ECOLOGY AND LOGGING IN A TROPICAL RAIN FOREST IN GUYANA

With recommendations for forest management

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ECOLOGY AND LOGGING IN A TROPICAL RAIN FOREST IN GUYANA

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The Tropenbos Series presents the results of studies and research activities related to the conservation and wise utilization of forest lands in the humid tropics. The series continues and integrates the former Tropenbos Scientific and Technical Series. The studies published in this series have been carried out within the international Tropenbos programme. Occasionally, this series may present the results of other studies which contribute to the objectives of the Tropenbos programme.

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The investigations reported in this book were carried out at the Tropenbos-Guyana Programme. Coordinating agencies of the programme are: The Guyana Natural Resources Agency and the Utrecht University. Implementing agencies are University of Guyana (Depts. Biology and Forestry) and Utrecht University (Depts. Physical Geography, Plant Ecology and Vegetation Sciency, Ecophysiology, Herbarium), with the Guyana Forestry Commission, National Agricultural Research Institute, Hydromet Department, Lands & Surveys Department, University of Wageningen (Depts. Water Resources and Forestry), Free University of Amsterdam (Dept. Earth Sciences), CIRAD-Forêts (France, Staring Centre-DLO (The Netherlands, National University ETH (Switzerland), Imperial College (UK), Forest Products Laboratory (USA) and MAB-UNESCO (France).

CONTENTS

PREFACE

This book summarises the results of the first phase of the Tropenbos-Guyana Programme (1989-1993). It is largely based upon an internal report prepared for the Tropenbos Foundation in 1994 but some new information has been added on the basis of work that has progressed further since. The book also summarises the contributions for all Tropenbos authors who participated in the Tropenbos-Guyana Symposium held in Georgetown, June 6-8, 1994.

The emphasis of the book is on presenting all results in an integrative manner and similar style, rather then presenting all sub-projects in separate chapters. The finalization has been a slow progress but we feel the results are now put in a proper perspective; but not all subjects have received a similar amount of discussion in relation to previous work. It is of course to the reader to decide whether we have succeeded in writing a comprehensive and understandable book.

Obviously such a report cannot be written without the help of all others involved in the programme and we would like to thank all who have contributed to this report either by:
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1 INTRODUCTION

1.1 The Tropenbos Foundation

The Tropenbos Foundation was established in July 1988 to continue and expand the International Tropenbos Programme which was set up in 1986 by the Government of The Netherlands.

The main objectives of the Foundation are (Tropenbos 1992):

- To contribute to the conservation and wise use of tropical rain forests by generating knowledge and developing methodologies.
- To involve and strengthen local research institutions and capacity in relation to tropical rain forests.

In close cooperation with research institutions and Governments in a number of tropical countries, several major research sites have been established where multi-disciplinary programmes have been set up to produce results which have significance for the application on a local as well as on a broader scale. Currently programmes are being executed in Cameroon, Colombia, Côte d'Ivoire, Guyana and Indonesia. In addition, some activities are being executed in Ecuador and Gabon.

The Tropenbos-Guyana Programme started on September 1st, 1989. Due to the presence of a joint programme of the Utrecht University and the University of Guyana a fast start was possible. Originally the first phase terminated by September 1st, 1992. This phase was extended by the Tropenbos Foundation up to the end of 1992. The programme continued in 1993 (ad interim) and the second phase has started in January 1994.

1.2 Forest Exploitation and Forest Policy in Guyana

Guyana has a land area of approximately 21.5 million hectares, 14 million of which are covered with forest. Approximately five million hectares have been allocated to logging companies, in a zone parallel to the coast (Figure 1). Presently 1.5 million hectares have been selectively logged (van der Hout 1992). The size of the timber and wood-using industry has remained more or less equal over recent decades in terms of employment (10,000), production volume (94,000 m^3) and export revenues (4 million US$) (Tropenbos 1991). Greenheart (*Chlorocardium rodiei*[1]) is Guyana's most renowned timber resource and has traditionally constituted 70% of the country's timber exports. Potentially such an emphasis on one single species may lead to under-utilization of the forest resource in general and to (economic) extinction (cf. Teak (*Tectona grandis*), Gajanseni & Jordan 1990) and/or to genetic erosion (cf. Mahogany (*Swietenia mahagoni*), Rodan *et al.*

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[1] names and authorities follow Mennega *et al.* 1988 (except in this particular case of *C. rodiei* (Schomb.) Rohwer, Richter & v.d. Werff [syn. *Ocotea rodiaei* (Schomb.) Mez], which was renamed recently). No further reference to authorities is made in this report. Mostly vernacular names are used in the report, unless no such name is available. When first used the vernacular name will be followed by the scientific name in parentheses.

1992) of the species selected. At present Greenheart is considered to be over-harvested (GNRA 1989). As the size of the human population is small (800,000) and concentrated in the coastal area, pressure on the forest is low. Luning (1987) estimated the annual deforestation rate in 1985 to be negligible, a condition only rivalled worldwide by the neighbouring countries, Suriname and French Guiana. FAO (1988 in Reid 1992) gives an annual deforestation in the 1980's of 2000 ha (but note that 1.5 million ha has been selectively logged).
However, as the National Forest Policy and National Forestry Action Plan suffer from constrained implementation and a concise plan for conservation of forests is still lacking (Lindeman & Mori 1989), this is only reason for moderate optimism. At a time when commercial logging in Guyana is receiving more attention from foreign companies and investors (e.g. Colchester 1994) it is also necessary to focus on long term management policies for the forestry belt.

In 1979 the Guyana Forestry Commission (GFC) was founded, replacing the former Forest Department. In 1989 the Commission was placed under the Guyana Natural Resources Agency (GNRA). In 1985 a Draft National Forest Policy was produced. This policy encompasses social, economic as well as ecological objectives. Although delineating a course of action which should be followed, the Policy has not been legislated so far and thus its implementation is constrained (Tropenbos 1991).

At the moment there are three forms of land tenure with respect to forest exploitation:

- Timber Sales Agreements (TSA), for periods of over 25 years in areas larger than 50,000 acres (20,243 ha).
- Woodcutting Leases (WL), valid for a period of 3-5 years in smaller areas, annually renewable.
- State Forest Permissions (SFP), valid only for one year for the removal of specified volumes in even smaller areas.

Only TSAs require the preparation of a management plan.

There is one nature reserve in Guyana, the Kaieteur National Park.

1.3 The Tropenbos-Guyana Programme

The major aims of the Tropenbos-Guyana Programme have been formulated as "*to achieve an understanding of the lowland tropical rain forest ecosystems in the area to such a degree that timber harvesting (and possibly other non-wood forest products) under a sustainable forest management system can be achieved without it leading to biodegradation and loss of proper hydrological functions of the exploited system, while at the same time a satisfactory level of biodiversity is maintained and an appropriate area of rain forest can be conserved*". To achieve these aims, fundamental, applied and extension studies are carried out.

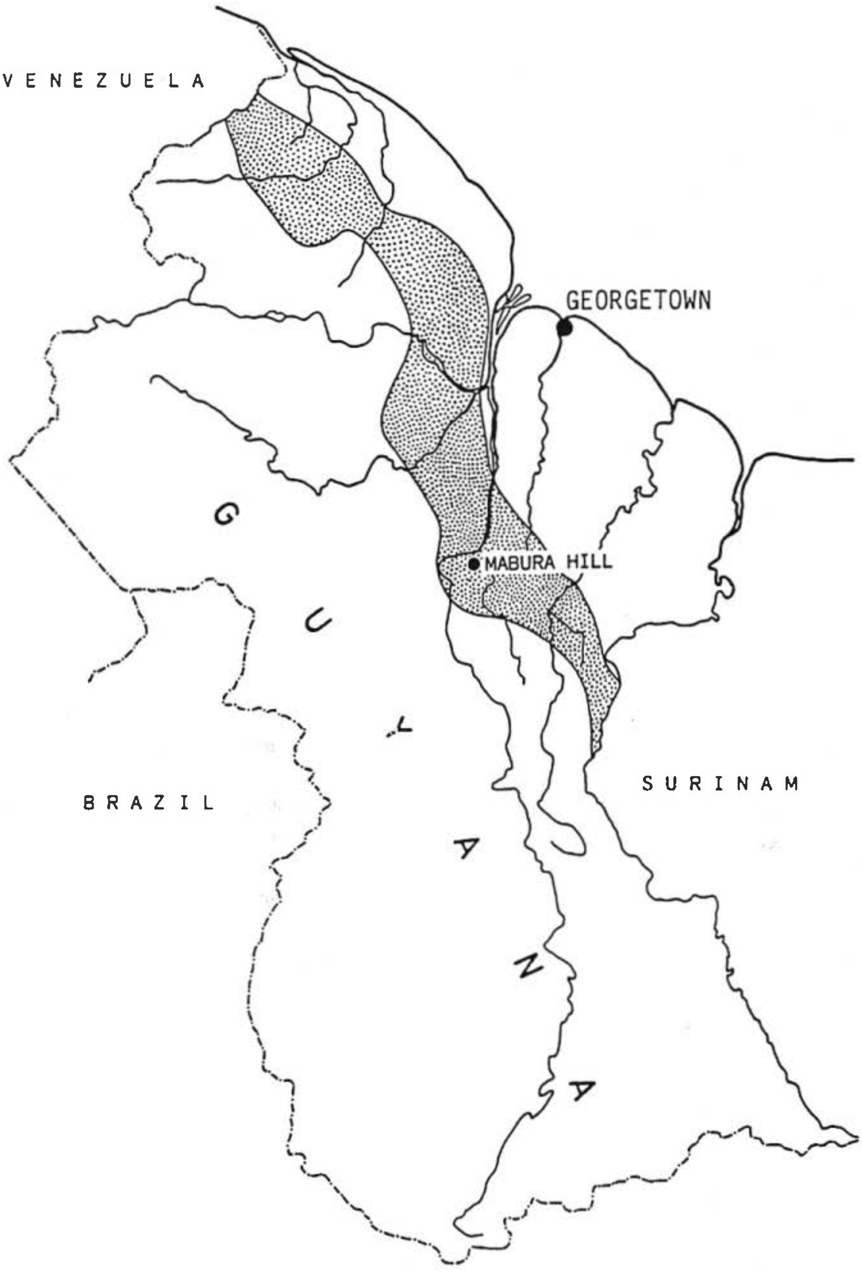


Figure 1. Map of Guyana with location of study site, Mabura Hill. The main forestry belt is shaded.

