EZBM	-	Roux
Apocynaceae	Ambelania	acida	8	3	2	AMBE	3	3	6	12	5	6	EZ	0.55	-
Apocynaceae	Aspidosperma	album	16	3	4	ASPA	0	0	33	33	5	35	AN	0.9	Massart
Apocynaceae	Aspidosperma	cruentum	16	3	4	ASPC	2	0	0	2	-	27	AN	0.9	Massart
Apocynaceae	Aspidosperma	excelsum	16	3	4	ASPE	0	0	0	0	3	35	AN	0.9	Massart
Apocynaceae	Aspidosperma	helstonei	16	3	4	ASPH	1	0	0	1	1	30	AN	0.9	Massart
Apocynaceae	Aspidosperma	marcgravianum	16	3	4	ASPM	3	4	0	7	5	30	AN	0.9	Massart
Apocynaceae	Aspidosperma	nitidum	16	3	4	ASPN	0	0	33	33	-	35	AN	0.9	Massart
Apocynaceae	Aspidosperma	oblongum	19	3	5	ASPO	4	0	0	4	5	40	AN	0.9	Massart
Apocynaceae	Aspidosperma	sandwithianum	12	3	3	ASPS	0	0	0	0	4	25	AN	0.9	Massart
Apocynaceae	Couma	guianensis	11	2	3	COMG	5	8	9	22	5	25	EZ	0.55	Rauh
Apocynaceae	Geissospermum	laevis	16	3	4	GEIL	17	0	0	17	5	30	EZ	0.85	Nozeran
Apocynaceae	Geissospermum	sericeum	11	2	3	GEIS	0	0	0	0	3	25	EZ	0.85	Nozeran
Apocynaceae	Himatanthus	articulatus	10	1	3	HIMA	0	1	1	2	6	25	AN	0.65	Koriba
Apocynaceae	Himatanthus	bracteatus	10	1	3	HIMB	0	1	0	1	1	25	AN	0.65	Koriba
Apocynaceae	Lacmellea	aculeata	8	3	2	LACA	1	6	0	7	5	12	EZ	0.6	Massart
Apocynaceae	Lacmellea	floribunda	8	3	2	LACF	3	16	40	59	-	12	EZ	0.6	Massart
Apocynaceae	Macoubea	guianensis	15	2	4	MACA	1	1	7	9	5	35	EZM	0.55	Scarrone
Apocynaceae	Malouetia	tamaquarina	10	1	3	MALO	0	0	0	0	5	20	AN	-	-
Apocynaceae	Parahancornia	fasciculata	18	2	5	PARA	0	0	4	4	5	40	SZ	0.6	-
Apocynaceae	Rauvolfia	paraensis	12	3	3	RAUV	0	2	0	2	-	20	EZ	-	-
Apocynaceae	Stemmadenia	grandiflora	6	1	2	STEM	0	0	0	0	4	10	EZMB	-	-
Apocynaceae	Tabernaemontana	albiflora	4	3	1	TACA	0	0	0	0	3	3	EZMB	-	-
Apocynaceae	Tabernaemontana	attenuata	8	3	2	TACB	0	0	13	13	3	10	EZMB	0.6	Leeuwenberg
Apocynaceae	Tabernaemontana	heterophylla	3	2	1	TACH	0	0	0	0	5	4	EZMB	-	-
Apocynaceae	Tabernaemontana	rupicola	4	3	1	TACR	0	0	0	0	3	3	EZMB	-	-
Apocynaceae	Tabernaemontana	siphilitica	8	3	2	TACS	0	0	0	0	5	6	EZMB	-	-
Apocynaceae	Tabernaemontana	undulata	8	3	2	TACU	0	1	0	1	5	8	EZMB	0.6	Leeuwenberg
Aquifoliaceae	Ilex	guianensis	8	3	2	ILEX	0	10	0	10	-	10	EZ	-	-
Araliaceae	Schefflera	decaphylla	15	2	4	SCHD	0	4	0	4	5	30	EZ	0.43	Leeuwenberg
Araliaceae	Schefflera	morototoni	15	2	4	SCHM	0	0	7	7	5	35	EZ	0.43	Leeuwenberg
Arecaceae	Acrocomia	lasiospatha	6	1	2	ACRL	0	0	0	0	3	12	SZ	-	-
Arecaceae	Astrocaryum	jauari	8	3	2	ASTJ	0	0	0	0	4	15	SZMR	-	-
Arecaceae	Astrocaryum	munbaca	8	3	2	ASTM	0	0	0	0	5	6	SZMR	-	-
Arecaceae	Astrocaryum	paramaca	4	3	1	ASTP	0	0	0	0	5	4	SZMR	-	-
Arecaceae	Astrocaryum	rodriguesii	8	3	2	ASTR	0	0	0	0	1	10	SZMR	-	-
...															

Family	Genus	Species	PFT	SG	HG	Code	NNOU	NPSE	NPAR	NTOT	VRI	Height	Disp.	Density	Architecture
...															
Arecaceae	Astrocaryum	sciophilum	8	3	2	ASTS	39	86	0	125	5	12	SZ	-	-
Arecaceae	Astrocaryum	vulgare	6	1	2	ASTV	0	0	0	0	5	9	SZ	-	-
Arecaceae	Bactris	acanthocarpoides	8	3	2	BACA	0	0	0	0	5	6	EZB	-	-
Arecaceae	Bactris	aubletiana	4	3	1	BACB	0	0	0	0	1	3	EZB	-	-
Arecaceae	Bactris	campestris	2	1	1	BACC	0	0	0	0	5	3	EZB	-	-
Arecaceae	Bactris	constanciae	4	3	1	BACD	0	0	0	0	1	4	EZB	-	-
Arecaceae	Bactris	elegans	3	2	1	BACE	0	0	0	0	5	4	EZB	-	-
Arecaceae	Bactris	gastoniana	4	3	1	BACG	0	0	0	0	5	3	EZB	-	-
Arecaceae	Bactris	humilis	4	3	1	BACH	0	0	0	0	4	4	EZB	-	-
Arecaceae	Bactris	major	8	3	2	BACM	0	0	0	0	5	8	EZB	-	-
Arecaceae	Bactris	maraja	8	3	2	BACN	0	1	0	1	5	12	EZB	-	-
Arecaceae	Bactris	oligocarpa	4	3	1	BACO	0	0	0	0	1	2	EZB	-	-
Arecaceae	Bactris	simplicifrons	3	2	1	BACS	0	0	0	0	5	4	EZB	-	-
Arecaceae	Elaeis	oleifera	2	1	1	ELAE	0	1	0	1	4	5	EZ	-	-
Arecaceae	Euterpe	oleracea	12	3	3	EUTE	10	1	0	11	6	20	EZBM	-	-
Arecaceae	Euterpe	precatoria	16	3	4	EUTP	0	0	0	0	5	27	EZBM	-	-
Arecaceae	Geonoma	baculifera	4	3	1	GEOB	0	0	0	0	4	4	EZ	-	-
Arecaceae	Geonoma	deversa	4	3	1	GEOD	0	0	0	0	1	3	EZ	-	-
Arecaceae	Geonoma	leptospadix	4	3	1	GEOL	0	0	0	0	2	3	EZ	-	-
Arecaceae	Geonoma	maxima	4	3	1	GEOM	0	7	0	7	5	5	EZ	-	-
Arecaceae	Geonoma	poiteauana	4	3	1	GEOP	0	0	0	0	1	3	EZ	-	-
Arecaceae	Geonoma	stricta	4	3	1	GEOS	0	0	0	0	1	2	EZ	-	-
Arecaceae	Geonoma	umbraculiformis	4	3	1	GEOU	0	0	0	0	1	3	EZ	-	-
Arecaceae	Hyospathe	elegans	4	3	1	HYOS	0	0	0	0	3	2	EZ	-	-
Arecaceae	Jessenia	bataua	11	2	3	JESS	14	26	0	40	3	20	EZBM	-	-
Arecaceae	Manicaria	saccifera	7	2	2	MANA	0	15	0	15	3	6	EZ	-	-
Arecaceae	Mauritia	flexuosa	14	1	4	MAUF	0	2	0	2	5	35	SZ	-	-
Arecaceae	Mauritiella	martiana	6	1	2	MAUM	0	0	0	0	0	11	EZ	-	-
Arecaceae	Maximiliana	maripa	10	1	3	MAXI	1	13	0	14	5	18	SZMR	-	-
Arecaceae	Oenocarpus	bacaba	11	2	3	OENO	3	25	0	28	4	20	EZBM	0.8	Corner
Arecaceae	Orbignya	polysticha	4	3	1	ORBI	0	6	0	6	-	-	SZ	-	-
Arecaceae	Orbignya	sagotii	3	2	1	ORBS	0	0	0	0	4	5	SZMR	-	-
Arecaceae	Scheleea	sp.	8	3	2	SCHN	0	4	0	4	5	6	SZ	-	-
Arecaceae	Socratea	exorrhiza	7	2	2	SOCR	5	1	0	6	5	12	EZBM	-	Corner
Arecaceae	Synagrus	inajai	8	3	2	SYNI	0	0	0	0	4	12	EZ	-	-
Arecaceae	Synagrus	stratincola	8	3	2	SYNS	0	0	0	0	1	14	EZ	-	-
Bignoniaceae	Jacaranda	copaia	14	1	4	JACC	16	11	42	69	5	35	AN	0.45	Scarrone
Bignoniaceae	Jacaranda	obtusifolia	10	1	3	JACO	0	0	0	0	5	20	AN	-	-
Bignoniaceae	Tabebuia	capitata	14	1	4	TABC	0	0	0	0	5	35	AN	-	-
Bignoniaceae	Tabebuia	fluviatilis	11	2	3	TABF	0	0	0	0	5	18	HY	-	-
Bignoniaceae	Tabebuia	insignis	17	1	5	TABI	0	2	0	2	5	40	AN	01.01.00	-
Bignoniaceae	Tabebuia	serratifolia	15	2	4	TABS	14	0	4	18	6	30	AN	01.01.00	Koriba
Bixaceae	Cochlospermum	orinocense	8	3	2	COCO	0	0	0	0	3	15	AN	-	-
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Bixaceae	Cochlospermum	vitifolium	8	3	2	COCV	0	0	0	0	1	12	AN	-	-
Bombacaceae	Bombacopsis	nervosa	13	0	4	BOMB	1	0	0	1	3	35	AN	-	-
Bombacaceae	Catostemma	fragrans	15	2	4	CATO	0	13	69	82	4	32	EZM	0.7	-
Bombacaceae	Ceiba	pentandra	17	1	5	CEIB	4	0	0	4	5	50	AN	0.4	Massart
Bombacaceae	Eriotheca	crassa	11	2	3	ERIC	0	0	0	0	4	20	AN	0.58	Rauh
Bombacaceae	Eriotheca	gobosa	12	3	3	ERIO	0	23	67	90	4	25	AN	0.58	Rauh
Bombacaceae	Eriotheca	surinamensis	19	3	5	ERIS	0	0	0	0	3	40	AN	0.58	Rauh
Bombacaceae	Pachira	aquatica	11	2	3	PACA	0	0	0	0	6	25	SZR	-	-
Bombacaceae	Pachira	insignis	14	1	4	PACH	0	0	0	0	3	35	SZR	-	-
Bombacaceae	Quararibea	guianensis	7	2	2	QUAG	1	0	0	1	5	15	SZ	-	-
Bombacaceae	Quararibea	lasiocalyx	8	3	2	QUAL	0	0	0	0	1	8	SZ	-	-
Bombacaceae	Quararibea	turbinata	8	3	2	QUAT	193	0	0	193	4	12	SZ	-	-
Boraginaceae	Cordia	bicolor	8	3	2	CORB	0	0	0	0	3	12	EZBM	-	Prevost
Boraginaceae	Cordia	fulva	12	3	3	CORF	0	0	0	0	1	20	EZBM	-	Prevost
Boraginaceae	Cordia	goeldiana	4	3	1	CORG	5	0	0	5	-	-	EZBM	-	Prevost
Boraginaceae	Cordia	hirta	12	3	3	CORH	0	0	0	0	1	20	EZBM	-	Prevost
Boraginaceae	Cordia	laevifrons	7	2	2	CORL	0	0	12	12	3	8	EZBM	0.4	Prevost
Boraginaceae	Cordia	lomatoloba	12	3	3	CORM	0	0	0	0	4	25	EZBM	-	Prevost
Boraginaceae	Cordia	nervosa	6	1	2	CORN	0	0	0	0	1	6	EZBM	-	Prevost
Boraginaceae	Cordia	nodosa	8	3	2	CORO	0	0	23	23	6	10	EZBM	0.45	Prevost
Boraginaceae	Cordia	panicularis	12	3	3	CORP	0	0	0	0	3	20	EZBM	-	Prevost
Boraginaceae	Cordia	sagotii	7	2	2	CORS	0	0	0	0	5	10	EZBM	-	Prevost
Boraginaceae	Cordia	tetrandra	12	3	3	CORT	0	0	0	0	5	18	EZBM	-	Prevost
Burseraceae	Crepidospermum	rhoifolium	12	3	3	CREP	1	0	0	1	5	25	EZ	-	-
Burseraceae	Dacryodes	nitens	10	1	3	DACR	0	16	0	16	1	20	EZ	0.6	Rauh
Burseraceae	Protium	altsonii	11	2	3	PRNZ	0	0	0	0	1	20	EZBMR	-	-
Burseraceae	Protium	apiculatum	8	3	2	PROA	10	0	0	10	2	15	EZBMR	0.7	Rauh
Burseraceae	Protium	aracouchini	8	3	2	PROB	6	32	0	38	5	10	EZBMR	0.7	Rauh
Burseraceae	Protium	decandrum	16	3	4	PROC	0	0	0	0	4	27	EZBMR	0.7	Rauh
Burseraceae	Protium	demerarense	16	3	4	PROD	23	0	0	23	-	35	EZBMR	0.7	Rauh
Burseraceae	Protium	giganteum	16	3	4	PROF	7	0	0	7	-	30	EZBMR	0.7	Rauh
Burseraceae	Protium	guianense	7	2	2	PROG	0	0	0	0	3	10	EZBMR	0.7	Rauh
Burseraceae	Protium	heptaphyllum	11	2	3	PROH	5	0	26	31	5	20	EZBMR	0.6	Rauh
Burseraceae	Protium	opacum	16	3	4	PROO	0	0	0	0	-	30	EZBMR	0.7	Rauh
Burseraceae	Protium	plagiocarpum	8	3	2	PROQ	0	0	0	0	2	8	EZBMR	0.7	Rauh
Burseraceae	Protium	polybotryum	11	2	3	PROR	0	0	0	0	5	24	EZBMR	-	-
Burseraceae	Protium	robustum	16	3	4	PROS	1	0	0	1	-	30	EZBMR	0.7	Rauh
Burseraceae	Protium	sagotianum	16	3	4	PROT	3	4	0	7	5	30	EZBMR	0.7	Rauh
Burseraceae	Protium	subserratum	16	3	4	PROU	0	9	20	29	-	30	EZBMR	0.7	Rauh
Burseraceae	Protium	tenuifolium	16	3	4	PROV	0	0	0	0	5	35	EZBMR	0.7	Rauh
Burseraceae	Protium	trifoliolatum	8	3	2	PROW	1	8	0	9	-	15	EZBMR	0.7	Rauh
Burseraceae	Tetragastris	altissima	16	3	4	TETA	17	0	0	17	4	30	EZMT	0.85	Rauh
Burseraceae	Tetragastris	hostmannii	11	2	3	TETH	0	0	0	0	5	25	EZMT	-	-
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Burseraceae	Tetragastris	panamensis	12	3	3	TETP	2	2	2	6	6	25	EZMT	0.85	Rauh
Burseraceae	Trattinnickia	burserifolia	6	1	2	TRAB	0	0	0	0	6	10	EZ	-	-
Burseraceae	Trattinnickia	demerarae	14	1	4	TRAD	0	0	0	0	5	30	EZ	-	-
Burseraceae	Trattinnickia	rhoifolia	15	2	4	TRAR	0	0	0	0	5	35	BA	-	-
Caesalpiniaceae	Bauhinia	cinnamonea	4	3	1	BAUH	0	0	0	0	2	5	EZ	-	-
Caesalpiniaceae	Bocoa	prouacensis	16	3	4	BOCO	29	60	257	346	5	35	EZM+Szbat	01.01.22	-