Logging affects the forest ecosystem in several ways:

- The population structure directly, by selectively taking out sound individuals of commercial species, thereby decreasing their absolute and relative abundance and increasing the same for non-commercial species (and defective individuals of commercial species).
- The hydrological cycle. While gross input (rain) will not change significantly with small-scale logging, processes such as interception, run-off, percolation, storage and stream discharge may change due to logging operations.
- The nutrient cycle. It is closely coupled to the hydrological cycle, as water is the main carrier for nutrients in the ecosystem. Changes in infiltration and run-off may speed up nutrient losses. Inevitably, logging will also change the nutrient cycle more directly as a large pulse of nutrients will be released from dead matter produced and a part of the nutrients will be exported from the system in the form of logs.
- Environmental circumstances. Due to the opening of the canopy, environmental factors and processes, such as light levels, average temperature, soil structure and decomposition all change in a specific manner. Not all species in the ecosystem will react similarly to such changes.

Based on the above-mentioned goals of the Foundation, the main effect of logging as listed above and the scientific expertise of the contributing agencies, the following comprehensive research programme was designed:

A: Inventory and projects of general value
The A projects include: A soil inventory of the DTL concession, resulting in a soil-landscape map; a vegetation map of the concession; a field guide, a hand lens key, a handbook on anatomical characteristics, a handbook on timber characteristics, and wood sample sets - all of 100 promising timber species of the Guyana forestry belt; a checklist of woody species of Guyana, checklists of the DTL area, and general common methodology wherever applicable. Additionally a literature compilation on publications and unpublished data related to forestry and ecology of tropical rain forests in Guyana has been carried out.

B: The hydrological balance and nutrient cycling
The B projects include: Gross input and output, influence of vegetation on input, influence of vegetation on output, moisture characteristics of the rooting zone - all these to be included in a water balance model. Nutrient concentrations in input and output, nutrient characteristics of mineral soil, nutrient characteristics of the organic part of the soil, integration of vegetation characteristics - all of this finally leading to a nutrient balance model.

C: Population structure, dynamics and reproduction of important tree species
The C projects include: Seedling survival and sapling establishment, seed rain dynamics, seed bank dynamics, and tree demography.

D: Growth and productivity in relation to environmental constraints.
The D projects include: Phenological studies, productivity and environmental constraints, nutrient limitation/shorter rotation, efficiency of nutrient utilization and acquisition of tree species growing on White Sands.

In a later stage two projects were added:

E: Logging intensities and botanical biodiversity
The E projects include: A thorough study of literature in relation to logging management trials, resulting in a logging intensity study, a study of botanical biodiversity and the effect of logging thereupon, the initiation of a field herbarium in Mabura Hill.

F: Radar remote sensing programme
The F project includes: A study of possible utilization of radar remote sensing in forest type recognition and biomass estimation.

1.4 Mabura Hill: previous work and site history

The field site of the Tropenbos-Guyana Programme is located near Mabura Hill (Figure 1), on the timber concession of Demerara Timbers Ltd (DTL). There is little or no agriculture in the area; and, apart from housing, some mining and hunting, there is no other significant land-use but logging.

Site development
Soil and forest-type maps of the area were prepared by Gross-Braun *et al.* (1966) and de Milde & de Groot (1970) respectively, in the framework of a national reconnaissance survey, sponsored by FAO and UNDP. Based on these results and an accessibility study carried out by Grayum (1970), further forest inventories were executed (The Great Falls Inventory, Guyana Forestry Commission 1970). A more detailed soil survey of the upper concession area, to investigate the possibilities of farming for the community to be established, was carried out in 1980 (Khan *et al.* 1980).
Subsequently, the state owned timber firm Demerara Woods Ltd. was founded and, with large investment from the Guyana Government, and through loans from the World Bank, IDB and EEC, building of a sawmillling complex and a township for staff and dependents took place from 1984 to 1986. The sawmill, at the time of construction said to be the largest on the South American continent, had a projected capacity of 230,000 m^3 of sawn wood per year. Production started in 1986 but the company ran into continuous financial problems. The company was put up for sale, as a part of a national divestment scheme, and was sold to a group of English investors, who merged their interest (now called Demerara Timbers Ltd.) into United Dutch Group (UDG). A management plan was developed in 1991 based on a 'Green Charter' of ten principles. In 1994 SGS-Forestry assessed and certified that DTL were adhering to their 'Green charter'. While this was not proof for sustainable forestry and several recommendations for improvement were made, the management of DTL was considered to have taken a very positive step towards wise forest management (SGS 1991). UDG encountered severe financial difficulties and since 1993 was in the hands of a receiver. UGG's principal bank continued to fund

DTL's activities until August 1995, when DTL was acquired by Primegroup Investments Ltd. The company continues to trade as DTL and stated that its commitment to wise forest management would be maintained.

Site research history
Plant collections in the area started in the 1800's, when botanists, such as R.H. Schomburgk and G.S. Jenman, visited the area (Ek 1990). The site became more accessible in the late 1970's and botanical collecting increased after that. Within the framework of the Flora of the Guianas programme, the first collections were made in 1981 by P.J.M. Maas and party, followed by Stoffers and party in 1982. By this time a good working relationship had been established between the University of Guyana and the Utrecht University on one hand, and the state owned Demerara Woods Ltd. on the other. A first Utrecht MSc project (on the ecology of epiphytes) was executed in the Mabura Hill area in 1985 (Comelissen & ter Steege 1988, ter Steege & Cornelissen 1988, 1989). Meanwhile the area kept attracting botanists and J. Pipoly and others made several collecting trips from 1986-1987. In 1989 the University of Guyana and the Utrecht University started a joint project and in the light of favourable logistics and good relations - Dr. G. Walcott was both Vice-Chancelor of the University of Guyana and a Director of Demerara Woods Ltd. - it was logical that the field site would be situated at Mabura Hill. This project was named "Forest Project Mabura Hill". Within the framework of this project an Ecological Reserve (900 ha) with a field station was established, botanical collections were made and several ecological research projects were carried out. In 1989 The Government of Guyana and the Government of The Netherlands agreed on establishing the Tropenbos-Guyana Programme, with the University of Guyana and Utrecht University as the main implementing agencies. The programme adopted and expanded the logistics of the Forest Project Mabura Hill. A comprehensive research programme was set up and several research projects were carried out (see above for general outline). A great number of MSc and PhD students worked in the area. The results of their projects were presented in a symposium in Georgetown, Guyana, June 1994 and form the basis of this book.

The research has been carried out exclusively in the central concession area of DTL, known as TSA/02/91. Several long term observation sites have been established and are to be regarded as permanent sampling plots. They include plots with observations on tree populations in logged and natural forest and gaps with observations on nutrient leaching. Unfortunately one logged PSP was accidentally destroyed by additional felling in December 1994. Main concentration points were the Ecological Reserve, the Waraputa compartment, and in a later stage Ekuk Compartment and West Pibiri Compartment. The location of sites with their names, abbreviations and short descriptions are given in Appendix 1.

1.5 Lay-out of this book

In the following chapter, a description of the forest ecosystem of the Mabura Hill area, based on the results of the research programme, is given. In chapter 3, the effects of logging on Greenheart bearing mixed forest are described. This chapter will also briefly review some earlier silvicultural work done in Guyana. In Chapter 4 some conclusions and recommendations for management are offered.

2 THE FOREST

2.1 Area description

Location
Guyana is situated on the north-eastern part of South America, between 56°20'W and 61°23'W and 1°10'N and 8°35'N. The main study site, Mabura Hill is located at approximately 5°13'N 58°48'W, in the main forestry belt (Figure 1).

Climate
The climate in Guyana is strongly influenced by the movement of the Intertropical Convergence Zone (ICZ). Due to the movement of the ICZ most climatic variables show a bi-modality through the year. There are two wet and two dry seasons but the dry season months have on average more than 100 mm of rain per month. A long wet season occurs from May to August and a short wet season from December to February. The remaining periods are drier, with October generally being the driest month. In November a thermic low pressure area develops in the Amazon basin, causing air masses to flow into the basin, thus diminishing the effect of the normal air convergence of the ICZ. Therefore, the December rainy season is less pronounced. Rainfall in Guyana is also strongly affected by the Pakaraima mountains in the west and Wilhelmina mountains in Suriname, in the east. As easterly winds prevail, orographic uplift and subsequent condensation causes a high annual rainfall of 4400 mm on the eastern sides of the mountains. The annual rainfall decreases to 1700 mm towards the east of the country, as this area and

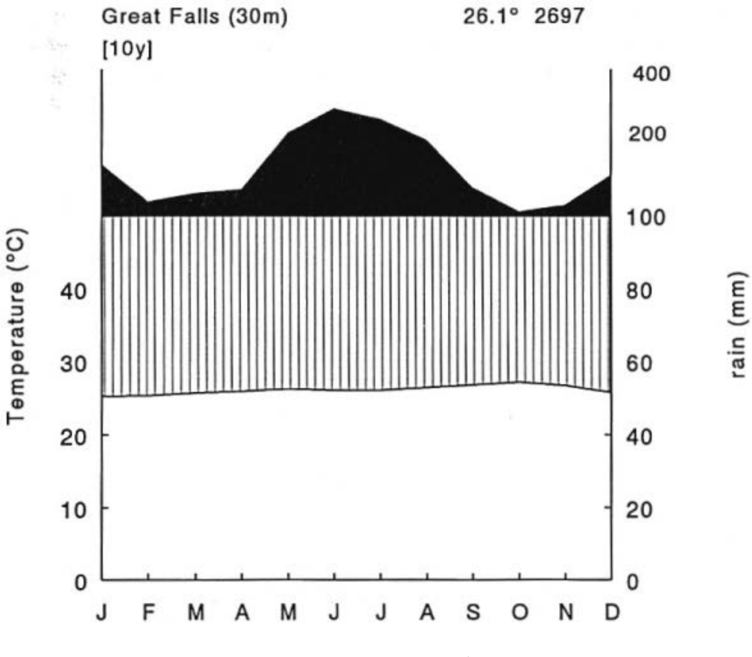


Figure 2. Climate diagram for Great Falls, 15 km east of Mabura Hill. After conventions of Walter & Lieth (1969).

western Suriname lie on the leeward side of the Wilhelmina mountains. The Mabura site lies immediately north-east of the Pakaraima mountains and has an annual rainfall of 2700 mm (Khan *et al.* 1980, see Figure 2). Year to year variation in rainfall may be high (ter Steege & Persaud 1990, Jetten 1994a). Monthly data for Mabura Hill from 1991 to 1993 are presented in Jetten (1994a).

The dry seasons are periods of lower cloud cover and thus have higher sunshine hours. On average sunshine amounts to 45% of the total day time (ter Steege 1994). Mean incoming short wave radiation (0.3-3 μm) is between 550 and 650 W m^{-2} at 2 p.m., while maximum values frequently exceed 800 W m^{-2}. Daily totals are between 11.3 to 14.2 MJ m^{-2} (Jetten 1994a). Based on the shortwave radiation measurements, an average daily PAR (Photosynthetic Active Radiation) of approximately 29.9 mol m^{-2} day^{-1} was calculated (ter Steege 1994). The values show good similarity with those of Borneo (4°58'N, 117°48'E, Brown 1993, Whitmore *et al.* 1993), who report 47% sunshine amounting to 5.7 hours per day, with an average of 35.3 mol m^{-2} day^{-1}. Average values reported from other tropical areas amount to: Costa Rica - 33 mol m^{-2} day^{-1} (Chazdon & Fetcher 1984), Costa Rica - 27 mol m^{-2} day^{-1} (Oberbauer & Strain 1985); Borneo - 31.2 mol m^{-2} day^{-1} (Raich 1989).

Annual potential evapotranspiration (PET) amounts to 1350-1500 mm, which corresponds well with values reported in neighbouring countries (Poels 1984, Fritsch 1990), although being on the higher end (cf. Bruijnzeel 1990).

Both temperature and relative humidity are closely related to incoming radiation. Average daily temperature is 25.9 °C and while the annual variation in daily average temperature is only about 2 °C, the average diurnal variation is about 6 °C. Warmest months are September and October, coldest are January and February.

These (micro-)meteorological values are important for the calibration of the hydrological models constructed (see below), and provide base line climatic data for most other ecological studies. The radiation data of 1991 and 1992 (Jetten 1993a & b) were also used to calibrate year round light estimations with the aid of hemispherical photographs (ter Steege 1994).

Geology, landforms and soils

Four main landscape types are distinguished in Guyana: the Pre-Cambrian Plateau, the Pakaraima Mountains, the White Sands Plateau (Berbice or Zanderij Formation) and the Coastal Plain (Daniel & Hons 1984, see also Jetten 1994a). The White Sands Plateau, in which the study site, Mabura Hill, is located, extends from the coast to about 200 km southwards. It is gently undulating but occasionally penetrated by Laterite-covered dolerite dykes, from the Pre-Cambrian Plateau forming ridges and hills. The White Sands Area has a typical drainage pattern of many small creeks. Despite their size they form wide valleys because of the coarseness of the sand. Where the White Sand layer is thin, as in the study area, the streams have cut through this layer into the brown (loamy) sands and sandy clay loams below. The latter soils are thought by some to be associated with the Pre-Cambrian Plateau (e.g. Jetten 1994a). Others, however, pointing out the similarities in particle size distribution between White and Brown Sands, consider White Sands a weathering product of Browns sands in situ (Krook 1984 in Poels 1987, van Kekem pers. obs.). In the classification below, the latter view is used.

In the study area the following landforms have been identified (van Kekem *et al.* 1995): hills, footslopes, dissected erosional plains, dissected sedimetary plains, alluvial plains. The parent material in the area consists of mainly basic, igneous dolerites and

Table 1. Soil types of the Mabura Hill region.

FAO Series	Guyana Series	Local Name[1]
on hills, footslopes and dissected erosional plains, formed on basic metamorphic and igneous rock:		
ferralic Cambisols, rudic phase	?	hill soils
dystric Leptosols, rudic phase	Mabura Gravelly Sandy Clay	Laterite
dystric Leptosols, petroferric phase	Ekuk Clay Loam	Laterite
dystric/lithic Leptosols	Seballi Gravelly Clay Loam	Laterite
acri-haplic Ferralsols, skeletic phase	Tiger Creek Gravelly Clay	Laterite
on dissected sedimentary plains, formed in the Berbice formation (White Sands plateau)		
albic Arenosols	Tiwiwid Sand	White Sand
carbic Podzols	Ituni Sand	White Sand
ferralic/luvic Arenosols	Tabela Sand	Brown Sand
acri-haplic/acri-xanthic Ferralsols	Kasarama Loamy Sand	Brown Sand
same	Ebini Sandy Loam	Brown Sand
in Alluvial plains		
terric Histosols	Anira Peat	pegasse
terric Histosols/gleyic Cambisols	Lama Muck	pegasse
gleyic Cambisols, Fluvisols	Barima Silt Loam	alluvial soils

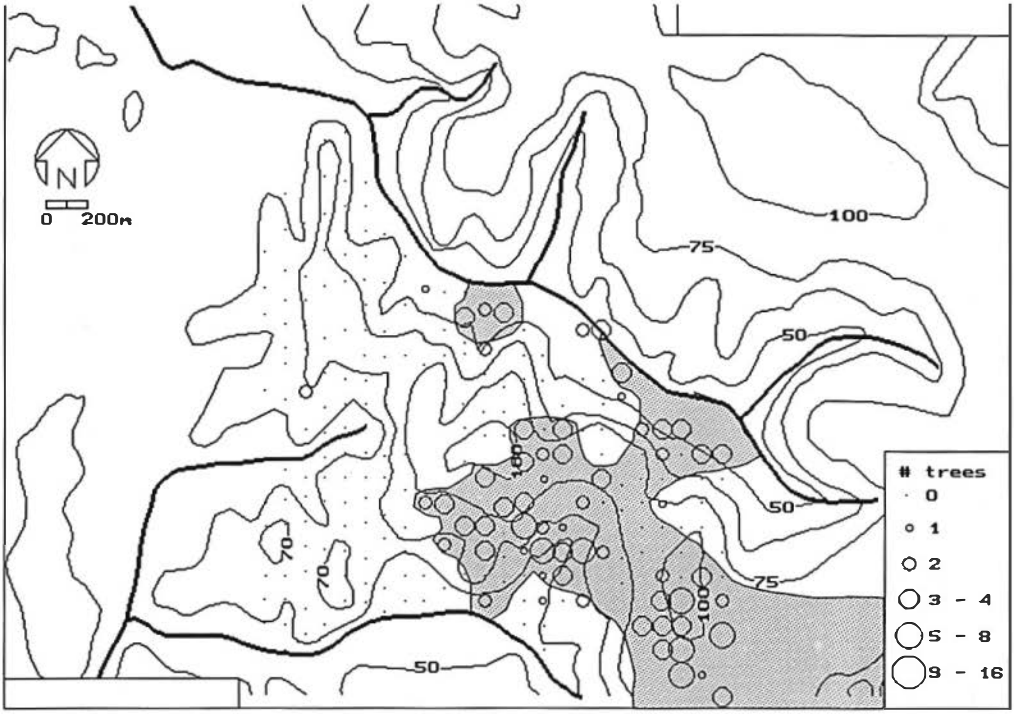
[1] These local names are used preferentially in the remaining chapters

metamorphic rocks, often accompanied by ironstone (Laterite), unconsolidated sediments (sands to clays) of the Plio-Pleistocene Berbice formation, alluvial sediments (riverine deposits and peat). The soils in the area, classified according to the FAO (FAO-Unesco 1988) and following the Guyana system, are summarized in Table 1.