Caesalpiniaceae	Candolleodendron	brachystachyum	8	3	2	CANB	0	0	0	0	0	15	EZ	-	-
Caesalpiniaceae	Cassia	cowanii	16	3	4	CASQ	0	0	0	0	1	30	HY	-	-
Caesalpiniaceae	Cassia	fastuosa	12	3	3	CASR	0	0	0	0	1	25	EZ	-	-
Caesalpiniaceae	Cassia	grandis	7	2	2	CASS	0	0	0	0	3	15	EZ	-	-
Caesalpiniaceae	Cassia	spruceana	12	3	3	CAST	0	0	0	0	1	25	EZ	-	-
Caesalpiniaceae	Chamaecrista	apoucouita	8	3	2	CHAM	0	0	0	0	1	15	EZ	-	-
Caesalpiniaceae	Copaifera	guianensis	18	2	5	COPA	0	1	0	1	6	40	EZM	0.75	-
Caesalpiniaceae	Crudia	aromatica	12	3	3	CRUA	0	0	0	0	3	25	AUT	-	-
Caesalpiniaceae	Crudia	glaberrima	11	2	3	CRUG	0	101	0	101	5	25	AUT	-	-
Caesalpiniaceae	Crudia	oblonga	8	3	2	CRUO	0	0	0	0	1	12	HY	-	-
Caesalpiniaceae	Crudia	spicata	3	2	1	CRUS	0	2	0	2	3	5	AUT	-	-
Caesalpiniaceae	Cynometra	hostmanniana	16	3	4	CYNH	0	0	0	0	5	27	SZR	-	-
Caesalpiniaceae	Cynometra	marginata	12	3	3	CYNM	0	0	0	0	4	20	SZR	-	-
Caesalpiniaceae	Cynometra	parviflora	8	3	2	CYNP	0	0	0	0	4	10	SZR	-	-
Caesalpiniaceae	Dialium	guianense	15	2	4	DIAL	0	1	0	1	5	35	EZM	01.05.00	-
Caesalpiniaceae	Dicorynia	guianensis	18	2	5	DICO	81	54	117	252	-	40	AN	0.78	Troll
Caesalpiniaceae	Dimorphandra	polyandra	15	2	4	DIMP	0	0	0	0	4	30	EZM	-	-
Caesalpiniaceae	Dimorphandra	pullei	19	3	5	DIMQ	0	0	0	0	3	50	EZM	-	-
Caesalpiniaceae	Elizabetha	princeps	16	3	4	ELIZ	0	0	0	0	4	29	EZM	-	-
Caesalpiniaceae	Eperua	falcata	15	2	4	EPEF	676	289	489	1454	5	32	SZ	0.85	Troll
Caesalpiniaceae	Eperua	grandiflora	15	2	4	EPEG	1	89	226	316	3	35	SZ	0.92	Troll
Caesalpiniaceae	Eperua	jenmanii	16	3	4	EPEJ	0	0	0	0	1	30	SZ	0.92	Troll
Caesalpiniaceae	Eperua	rubiginosa	15	2	4	EPER	75	0	0	75	4	30	SZ	0.85	Troll
Caesalpiniaceae	Heterostemon	mimosoides	8	3	2	HETE	0	0	0	0	1	15	EZ	-	-
Caesalpiniaceae	Hymenaea	courbaril	15	2	4	HYMC	3	0	0	3	6	35	SZRM	0.83	Troll
Caesalpiniaceae	Lecointea	amazonica	12	3	3	LECA	0	0	0	0	0	25	EZ	-	-
Caesalpiniaceae	Macrolobium	acaciifolium	11	2	3	MACB	0	0	0	0	5	17	HY	-	-
Caesalpiniaceae	Macrolobium	angustifolium	15	2	4	MACC	0	0	0	0	6	30	HY	-	-
Caesalpiniaceae	Macrolobium	bifolium	11	2	3	MACD	136	0	0	136	5	25	HY	0.75	-
Caesalpiniaceae	Macrolobium	multijugum	11	2	3	MACH	0	0	0	0	4	20	HY	-	-
Caesalpiniaceae	Martiodendron	parviflorum	16	3	4	MART	0	0	0	0	4	35	AN	-	-
Caesalpiniaceae	Paloue	guianensis	8	3	2	PALO	0	0	0	0	3	8	HY	-	-
Caesalpiniaceae	Paloue	riparia	8	3	2	PALR	0	0	0	0	2	10	HY	-	-
Caesalpiniaceae	Peltogyne	paniculata	18	2	5	PELP	0	1	1	2	6	40	EZM	0.9	Troll
Caesalpiniaceae	Peltogyne	venosa	16	3	4	PELV	0	6	4	10	6	35	EZM	0.84	Troll
Caesalpiniaceae	Recordoxylon	speciosum	15	2	4	RECO	0	0	82	82	3	30	EZ	0.95	-
Caesalpiniaceae	Sclerolobium	albiflorum	15	2	4	SCLA	0	0	0	0	5	30	AN	0.55	-
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Caesalpiniaceae	Sclerolobium	guianense	18	2	5	SCLG	0	0	0	0	4	40	AN	-	-
Caesalpiniaceae	Sclerolobium	melinonii	15	2	4	SCLM	146	16	38	200	6	30	AN	0.55	Petit
Caesalpiniaceae	Senna	multijuga	8	3	2	SENM	0	0	0	0	6	12	HY	-	-
Caesalpiniaceae	Senna	quinquangulata	6	1	2	SENQ	0	0	0	0	6	6	EZ	-	-
Caesalpiniaceae	Senna	reticulata	6	1	2	SENR	0	0	0	0	6	8	EZ	-	-
Caesalpiniaceae	Senna	silvestris	8	3	2	SENS	0	0	0	0	3	10	HY	-	-
Caesalpiniaceae	Swartzia	arborescens	10	1	3	SWAA	0	3	1	4	5	23	SZRMbat	1	Troll
Caesalpiniaceae	Swartzia	benthamiana	16	3	4	SWAB	48	0	0	48	5	30	SZRMbat	1	Troll
Caesalpiniaceae	Swartzia	grandifolia	12	3	3	SWAG	0	1	0	1	3	18	SZRMbat	1	Troll
Caesalpiniaceae	Swartzia	guianensis	11	2	3	SWAH	1	4	31	36	3	20	SZRMbat	0.9	Troll
Caesalpiniaceae	Swartzia	laevicarpa	16	3	4	SWAK	0	0	0	0	1	30	SZRMbat	-	-
Caesalpiniaceae	Swartzia	leblondii	3	2	1	SWAL	38	0	0	38	-	-	SZRMbat	1	Troll
Caesalpiniaceae	Swartzia	longicarpa	7	2	2	SWAM	0	1	0	1	3	12	SZRMbat	1	Troll
Caesalpiniaceae	Swartzia	panacoco	16	3	4	SWAP	1	5	17	23	5	30	SZRMbat	01.01.00	Troll
Caesalpiniaceae	Swartzia	polyphylla	16	3	4	SWAQ	0	0	36	36	1	35	SZRMbat	1	Troll
Caesalpiniaceae	Swartzia	remiger	16	3	4	SWAR	4	18	0	22	4	30	SZRMbat	-	Troll
Caesalpiniaceae	Tachigali	myrmecophila	4	3	1	TACV	16	0	0	16	-	-	AN	-	-
Caesalpiniaceae	Tachigali	paniculata	16	3	4	TACW	0	1	0	1	5	30	AN	-	-
Caesalpiniaceae	Vouacapoua	americana	15	2	4	VOUA	460	35	178	673	4	35	SZR	0.92	Troll
Caricaceae	Jacaratia	spinosa	10	1	3	JACS	38	0	0	38	4	20	EZBM	-	-
Caryocaraceae	Caryocar	glabrum	18	2	5	CARK	15	10	36	61	3	50	SZRbat	0.79	-
Caryocaraceae	Caryocar	microcarpum	11	2	3	CARM	0	0	0	0	4	25	SZRbat	0.79	-
Caryocaraceae	Caryocar	nuciferum	18	2	5	CARN	0	0	0	0	3	45	SZRbat	0.79	-
Caryocaraceae	Caryocar	villosum	18	2	5	CARV	0	0	0	0	1	45	SZRbat	0.79	-
Cecropiaceae	Cecropia	latiloba	6	1	2	CECL	0	0	0	0	3	10	EZBMbat	0.35	Rauh
Cecropiaceae	Cecropia	obtusa	6	1	2	CECO	184	2	0	186	5	15	EZBMbat	0.35	Rauh
Cecropiaceae	Cecropia	palmata	6	1	2	CECP	0	0	0	0	3	15	EZBMbat	0.35	Rauh
Cecropiaceae	Cecropia	peltata	6	1	2	CECQ	0	0	0	0	5	15	EZBMbat	0.35	Rauh
Cecropiaceae	Cecropia	sciadophylla	14	1	4	CECS	42	1	6	49	5	30	EZBMbat	0.35	Rauh
Cecropiaceae	Pourouma	bicolor	10	1	3	POUB	25	0	0	25	-	25	EZBMbat	0.4	Rauh
Cecropiaceae	Pourouma	cecropiaefolia	2	1	1	POUC	2	0	0	2	-	-	EZBMbat	0.4	Rauh
Cecropiaceae	Pourouma	guianensis	10	1	3	POUG	5	0	4	9	5	25	EZBMbat	0.4	Rauh
Cecropiaceae	Pourouma	melinonii	10	1	3	POUM	0	0	0	0	1	20	EZBMbat	0.4	Rauh
Cecropiaceae	Pourouma	minor	10	1	3	POUN	211	0	0	211	3	25	EZBMbat	0.4	Rauh
Cecropiaceae	Pourouma	mollis	10	1	3	POUO	4	0	0	4	5	25	EZBMbat	0.4	Rauh
Cecropiaceae	Pourouma	saulensis	6	1	2	POUP	0	0	0	0	1	11	EZBMbat	-	-
Cecropiaceae	Pourouma	tomentosa	10	1	3	POUT	17	0	0	17	1	20	EZBMbat	0.4	Rauh
Cecropiaceae	Pourouma	velutina	6	1	2	POUV	0	0	0	0	3	15	EZBMbat	0.4	Rauh
Cecropiaceae	Pourouma	villosa	14	1	4	POUW	1	2	0	3	5	30	EZBMbat	0.4	Rauh
Celastraceae	Goupia	glabra	14	1	4	GOUP	11	0	54	65	5	35	EZBM	0.78	Roux
Celastraceae	Maytenus	myrsinoides	16	3	4	MAYM	0	0	0	0	1	35	EZBM	-	-
Celastraceae	Maytenus	sp.	11	2	3	MAYT	0	5	1	6	1	20	EZBM	0.75	-
Chrysobalanaceae	Chrysobalanus	icaco	6	1	2	CHRA	0	0	0	0	4	6	EZ	-	-
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Chrysobalanaceae	Couepia	bracteosa	11	2	3	COEB	0	6	86	92	1	25	SZRbat	0.95	Troll
Chrysobalanaceae	Couepia	caryophylloides	11	2	3	COEC	0	9	304	313	4	25	SZRbat	0.95	Troll
Chrysobalanaceae	Couepia	guianensis	18	2	5	COEG	0	5	33	38	5	45	SZRbat	0.95	Troll
Chrysobalanaceae	Couepia	parillo	10	1	3	COEP	0	13	0	13	5	20	SZRbat	0.95	Troll
Chrysobalanaceae	Exellodendron	barbatum	12	3	3	EXEL	0	0	0	0	2	25	EZ	-	-
Chrysobalanaceae	Hirtella	bicornis	15	2	4	HIRB	0	4	3	7	4	28	EZ	0.9	Troll
Chrysobalanaceae	Hirtella	ciliata	5	0	2	HIRC	0	0	0	0	1	12	EZ	-	-
Chrysobalanaceae	Hirtella	glandulosa	10	1	3	HIRG	0	2	0	2	2	25	EZ	0.9	Troll
Chrysobalanaceae	Hirtella	hispidula	8	3	2	HIRH	0	0	0	0	3	15	EZ	-	-
Chrysobalanaceae	Hirtella	obidensis	12	3	3	HIRO	0	0	0	0	3	25	EZ	-	-
Chrysobalanaceae	Hirtella	paniculata	1	0	1	HIRP	0	0	0	0	6	4	EZ	-	-
Chrysobalanaceae	Hirtella	physophora	8	3	2	HIRQ	0	0	0	0	3	7	EZ	-	-
Chrysobalanaceae	Hirtella	silicea	8	3	2	HIRS	0	0	0	0	3	10	EZ	-	-
Chrysobalanaceae	Licania	affinis	8	3	2	LIAA	0	1	0	1	1	15	SZR(Mbat)	0.98	Troll
Chrysobalanaceae	Licania	alba	16	3	4	LIAB	5	113	619	737	3	35	SZR(Mbat)	0.98	Troll
Chrysobalanaceae	Licania	apetala	18	2	5	LIAC	0	0	0	0	5	40	SZR(Mbat)	-	-
Chrysobalanaceae	Licania	canescens	11	2	3	LICA	3	23	44	70	3	20	SZR(Mbat)	0.98	Troll
Chrysobalanaceae	Licania	coriacea	11	2	3	LICB	0	0	0	0	1	25	SZR(Mbat)	-	-
Chrysobalanaceae	Licania	davillifolia	11	2	3	LIDA	0	0	0	0	3	20	SZR(Mbat)	-	-
Chrysobalanaceae	Licania	densiflora	12	3	3	LIDB	0	5	39	44	3	25	SZR(Mbat)	0.98	Troll
Chrysobalanaceae	Licania	discolor	19	3	5	LIDC	0	0	0	0	1	40	SZR(Mbat)	-	-
Chrysobalanaceae	Licania	elliptica	12	3	3	LIEA	0	0	0	0	2	20	SZR(Mbat)	-	-
Chrysobalanaceae	Licania	granvillei	12	3	3	LIGA	2	22	83	107	-	25	SZR(Mbat)	0.98	Troll
Chrysobalanaceae	Licania	heteromorpha	16	3	4	LIGB	2	19	0	21	6	30	SZR(Mbat)	0.98	Troll
Chrysobalanaceae	Licania	hypoleuca	11	2	3	LIHA	0	1	115	116	4	25	SZR(Mbat)	0.98	Troll
Chrysobalanaceae	Licania	incana	5	0	2	LIHB	0	0	0	0	5	10	SZR(Mbat)	-	-
Chrysobalanaceae	Licania	irwinii	12	3	3	LIHC	0	0	0	0	1	25	SZR(Mbat)	0.98	Troll
Chrysobalanaceae	Licania	kunthiana	11	2	3	LIHK	0	0	0	0	3	25	SZR(Mbat)	0.98	Troll
Chrysobalanaceae	Licania	latistipula	4	3	1	LILA	1	10	0	11	-	-	SZR(Mbat)	0.98	Troll
Chrysobalanaceae	Licania	laxiflora	16	3	4	LILB	0	7	0	7	1	30	SZR(Mbat)	0.98	Troll
Chrysobalanaceae	Licania	leptostachya	6	1	2	LILC	0	0	0	0	4	8	SZR(Mbat)	-	-
Chrysobalanaceae	Licania	licaniiflora	14	1	4	LILD	0	0	0	0	3	30	SZR(Mbat)	-	-
Chrysobalanaceae	Licania	macrophylla	15	2	4	LIMA	0	0	0	0	4	30	SZR(Mbat)	-	-
Chrysobalanaceae	Licania	majuscula	16	3	4	LIMB	12	0	0	12	4	30	SZR(Mbat)	0.98	Troll
Chrysobalanaceae	Licania	membranacea	16	3	4	LIMC	0	3	2	5	1	30	SZR(Mbat)	0.98	Troll
Chrysobalanaceae	Licania	micrantha	12	3	3	LIMD	0	14	56	70	5	25	SZR(Mbat)	0.98	Troll
Chrysobalanaceae	Licania	minutiflora	19	3	5	LIME	0	0	0	0	1	45	SZR(Mbat)	0.98	Troll
Chrysobalanaceae	Licania	octandra	10	1	3	LIMF	0	0	0	0	1	25	SZR(Mbat)	-	-