All soils have a very low fertility and are only marginally suitable for agriculture with sufficient nutrient inputs (Khan *et al.* 1980, Eernisse 1991, see also Walmsley 1989) or for plantation forestry (ter Steege 1990). The soils have a low pH of 4 to 4.5 in topsoils and 5 in subsoils, low total bases and low Cation Exchange Capacity (CEC, 1.5 - 2 meq/100g for Arenosols, between 2 to 6 for Ferralsols and Fluvisols and between 2.5 to 5 for Histosols). Soil drainage ranges from excessively drained (albic Arenosols) to poorly drained floodplains (gleyic Cambisols). Soil hydrological properties vary largely between soil types, the Arenosols (with lowest clay content) having the lowest water retention capacity. Moreover, soil hydrological properties show a large variation at a small spatial level (Jetten *et al.* 1993, see below). For more information on soil types the reader is referred to Jetten (1994a) or van Kekem *et al.* (1995).

Forest types

Forests cover some 80% of Guyana and can broadly be classified as swamp forest in the coastal belt and rain forest, seasonal forest and dry evergreen forest in the interior (Fanshawe 1952). The tropical rain forest of Guyana is peculiar in that large parts are dominated by a few or one species (Davis & Richards 1934, Fanshawe 1952). Dominance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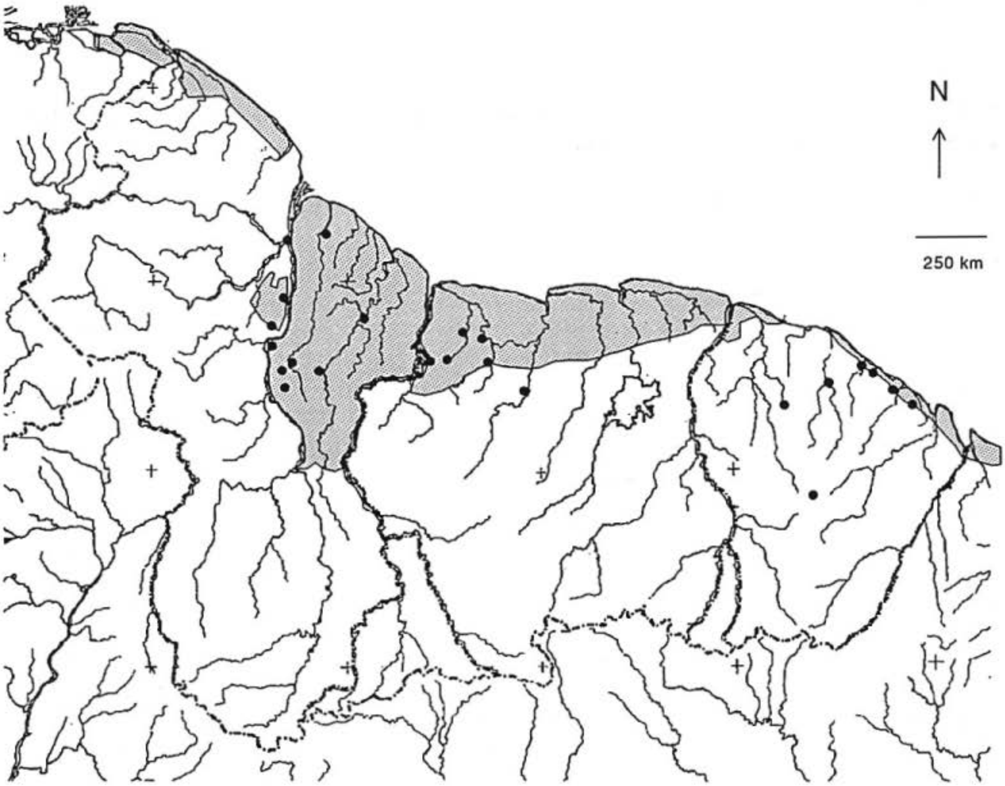
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◂ **Figure 3.** Distribution of Ituri wallaba in the Waraputa watershed area (ter Steege *et al.* 1993). The shaded area indicates the areas with a clay content <5% (=White Sand, Jetten 1994a).

may result in clearly identifiable forest types that are often associated with particular soil types or conditions.

In the Mabura Hill region the relations between vegetation and soils were investigated in a small watershed area of 480 ha (ter Steege *et al.* 1993, Jetten 1994a). There are strong relationships between soil types and forest types. Not unexpectedly, the results show that the largest differences are found between forests on White Sands and forests on Brown Sands. Two main environmental gradients explain most of the variation found in canopy tree composition: White vs. Brown Sands and drainage class. As will be seen below, Brown and White Sands differ in a number of characteristics such as: total and available nutrient content, aluminium and iron content, pH (section 2.4) and water retention (section 2.2). Differences in species composition between Brown and White Sand may thus be related to different nutrient requirements or water availability, or to different tolerances to low pH and related problems (see 2.4). The strong correlation between Ituri wallaba (*Eperua grandiflora*) and White Sand is shown in Figure 3 for the Waraputa watershed area. Even on a more regional scale the relation seems to hold (Figure 4).

The forest vegetation on such a small watershed is rich in canopy species. In 252 plots of 0.05 ha 111 species of trees > 20 cm DBH were found. Most common families are Lecythidaceae (Brazil nut family), Caesalpiniaceae, Papilionaceae, Sapotaceae, and Chrysobalanaceae. The Leguminosae s.l. account for 23% of all species and 64% of all individuals. Seven species are especially abundant in the area, being in order of importance: Watafa (*Eperua rubiginosa*), Clump wallaba (*Dicymbe altsonii*), Ituri wallaba (*E. grandiflora*), Soft wallaba (*E. falcata*), Black kakaralli (*Eschweilera sagotiana*), Greenheart and Morabukea (*Mora gonggrijpii*). The two most common species Watafa and Clump wallaba, both non-commercial, account for 46% of the total basal area in the watershed area (ter Steege *et al.* 1993).

Based on computer analysis (TWINSPAN, Hill 1979a, DECORANA, Hill 1979b) 5 forest types were distinguished in the watershed area (with general forest formation type between brackets):

- **poorly-drained mixed forest** (evergreen rain forest) in low-lying small creek heads and valleys, mainly on Brown Sands (ferralic Arenosols and Ferralsols). Watafa is strongly dominant here. Black kakaralli (*Eschweilera sagotiana*), Greenheart (*Chlorocardium rodiei*) and Morabukea (*Mora gonggrijpii*) may be co-dominant.
- **well-drained mixed forest** (evergreen rain forest) on Brown Sands (ferralic Arenosols and Ferralsols), but better drained than the former type. Greenheart, Black kakaralli (plus other Lecythidaceae) and Clump wallaba (*Dicymbe altsonii*) dominate these areas, alone or in combination.
- **dry evergreen forest** (high, well developed heath forest) on excessively drained White Sands (albic Arenosols). Dominant species are Soft wallaba (*Eperua falcata*) and Ituri wallaba (*E. grandiflora*). Other common species are Awasokule

◂ **Figure 4.** Distribution of the Berbice (Zanderij) formation (shaded area, after Cooper 1979, Fanshawe 1952 and Poels 1987) and Ituri wallaba in the Guianas (ter Steege 1990 and unpublished data).

(*Tovomita* sp.), Itikiboroballi (*Swartzia* sp.), Yareola (*Aspidosperma excelsum*) and Baromalli (*Catostemma* cf. *fragrans*). Korokororo (*Ormosia coutinhoi*) is found near the borders with lower, swampy areas.

- **palm-swamp forest** (fresh water swamp forest) on peaty soils (Histosols). Dominant species are Soft wallaba and Ituri wallaba. Common species are Charcoal barabara (*Diospyros ierensis*), Turu (*Jessenia bataua*), White cedar (*Tabebuia insignis*), Kirikaua (*Iryanthera lancifolia*), Manni (*Symphonia globulifera*), and Wadara (*Couratari* cf. *gloriosa*). The forest is very open and a dense herb layer of *Rapatea paludosa* may be present.
- **creek forest** (evergreen rain forest) on alluvial soils (gleyic Arenosols and gleyic Cambisols). Dominant species are Soft wallaba and Baromalli (*Catostemma* sp.), Watafa (*Eperua rubiginosa*), Imirimiaballi (*Chamaecrista adiantifolia*) and Charcoal barabara are often found.

Although two forest types were distinguished on Brown Sand, both a direct gradient analysis (ter Steege *et al.* 1993) and fuzzy cluster analysis (Jetten 1994a) showed that in reality there exists a gradient from wetter sites to drier sites. The variation on this gradient could largely be explained by clay content (Jetten 1994a). Many species have a rather broad range on this gradient. On particular sites along this gradient, species such as Greenheart, Morabukea, Clump wallaba or Black kakaralli may become dominant. It can be concluded that water availability, more than nutrient content (see below) may explain differences between forest types in central Guyana. The somewhat sharper distinction between forest on White Sands and Brown Sand may be attributable to the fact that White Sands are the only soils that may regularly experience drought (water potentials below wilting point), as shown by computer modelling of the hydrological cycle (Jetten 1994a). A similar conclusion was drawn for the occurrence of heath forest in south-east-Asia (see Whitmore 1990). As roots of full grown trees have been shown to reach as deep as 4m (Eernisse 1994) and may possibly reach much deeper, such drought will mainly affect the establishment of seedlings and survival of saplings (see also ter Steege 1993, 1994c). A typical characteristic of dry evergreen forest (Wallaba forest) is its extremely even canopy, easily visible on aerial photographs. This evenness is thought to be an aerodynamic adaptation of the forest to drought (Whitmore 1990).