Chrysobalanaceae	Licania	ovalifolia	19	3	5	LIMG	0	5	0	5	1	40	SZR(Mbat)	0.98	Troll
Chrysobalanaceae	Licania	persaudii	4	3	1	LIMH	0	10	0	10	-	-	SZR(Mbat)	0.98	Troll
Chrysobalanaceae	Licania	robusta	12	3	3	LIMR	0	0	0	0	3	25	SZR(Mbat)	-	-
Chrysobalanaceae	Parinari	campestris	11	2	3	PARC	0	0	48	48	4	25	ZMRbat	1	Troll
Chrysobalanaceae	Parinari	excelsa	19	3	5	PARE	0	3	0	3	2	40	ZMRbat	1	Troll
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Chrysobalanaceae	Parinari	montana	3	2	1	PARM	0	1	0	1	-	-	ZMRbat	1	Troll
Chrysobalanaceae	Parinari	rodolphii	18	2	5	PARR	0	1	0	1	1	40	ZMRbat	1	Troll
Clusiaceae	Calophyllum	brasiliense	14	1	4	CALB	0	0	0	0	5	27	EZ	-	-
Clusiaceae	Caraipa	densifolia	16	3	4	CARD	0	12	16	28	5	30	AN	0.7	-
Clusiaceae	Caraipa	punctulata	12	3	3	CARE	0	0	0	0	3	25	AN	-	-
Clusiaceae	Caraipa	richardiana	12	3	3	CARF	0	0	0	0	3	20	AN	-	-
Clusiaceae	Clusia	fockeana	5	0	2	CLUA	0	0	0	0	5	11	EZBM	-	-
Clusiaceae	Clusia	leprantha	6	1	2	CLUB	0	0	0	0	4	13	EZBM	-	-
Clusiaceae	Clusia	melchiori	7	2	2	CLUC	0	0	0	0	2	15	EZBM	-	-
Clusiaceae	Clusia	minor	7	2	2	CLUD	0	0	0	0	3	6	EZBM	-	-
Clusiaceae	Mahurea	exstipulata	12	3	3	MAHE	0	0	0	0	1	20	AN	-	-
Clusiaceae	Mahurea	palustris	8	3	2	MAHU	0	2	0	2	1	10	AN	-	-
Clusiaceae	Moronobea	coccinea	18	2	5	MONO	0	18	94	112	1	40	EZ	0.88	-
Clusiaceae	Platonia	insignis	15	2	4	PLAI	1	7	16	24	4	35	EZM	0.85	Massart
Clusiaceae	Rheedia	acuminata	6	1	2	RHEA	0	2	49	51	5	15	EZ	0.75	Attims
Clusiaceae	Rheedia	benthamiana	8	3	2	RHEB	0	10	0	10	5	15	EZ	0.75	Attims
Clusiaceae	Rheedia	macrophylla	12	3	3	RHEM	1	0	0	1	3	20	EZ	0.75	Attims
Clusiaceae	Symphonia	globulifera	15	2	4	SYMG	10	43	229	282	5	30	EZ	0.71	Roux
Clusiaceae	Tovomita	brevistaminea	8	3	2	TOVB	0	0	0	0	3	15	EZ	-	-
Clusiaceae	Tovomita	cephalostigma	12	3	3	TOVC	0	3	0	3	4	25	EZ	0.92	Fagerlind
Clusiaceae	Tovomita	choisyana	12	3	3	TOVD	5	7	185	197	4	20	EZ	0.92	Fagerlind
Clusiaceae	Tovomita	grata	8	3	2	TOVG	0	0	0	0	1	10	EZ	-	-
Clusiaceae	Tovomita	secunda	7	2	2	TOVS	0	0	0	0	3	12	EZ	-	-
Clusiaceae	Vismia	cayennensis	6	1	2	VISC	0	0	9	9	6	12	EZ	0.55	Roux
Clusiaceae	Vismia	latifolia	10	1	3	VISL	0	0	0	0	3	18	EZ	-	-
Clusiaceae	Vismia	macrophylla	6	1	2	VISM	0	0	0	0	5	12	EZ	-	-
Clusiaceae	Vismia	sessilifolia	2	1	1	VIST	0	2	0	2	-	-	EZ	0.55	Roux
Clusiaceae	Vismia	guianensis	6	1	2	VISG	4	0	0	4	4	9	EZ	0.55	Roux
Combretaceae	Buchenavia	tetraphylla	19	3	5	BUCT	0	1	0	1	3	50	EZBM	0.78	-
Combretaceae	Buchenavia	grandis	18	2	5	BUCG	0	0	0	0	-	50	EZBM	0.78	-
Combretaceae	Buchenavia	macrophylla	12	3	3	BUCM	0	0	0	0	1	20	EZBM	0.78	-
Combretaceae	Buchenavia	nitidissima	18	2	5	BUCN	0	0	0	0	-	50	EZBM	0.78	-
Combretaceae	Conocarpus	erecta	5	0	2	CONR	0	0	0	0	5	8	HY	-	-
Combretaceae	Terminalia	amazonia	11	2	3	TERA	0	0	3	3	5	25	HY	0.75	Aubreville
Combretaceae	Terminalia	dichotoma	11	2	3	TERD	0	0	0	0	5	20	HY	0.75	Aubreville
Combretaceae	Terminalia	guyanensis	3	2	1	TERG	6	0	0	6	-	-	SZ	0.75	Aubreville
Combretaceae	Terminalia	lucida	9	0	3	TERL	0	0	0	0	2	20	SZ	-	-
Connaraceae	Connarus	coriaceus	4	3	1	COND	0	0	0	0	3	5	EZB	-	-
Connaraceae	Connarus	erianthus	4	3	1	CONE	0	0	0	0	1	5	EZB	-	-
Connaraceae	Connarus	fasciculatus	4	3	1	CONF	0	0	0	0	1	4	EZB	-	-
Connaraceae	Connarus	perrottetii	8	3	2	CONP	0	0	0	0	4	8	EZB	-	-
Connaraceae	Connarus	punctuatus	8	3	2	CONQ	0	0	0	0	3	7	EZB	-	-
Cyrillaceae	Cyrilla	racemiflora	5	0	2	CYRI	0	0	0	0	3	6	HY	-	-
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Dichapetalaceae	Tapura	amazonica	8	3	2	TAUA	0	0	0	0	1	12	SZ	0.68	Cook
Dichapetalaceae	Tapura	capitulifera	12	3	3	TAUC	0	0	0	0	4	20	SZ	0.68	Cook
Dichapetalaceae	Tapura	singularis	16	3	4	TAUS	0	0	94	94	-	35	SZ	0.68	Cook
Dilleniaceae	Curatella	americana	5	0	2	CURA	0	0	0	0	5	6	EZB	-	-
Ebenaceae	Diospyros	carbonaria	4	3	1	DIOC	1	0	0	1	-	-	EZ	0.8	Massart
Ebenaceae	Diospyros	guianensis	8	3	2	DIOG	0	0	8	8	5	10	EZ	0.8	Massart
Ebenaceae	Diospyros	lissocarpodes	8	3	2	DIOL	0	1	0	1	1	6	EZ	0.8	Massart
Ebenaceae	Diospyros	melinonii	12	3	3	DIOM	0	1	0	1	4	18	EZ	0.8	Massart
Ebenaceae	Diospyros	dichroa	16	3	4	DIOD	0	0	0	0	4	30	EZ	0.8	Massart
Ebenaceae	Diospyros	duckei	12	3	3	DIOE	0	0	0	0	3	25	EZ	0.8	Massart
Ebenaceae	Diospyros	martinii	8	3	2	DIOL	0	0	0	0	4	7	EZ	0.8	Massart
Ebenaceae	Diospyros	tetrandra	8	3	2	DION	0	0	0	0	1	8	EZ	0.8	Massart
Elaeocarpaceae	Sloanea	brevipes	4	3	1	SLOB	0	1	0	1	-	-	EZBM	0.9	Aubreville
Elaeocarpaceae	Sloanea	grandiflora	12	3	3	SLOH	0	2	108	110	3	18	EZBM	0.9	Aubreville
Elaeocarpaceae	Sloanea	guianensis	11	2	3	SLOI	0	0	436	436	5	18	EZBM	0.9	Aubreville
Elaeocarpaceae	Sloanea	latifolia	4	3	1	SLOL	0	1	0	1	-	-	EZBM	0.9	Aubreville
Elaeocarpaceae	Sloanea	echinocarpa	15	2	4	SLOE	0	0	0	0	1	30	EZBM	-	-
Elaeocarpaceae	Sloanea	eichleri	12	3	3	SLOF	0	0	0	0	4	20	EZBM	-	-
Elaeocarpaceae	Sloanea	garckeana	12	3	3	SLOG	0	0	0	0	3	16	EZBM	0.9	Aubreville
Elaeocarpaceae	Sloanea	parviflora	11	2	3	SLOP	0	0	0	0	5	16	EZBM	-	-
Elaeocarpaceae	Sloanea	rufa	8	3	2	SLOR	0	0	0	0	1	15	EZBM	-	-
Erythroxylaceae	Erythroxylum	amazonicum	5	0	2	ERYD	0	0	0	0	3	8	EZ	-	Rauh
Erythroxylaceae	Erythroxylum	amplum	7	2	2	ERYE	0	0	0	0	1	10	EZ	-	Rauh
Erythroxylaceae	Erythroxylum	citrifolium	2	1	1	ERYF	0	0	0	0	4	5	EZ	-	Rauh
Erythroxylaceae	Erythroxylum	kapplerianum	6	1	2	ERYG	0	0	0	0	4	8	EZ	-	Rauh
Erythroxylaceae	Erythroxylum	ligustrinum	2	1	1	ERYH	0	1	0	1	-	-	EZ	-	Rauh
Erythroxylaceae	Erythroxylum	macrophyllum	6	1	2	ERYM	0	0	0	0	4	12	EZ	-	Rauh
Erythroxylaceae	Erythroxylum	squamatum	6	1	2	ERYS	0	0	0	0	1	10	EZ	-	Rauh
Euphorbiaceae	Acalphya	diversifolia	8	3	2	ACAL	0	1	0	1	3	8	EZ	-	Koriba
Euphorbiaceae	Alchornea	schomburgkii	8	3	2	ALCS	0	0	0	0	0	10	EZ	0.7	Champagnat
Euphorbiaceae	Alchornea	triplinervia	11	2	3	ALCT	0	0	1	1	4	20	EZ	0.7	Champagnat
Euphorbiaceae	Alchorneopsis	floribunda	12	3	3	ALDF	0	0	0	0	4	20	EZ	-	-
Euphorbiaceae	Amanoa	guianensis	10	1	3	AMAN	0	2	41	43	5	20	EZ	0.94	-
Euphorbiaceae	Aparisthmium	cordatum	7	2	2	APAR	0	0	0	0	5	15	AUT	-	Koriba
Euphorbiaceae	Chaetocarpus	schomburgkianus	11	2	3	CHAE	0	24	111	135	4	25	EZM	01.01.13	-
Euphorbiaceae	Conceveiba	guianensis	7	2	2	CONC	0	4	64	68	5	15	EZ	0.68	-
Euphorbiaceae	Croton	cuneatus	4	3	1	CROC	0	0	0	0	4	4	EZ	-	-
Euphorbiaceae	Croton	hostmanii	1	0	1	CROH	0	0	0	0	2	3	EZ	-	-
Euphorbiaceae	Croton	matourensis	11	2	3	CROM	1	0	0	1	5	25	EZ	-	-
Euphorbiaceae	Croton	schiedeanus	8	3	2	CROS	0	0	0	0	2	8	EZ	-	-
Euphorbiaceae	Dodecastigma	integrifolia	12	3	3	DODI	0	0	0	0	1	18	EZ	-	-
Euphorbiaceae	Drypetes	variabilis	12	3	3	DRYP	8	20	92	120	5	25	EZM	0.86	Roux
Euphorbiaceae	Glycydendron	amazonicum	16	3	4	GLYC	0	3	12	15	1	30	EZ	0.71	-
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Euphorbiaceae	Hevea	guianensis	11	2	3	HEVE	0	12	47	59	5	25	SZ	0.6	Rauh
Euphorbiaceae	Hura	crepitans	17	1	5	HURA	0	0	0	0	4	40	EZ	-	-
Euphorbiaceae	Hyeronima	alchorneoides	14	1	4	HYER	16	0	19	35	5	30	EZBM	0.7	-
Euphorbiaceae	Mabea	piriri	8	3	2	MABE	0	0	29	29	5	15	EZ	0.7	Nozeran
Euphorbiaceae	Mabea	speciosa	8	3	2	MABS	0	0	0	0	4	7	EZ	-	-
Euphorbiaceae	Manihot	brachyloba	2	1	1	MANB	0	0	0	0	1	5	EZ	-	-
Euphorbiaceae	Maprounea	guianensis	10	1	3	MAPR	0	0	0	0	5	25	EZ	-	-
Euphorbiaceae	Margaritaria	nobilis	7	2	2	MARG	0	0	0	0	5	14	HY	-	-
Euphorbiaceae	Micrandra	elata	11	2	3	MIDA	0	1	0	1	2	22	EZ	-	-
Euphorbiaceae	Pausandra	martinii	8	3	2	PAUW	0	0	0	0	3	12	EZ	-	-
Euphorbiaceae	Pera	bicolor	9	0	3	PERB	0	0	0	0	4	25	EZ	-	-
Euphorbiaceae	Pera	glabrata	5	0	2	PERC	0	0	0	0	3	15	EZ	-	-
Euphorbiaceae	Phyllanthus	attenuatus	5	0	2	PHYA	0	0	0	0	1	10	EZ	-	-
Euphorbiaceae	Phyllanthus	juglandifolius	5	0	2	PHYB	0	0	0	0	1	10	EZ	-	-
Euphorbiaceae	Pogonophora	schomburgkiana	11	2	3	POGO	0	3	0	3	4	20	EZ	-	-
Euphorbiaceae	Sagotia	racemosa	7	2	2	SAGR	0	110	170	280	4	15	EZ	0.7	-
Euphorbiaceae	Sandwithia	guianensis	8	3	2	SANG	0	0	0	0	1	12	EZ	-	-
Euphorbiaceae	Sapium	glandulosum	11	2	3	SAPG	0	0	0	0	4	23	EZ	-	-
Euphorbiaceae	Sapium	paucinervium	7	2	2	SAPP	5	0	0	5	4	12	EZ	-	-
Euphorbiaceae	Senefeldera	macrophylla	8	3	2	SENE	0	0	0	0	1	10	EZ	-	-
Fabaceae	Alexa	washenheimii	11	2	3	ALEX	0	0	0	0	5	25	EZ	-	-
Fabaceae	Andira	coriacea	15	2	4	ANDC	0	8	23	31	5	30	SZR	0.89	Champagnat
Fabaceae	Andira	inermis	11	2	3	ANDI	0	0	0	0	5	20	SZR	0.89	Champagnat
Fabaceae	Andira	surinamensis	15	2	4	ANDS	0	0	0	0	5	35	SZR	0.89	Champagnat
Fabaceae	Bowdichia	virgilioides	5	0	2	BOWD	0	0	0	0	1	10	EZ	-	-
Fabaceae	Clathrotropis	brachypetala	11	2	3	CLAB	0	0	0	0	5	20	EZ	-	-
Fabaceae	Diplotropis	purpurea	19	3	5	DIPL	13	0	14	27	5	40	AN	0.92	-
Fabaceae	Dipteryx	odorata	16	3	4	DIPO	4	1	6	11	5	30	SZRbat	01.01.00	Attims
Fabaceae	Dipteryx	punctuata	15	2	4	DIPP	0	0	0	0	3	35	SZRbat	-	-
Fabaceae	Dussia	discolor	19	3	5	DUSS	5	0	0	5	2	40	SZ	-	-
Fabaceae	Erythrina	amazonica	7	2	2	ERYA	0	0	0	0	0	10	EZ	-	
Fabaceae	Erythrina	fusca	7	2	2	ERYB	0	0	0	0	4	12	EZ	-	
Fabaceae	Hymenolobium	flavum	18	2	5	HYMF	0	0	1	1	4	50	AN	0.75	
Fabaceae	Hymenolobium	petraeum	17	1	5	HYMP	0	0	0	0	1	45	AN	0.75	
Fabaceae	Lonchocarpus	hedyosmus	7	2	2	LONB	0	0	0	0	3	15	AN	-	
Fabaceae	Lonchocarpus	heptaphyllus	11	2	3	LONC	8	0	0	8	1	20	AN	-	
Fabaceae	Muellera	frutescens	5	0	2	MUEL	0	0	0	0	5	6	HY	-	
Fabaceae	Ormosia	cinerea	19	3	5	ORMA	0	0	0	0	1	40	EZ	-	
Fabaceae	Ormosia	coarctata	16	3	4	ORMB	0	0	0	0	1	30	EZ	-	
Fabaceae	Ormosia	coccinea	8	3	2	ORMC	0	0	0	0	5	15	EZ	-	
Fabaceae	Ormosia	coutinhoi	18	2	5	ORMD	2	1	14	17	3	40	EZ	0.8	
Fabaceae	Ormosia	flava	11	2	3	ORME	0	0	0	0	3	20	EZ	-	
Fabaceae	Ormosia	melanocarpa	12	3	3	ORMM	0	0	0	0	2	25	EZ	-	
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Fabaceae	Ormosia	paraensis	12	3	3	ORMP	0	0	0	0	4	25	EZ	-	
Fabaceae	Ormosia	stipularis	11	2	3	ORMS	0	0	0	0	4	25	EZ	-	
Fabaceae	Paramachaerium	ormosioides	12	3	3	PARB	0	0	0	0	0	25	AN	-	
Fabaceae	Platymiscium	trinitatis	16	3	4	PLAT	0	0	0	0	1	35	AN	-	-
Fabaceae	Platymiscium	ulei	16	3	4	PLAU	0	0	0	0	4	30	AN	-	-
Fabaceae	Poecilanthe	effusa	8	3	2	POEB	0	0	0	0	1	12	EZ	-	-
Fabaceae	Poecilanthe	hostmanni	8	3	2	POEC	0	1	19	20	1	15	EZ	0.65	-
Fabaceae	Pterocarpus	officinalis	15	2	4	PTEO	32	4	38	74	5	32	HY	0.6	Troll
Fabaceae	Pterocarpus	rohrii	15	2	4	PTER	0	0	0	0	5	30	HY	-	-
Fabaceae	Pterocarpus	santalinoides	15	2	4	PTES	4	0	0	4	5	32	HY	0.6	Troll
Fabaceae	Spirotropsis	longifolia	7	2	2	SPIL	0	0	0	0	1	15	EZ	-	-
Fabaceae	Taralea	oppositifolia	15	2	4	TARO	0	0	0	0	3	30	HY	-	-
Fabaceae	Vatairea	guianensis	18	2	5	VATG	0	1	0	1	3	40	HY	0.8	-
Fabaceae	Vatairea	paraensis	18	2	5	VATP	0	0	0	0	1	40	AN	-	-
Fabaceae	Vataireopsis	surinamensis	18	2	5	VATS	1	1	2	4	3	40	AN	0.69	-
Flacourtiaceae	Banara	guianensis	6	1	2	BANG	0	0	0	0	5	12	EZ	-	-
Flacourtiaceae	Carpotroche	longifolia	8	3	2	CARG	0	0	0	0	2	12	EZB	-	-
Flacourtiaceae	Carpotroche	surinamensis	8	3	2	CARH	0	0	0	0	5	8	EZB	-	-
Flacourtiaceae	Casearia	acuminata	1	0	1	CASA	0	0	0	0	4	4	EZ	0.9	Cook
Flacourtiaceae	Casearia	arborea	12	3	3	CASB	0	0	0	0	5	16	EZ	0.9	Cook
Flacourtiaceae	Casearia	combaymensis	9	0	3	CASC	0	1	0	1	4	20	EZM	0.9	Cook
Flacourtiaceae	Casearia	commersoniana	6	1	2	CASD	0	0	0	0	4	6	EZ	0.9	Cook
Flacourtiaceae	Casearia	decandra	12	3	3	CASF	0	0	1	1	1	18	EZ	0.9	Cook
Flacourtiaceae	Casearia	grandiflora	8	3	2	CASG	0	0	0	0	1	15	EZ	0.9	Cook
Flacourtiaceae	Casearia	guianensis	6	1	2	CASH	0	0	0	0	1	15	EZ	0.9	Cook
Flacourtiaceae	Casearia	javitensis	11	2	3	CASJ	0	4	11	15	6	18	EZ	0.9	Cook
Flacourtiaceae	Casearia	mariquitensis	7	2	2	CASK	0	0	0	0	5	10	EZ	0.9	Cook
Flacourtiaceae	Casearia	negrensis	8	3	2	CASL	0	0	0	0	1	8	EZ	0.9	Cook
Flacourtiaceae	Casearia	pitumba	6	1	2	CASM	0	0	1	1	5	12	EZ	0.9	Cook
Flacourtiaceae	Casearia	rusbyana	11	2	3	CASN	0	0	0	0	1	20	EZ	0.9	Cook
Flacourtiaceae	Casearia	sylvestris	6	1	2	CASO	0	0	0	0	5	15	EZ	0.9	Cook
Flacourtiaceae	Casearia	ulmifolia	6	1	2	CASP	0	0	0	0	1	12	EZ	0.9	Cook
Flacourtiaceae	Homalium	guianense	12	3	3	HOMG	0	0	0	0	5	20	HY	-	-
Flacourtiaceae	Homalium	racemosum	8	3	2	HOMR	0	0	0	0	4	12	HY	-	-
Flacourtiaceae	Laetia	procera	17	1	5	LAET	2	7	13	22	-	40	EZ	0.75	-
Flacourtiaceae	Ryania	pyrifera	8	3	2	RYAP	0	0	0	0	3	8	EZ	-	-
Flacourtiaceae	Ryania	speciosa	8	3	2	RYAS	0	0	0	0	1	10	EZ	-	-
Hernandiaceae	Hernandia	guianensis	10	1	3	HERG	0	0	0	0	3	20	EZ	-	-
Hippocrataceae	Cheiloclinium	cognatum	8	3	2	CHEI	0	4	0	4	5	12	EZM	0.75	-
Hugoniaceae	Hebepetalum	humiriifolium	12	3	3	HEBE	1	13	25	39	4	20	EZ	1	-
Humiriaceae	Humiria	balsamifera	17	1	5	HUMB	0	0	0	0	5	40	EZBM	0.9	-
Humiriaceae	Humiriastrum	exelsum	16	3	4	HUME	0	1	0	1	-	35	EZ	-	-
Humiriaceae	Humiriastrum	subcrenatum	16	3	4	HUMS	0	7	0	7	-	35	EZ	-	-
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Humiriaceae	Sacoglottis	cydonioides	16	3	4	SACC	0	0	21	21	3	30	EZM	0.9	-
Humiriaceae	Sacoglottis	guianensis	14	1	4	SACG	0	2	0	2	5	30	EZ	0.9	-
Humiriaceae	Schistostemon	dichotomum	12	3	3	SCID	0	0	0	0	1	25	EZM	-	-
Humiriaceae	Schistostemon	sylvaticum	12	3	3	SCIS	0	9	0	9	-	25	EZ	-	-
Humiriaceae	Vantanea	guianensis	16	3	4	VANG	0	0	0	0	1	35	EZ	-	-
Humiriaceae	Vantanea	parviflora	16	3	4	VANP	0	0	0	0	1	35	EZ	0.9	-
Icacinaceae	Dendrobangia	boliviana	11	2	3	DEND	13	24	55	92	5	25	EZ	0.75	-
Icacinaceae	Discophora	guianensis	8	3	2	DISC	0	1	0	1	4	13	EZ	-	-
Icacinaceae	Emmotum	fagifolium	5	0	2	EMMO	0	1	0	1	1	15	EZ	-	-
Icacinaceae	Poraqueiba	guianensis	12	3	3	PORA	58	27	3	88	4	23	EZ	0.9	-
Lascistemataceae	Lascistema	grandifolium	10	1	3	LASC	1	0	0	1	4	18	EZ	-	-
Lascistemataceae	Lascistema	polystachyum	8	3	2	LASP	0	0	0	0	0	8	EZ	-	-
Lauraceae	Aiouea	guianensis	15	2	4	AIOU	0	0	0	0	4	35	EZBM	-	-
Lauraceae	Aniba	citrifolia	16	3	4	ANIC	0	0	0	0	1	27	EZBM	0.6	Rauh
Lauraceae	Aniba	guianensis	8	3	2	ANIG	0	0	0	0	1	15	EZBM	0.6	Rauh
Lauraceae	Aniba	hostmanniana	12	3	3	ANIH	0	0	9	9	5	20	EZBM	0.6	Rauh
Lauraceae	Aniba	jenmanii	7	2	2	ANIJ	0	0	0	0	1	10	EZBM	0.6	Rauh
Lauraceae	Aniba	kappleri	7	2	2	ANIK	0	0	0	0	3	13	EZBM	0.6	Rauh
Lauraceae	Aniba	megaphylla	11	2	3	ANIM	0	0	0	0	3	25	EZBM	0.6	Rauh
Lauraceae	Aniba	panurensis	14	1	4	ANIP	0	0	0	0	1	35	EZBM	0.6	Rauh
Lauraceae	Aniba	parviflora	12	3	3	ANIQ	0	0	0	0	1	20	EZBM	0.6	Rauh
Lauraceae	Aniba	rosaeodora	15	2	4	ANIR	0	0	0	0	3	30	EZBM	0.6	Rauh
Lauraceae	Aniba	taubertiana	7	2	2	ANIT	0	0	0	0	3	15	EZBM	0.6	Rauh
Lauraceae	Aniba	williamsii	16	3	4	ANIW	0	0	0	0	1	30	EZBM	0.6	Rauh
Lauraceae	Chlorocardium	rodiei	19	3	5	CHLO	0	0	0	0	3	40	EZBM	-	-
Lauraceae	Cinnamomum	cinnamomifolia	8	3	2	CINN	0	0	0	0	0	7	EZBM	-	-
Lauraceae	Cryptocarya	guianensis	16	3	4	CRYP	0	0	0	0	1	35	EZBM	-	-
Lauraceae	Endlicheria	bracteolata	16	3	4	ENDA	0	0	0	0	1	30	EZBM	-	-
Lauraceae	Endlicheria	endlicheriopsis	12	3	3	ENDB	0	0	0	0	2	25	EZBM	-	-
Lauraceae	Endlicheria	multiflora	12	3	3	ENDC	0	0	0	0	5	18	EZBM	-	-
Lauraceae	Endlicheria	punctulata	4	3	1	ENDD	0	0	0	0	1	5	EZBM	-	-
Lauraceae	Endlicheria	pyriformis	11	2	3	ENDE	0	0	0	0	4	25	EZBM	-	-
Lauraceae	Kubizkia	mezii	7	2	2	KUBI	0	0	0	0	3	7	EZBM	-	-
Lauraceae	Licaria	cannella	15	2	4	LIRC	0	0	7	7	4	30	EZBM	1	-
Lauraceae	Licaria	chrysophylla	4	3	1	LIRD	11	0	0	11	-	-	EZBM	-	-
Lauraceae	Licaria	debilis	8	3	2	LIRE	0	0	0	0	4	15	EZBM	-	-
Lauraceae	Licaria	globifera	12	3	3	LIRG	0	0	7	7	-	25	EZBM	0.7	-
Lauraceae	Licaria	guianensis	15	2	4	LIRH	0	0	0	0	5	30	EZBM	-	-
Lauraceae	Licaria	martiniana	12	3	3	LIRM	0	0	0	0	4	20	EZBM	-	-
Lauraceae	Licaria	polyphylla	16	3	4	LIRP	0	0	0	0	4	30	EZBM	-	-
Lauraceae	Licaria	rigida	16	3	4	LIRR	0	0	1	1	4	30	EZBM	0.7	-
Lauraceae	Licaria	subbullata	8	3	2	LIRS	0	0	0	0	3	12	EZBM	-	-
Lauraceae	Licaria	vernicosa	8	3	2	LIRV	0	0	0	0	1	12	EZBM	-	-
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Lauraceae	Mezilaurus	itauba	18	2	5	MEZI	0	0	0	0	1	40	EZBM	-	-
Lauraceae	Nectandra	cissiflora	12	3	3	NECC	0	0	0	0	2	25	EZBM	-	-
Lauraceae	Nectandra	cuspidata	16	3	4	NECD	0	0	0	0	2	30	EZBM	-	-
Lauraceae	Nectandra	globosa	15	2	4	NECG	0	0	0	0	5	30	EZBM	-	-
Lauraceae	Nectandra	pearcei	12	3	3	NECP	0	0	0	0	1	20	EZBM	-	-
Lauraceae	Nectandra	reticulata	12	3	3	NECR	0	0	0	0	1	25	EZBM	-	-
Lauraceae	Ocotea	aciphylla	12	3	3	OCOA	0	0	0	0	1	18	EZBM	0.6	Massart
Lauraceae	Ocotea	argyrophylla	8	3	2	OCOB	7	2	0	9	1	15	EZBM	0.6	Massart
Lauraceae	Ocotea	canaliculata	16	3	4	OCOC	0	0	4	4	3	28	EZBM	0.6	Massart
Lauraceae	Ocotea	cernua	12	3	3	OCOD	0	0	0	0	4	20	EZBM	-	-
Lauraceae	Ocotea	cymbarum	16	3	4	OCOE	0	0	0	0	0	30	EZBM	-	-
Lauraceae	Ocotea	discrepens	12	3	3	OCOF	0	1	0	1	3	25	EZBM	0.6	Massart
Lauraceae	Ocotea	fasciculata	8	3	2	OCOG	0	0	0	0	1	12	EZBM	-	-
Lauraceae	Ocotea	floribunda	16	3	4	OCOH	0	0	0	0	4	28	EZBM	0.6	Massart
Lauraceae	Ocotea	glomerata	16	3	4	OCOI	0	0	9	9	5	32	EZBM	0.6	Massart
Lauraceae	Ocotea	guianensis	10	1	3	OCOJ	1	0	13	14	4	25	EZBM	0.6	Massart
Lauraceae	Ocotea	indirectinervia	12	3	3	OCOK	0	0	0	0	1	25	EZBM	-	-
Lauraceae	Ocotea	oblonga	16	3	4	OCOO	0	0	2	2	3	30	EZBM	0.6	Massart
Lauraceae	Ocotea	petalanthera	12	3	3	OCOP	0	0	0	0	6	25	EZBM	-	-
Lauraceae	Ocotea	puberula	16	3	4	OCOQ	0	0	0	0	4	30	EZBM	-	-
Lauraceae	Ocotea	rubra	15	2	4	OCOR	35	3	45	83	5	30	EZBM	0.6	Massart
Lauraceae	Ocotea	schomburgkiana	10	1	3	OCOS	0	4	0	4	5	25	EZBM	0.6	Massart
Lauraceae	Ocotea	splendens	12	3	3	OCOT	0	0	0	0	3	22	EZBM	0.6	Massart
Lauraceae	Persea	nivea	10	1	3	PERN	0	0	0	0	3	20	EZBM	-	-
Lauraceae	Rhodostemonodaphne	grandis	16	3	4	RHOD	0	2	0	2	5	30	EZBM	-	-
Lauraceae	Rhodostemonodaphne	kunthiana	7	2	2	RHOK	0	0	0	0	3	15	EZBM	-	-
Lecythidaceae	Bertholletia	excelsa	19	3	5	BERE	0	0	0	0	3	45	SZR	-	-
Lecythidaceae	Couratari	gloriosa	14	1	4	COUF	0	0	0	0	3	35	AN	-	Massart
Lecythidaceae	Couratari	guianensis	19	3	5	COUG	5	3	0	8	5	55	AN	-	Massart
Lecythidaceae	Couratari	multiflora	18	2	5	COUH	3	9	137	149	5	40	AN	0.65	Massart
Lecythidaceae	Couratari	oblongifolia	19	3	5	COUI	0	0	0	0	4	45	AN	-	Massart
Lecythidaceae	Couratari	stellata	19	3	5	COUJ	0	0	0	0	4	45	AN	-	Massart
Lecythidaceae	Couroupita	guianensis	19	3	5	COUK	0	0	0	0	5	40	EZ	-	-
Lecythidaceae	Eschweilera	apiculata	4	3	1	ESCA	0	14	0	14	-	-	SZR	1	Troll
Lecythidaceae	Eschweilera	collina	16	3	4	ESCD	0	0	0	0	1	30	SZR	1	Troll
Lecythidaceae	Eschweilera	congestiflora	15	2	4	ESCE	0	0	49	49	2	28	SZR	1	Troll