In wider floodplains the poorly drained mixed forest and or creek forests are replaced by:

- **riverine floodplain forest** (evergreen rain forest) on alluvial soils. This forest is often strongly dominated by Mora (*Mora excelsa*), though with abundance of Watafa, Crabwood (*Carapa guianensis*), Trysil (*Pentaclethra macroloba*), Corkwood (*Pterocarpus officinalis*) and Sarebebe (*Macrolobium bifolium*).

Forests on Laterite have thus far not been inventoried in a similar manner. Based upon air photo interpretation and ground information at least two forest types are present on Laterite in the Ecological Reserve:

- **mixed forest** (evergreen rain forest) on gravelly clay Laterite (Leptosols, petroferric and rudic phase) with species such as Morabukea, Greenheart, Kakaralli (*Lecythis* spp.), Itikiboroballi/Parakusan (*Swartzia* spp.) and

Sarebebeballi (*Vouacapoua macropetala*). It is unknown if species composition differs significantly from mixed forest on Brown Sands.
- **xeric mixed forest** on rocky lateritic soils (Leptosols lithic phase). A low open forest with relatively high abundance of Wild guavas (Myrtaceae). Further species composition is unknown.

On excessively-drained White Sands in the north and south of the concession are found:

- **dry evergreen low forest** (low heath forest) on White Sands (albic Arenosols), dominated by Dakama (*Dimorphandra conjugata*) and with high abundance of Duka (*Tapirira* sp.).
- **dry evergreen scrub** (low, poorly developed heath forest) on excessively drained White Sands. A very low and open vegetation, dominated by Dakama and Muri (*Humiria balsamifera* var. *guianensis*).

Species unknown to the rest of the concession may become strongly dominant at a local scale. For example, Potaro kakaralli (*Eschweilera potaroensis*) is 'almost' dominant on lateritic hills and Brown Sands in the north-west part of the concession, but appears to be absent in the rest of the area. Furthermore, species such as Watafa and Clump wallaba, which are local dominant species in the northern part of the concession, appear to be absent in the southern part (Van der Hout 1995). Parts of the south-east are covered by:

- **seasonal forest** (semi evergreen rain forest) on gently undulating terrain, mainly (brown) sandy soils with species such as Kabukalli (*Goupia glabra*), Simarupa (*Simarouba amara*), Koraroballi (*Hymenolobium* sp.), Iteballi (*Vochysia* spp.), Tatabu (*Diplotropis purpurea*) and other Mimosaceae and Vochysiaceae.

The term Seasonal Forest has been in use in Guyana for the latter forest types since the sixties and is based upon the fact that several species in this forest type may lose their leaves for a short time span - semi-evergreen rain forest (T.C. Whitmore, pers. com.) or semi-deciduous might be a more exact term.
Different forest types differ in their structural canopy characteristics; consequently forest types can be recognized on aerial photographs. The good correlation between forest types and soils makes it possible to construct a soil map on the basis of a forest map (air photo interpretation) and geomorphology, complemented with limited field work. Such a map is under construction (van Kekem *et al.* 1995 in prep). Radar remote sensing can also utilise the structural differences among forest types (van der Sanden & Hoekman 1993, Verhoeven & Vissers 1993, Hoekman *et al.* 1994). However, the use in forests classification appears to be limited at present.

The Mabura Hill area has a high botanical diversity. The total number of vascular plant species collected amounts to 1323 species (June 1995). Most common families are Orchidaceae (117), Leguminosae s.l. (112 species), Rubiaceae (65) and Melastomataceae (40) (Figure 5). Compared to three western Amazonian sites (La Selva, Barro Colorado Island, and Cocha Cashu, Gentry 1990) and two other eastern Amazonian sites (Ducke Reserve, Gentry 1990 and Saül, Cremers *et al.* 1993) it is apparent that apart from families that are typically among the top twenty at all neotropical sites, such as

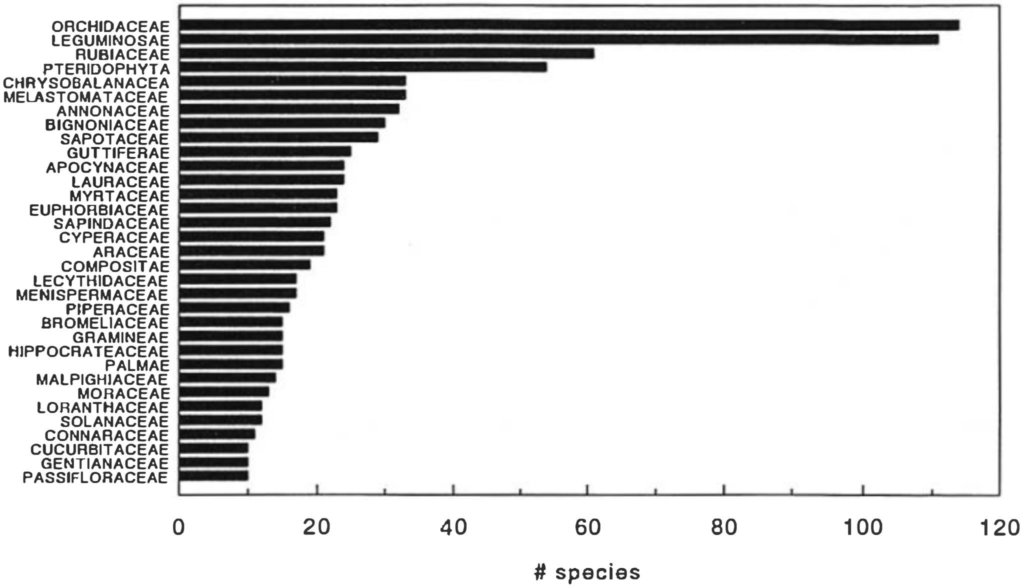


Figure 5. Species richness of the first 20 families around Mabura Hill. In accordance with the eastern Amazonian situation, Chrysobalanaceae, and Lecythidaceae are among the more speciose families.

Leguminosae, Orchidaceae, Rubiaceae, Melastomataceae (Figure 5), some families are typically dominant (in species diversity) in eastern Amazonia and thus in the Mabura Hill area. Such families include Annonaceae, Chrysobalanaceae, Lecythidaceae and Sapotaceae. Another site, Araracuara, is intermediate between Guyana and the sub-Andean sites in some respects, which may represent a Guayana shield floristic component (Duivenvoorden & Lips 1995). Among Legumes, the Caesalpiniaceae are more common at Mabura Hill and the other eastern Amazonia and Guayanan sites (Mabura 42%, Araracuara 40%, Saül 33%, Ducke 27%) when compared to western Amazonian and central American sites (Cocha Cashu 16%, BCI 14%, La Selva 13%). A checklist of the vascular plant species collected at Mabura Hill is given in Appendix 2. A list of non-vascular plants (172 spp.) collected in 1995 in the northern part of the area can be found in Cornelissen & Gradstein (1990).

Animals

The area is rich in both mammal and bird species. Although no work on animal diversity was carried out, within the programme several checklists were kept. The total mammal list amounts to 76 species and is given in Appendix 3.

The list of birds sighted amounts to 302. A checklists of birds is given in Appendix 4.

Due to previous low population pressure in the area and minimal access, hunting pressure has been limited. However, with a substantial increase in road construction, access to previously uninhabited areas has led to an increase in hunting, mainly on such species as Deer (*Mazama* spp.), Tapir (*Tapirus terrestris*), Peccary (*Tayassu* spp.), Laba (*Agouti paca*), Powis (*Crax alector*).

2.2 Hydrological and nutrient balance

The research on the hydrological balance and nutrient cycling is mainly concentrated in two catchments and two artificial gaps (medium and large) plus surrounding forest on Brown and White Sand. The first catchment (6.2 ha) is located in the Ecological Reserve and serves as a reference catchment. The second catchment (5.5) is located a few hundred meters north of the Ecological Reserve and was logged in October 1992. The artificial gaps are situated at the south-western edge of the reserve. A fully automatic meteorological station was set up on a large gap between the two sites. Both catchments have been monitored over a year prior to logging and subsequently for two years after logging. The components of the water balance were measured and monitored on a small time-step basis, using automatic, digital recording equipment. Apart from the standard set of meteorological variables and parameters (incoming and outgoing radiation, air and soil temperature, wind speed, and relative humidity) the measurements comprised evapotranspiration, rain interception and throughfall, infiltration, groundwater flow, surface runoff, and streamflow discharge. In connection with these processes waterbound chemical fluxes were measured together with litter fall, litter decomposition and nutrient re-translocation. Elements (ions) that were analyzed comprised: P, N, K, Ca, Na, S, Mg, Mn, Si, Cl, Fe, Al, and H. Emphasis was put on P, N, K, Mg and Ca.