Lecythidaceae	Eschweilera	coriacea	16	3	4	ESCF	721	13	0	734	5	30	SZR	1	Troll
Lecythidaceae	Eschweilera	decolorans	16	3	4	ESCG	0	19	0	19	1	35	SZR	1	Troll
Lecythidaceae	Eschweilera	grandiflora	4	3	1	ESCH	2	1	0	3	-	-	SZR	1	Troll
Lecythidaceae	Eschweilera	micrantha	16	3	4	ESCM	2	166	0	168	2	35	SZR	1	Troll
Lecythidaceae	Eschweilera	parviflora	4	3	1	ESCP	5	62	0	67	-	-	SZR	1	Troll
Lecythidaceae	Eschweilera	pedicellata	16	3	4	ESCQ	0	10	0	10	5	30	SZR	1	Troll
Lecythidaceae	Eschweilera	sagotiana	16	3	4	ESCS	1	117	937	1055	3	35	SZR	1	Troll
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Lecythidaceae	Eschweilera	simiorum	12	3	3	ESCT	0	0	2	2	3	25	SZR	1	Troll
Lecythidaceae	Eschweilera	subglandosa	18	2	5	ESCU	0	0	0	0	5	40	SZR	-	-
Lecythidaceae	Eschweilera	wachenheimii	12	3	3	ESCV	0	0	0	0	1	25	SZR	-	-
Lecythidaceae	Gustavia	augusta	7	2	2	GUSA	0	0	0	0	6	10	ZMR	0.85	-
Lecythidaceae	Gustavia	hexapetala	8	3	2	GUSH	5	19	136	160	5	12	ZMR	0.85	-
Lecythidaceae	Lecythis	chartacea	16	3	4	LECB	0	0	0	0	5	35	SZR	-	-
Lecythidaceae	Lecythis	confertiflora	16	3	4	LECC	13	1	0	14	1	35	SZR	1	Troll
Lecythidaceae	Lecythis	corrugata	12	3	3	LECD	0	26	737	763	6	25	SZR	1	Troll
Lecythidaceae	Lecythis	holcogyne	16	3	4	LECH	0	0	0	0	0	35	SZR	1	Troll
Lecythidaceae	Lecythis	idatimon	12	3	3	LECI	32	321	1	354	4	20	SZR	1	Troll
Lecythidaceae	Lecythis	persistens	12	3	3	LECP	58	198	1	257	-	25	SZR	1	Troll
Lecythidaceae	Lecythis	poiteaui	19	3	5	LECQ	0	17	52	69	3	40	SZR	1	Troll
Lecythidaceae	Lecythis	simiorum	12	3	3	LECS	0	1	0	1	-	20	SZR	1	Troll
Lecythidaceae	Lecythis	zabucajo	18	2	5	LECZ	11	1	13	25	5	45	SZR	1	Troll
Loganiaceae	Antonia	ovata	14	1	4	ANTO	0	0	13	13	4	30	AN	0.54	-
Malpighiaceae	Byrsonima	crassifolia	5	0	2	BYRC	0	0	0	0	6	10	EZ	0.75	Aubreville
Malpighiaceae	Byrsonima	eugeniifolia	9	0	3	BYRE	0	0	0	0	1	20	EZ	0.75	Aubreville
Malpighiaceae	Byrsonima	spicata	13	0	4	BYRS	0	0	0	0	5	35	EZ	0.75	Aubreville
Malpighiaceae	Byrsonima	stipulacea	14	1	4	BYRT	1	0	0	1	-	30	EZ	0.75	Aubreville
Malpighiaceae	Byrsonima	verbascifolia	1	0	1	BYRV	0	0	0	0	4	5	EZ	0.75	Aubreville
Malpighiaceae	Spachea	elegans	11	2	3	SPAE	0	0	0	0	5	25	AUT	-	-
Malpighiaceae	Byrsonima	aerugo	14	1	4	BYRA	0	0	0	0	-	35	EZ	0.75	Aubreville
Malpighiaceae	Byrsonima	densa	14	1	4	BYRD	0	0	0	0	-	35	EZ	0.75	Aubreville
Malpighiaceae	Byrsonima	laevigata	14	1	4	BYRL	0	0	0	0	4	30	EZ	0.75	Aubreville
Melastomataceae	Bellucia	grossularioides	14	1	4	BELL	2	0	0	2	-	30	EZ	-	Leeuwenberg
Melastomataceae	Henriettea	maroniensis	6	1	2	HENA	0	0	0	0	3	11	EZB	-	-
Melastomataceae	Henriettea	multiflora	6	1	2	HENC	0	0	0	0	4	15	EZB	-	-
Melastomataceae	Henriettea	ramiflora	6	1	2	HENE	0	0	0	0	3	11	EZB	-	-
Melastomataceae	Henriettea	succosa	6	1	2	HENG	0	0	0	0	6	10	EZB	-	-
Melastomataceae	Henriettella	caudata	7	2	2	HENK	0	0	0	0	3	6	EZB	-	-
Melastomataceae	Loreya	mespiloides	6	1	2	LORE	0	0	1	1	6	15	EZB	0.7	Leeuwenberg
Melastomataceae	Miconia	argyrophylla	7	2	2	MICA	1	0	0	1	3	9	EZB	0.7	Mangenot
Melastomataceae	Miconia	chrysophylla	7	2	2	MICC	0	0	0	0	4	12	EZB	-	Mangenot
Melastomataceae	Miconia	holosericea	6	1	2	MICH	0	0	0	0	5	9	EZB	0.7	Mangenot
Melastomataceae	Miconia	kappleri	10	1	3	MICK	0	0	0	0	3	20	EZB	-	Mangenot
Melastomataceae	Miconia	lepidota	10	1	3	MICL	0	0	0	0	4	20	EZB	-	Mangenot
Melastomataceae	Miconia	longifolia	6	1	2	MICM	0	0	0	0	5	13	EZB	-	Mangenot
Melastomataceae	Miconia	mirabilis	11	2	3	MICN	0	0	0	0	5	20	EZB	0.7	Mangenot
Melastomataceae	Miconia	myriantha	5	0	2	MICO	0	0	0	0	5	10	EZB	-	Mangenot
Melastomataceae	Miconia	plukenetii	8	3	2	MICP	0	0	0	0	4	9	EZB	0.7	Mangenot
Melastomataceae	Miconia	poeppigii	15	2	4	MICQ	0	0	0	0	4	27	EZB	-	Mangenot
Melastomataceae	Miconia	prasina	11	2	3	MICR	0	0	0	0	5	18	EZB	0.7	Mangenot
Melastomataceae	Miconia	pubipetala	7	2	2	MICS	0	0	0	0	4	7	EZB	-	Mangenot
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Melastomataceae	Miconia	ruficalyx	7	2	2	MICT	1	0	0	1	3	10	EZB	0.7	Mangenot
Melastomataceae	Miconia	serrulata	3	2	1	MICU	0	0	0	0	4	4	EZB	-	Mangenot
Melastomataceae	Miconia	tomentosa	6	1	2	MICV	0	0	0	0	6	13	EZB	-	Mangenot
Melastomataceae	Miconia	trimera	6	1	2	MICT	0	0	34	34	-	10	EZB	0.7	Mangenot
Melastomataceae	Miconia	tschudyoides	4	3	1	MICU	0	2	0	2	1	5	EZB	0.7	Mangenot
Melastomataceae	Mouriri	acutiflora	15	2	4	MOUA	0	0	0	0	3	30	EZBM	-	Mangenot
Melastomataceae	Mouriri	collocarpa	15	2	4	MOUC	0	0	80	80	1	30	EZBM	01.01.00	Mangenot
Melastomataceae	Mouriri	crassifolia	16	3	4	MOUD	1	5	17	23	-	29	EZBM	01.01.00	Mangenot
Melastomataceae	Mouriri	dumetosa	8	3	2	MOUE	0	0	0	0	1	15	EZBM	-	Mangenot
Melastomataceae	Mouriri	francavillana	8	3	2	MOUF	0	0	0	0	3	14	EZBM	-	Mangenot
Melastomataceae	Mouriri	grandiflora	11	2	3	MOUG	0	0	0	0	5	25	EZBM	-	Mangenot
Melastomataceae	Mouriri	guianensis	7	2	2	MOUH	0	0	0	0	3	15	EZBM	-	Mangenot
Melastomataceae	Mouriri	huberi	15	2	4	MOUI	0	0	0	0	-	30	EZBM	01.01.00	Mangenot
Melastomataceae	Mouriri	nervosa	7	2	2	MOUM	0	1	0	1	-	12	EZBM	01.01.00	Mangenot
Melastomataceae	Mouriri	nigra	11	2	3	MOUN	0	0	0	0	4	25	EZBM	-	Mangenot
Melastomataceae	Mouriri	oligantha	12	3	3	MOUO	0	0	0	0	1	20	EZBM	-	Mangenot
Melastomataceae	Mouriri	sagotiana	7	2	2	MOUS	0	1	0	1	-	15	EZBM	01.01.00	Mangenot
Melastomataceae	Mouriri	sideroxylon	15	2	4	MOUT	0	0	0	0	1	28	EZBM	-	Mangenot
Melastomataceae	Mouriri	subumbellata	12	3	3	MOUU	0	0	0	0	1	25	EZBM	-	Mangenot
Melastomataceae	Mouriri	vernicosa	10	1	3	MOUV	0	0	0	0	-	25	EZBM	01.01.00	Mangenot
Melastomataceae	Myriaspora	egensis	7	2	2	MYRX	0	0	0	0	3	7	EZB	-	-
Melastomataceae	Tococa	guianensis	6	1	2	TOCG	0	0	0	0	5	6	EZB	-	-
Melastomataceae	Votomita	guianensis	12	3	3	VOTG	0	0	0	0	1	20	EZ	-	-
Meliaceae	Carapa	guianensis	15	2	4	CARG	0	0	0	0	6	35	SZ	0.7	Cook
Meliaceae	Carapa	procera	15	2	4	CARF	226	16	147	389	6	35	SZRM	0.7	Cook
Meliaceae	Cedrela	odorata	18	2	5	CEDR	4	0	0	4	4	40	AN	0.46	Chamberlain
Meliaceae	Guarea	costata	12	3	3	GUAC	0	0	0	0	3	18	EZ	-	-
Meliaceae	Guarea	gomma	12	3	3	GUAD	0	0	0	0	3	25	EZ	-	-
Meliaceae	Guarea	grandifolia	19	3	5	GUAE	0	0	0	0	3	50	EZ	-	-
Meliaceae	Guarea	guidonia	12	3	3	GUAG	1	0	0	1	5	20	EZ	0.7	-
Meliaceae	Guarea	kunthiana	16	3	4	GUAK	0	0	0	0	5	35	EZ	0.7	-
Meliaceae	Guarea	macrophylla	12	3	3	GUAM	0	0	0	0	0	25	EZ	0.7	-
Meliaceae	Guarea	pubescens	8	3	2	GUAP	0	0	0	0	3	15	EZ	0.7	-
Meliaceae	Guarea	scabra	12	3	3	GUAQ	0	0	0	0	1	20	EZ	-	-
Meliaceae	Guarea	silvatica	12	3	3	GUAR	0	0	27	27	0	20	EZ	0.7	-
Meliaceae	Trichilia	cipo	12	3	3	TRIC	0	0	0	0	1	20	EZ	-	Rauh
Meliaceae	Trichilia	euneura	12	3	3	TRIE	0	0	0	0	1	20	EZ	0.8	Rauh
Meliaceae	Trichilia	martiana	15	2	4	TRIL	0	0	0	0	3	35	EZ	-	Rauh
Meliaceae	Trichilia	micrantha	10	1	3	TRIM	0	0	0	0	5	20	EZ	0.8	Rauh
Meliaceae	Trichilia	pallida	11	2	3	TRIP	2	0	0	2	5	18	EZ	0.8	Rauh
Meliaceae	Trichilia	quadrijuga	16	3	4	TRIQ	0	0	0	0	4	30	EZ	0.8	Rauh
Meliaceae	Trichilia	schomburgkii	12	3	3	TRIS	0	0	0	0	4	18	EZ	0.8	Rauh
Meliaceae	Trichilia	septentrionalis	16	3	4	TRIT	0	0	0	0	3	30	EZ	0.8	Rauh
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Meliaceae	Trichilia	surinamensis	16	3	4	TRIU	0	0	0	0	5	35	EZ	0.8	Rauh
Mimosaceae	Abarema	jupunba	18	2	5	ABAR	4	1	1	6	6	37	EZM	0.66	-
Mimosaceae	Abarema	laeta	8	3	2	ABAL	0	0	0	0	1	6	EZ	-	-
Mimosaceae	Anadenanthera	peregrina	16	3	4	ANBP	0	0	0	0	1	30	EZ	-	-
Mimosaceae	Balizia	pedicellaris	12	3	3	BALI	4	0	12	16	5	25	EZ	0.6	-
Mimosaceae	Calliandra	surinamensis	3	2	1	CALA	0	0	0	0	4	5	AUT	-	-
Mimosaceae	Cedrelinga	cateniformis	18	2	5	CEDP	0	0	0	0	3	60	SZMB	-	-
Mimosaceae	Enterolobium	oldemanii	3	2	1	ENTO	2	0	0	2	-	-	EZ	0.75	-
Mimosaceae	Enterolobium	schomburgkii	18	2	5	ENTS	0	1	23	24	5	40	EZ	0.75	-
Mimosaceae	Hydrochorea	corymbosa	10	1	3	HYDC	0	0	22	22	-	25	EZ	0.55	-
Mimosaceae	Hydrochorea	gonggrijpii	10	1	3	HYDG	0	0	0	0	4	20	EZ	-	-
Mimosaceae	Inga	acreana	12	3	3	INAA	15	0	0	15	3	25	EZMB	0.65	Troll
Mimosaceae	Inga	acrocephala	12	3	3	INAB	20	0	0	20	3	25	EZMB	0.65	Troll
Mimosaceae	Inga	alata	3	2	1	INAC	26	0	0	26	-	-	EZMB	0.65	Troll
Mimosaceae	Inga	alba	15	2	4	INAD	52	1	33	86	5	35	EZMB	0.65	Troll
Mimosaceae	Inga	auristellae	8	3	2	INAE	14	1	0	15	3	15	EZMB	0.65	Troll
Mimosaceae	Inga	bourgoni	15	2	4	INBA	53	0	0	53	5	30	EZMB	0.65	Troll
Mimosaceae	Inga	brachystachys	8	3	2	INBB	3	0	0	3	1	8	EZMB	0.65	Troll
Mimosaceae	Inga	bracteosa	7	2	2	INBC	0	0	0	0	0	15	EZMB	-	-
Mimosaceae	Inga	capitata	12	3	3	INCA	18	0	0	18	5	20	EZMB	0.65	Troll
Mimosaceae	Inga	cayennensis	7	2	2	INCB	4	0	38	42	4	15	EZMB	0.65	Troll
Mimosaceae	Inga	crassiflora	3	2	1	INCC	2	0	0	2	-	-	EZMB	0.65	Troll
Mimosaceae	Inga	disticha	12	3	3	INDA	0	0	0	0	3	20	EZMB	-	-
Mimosaceae	Inga	edulis	15	2	4	INEA	23	0	0	23	5	30	EZMB	0.65	Troll
Mimosaceae	Inga	fanchoniana	3	2	1	INFA	13	7	0	20	-	-	EZMB	0.65	Troll
Mimosaceae	Inga	fastuosa	3	2	1	INFB	18	0	0	18	-	-	EZMB	0.65	Troll
Mimosaceae	Inga	flagelliformis	3	2	1	INFC	9	0	0	9	-	-	EZMB	0.65	Troll
Mimosaceae	Inga	gracilifolia	7	2	2	INGA	8	0	0	8	1	13	EZMB	0.65	Troll
Mimosaceae	Inga	heterophylla	5	0	2	INHA	0	0	0	0	6	12	EZMB	-	-
Mimosaceae	Inga	huberi	4	3	1	INHB	105	0	26	131	3	-	EZMB	0.65	Troll