Hydrological balance
The three major physiographic units: White Sands, Brown Sands and Laterite are well defined on the basis of soil hydrological characteristics, indicating the sharp landscape boundaries (Hoefsloot & van Rossum 1991, Jetten *et al.* 1993, Jetten 1994a). Each of the units has a different combination of soil properties that explains the variance in infiltration and sorptivity of the soil. However, soils are far from homogeneous and almost all soil properties exhibit large short range spatial variability. In White Sands, properties such as bulk density, saturated hydraulic conductivity and rooting characteristics have a spatial correlation of 20 m. Brown Sands have high noise levels (variation at a distance of less than 2 m.) for almost all properties and spatial patterns, which vary at distances of less than 20m. There is no difference in spatial variability of the infiltration process if it is measured directly, or if the process is modelled with basic hydrological properties. In view of this it is to be concluded that it is not feasible to map any of the hydrological properties within the different soil units. The number of sample points required to represent the spatial structure adequately is prohibitive. Therefore, the best strategy is random sampling, to ensure that the values of the soil properties are good representatives of the areal mean and variance. However, it must be understood that hydrological models based upon such random sampling will provide general results with high variance levels.

The rain forest water balance in principle is not very different from that of other forests. The trees intercept most of the rainfall, of which the largest part then drains to the ground. Uptake of water depends on the atmospheric demand and the root distribution in the soil. Because the rain forest has such a complex structure it shows a large spatial variability in interception and probably also in uptake fluxes. This variability however is extremely difficult to quantify and average values have to be calculated. When logging takes place and the plant layer is removed, this spatial structure becomes very important in terms of hydrological response. Nevertheless the average water fluxes can be quantified and are representative of the research area.

A breakdown of the rainfall into individual rainstorms, reveals that about 70 % of the rain falls in showers of less than 2 mm. Larger rainstorms (of up to 50 mm) of course do occur with peak intensities that are usually more than 70 mm/hr. Most rain falls in the late afternoon and early evening (Jetten 1994a). Average annual rainfall in the area is approximately 2700 mm. The Penman potential evaporation is between 1350 and 1500 per year on ground level, with daily values ranging from 1 to 7 mm (see also climate above). On canopy level the potential evapotranspiration is about 1520 mm, due to increased wind speeds.

These values constitute the atmospheric input and output for the log catchment. The rest of the water is (temporarily) stored as groundwater and leaves the catchment as streamflow with an average of 165 m^3 per day (from 70 m^3/d in the dry season to 520 m^3/d in the wet season). The partition of water over the various compartments of the water balance is shown in Figure 6. Evapotranspiration dominates the water balance and is nearly identical in all forest type - soil combinations (Jetten 1994a). As a result total yearly water fluxes are quite identical for all soil-forest combinations investigated (Jetten 1994a).

About 16 % of the rainfall is intercepted by the canopy (Jetten 1994a), which is near to the average value for interception in tropical forests (see Bruijnzeel 1990). Measured over a period of 17 months, data showed that there was no significant difference between dry evergreen forest and mixed forest in throughfall and stemflow. The interception decreases with rainstorm size and peak intensity. In order to model the exact throughfall intensities a new interception model (the CASCADE model, Jetten 1994a,b) was developed and validated. The interception model can be used alone or as a component of a more complete water balance model, SOAP (SOil Atmosphere Plant model; Jetten 1994a,b).
Due to the sandy nature of the soils, nearly all throughfall infiltrates at first. Infiltration rates are very high and vary between 2000 and 5700 cm/day for White Sands and between 50 and 500 cm/day for Brown Sands. Although the Brown Sands have a sandy-loam to sandy clay-loam texture, the iron oxides form very stable microaggregates which have the size of fine sand. Therefore these soils too have very "sandy" hydrological properties. The hydraulic conductivity decreases very rapidly with moisture content and the redistribution of water after infiltration from the surface to below the root zone may take 2 to 5 days. Part of the water is used by the plants as transpiration (about 40% of the rainfall).
Soil moisture shows a seasonal fluctuation around field capacity. Only White Sands will experience water stress in the dry season with potentials up to pF 4.2 (pF = -log(H_2O suction)) just below the root mat. Mixed forest on Brown Sands never experiences pF values lower than 2.7, thus transpiration is never reduced. In this case actual evapotranspiration equals the potential evapotranspiration of 1520 mm. Thus approximately 57% of the annual rainfall is evapotranspired and percolation plus runoff (=discharge) amounts to 43%. The actual evaporation is lower than the value found by Poels (1987) in Suriname (1630 but this value is probably overestimated [Bruijnzeel 1990]) and rather equal to values found in French Guiana (1470-1537 mm [given as 43-47% of approx. 3420 mm annual rain] in four different catchments, Fritsch 1989). Evapotranspiration for the Mabura site is higher than the average for several tropical sites (1430 mm, Bruijnzeel 1990).

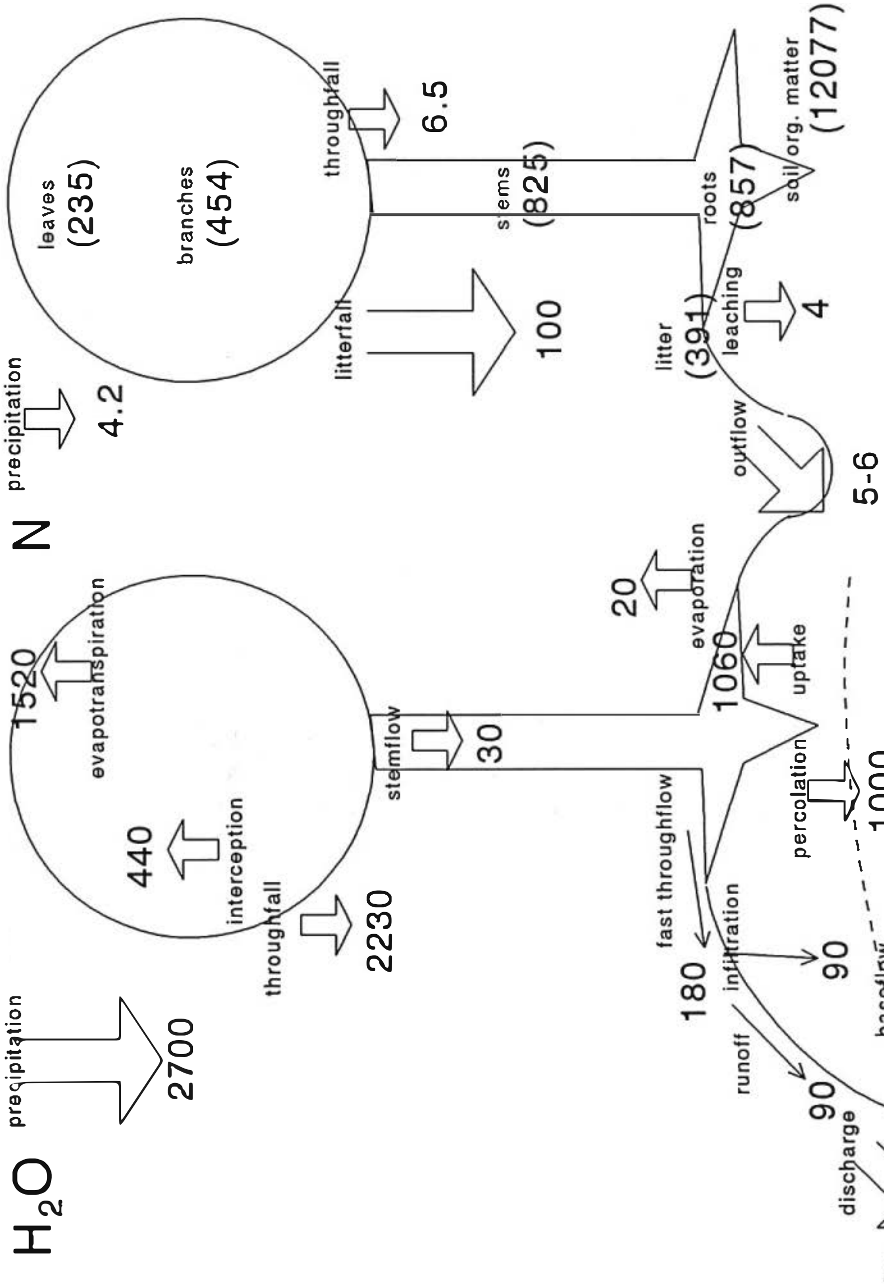


Figure 6. Water balance and Nitrogen budget for a mixed rain forest on a Brown Sand (Ferralsol) i Guyana. Left: water balance: water movements in mm year^{-1} (Jetten 1994a). Right: Nitrogen budget: i parentheses Nitrogen standing stocks in kg ha^{-1} (Suriname, Poels 1987), and Nitrogen fluxes in kg ha^{-1} year^{-} (Brouwer 1994).

The groundwater flow in porous sandy media is relatively fast (depending on the gradient). Since the response time of the catchment base flow is in the order of 40 days, and the groundwater surface is on average 20 meters below the surface, the vertical water movement can be estimated at roughly 60 cm per day. Simulation of the redistribution with SOAP resulted in similar fluxes. The groundwater fluctuation measured around the creek and on the lower slopes were in the order of several cm per week. Lateral surface flow amounting to between 2 and 12 % of the rainfall (depending on slope angle) has been measured in field plots. Further experiments on large soil samples showed that the lateral flow is not actual surface runoff, but fast subsurface flow at the contact zone between the litter layer and the mineral soil. Flow velocities were measured at one to several hundred meters per day (Rotmans, 1993). In the field most of the water infiltrates before it reaches the creek on the (usually) flat floodplain. The peak flow in the creek, about 3 to 5 % of each rainstorm with water levels rising to more than 10 times the base flow level, follows within 60 minutes after the peak in rainfall. It follows that this peak discharge is generated by rain falling on the stream itself and the banks, swamps and convolutions of the channel, and is not directly related to the fast subsurface flow.
From the above it follows that the rainfall pattern is strongly buffered and delayed. Changes in the various water flows caused by logging may be buffered as well (see chapter 3), because most of the water will still infiltrate even though the hydrological characteristics of the soils are altered.

Nutrient balance
The main nutrient pools in the landscape ecosystem are the standing biomass and the soil organic matter. No total estimates of the standing biomass are available for the research area but there is no reason to assume that this nutrient pool will differ much from comparable forests of surrounding countries (e.g Suriname, Poels 1987, see Figure 6). Measurements of nutrient levels in leaves and leaf litter show that these are extremely low for Phosphorus and low for Calcium and Potassium (van Zanten 1991, den Ouden 1992, van der Marel 1993, Brouwer 1994). This indicates limitations in availability and probably a high efficiency in use.

Soils are extremely poor in 'plant available' or 'easily extractable' nutrients except for Nitrogen, which occurs in somewhat larger amounts. However, the usefulness of measuring only 'plant available' nutrients is strongly doubted in the case of (tropical rain) forests, firstly as it may differ greatly among species and secondly being developed for agriculture it implies availability at short time spans (one growing season). Therefore, total nutrient contents have been determined as well. These stocks are somewhat larger, although still very low. In general, clayey lateritic soils are slightly less poor than the loamy Brown Sands. The White Sands have the lowest total nutrient contents, except for Calcium, which is low in all soils. Due to the low pH and high content of Iron and Aluminium in the loamy Brown Sand and Laterite soils, Phosphorus availability is strongly limited. The quantity of exchangeable cations in the soil is equal to the annual flux of cations in small litterfall (see below) in order of magnitude (kg/ha, Brouwer 1994). This means there is only limited buffer capacity of these soils concerning cations, and recovery of biomass nutrient to original levels after exploitation might take a long time.

Table 2. Nutrient fluxes in natural mixed forest, a medium gap and a large gap. Fluxes are in kg per ha per year, except logging which is a single event output in kg per ha (Brouwer 1994).

	Ca	K	Mg	N
rain	2.8	3.1	1.3	4.2
Natural mixed forest				
throughfall Wallaba forest	4.7	14.0	4.5	5.6
throughfall Greenheart forest	3.1	16.0	3.8	7.6
fine litterfall Wallaba forest	32.6	14.5	12.7	80.8
fine litterfall Greenheart forest	33.8	16.7	18.2	119.8
Exploited forest				
creek 'Log catchment'	2.5	3.2	7.0	4.6
leaching large gap[1]	28.2	45.6	29.3	174.1
leaching medium gap[1]	24.7	21.5	14.6	78.8
leaching forest[2]	5.2	7.4	2.1	3.9
output timber large gap	74	73	32	781

[1] Figures based upon the first 22 months after logging.
[2] Figures based upon the first 550 days after logging.

Inputs from the atmosphere were measured with duplicate rainfall gauges over a period of almost three years. The collected rain water was sampled weekly or at fortnightly intervals, depending on the amount of rain. Collected inputs from known wet, and an unknown quantity of dry deposition, slightly underestimate total inputs (Brouwer 1994). Atmospheric inputs are very low, a condition expected for remote inland areas (cf e.g. Herrera 1979, Russel 1983, Buschbacher 1984, Lewis *et al.* 1987, Poels 1987). Inputs of Nitrogen (Figure 6) and Phosphorus from this source (data not shown) may not represent true inputs for the ecosystem as a whole, since it is known that tropical rain forests can generate their own aerosols, which can be returned to the system via deposition. Concentrations of nutrients are negatively correlated with amounts of rainfall.
Drainage water, in the form of streamflow water, groundwater and soil water below the rooting zone, are as poor in nutrients as is rainwater, reflecting the closed nutrient cycle, at least under the natural forest condition. Inputs from weathering are not easily measured (Eernisse 1993), though these are expected to be very low. The presence of fine roots near weathering rock (Eernisse 1993) and Magnesium outflies (creek) in excess of rain input (Brouwer 1994) may be an indication that weathering does affect the nutrient balance and that some nutrients may become available to the vegetation due to weathering.

"Within-ecosystem" nutrient fluxes (i.e. nutrient-fluxes in the biomass and the soil root zone) are considerably larger than inputs and outputs (Table 2, Figure 6). For most nutrients litterfall is the most important means of returning nutrients from the biomass to the forest floor. Fine litterfall, which is sometimes considered a measure of production rate in tropical forests amounted to 7.5-10.5 ton/ha and falls within the range found for South-American tropical forests (4.7-21 ton/ha, see Brouwer 1994, or ter Steege 1990, table 2 for references). Variation in litterfall from month to month (temporal variation) is considerably larger than spatial variation (Brouwer 1994), emphasizing the seasonality of this process of the study site. The largest peak in leaf litterfall is observed in the September-October dry season, just after the long rainy season (Figure 7). Small non-leaf litterfall (twigs, fruits, flowers) is more irregular and related to phenological phenomena (ter Steege & Persaud 1991, see below) and the occurrence of storms. Large litterfall (stems and branches) and root turnover are not measured due to methodological problems and the enormous amount of work involved. However, especially the contribution of roots to total litter production should not be underestimated.

Throughfall is the second mechanism for transport of nutrients from canopy to soil. For most nutrients this is not as important as litterfall, however, it plays a major role in the Potassium cycle. Although throughfall must be considered as a net result of dry deposition and canopy interactions with rainwater, it is expected that dry deposition is only of minor importance since there are no major source areas for dust in the vicinity. This is confirmed by the extremely low contents of typical soil-associated elements (e.g. Silica, Iron and Aluminium) in the throughfall water.

Nutrient retranslocation percentages are high and thus form an important nutrient conserving mechanism. For phosphorus this can be as high as 50-87% and for Nitrogen 33-66% (Prinsen & Straatsma 1992, Brouwer 1994, Raaimakers 1994). Retranslocation is less important for Potassium and Magnesium.

The decomposition process is the main pathway of breaking down organic compounds into mineral nutrients that then can be used for plant growth. Decomposition was studied with three different methods: cotton strips, litter standing stock and litterbags. Cellulose (cotton strips) decomposed significantly faster on the Brown Sands compared to the White Sands, probably due to a higher average moisture and higher organic matter content on the Brown Sand soils (Brouwer 1994). The figures are comparable with other studies in tropical rain forest soils. Decomposition rates, calculated using the ratio of litterfall to standing litter stock, gave turnover times of litter between 4 to 12 months (Brouwer 1994). This can be considered low to average in comparison with other sites (ter Steege 1990, Brouwer 1994). Interestingly, decomposition rates of small materials, as assessed using litter bags, were quite similar on White Sand (48-78%/y) and Brown Sand (56-71%)(Brouwer 1994). Clump wallaba litter, however, decomposed more rapidly on white sand. This is probably caused by the nature of the decomposing material, which may be more recalcitrant on Brown Sand with mixed forest (Prinsen & Straatsma 1992). Overall it appears that decomposition rates are mainly determined by resource quality and not by soil type (Brouwer 1994).

2.3 Population structure and dynamics

Phenology of timber trees

Phenology is the regular yearly pattern of (visible) events in a natural system. Flowering and fruiting of 190 tree species have been recorded in Guyana for over a century (ter Steege & Persaud 1991). Most tree species show a clear flowering peak in the period

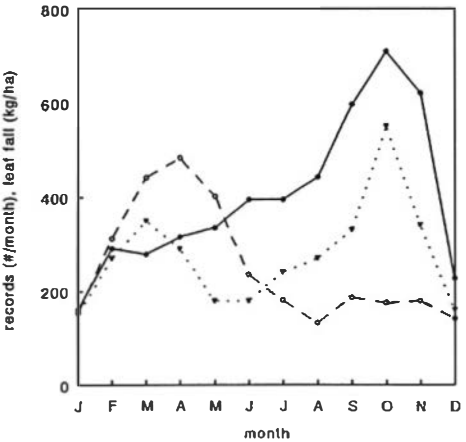


Figure 7. Phenology of the timber belt of Guyana. Flowering (●) and fruiting (○) after ter Steege & Persaud (1991), leaf fall (▼) after Brouwer (1994).