Mimosaceae	Inga	ingoides	6	1	2	INIA	0	0	0	0	5	10	EZMB	-	-
Mimosaceae	Inga	jenmanii	3	2	1	INJA	23	0	0	23	-	-	EZMB	0.65	Troll
Mimosaceae	Inga	lateriflora	10	1	3	INLA	1	0	0	1	5	25	EZMB	0.65	Troll
Mimosaceae	Inga	laurina	12	3	3	INLB	0	0	0	0	2	20	EZMB	-	-
Mimosaceae	Inga	leiocalycina	11	2	3	INLC	56	0	0	56	3	22	EZMB	0.65	Troll
Mimosaceae	Inga	lomatophylla	3	2	1	INLD	2	0	0	2	-	-	EZMB	0.65	Troll
Mimosaceae	Inga	melinonis	3	2	1	INMA	22	0	9	31	-	-	EZMB	0.65	Troll
Mimosaceae	Inga	nobilis	11	2	3	INMB	0	0	0	0	6	25	EZMB	-	-
Mimosaceae	Inga	nouragensis	3	2	1	INNA	4	0	0	4	-	-	EZMB	0.65	Troll
Mimosaceae	Inga	nuda	12	3	3	INNB	0	0	0	0	1	20	EZMB	-	-
Mimosaceae	Inga	paraensis	3	2	1	INPA	22	0	0	22	-	-	EZMB	0.65	Troll
Mimosaceae	Inga	pezizifera	12	3	3	INPB	15	0	0	15	5	25	EZMB	0.65	Troll
Mimosaceae	Inga	pilosula	4	3	1	INPC	0	1	0	1	4	-	EZMB	0.65	Troll
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Mimosaceae	Inga	poeppigiana	3	2	1	INPD	3	0	0	3	-	-	EZMB	0.65	Troll
Mimosaceae	Inga	retinocarpa	3	2	1	INRA	1	0	0	1	-	-	EZMB	0.65	Troll
Mimosaceae	Inga	rubiginosa	12	3	3	INRB	31	0	0	31	5	25	EZMB	0.65	Troll
Mimosaceae	Inga	semialata	12	3	3	INSB	8	0	5	13	1	20	EZMB	0.65	Troll
Mimosaceae	Inga	splendens	16	3	4	INSC	4	0	0	4	5	30	EZMB	0.65	Troll
Mimosaceae	Inga	sterulifera	12	3	3	INSD	0	0	0	0	5	20	EZMB	-	-
Mimosaceae	Inga	stipularis	11	2	3	INSE	6	3	0	9	5	25	EZMB	0.65	Troll
Mimosaceae	Inga	thibaudiana	10	1	3	INTA	20	2	0	22	6	25	EZMB	0.65	Troll
Mimosaceae	Inga	tubaeformis	11	2	3	INTB	0	0	7	7	-	25	EZMB	0.65	Troll
Mimosaceae	Inga	umbellifera	7	2	2	INUA	0	0	0	0	3	10	EZMB	0.65	Troll
Mimosaceae	Inga	virgultosa	6	1	2	INVA	0	0	0	0	1	15	EZMB	0.65	Troll
Mimosaceae	Macrosamanea	kegelii	8	3	2	MACK	0	0	0	0	1	12	EZ	-	-
Mimosaceae	Parkia	nitida	18	2	5	PAUN	6	0	0	6	5	50	ZMR	0.45	-
Mimosaceae	Parkia	pendula	19	3	5	PAUP	2	0	5	7	5	40	ZMR	0.45	-
Mimosaceae	Parkia	ulei	19	3	5	PAUU	1	0	0	1	5	45	ZMR	0.45	-
Mimosaceae	Parkia	velutina	18	2	5	PAUV	2	0	36	38	-	45	ZMR	0.45	-
Mimosaceae	Penthaclethra	macroloba	11	2	3	PENT	0	0	0	0	5	25	HY	-	-
Mimosaceae	Pseudopiptadenia	psilostachya	16	3	4	PSEC	2	0	0	2	1	30	AN	0.79	-
Mimosaceae	Pseudopiptadenia	suaveolens	17	1	5	PSED	131	1	0	132	5	50	AN	0.79	-
Mimosaceae	Stryphnodendron	guianense	6	1	2	STRG	1	0	0	1	1	12	EZ	-	-
Mimosaceae	Stryphnodendron	moricolor	4	3	1	STRM	1	0	0	1	-	-	EZ	-	-
Mimosaceae	Stryphnodendron	polystachyum	19	3	5	STRP	1	0	0	1	4	45	EZ	-	-
Mimosaceae	Zygia	cataractae	8	3	2	ZYGC	0	0	0	0	3	10	EZ	-	-
Mimosaceae	Zygia	inaequalis	11	2	3	ZYGI	0	0	0	0	4	25	EZ	-	-
Mimosaceae	Zygia	latifolia	11	2	3	ZYGL	0	0	0	0	4	20	EZ	-	-
Mimosaceae	Zygia	morii	16	3	4	ZYGM	1	0	0	1	-	30	EZ	01.03.00	-
Mimosaceae	Zygia	racemosa	16	3	4	ZYGR	8	3	0	11	4	30	EZ	01.03.00	-
Monimiaceae	Siparuna	cuspidata	6	1	2	SIPC	0	0	0	0	4	10	SZC	-	-
Monimiaceae	Siparuna	cristata	4	3	1	SIPB	3	0	0	3	-	-	SZ	0.8	Roux
Monimiaceae	Siparuna	decipiens	7	2	2	SIPD	0	6	1	7	5	15	SZ	0.8	Roux
Monimiaceae	Siparuna	guianensis	7	2	2	SIPG	0	0	0	0	6	12	SZ	0.8	Roux
Moraceae	Bagassa	guianensis	18	2	5	BAGS	18	0	0	18	-	45	EZMR	0.75	Rauh
Moraceae	Batocarpus	amazonicus	4	3	1	BATO	1	0	0	1	-	-	EZ	-	-
Moraceae	Brosimum	acutifolium	16	3	4	BROA	0	1	5	6	3	35	EZMR	1	Troll
Moraceae	Brosimum	guianense	19	3	5	BROG	0	3	10	13	6	45	EZMR	1	Troll
Moraceae	Brosimum	lactescens	18	2	5	BROL	0	0	0	0	3	45	EZMR	1	Troll
Moraceae	Brosimum	parinarioides	19	3	5	BROP	0	0	0	0	3	40	EZMR	1	Troll
Moraceae	Brosimum	rubescens	19	3	5	BROR	0	5	29	34	5	40	EZMR	1	Troll
Moraceae	Brosimum	utile	19	3	5	BROU	0	0	0	0	1	50	EZMR	1	Troll
Moraceae	Clarisia	ilicifolia	10	1	3	CLAA	0	0	0	0	5	20	EZM	-	-
Moraceae	Ficus	broadwayi	11	2	3	FICB	0	0	0	0	2	20	EZ	0.4	Rauh
Moraceae	Ficus	catappifolia	6	1	2	FICC	0	0	0	0	1	15	EZ	0.4	Rauh
Moraceae	Ficus	gomelleira	17	1	5	FICG	0	0	0	0	1	40	EZ	0.4	Rauh
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Moraceae	Ficus	guianensis	6	1	2	FICH	0	0	0	0	4	12	EZ	0.4	Rauh
Moraceae	Ficus	insipida	17	1	5	FICI	0	0	0	0	1	40	EZ	0.4	Rauh
Moraceae	Ficus	malacocarpa	10	1	3	FICM	0	0	0	0	1	20	EZ	0.4	Rauh
Moraceae	Ficus	maxima	18	2	5	FICN	0	0	3	3	5	40	EZ	0.4	Rauh
Moraceae	Ficus	nymphaeifolia	14	1	4	FICO	0	0	0	0	2	35	EZ	0.4	Rauh
Moraceae	Ficus	paludica	10	1	3	FICP	0	0	0	0	4	20	EZ	0.4	Rauh
Moraceae	Ficus	pertusa	14	1	4	FICQ	0	0	0	0	5	30	EZ	0.4	Rauh
Moraceae	Ficus	pulchella	16	3	4	FICR	0	0	0	0	1	30	EZ	0.4	Rauh
Moraceae	Ficus	schumacheri	15	2	4	FICS	0	0	0	0	1	30	EZ	0.4	Rauh
Moraceae	Ficus	trigona	14	1	4	FICT	0	0	0	0	5	30	EZ	0.4	Rauh
Moraceae	Helicostylis	pedunculata	11	2	3	HELP	0	0	0	0	2	25	EZM	-	-
Moraceae	Helicostylis	tomentosa	15	2	4	HELT	3	2	19	24	4	30	EZ	0.6	-
Moraceae	Maquira	guianensis	10	1	3	MAQG	0	0	1	1	4	25	EZ	0.93	-
Moraceae	Maquira	sclerophylla	14	1	4	MAQS	0	1	0	1	1	30	EZ	0.93	-
Moraceae	Naucleopsis	glabra	10	1	3	NAUF	0	0	0	0	1	20	EZM	-	-
Moraceae	Naucleopsis	guianensis	11	2	3	NAUG	1	0	1	2	3	20	EZ	0.8	-
Moraceae	Perebea	guianensis	12	3	3	PERG	0	1	6	7	1	20	EZ	0.68	Roux
Moraceae	Perebea	mollis	15	2	4	PERH	0	0	0	0	4	30	EZM	-	-
Moraceae	Pseudolmedia	laevis	17	1	5	PSEB	0	0	0	0	5	40	EZBM	-	-
Moraceae	Trymatococcus	oligandrus	11	2	3	TRYO	0	1	33	34	4	20	EZ	0.75	Troll
Moraceae	Trymatococcus	paraensis	15	2	4	TRYP	0	0	0	0	5	30	EZ	0.75	Troll
Myristicaceae	Iryanthera	paraensis	12	3	3	IRYP	0	0	0	0	5	23	EZBM	-	-
Myristicaceae	Virola	melinonii	11	2	3	VIRL	0	0	0	0	5	25	EZBM	-	-
Myristicaceae	Virola	sebifera	11	2	3	VIRS	0	0	0	0	4	20	EZBM	-	-
Myristicaceae	Iryanthera	hostmannii	12	3	3	IRYH	0	22	121	143	4	20	EZBM	0.75	Massart
Myristicaceae	Iryanthera	sagotiana	16	3	4	IRYS	21	36	109	166	5	30	EZBM	0.75	Massart
Myristicaceae	Virola	michelii	15	2	4	VIRM	30	13	46	89	-	35	EZBM	0.48	Massart
Myristicaceae	Virola	multicostata	15	2	4	VIRN	31	0	0	31	-	35	EZBM	0.48	Massart
Myristicaceae	Virola	surinamensis	15	2	4	VIRT	3	1	0	4	6	35	EZBM	0.46	Massart
Myrsinaceae	Ardisia	guianensis	3	2	1	ARDG	0	0	0	0	2	4	EZB	-	-
Myrsinaceae	Cybianthus	fulvopuverulentus	7	2	2	CYBF	0	0	0	0	5	15	EZB	-	-
Myrsinaceae	Cybianthus	microbotrys	7	2	2	CYBM	0	0	0	0	1	6	EZB	-	-
Myrsinaceae	Cybianthus	surinamensis	6	1	2	CYBS	0	0	0	0	5	12	EZB	-	-
Myrsinaceae	Myrsine	guianensis	6	1	2	MYRY	0	0	0	0	5	11	EZB	-	-
Myrsinaceae	Stylogyne	surinamensis	8	3	2	STYL	0	0	0	0	4	8	EZB	-	-
Myrtaceae	Calycolpus	goetheanus	8	3	2	CALC	0	0	0	0	2	12	EZBM	-	-
Myrtaceae	Calycolpus	revolutus	6	1	2	CALD	0	0	0	0	6	10	EZBM	-	-
Myrtaceae	Calycorectes	bergii	11	2	3	CALE	0	0	0	0	4	18	EZBM	-	-
Myrtaceae	Calycorectes	grandifolius	8	3	2	CALG	0	0	0	0	4	7	EZBM	-	-
Myrtaceae	Calyptranthes	amshoffae	10	1	3	CALK	0	0	0	0	1	17	EZBM	-	-
Myrtaceae	Calyptranthes	fasciculata	8	3	2	CALL	0	0	0	0	4	12	EZBM	-	-
Myrtaceae	Calyptranthes	lucida	8	3	2	CALP	0	0	0	0	1	15	EZBM	-	-
Myrtaceae	Calyptranthes	speciosa	6	1	2	CALS	0	0	0	0	5	10	EZBM	-	-
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Myrtaceae	Campomanesia	aromatica	6	1	2	CAMA	0	0	0	0	3	10	EZBM	-	-
Myrtaceae	Campomanesia	grandiflora	7	2	2	CAMG	0	0	0	0	3	10	EZBM	-	-
Myrtaceae	Eugenia	albicans	8	3	2	EUGA	0	0	0	0	3	10	EZBM	0.9	-
Myrtaceae	Eugenia	anastomosans	12	3	3	EUGA	0	0	0	0	1	23	EZBM	0.9	-
Myrtaceae	Eugenia	citrifolia	8	3	2	EUGB	0	0	0	0	1	14	EZBM	0.9	-
Myrtaceae	Eugenia	coffeifolia	8	3	2	EUGC	0	2	29	31	5	15	EZBM	0.9	-
Myrtaceae	Eugenia	cucullata	8	3	2	EUGD	0	0	0	0	-	10	EZBM	0.9	-
Myrtaceae	Eugenia	excelsa	8	3	2	EUGE	0	0	0	0	1	8	EZBM	0.9	-
Myrtaceae	Eugenia	feijoi	8	3	2	EUGF	0	0	0	0	1	15	EZBM	0.9	-
Myrtaceae	Eugenia	florida	11	2	3	EUGG	0	0	0	0	4	16	EZBM	0.9	-
Myrtaceae	Eugenia	lambertiana	8	3	2	EUGK	0	0	0	0	3	12	EZBM	0.9	-
Myrtaceae	Eugenia	latifolia	7	2	2	EUGL	0	0	0	0	1	8	EZBM	0.9	-
Myrtaceae	Eugenia	macrocalyx	8	3	2	EUGM	0	0	0	0	4	10	EZBM	0.9	-
Myrtaceae	Eugenia	omissa	6	1	2	EUGO	0	0	0	0	1	12	EZBM	0.9	-
Myrtaceae	Eugenia	patrisii	8	3	2	EUGP	0	1	0	1	5	15	EZBM	0.9	-
Myrtaceae	Eugenia	pseudopsidium	5	0	2	EUGQ	0	0	0	0	4	10	EZBM	0.9	-
Myrtaceae	Eugenia	punicifolia	1	0	1	EUGR	0	0	0	0	5	5	EZBM	0.9	-
Myrtaceae	Eugenia	ramiflora	3	2	1	EUGS	0	0	0	0	2	3	EZBM	0.9	-
Myrtaceae	Eugenia	tapacumensis	2	1	1	EUGT	0	0	0	0	4	4	EZBM	0.9	-
Myrtaceae	Marlierea	montana	9	0	3	MARM	0	0	0	0	5	17	EZBM	-	-
Myrtaceae	Marlierea	schomburgkiana	6	1	2	MARS	0	0	0	0	1	15	EZBM	-	-
Myrtaceae	Myrcia	amazonica	9	0	3	MYRA	0	0	0	0	5	17	EZBM	-	-
Myrtaceae	Myrcia	bracteata	5	0	2	MYRB	0	0	0	0	4	6	EZBM	-	-
Myrtaceae	Myrcia	citrifolia	5	0	2	MYRC	0	0	0	0	1	13	EZBM	-	-
Myrtaceae	Myrcia	decorticans	14	1	4	MYRD	0	0	0	0	1	30	EZBM	-	-
Myrtaceae	Myrcia	deflexa	7	2	2	MRYE	0	0	0	0	2	15	EZBM	-	-
Myrtaceae	Myrcia	fallax	10	1	3	MYRF	0	0	0	0	5	16	EZBM	-	-
Myrtaceae	Myrcia	graciliflora	5	0	2	MYRG	0	0	0	0	3	6	EZBM	-	-
Myrtaceae	Myrcia	guianensis	5	0	2	MYRH	0	0	0	0	6	15	EZBM	-	-
Myrtaceae	Myrcia	inaequiloba	5	0	2	MYRI	0	0	0	0	3	14	EZBM	-	-
Myrtaceae	Myrcia	magnoliifolia	11	2	3	MYRJ	0	0	0	0	3	22	EZBM	-	-
Myrtaceae	Myrcia	multiflora	5	0	2	MYRK	0	0	0	0	1	10	EZBM	-	-
Myrtaceae	Myrcia	pistrinalis	5	0	2	MYRM	0	0	0	0	1	15	EZBM	-	-
Myrtaceae	Myrcia	pyrifolia	6	1	2	MYRN	0	0	0	0	5	10	EZBM	-	-
Myrtaceae	Myrcia	rufipila	8	3	2	MYRO	0	0	0	0	1	15	EZBM	-	-
Myrtaceae	Myrcia	saxatilis	1	0	1	MYRP	0	0	0	0	1	5	EZBM	-	-
Myrtaceae	Myrcia	servata	14	1	4	MYRR	0	0	0	0	1	30	EZBM	-	-
Myrtaceae	Myrcia	spendens	7	2	2	MYRS	0	0	0	0	4	8	EZBM	-	-
Myrtaceae	Myrcia	sylvatica	5	0	2	MYRT	0	0	0	0	5	6	EZBM	-	-
Myrtaceae	Myrcia	tomentosa	6	1	2	MYRU	0	0	0	0	1	13	EZBM	-	-
Myrtaceae	Myrciaria	floribunda	8	3	2	MYRV	0	0	0	0	6	10	EZBM	-	-
Myrtaceae	Myrciaria	vismiifolia	6	1	2	MYRW	0	0	0	0	5	10	EZBM	-	-
Myrtaceae	Psidium	guineense	5	0	2	PSIG	0	0	0	0	4	7	EZBM	-	-
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Nyctaginaceae	Guapira	olfersiana	14	1	4	GUAA	0	0	0	0	5	30	EZBM	-	-
Nyctaginaceae	Neea	floribunda	12	3	3	NEEA	827	0	5	832	4	20	EZ	0.75	-
Ochnaceae	Ouratea	decagyna	10	1	3	OURD	0	0	0	0	4	25	EZB	-	-
Ochnaceae	Ouratea	guianensis	2	1	1	OURG	0	2	0	2	4	5	EZ	-	Roux
Ochnaceae	Ouratea	melinonii	2	1	1	OURM	0	17	0	17	-	-	EZ	-	Roux
Olacaceae	Chaunochiton	kappleri	12	3	3	CHAU	0	0	18	18	5	25	EZBM	0.58	-
Olacaceae	Dulacia	guianensis	16	3	4	DULA	0	0	1	1	1	30	EZBM	0.8	-
Olacaceae	Heisteria	cauliflora	8	3	2	HEIC	0	0	0	0	6	7	EZBM	0.8	-
Olacaceae	Heisteria	densifrons	8	3	2	HEID	7	1	10	18	4	15	EZBM	0.8	-
Olacaceae	Minquartia	guianensis	15	2	4	MING	0	5	7	12	5	30	EZBM	0.9	Nozeran
Olacaceae	Ptychopetalum	olacoides	11	2	3	PTYO	2	0	0	2	5	20	EZBM	-	-
Piperaceae	Piper	arboreum	7	2	2	PIPA	0	0	0	0	5	7	EZBRC	-	-
Polygonaceae	Coccoloba	latifolia	6	1	2	COCL	0	0	0	0	5	12	EZBM	-	-
Polygonaceae	Coccoloba	mollis	14	1	4	COCM	0	0	0	0	5	30	EZBM	-	-
Polygonaceae	Triplaris	surinamensis	10	1	3	TRIV	0	0	0	0	4	25	AN	-	-
Proteaceae	Euplassa	pinnata	12	3	3	EUPL	0	1	0	1	1	18	AN	-	-
Proteaceae	Panopsis	sessilifolia	12	3	3	PANS	0	0	0	0	6	20	HY	-	-
Proteaceae	Roupala	montana	6	1	2	ROUM	0	0	0	0	4	7	AN	-	-
Quiinaceae	Lacunaria	crenata	8	3	2	LACC	0	4	23	27	5	13	EZM	0.98	-
Quiinaceae	Lacunaria	jenmani	7	2	2	LACJ	0	0	0	0	5	15	EZM	-	-
Quiinaceae	Lacunaria	umbonata	6	1	2	LACU	0	0	0	0	0	6	EZM	-	-
Quiinaceae	Quiina	guianensis	7	2	2	QUIG	0	0	0	0	3	7	EZ	-	-
Quiinaceae	Quiina	macrophylla	12	3	3	QUIM	0	0	0	0	0	18	EZ	-	-
Quiinaceae	Quiina	obovata	15	2	4	QUII	0	0	0	0	5	30	EZ	-	Chamberlain
Quiinaceae	Quiina	oiapocensis	14	1	4	QUIJ	0	0	0	0	0	30	EZ	-	Chamberlain
Quiinaceae	Quiina	sessilis	6	1	2	QUIS	0	0	0	0	0	10	EZ	-	-
Quiinaceae	Touroulia	guianensis	7	2	2	TOUG	1	0	0	1	3	15	EZ	-	-
Rhabdodendraceae	Rhabdodedron	amazonicum	7	2	2	RHAB	0	2	0	2	4	15	EZ	-	-
Rhamnaceae	Ziziphus	cinamomum	4	3	1	ZIZI	3	0	0	3	-	-	EZ	-	-
Rhizophoraceae	Cassipourea	guianensis	14	1	4	CASU	0	19	0	19	5	30	EZ(myrmec)		Roux
Rhizophoraceae	Rhizophora	racemosa	7	2	2	RHIZ	0	0	0	0	4	10	AUT	-	-
Rosaceae	Prunus	myrtifolia	11	2	3	PRUN	0	0	0	0	3	20	EZ	-	-
Rubiaceae	Alibertia	edulis	4	3	1	ALIE	0	0	0	0	3	5	EZ	-	-
Rubiaceae	Alibertia	myrciifolia	5	0	2	ALIM	0	0	0	0	4	11	EZM	-	-
Rubiaceae	Alibertia	surinamensis	2	1	1	ALIS	0	0	0	0	1	5	EZ	-	-
Rubiaceae	Alseis	longifolia	7	2	2	ALSE	0	0	0	0	1	15	AN	-	-
Rubiaceae	Amaioua	corymbosa	6	1	2	AMAC	0	0	0	0	3	10	EZ	0.7	-
Rubiaceae	Amaioua	guianensis	7	2	2	AMAG	0	0	0	0	5	15	EZ	0.7	-
Rubiaceae	Bertiera	guianensis	4	3	1	BERG	0	0	0	0	3	5	EZ	-	-
Rubiaceae	Capirona	decorticans	16	3	4	CAPI	8	0	0	8	4	30	AN	-	-
Rubiaceae	Chimarrhis	turbinata	19	3	5	CHIM	25	2	18	45	4	37	EZ	0.85	Petit
Rubiaceae	Chomelia	tenuiflora	3	2	1	CHOM	0	0	0	0	3	3	EZ	-	-
Rubiaceae	Coussarea	mapourioides	4	3	1	COUL	0	0	0	0	3	5	EZ	-	-
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Rubiaceae	Coussarea	micrococca	4	3	1	COUM	0	0	0	0	1	5	EZ	-	-
Rubiaceae	Coussarea	paniculata	8	3	2	COUN	0	0	0	0	4	12	EZ	-	-
Rubiaceae	Coussarea	racemosa	8	3	2	COUO	0	0	2	2	3	12	EZ	0.8	-
Rubiaceae	Coutarea	hexandra	2	1	1	COUP	0	0	0	0	3	5	AN	-	-
Rubiaceae	Duroia	amapana	7	2	2	DURA	0	0	0	0	3	15	EZBM	0.9	Fagerlind
Rubiaceae	Duroia	aquatica	8	3	2	DURB	2	2	11	15	4	15	EZBM	0.9	Fagerlind
Rubiaceae	Duroia	eriopila	7	2	2	DURE	0	0	20	20	5	15	EZBM	0.9	Fagerlind
Rubiaceae	Duroia	longiflora	16	3	4	DURL	0	0	0	0	3	27	EZBM	0.9	Fagerlind
Rubiaceae	Duroia	micrantha	4	3	1	DURM	0	3	0	3	-	-	EZBM	0.9	Fagerlind
Rubiaceae	Faramea	corymbosa	8	3	2	FARA	0	0	0	0	1	6	EZ	-	-
Rubiaceae	Faramea	costata	4	3	1	FARC	0	0	0	0	4	5	EZ	-	-
Rubiaceae	Faramea	guianensis	4	3	1	FARG	0	0	0	0	3	3	EZ	-	-
Rubiaceae	Faramea	multiflora	8	3	2	FARM	0	0	0	0	4	10	EZ	-	-
Rubiaceae	Faramea	occidentalis	8	3	2	FARO	0	0	0	0	5	12	EZ	-	-
Rubiaceae	Faramea	quadricostata	4	3	1	FARQ	0	0	0	0	4	4	EZ	-	-
Rubiaceae	Ferdinandusa	paraensis	11	2	3	FERD	0	1	0	1	3	20	AN	-	-
Rubiaceae	Genipa	americana	12	3	3	GENA	0	0	0	0	5	25	EZ	-	-
Rubiaceae	Genipa	spruceana	12	3	3	GENS	0	0	0	0	4	20	EZ	-	-
Rubiaceae	Gonzalagunia	dicocca	4	3	1	GONZ	0	0	0	0	4	4	EZ	-	-
Rubiaceae	Guettarda	acreana	10	1	3	GUEA	103	0	0	103	4	20	EZ	-	Aubreville
Rubiaceae	Guettarda	macrantha	7	2	2	GUAM	0	0	0	0	1	8	EZ	-	-
Rubiaceae	Isertia	coccinea	6	1	2	ISEC	0	0	0	0	5	12	EZ	-	-
Rubiaceae	Isertia	hypoleuca	7	2	2	ISEH	0	0	0	0	5	15	EZ	-	-
Rubiaceae	Isertia	parviflora	5	0	2	ISEP	0	0	0	0	5	12	EZ	-	-
Rubiaceae	Isertia	spiciformis	6	1	2	ISES	0	0	0	0	5	12	EZ	-	-
Rubiaceae	Ixora	gracilifolia	4	3	1	IXOR	0	0	0	0	5	5	EZ	-	-
Rubiaceae	Pagamea	guianensis	5	0	2	PAGG	0	0	0	0	6	13	EZ	-	-
Rubiaceae	Palicourea	calophylla	2	1	1	PALC	0	0	0	0	4	5	EZ	-	-
Rubiaceae	Palicourea	crocea	8	3	2	PALD	0	0	0	0	6	6	EZ	-	-
Rubiaceae	Palicourea	guianensis	6	1	2	PALI	3	0	2	5	6	15	EZ	0.63	-
Rubiaceae	Palicourea	longiflora	6	1	2	PALL	0	0	0	0	5	15	EZ	-	-
Rubiaceae	Palicourea	rigida	1	0	1	PALM	0	0	0	0	3	5	EZ	-	-
Rubiaceae	Posoqueria	latifolia	7	2	2	POSO	1	14	85	100	-	12	EZ	0.71	-
Rubiaceae	Psychotria	erecta	3	2	1	PSYE	0	0	0	0	4	3	EZ	-	-
Rubiaceae	Psychotria	racemosa	4	3	1	PSYR	0	0	0	0	4	4	EZ	-	-
Rubiaceae	Rudgea	cornigera	4	3	1	RUDC	0	0	0	0	3	5	EZ	-	-
Rubiaceae	Rudgea	hostmanniana	8	3	2	RUDH	0	0	0	0	5	6	EZ	-	-
Rubiaceae	Tocoyena	guianensis	7	2	2	TOCK	0	0	0	0	3	7	EZ	-	-
Rutaceae	Erythrochiton	brasiliensis	8	3	2	ERYC	0	0	0	0	4	6	AUT	-	-
Rutaceae	Esenbeckia	cowanii	8	3	2	ESEC	0	0	0	0	0	6	SZ(myrm)	-	-
Rutaceae	Esenbeckia	pilocarpoides	8	3	2	ESEP	0	0	0	0	1	10	SZ(myrm)	-	-
Rutaceae	Galipea	trifoliata	7	2	2	GALI	0	0	0	0	3	15	AUT	-	-
Sapindaceae	Cupania	diphylla	8	3	2	CUPD	0	0	0	0	2	10	EZ	-	-
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Sapindaceae	Cupania	hirsuta	7	2	2	CUPH	0	1	0	1	4	15	EZ	-	-
Sapindaceae	Cupania	scrobiculata	7	2	2	CUPS	0	2	1	3	6	10	EZ	0.85	-
Sapindaceae	Dodonaea	viscosa	4	3	1	DODV	0	0	0	0	4	4	HY	-	-
Sapindaceae	Matayba	arborescens	7	2	2	MATA	0	1	3	4	6	15	EZ	0.9	-
Sapindaceae	Matayba	guianensis	8	3	2	MATG	0	0	0	0	3	15	EZ	-	-
Sapindaceae	Matayba	opaca	9	0	3	MATO	0	0	0	0	5	20	EZ	-	-
Sapindaceae	Pseudima	frutescens	8	3	2	PSEA	0	0	0	0	5	14	EZ	-	-
Sapindaceae	Talisia	elephantipes	16	3	4	TALE	0	0	0	0	1	30	EZ	-	-
Sapindaceae	Talisia	furfuracea	16	3	4	TALF	0	0	0	0	0	30	EZ	-	-
Sapindaceae	Talisia	guianensis	8	3	2	TALG	0	0	0	0	3	13	EZ	-	-
Sapindaceae	Talisia	longifolia	8	3	2	TALL	0	0	0	0	4	12	EZ	-	-
Sapindaceae	Talisia	megaphylla	8	3	2	TALM	0	0	112	112	6	15	EZ	0.9	Chamberlain
Sapindaceae	Talisia	micrantha	4	3	1	TALN	0	0	0	0	4	4	EZ	-	-
Sapindaceae	Talisia	mollis	8	3	2	TALO	0	0	0	0	3	8	EZ	-	-
Sapindaceae	Talisia	praealta	12	3	3	TALP	0	0	0	0	4	20	EZ	-	-
Sapindaceae	Talisia	retusa	12	3	3	TALR	0	0	0	0	0	20	EZ	-	-
Sapindaceae	Talisia	sylvatica	8	3	2	TALS	0	0	0	0	4	15	EZ	-	-
Sapindaceae	Toulicia	guianensis	8	3	2	TOUG	0	0	0	0	1	15	AN	-	-
Sapindaceae	Toulicia	pulvinata	8	3	2	TOUP	0	0	0	0	5	15	AN	-	-
Sapindaceae	Vouarana	guianensis	8	3	2	VOUG	0	0	0	0	3	15	EZ	-	-
Sapotaceae	Chrysophyllum	argenteum	12	3	3	CHRB	3	1	0	4	4	20	EZ	1	-
Sapotaceae	Chrysophyllum	cuneifolium	11	2	3	CHRC	3	0	0	3	5	20	EZ	1	-
Sapotaceae	Chrysophyllum	lucentifolium	4	3	1	CHRL	58	0	0	58	-	-	EZ	1	-
Sapotaceae	Chrysophyllum	pomiferum	15	2	4	CHRO	5	3	2	10	2	35	EZM	1	-
Sapotaceae	Chrysophyllum	prieurii	16	3	4	CHRR	1	2	74	77	4	30	EZ	01.05.00	-
Sapotaceae	Chrysophyllum	sanguinolentum	12	3	3	CHRS	5	6	39	50	3	25	EZ	0.7	-
Sapotaceae	Chrysophyllum	venezuelanense	4	3	1	CHRV	1	0	0	1	-	-	EZ	1	-
Sapotaceae	Ecclinusa	guianensis	15	2	4	ECCG	2	14	18	34	5	30	EZ	0.7	-
Sapotaceae	Ecclinusa	ramiflora	4	3	1	ECCR	1	0	0	1	-	-	EZ	0.7	-
Sapotaceae	Manilkara	bidentata	19	3	5	MANC	17	2	25	44	5	40	EZ	01.01.00	Aubreville
Sapotaceae	Manilkara	huberi	16	3	4	MANH	1	0	0	1	4	30	EZ	01.01.00	Aubreville
Sapotaceae	Micropholis	cayennensis	4	3	1	MIDC	6	0	0	6	-	-	EZ	0.78	-
Sapotaceae	Micropholis	egensis	12	3	3	MIDE	1	3	0	4	3	20	EZ	0.78	-
Sapotaceae	Micropholis	guyanensis	18	2	5	MIDG	19	8	216	243	6	40	EZ	0.78	-
Sapotaceae	Micropholis	longipedicellata	4	3	1	MIDL	5	0	0	5	-	-	EZ	0.78	-
Sapotaceae	Micropholis	mensalis	4	3	1	MIDN	4	0	0	4	-	-	EZ	0.78	-
Sapotaceae	Micropholis	porphyrocarpa	4	3	1	MIDP	1	0	0	1	-	-	EZ	0.78	-
Sapotaceae	Micropholis	venulosa	16	3	4	MIDV	0	4	1	5	4	35	EZ	0.78	-
Sapotaceae	Pouteria	ambelaniifolia	4	3	1	PPAA	1	0	0	1	-	-	EZ	-	Aubreville
Sapotaceae	Pouteria	bangii	16	3	4	PPAZ	0	0	0	0	4	30	EZ	-	-
Sapotaceae	Pouteria	bilocularis	4	3	1	PPBA	0	2	0	2	-	-	EZ	-	Aubreville
Sapotaceae	Pouteria	caimito	19	3	5	PPCA	0	0	0	0	3	40	EZ	-	Aubreville
Sapotaceae	Pouteria	cicatricata	4	3	1	PPCB	0	1	0	1	-	-	EZ	-	Aubreville
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Sapotaceae	Pouteria	cladantha	11	2	3	PPCC	0	0	0	0	3	20	EZ	-	-
Sapotaceae	Pouteria	coriacea	7	2	2	PPCD	0	0	0	0	3	15	EZ	-	Aubreville
Sapotaceae	Pouteria	cuspidata	16	3	4	PPCE	0	6	0	6	4	27	EZ	-	Aubreville
Sapotaceae	Pouteria	decorticans	4	3	1	PPDA	4	0	0	4	-	-	EZ	-	Aubreville
Sapotaceae	Pouteria	egregia	19	3	5	PPEA	0	0	0	0	1	40	EZ	-	Aubreville
Sapotaceae	Pouteria	engleri	11	2	3	PPEB	0	2	0	2	6	25	EZ	-	Aubreville
Sapotaceae	Pouteria	eugeniifolia	4	3	1	PPEC	7	0	0	7	-	-	EZ	-	Aubreville
Sapotaceae	Pouteria	filipes	12	3	3	PPFA	0	0	0	0	1	25	EZ	-	Aubreville
Sapotaceae	Pouteria	glomerata	4	3	1	PPGA	8	0	0	8	-	-	EZ	-	Aubreville
Sapotaceae	Pouteria	gonggrijpii	12	3	3	PPGB	17	1	3	21	4	25	EZ	1	Aubreville
Sapotaceae	Pouteria	grandis	16	3	4	PPGC	0	1	0	1	1	30	EZ	-	Aubreville
Sapotaceae	Pouteria	guianensis	16	3	4	PPGD	29	4	169	202	5	35	EZM	01.01.15	Aubreville
Sapotaceae	Pouteria	hispida	11	2	3	PPHA	0	0	0	0	2	17	EZ	-	Aubreville
Sapotaceae	Pouteria	jariensis	4	3	1	PPJA	2	0	0	2	-	-	EZ	-	Aubreville
Sapotaceae	Pouteria	laevigata	4	3	1	PPLA	2	0	0	2	-	-	EZ	-	Aubreville
Sapotaceae	Pouteria	melanopoda	16	3	4	PPMA	4	0	57	61	4	30	EZ	01.05.00	Aubreville
Sapotaceae	Pouteria	oblanceolata	4	3	1	PPOA	2	0	0	2	-	-	EZ	-	Aubreville
Sapotaceae	Pouteria	reticulata	4	3	1	PPRA	0	1	0	1	-	-	EZ	-	Aubreville
Sapotaceae	Pouteria	retinervis	4	3	1	PPRB	0	1	0	1	-	-	EZ	-	Aubreville
Sapotaceae	Pouteria	sagotiana	7	2	2	PPSA	1	0	0	1	4	12	EZ	-	Aubreville
Sapotaceae	Pouteria	singularis	4	3	1	PPSB	1	0	0	1	-	-	EZ	-	Aubreville
Sapotaceae	Pouteria	torta	4	3	1	PPTA	1	4	0	5	-	-	EZ	-	Aubreville
Sapotaceae	Pouteria	trigonosperma	10	1	3	PPTB	0	0	0	0	5	25	EZ	-	-
Sapotaceae	Pouteria	venosa	16	3	4	PPVA	0	0	0	0	3	35	EZ	-	Aubreville
Sapotaceae	Pouteria	virescens	4	3	1	PPVB	0	1	0	1	-	-	EZ	-	Aubreville
Sapotaceae	Pradosia	cochlearia	19	3	5	PRAC	0	0	175	175	-	40	EZ	0.9	-
Sapotaceae	Pradosia	ptychandra	12	3	3	PRAP	11	8	1	20	4	25	EZ	0.87	-
Sapotaceae	Pradosia	surinamensis	12	3	3	PRAS	0	0	0	0	4	25	EZ	-	-
Simaroubaceae	Quassia	amara	3	2	1	QUAV	0	0	0	0	5	4	EZ	-	-
Simaroubaceae	Simaba	cedron	7	2	2	SIMC	0	0	109	109	3	10	EZ	0.55	-
Simaroubaceae	Simaba	morettii	4	3	1	SIMM	0	1	0	1	-	-	EZ	0.55	-
Simaroubaceae	Simaba	multiflora	8	3	2	SIMN	0	0	20	20	5	15	EZ	0.55	-
Simaroubaceae	Simarouba	amara	15	2	4	SINA	0	1	1	2	5	30	EZM	0.45	Scarrone
Solanaceae	Brunfelsia	guianensis	3	2	1	BRUN	0	0	0	0	2	4	EZ	-	-
Solanaceae	Solanum	asperum	6	1	2	SOLA	0	0	0	0	6	6	EZ	-	-
Solanaceae	Solanum	crinitum	2	1	1	SOLC	0	0	0	0	5	5	EZ	-	-
Solanaceae	Solanum	leucocarpon	6	1	2	SOLL	0	0	0	0	6	8	EZ	-	-
Solanaceae	Solanum	paludosum	2	1	1	SOLP	0	0	0	0	6	5	EZ	-	-
Solanaceae	Solanum	rugosum	2	1	1	SOLR	0	0	0	0	5	5	EZ	-	-
Sterculiaceae	Guazuma	ulmifolia	12	3	3	GUAZ	0	0	0	0	3	20	EZM	-	-
Sterculiaceae	Herrania	kanukuensis	8	3	2	HERK	0	0	0	0	4	8	EZ	-	-
Sterculiaceae	Sterculia	excelsa	15	2	4	STEE	6	0	0	6	6	33	SZRM	0.57	Rauh
Sterculiaceae	Sterculia	frondosa	15	2	4	STEF	2	0	0	2	-	35	SZRM	0.57	Rauh
...															

Family	Genus	Species	PFT	SG	HG	Code	NNOU	NPSE	NPAR	NTOT	VRI	Height	Disp.	Density	Architecture
...															
Sterculiaceae	Sterculia	pruriens	15	2	4	STEP	18	5	82	105	6	34	SZRM	0.57	Rauh
Sterculiaceae	Theobroma	subincanum	12	3	3	THES	3	1	62	66	1	18	EZM	0.55	Nozeran
Styracaceae	Styrax	glabratus	11	2	3	STYR	0	0	0	0	4	20	EZ	-	Roux
Symplocaceae	Symplocos	guianensis	5	0	2	SYMP	0	0	0	0	6	8	EZ	-	-
Theaceae	Gordonia	fruticosa	11	2	3	GORD	0	0	0	0	4	25	AN	-	-
Theophrastaceae	Clavija	lancifolia	4	3	1	CLAC	0	0	0	0	5	4	EZ	-	-
Tiliaceae	Apeiba	echinata	14	1	4	APEE	0	0	29	29	6	35	EZ	0.38	Troll
Tiliaceae	Apeiba	glabra	14	1	4	APEG	3	0	0	3	4	30	EZ	0.38	Troll
Tiliaceae	Apeiba	petoumo	14	1	4	APEP	4	0	0	4	-	30	EZ	0.38	Troll
Tiliaceae	Apeiba	tibourbou	10	1	3	APET	0	0	0	0	5	25	EZ	0.38	Troll
Tiliaceae	Luehea	speciosa	7	2	2	LUEH	0	0	0	0	1	10	AN	-	Troll
Tiliaceae	Lueheopsis	rosea	14	1	4	LUER	0	0	2	2	-	30	AN	0.4	-
Tiliaceae	Lueheopsis	rugosa	14	1	4	LUES	0	0	9	9	3	35	AN	0.65	-
Ulmaceae	Trema	micrantha	6	1	2	TREM	0	0	0	0	6	8	EZ	-	-
Verbenaceae	Aegiphila	integrifolia	6	1	2	AEGI	0	0	0	0	4	8	EZ	-	-
Verbenaceae	Citharexylum	macrophyllum	11	2	3	CITM	0	0	0	0	5	20	EZ	-	-
Verbenaceae	Citharexylum	spinosum	6	1	2	CITS	0	0	0	0	4	15	EZ	-	-
Verbenaceae	Vitex	compressa	10	1	3	VITE	0	1	0	1	6	20	EZ	-	-
Verbenaceae	Vitex	triflora	6	1	2	VITT	0	0	0	0	4	13	EZ	-	-
Violaceae	Leonia	glycycarpa	11	2	3	LEON	0	0	6	6	5	20	EZM	0.7	-
Violaceae	Paypayrola	guianensis	7	2	2	PAYP	0	0	0	0	5	10	AUT	-	-
Violaceae	Rinorea	flavescens	8	3	2	RINF	0	0	0	0	1	10	AUT	-	-
Violaceae	Rinorea	pectino-squamata	8	3	2	RINO	0	6	11	17	4	10	AUT	0.75	Fagerlind
Violaceae	Rinorea	pubiflora	8	3	2	RINP	0	0	0	0	5	8	AUT	-	-
Violaceae	Rinorea	riana	4	3	1	RINR	0	0	0	0	4	4	AUT	-	-
Vochysiaceae	Erisma	uncinatum	15	2	4	ERIU	34	0	0	34	4	35	AN	0.58	-
Vochysiaceae	Qualea	caercula	18	2	5	QUAC	0	0	0	0	5	45	AN	-	-
Vochysiaceae	Qualea	dinizii	17	1	5	QUAD	0	0	0	0	5	40	AN	-	-
Vochysiaceae	Qualea	rosea	18	2	5	QUAE	65	1	181	247	5	50	AN	0.71	Massart
Vochysiaceae	Ruizterania	albiflora	18	2	5	RUIZ	3	1	23	27	5	45	AN	0.7	-
Vochysiaceae	Vochysia	densiflora	14	1	4	VOCD	0	0	0	0	5	30	AN	-	-
Vochysiaceae	Vochysia	guyanensis	15	2	4	VOCG	0	1	0	1	4	35	AN	-	-
Vochysiaceae	Vochysia	surinamensis	15	2	4	VOCS	0	0	0	0	4	30	AN	-	-
Vochysiaceae	Vochysia	tetraphylla	18	2	5	VOCT	0	0	0	0	6	40	AN	-	-
Vochysiaceae	Vochysia	tomentosa	18	2	5	VOCU	2	2	3	7	6	50	AN	0.45	-

Danksagung

Diese Arbeit entstand am Wissenschaftlichen Zentrum für Umweltsystemforschung (WZIII), einem interdisziplinären Institut an der Universtät Gesamthochschule Kassel.

Danken möchte ich an dieser Stelle Herrn Bossel für seine Bereitschaft, selbst nach der Emeritierung dieser Arbeit als Erstgutachter zur Verfügung zu stehen. Durch die Offenheit des Fachbereiches Physik fachfremden Themen gegenüber konnte die Arbeit in der vorliegenden Form verwirklicht werden. Insbesondere Herrn Fricke sei an dieser Stelle für die Zweitbegutachtung sowie für die Möglichkeit zur Einreichung der Arbeit in seiner momentanen Form gedankt. Weiterer Dank gebührt Andreas Huth für die Betreuung dieser Arbeit in angenehmer, freundschaftlicher Atmosphäre. Mit ihm und Thomas Ditzer fanden etliche fruchtbare Fachdiskussionen statt. Ein dreimonatiger Forschungsaufenthalt in den Wäldern Borneos wurde durch ihr DFG-Projekt möglich gemacht. Kai Reinhard, Frank Kaspar und Thomas Noll als Raumteiler und Mitstudenten verdanke ich etliche hilfreiche Tipps und eine entspannte Arbeitsatmosphäre.

Allen anderen Mitgliedern des WZIII danke ich für die angenehme Arbeitsatmosphäre, insbesondere Ulla Marquard für die leckeren Kuchen.

Ohne unsere nationalen und internationalen Kooperationspartner hätte diese Arbeit in ihrem Umfang nicht durchgeführt werden können. Dem Malaysian-German Sustainable Forest Management Project am Forestry Department in Sandakan und allen Mitgliedern verdanke ich eine lehrreiche und wundervolle Zeit in Sabah, Malaysia. Insbesondere Robert Ong und Peter Lagan möchte ich für ihren freundlichen Empfang danken. Reinhold Glauner von der Bundesanstalt für Holz- und Forstwirtschaft, Hamburg, gebührt Dank für die Einführung in das malayische Forestry Department, sowie für fachliche Unterstützung der Kasseler Modellierungsprojekte. Masirom Rundi danke ich für sein Wissen über Lichtbedarf einzelner Baumarten. Mit Artur Gralla verbrachte ich eine angenehme Zeit im Regenwald. Zainal Abidin Jaafar und Hubert ”We are onto somethingPerol haben den notwendigen Humor mitgebracht.

Ludwig Kammesheidt (Institut für Waldbau, Universität Göttingen) und Jérôme Chave (Service de Physique de l'État condensé, Université Paris-Sud and Department of Ecology and Evolutionary Biology, Princeton University) danke ich für die erfolgreiche Zusammenarbeit und ihr Wissen über südamerikanische Wälder. Ihre Arbeiten haben eine Modellanwendung in Venezuela und Französisch Guayana erst möglich gemacht. Freundlicherweise haben sie mir ihre Artenlisten für den Anhang dieser Arbeit zur Verfügung gestellt.

Für die Verwendung etlicher Felddaten aus unterschiedlichsten Projekten bin ich allen Beteiligten dankbar, insbesondere Michael Kleine, Robert Ong, Mark Schlensog (Sabah), Ludwig Kammesheidt (Venezuela), Jérôme Chave und Bernard Riéra (Französisch Guayana).

Finanziert wurde diese Arbeit durch ein Projekt der Deutschen Forschungsgemeinschaft (DFG) und ein Promotionsstipendium des Otto-Braun-Fonds an der Universität Gesamthochschule Kassel.

Mein Dank gilt auch Susa Lewit und Robin Phipps für ihre Fehlerkorrekturen.

Meinen zwei Frauen, Dagi und Hannah Schneider, danke ich für all den Rest.