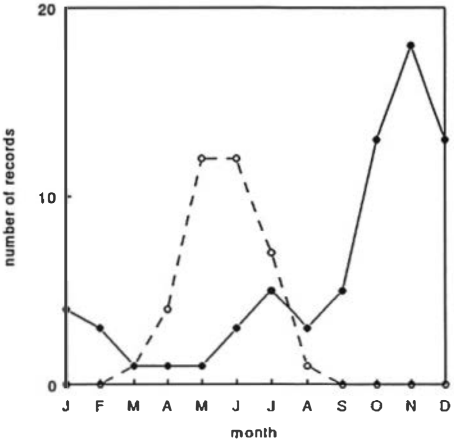


Figure 8. Flowering (●) and fruiting (○) of Sawari nut (*Caryocar nuciferum*) in the timber belt in Guyana (after ter Steege & Persaud 1991).

between September and November (Figure 7), when peak sunshine hours (ter Steege & Persaud 1991) and fresh new leaves (Figure 7) allow for high production. Fruit/seed fall is slightly ahead of the wet season, ensuring moist conditions suitable for germination and early seedling growth. It is envisaged that these data on individual tree species will help foresters and forest ecologists plan their collecting of flowers, fruits, seeds, seedlings and the timing of silvicultural interventions. Information includes species of local economic importance, such as Sawari nut (*Caryocar nuciferum*, nuts are collected and locally sold for consumption, fruiting time May-June, Figure 8). Phenology patterns on flowering and fruiting in Guyana are quite comparable to those of French Guiana (Sabatier 1985, Sabatier & Puig 1985) and Suriname (van Roosmalen, unpublished data), although slightly more bi-modal (ter Steege & Persaud 1991). Leaf fall appears to be equal in amount to French Guiana (8-10 ton ha^{-1}, Puig & Delobelle 1988), but peaks one month later in Guyana.

Population structures

For most tropical tree species the driving force behind regeneration is their seed production. The timing of seed production, the size of the seed crop and the area over which the seeds are dispersed, are all important parameters determining the probability of germination and seedling establishment. Species differ in these properties, which consequently affects their regeneration.

The population structure of the total forest in the Waraputa watershed area shows the usual positive stand table for any tropical forest. Some species show similar curves e.g.: Soft wallaba, Ituri wallaba (ter Steege *et al.* 1993). Other species may show different population structures, probably based on different modes of recruitment (Bongers &

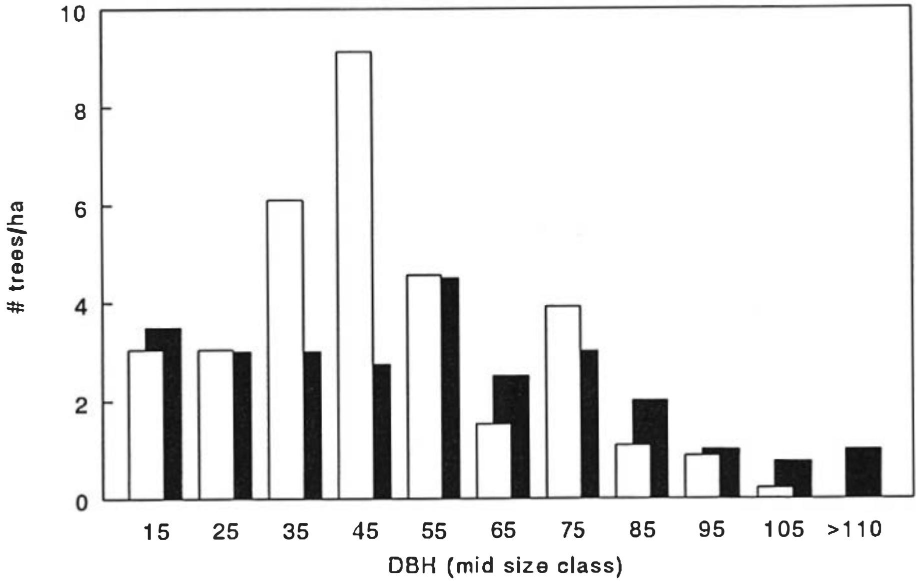


Figure 9. Size class distribution of Greenheart in the Waraputa Compartment (□, ter Steege *et al.* 1993 and Ecological Reserve (■, Bokdam & Dobbelsteen 1990).

Popma 1988). Greenheart is renowned for its dip in the population structure (Fanshawe 1947, Richards 1952, Maas 1971, Bokdam & Dobbelsteen 1990, ter Steege *et al.* 1993, Figure 9). Possibly, this relates to irregular recruitment (ter Steege 1990). Given the low growth figure of Greenheart (see below), such a negative stand table may have profound consequences for sustainable forestry (Chapter 3), although the dynamics as a whole will be more indicative.

Temporal and spatial patterns in seed production

Various aspects of seed rain dynamics are studied for Greenheart and Clump wallaba. For Greenheart the total seed production amounted to 4000, 6000 and 2500 seeds per ha in 1992, 1993 and 1994, respectively, as measured on two plots in natural forest (Zagt 1994). The spatial variation in the number of seeds was considerable (range 0.04 - 18.8 m^{-2}). Locally density may be as high as 30 seeds m^{-2}. This reflects the patchy distribution pattern of adult trees and poor dispersal of seeds (Zagt 1994). Seed production also varied considerably among individuals, ranging from 0 to 523 in 16 individuals (median = 50). The period of seedfall for Greenheart is usually long; about six months (Figure 10). A breakdown of the total showed that the timing of seed production differs among plots and trees (Zagt unpubl. data). Some trees peak in January, others in April, while others release a regular but low amount of seeds every week.

Clump wallaba (*Dicymbe altsonii*), a species that is co-dominant with Greenheart in a large part of the study area is much more profuse in its seed production, which amounted to 57,000 and 37,000 per ha in 1991 and 1994, respectively. However, Clump wallaba only set seed once every two years, which may in part account for the large seed crop.

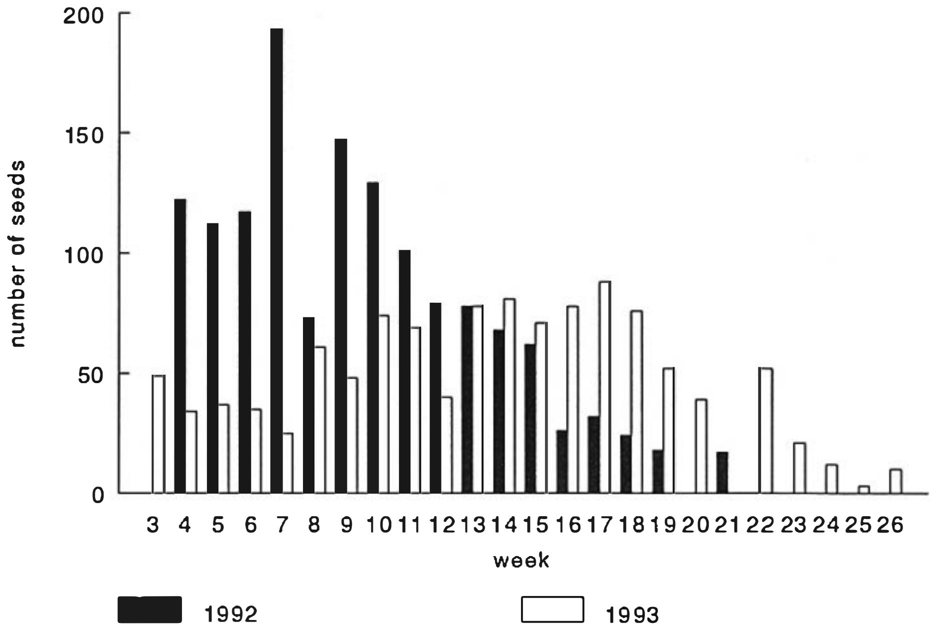


Figure 10. Seed fall of Greenheart in 1992 and 1993 (Zagt 1994).

Predators of Greenheart seeds

Three characteristics of seeds may contribute to an increased likelihood of predator attack: 1) a large seed mass, 2) long development time at the mother tree and 3) a prolonged dormancy and/or slow cotyledon depletion. Average fresh seed weight in Greenheart is 60-65 g and seeds may show germination up to two years after dispersal and show very slow cotyledon depletion afterwards (see below). This is the longest germination period recorded for a seed of this size in the neotropics. These attributes support a large array of primary and secondary invertebrate infestations. Invertebrate infestations encountered more than twice are listed in Table 3.

Pre-dispersal attack was found in 10% of all seeds investigated (Luis Cervantes, unpubl. data). In all cases the predator was *Stenoma catenifer*, a common predator of Avocado seeds (*Persaea americana*, Lauraceae) in the tropics. Invertebrate attack is also be a major factor in seedling mortality, as many seedlings have shoot borers (Brown in ter Welle *et al.* 1988), which are also *Stenoma catenifer* individuals. Scolytid beetle attack on seeds is especially high in the understorey near the parent tree (Hammond & Brown 1993), as predicted by distance-dependent mortality models (Janzen 1971, Connell 1970). Several vertebrate predators/dispersers feed on the fallen fruits of Greenheart (Hammond, unpubl. data). Red acouchi (*Myoprocta acouchy*) and Red-rumped agouti (*Dasyprocta leporina*) probably account for most of the attacks on the seeds, though Laba (*Agouti paca*), Guianan squirrel (*Sciurus aestuans*) and several Spiny rats (*Echimys* spp., *Mesomys* sp. and *Proechimys* sp.) also reduce the number of seeds available for germination. Fungal attack on the seeds occurs mainly by soil borne generalist

Table 3. Invertebrate attack on seeds of Greenheart (Hammond & Brown 1992).

species	(Sub)Family	Order	Use[1]	Stages[2]	% of. seeds	% of seedlings
Pre-dispersal[3]						
Invertebrates						
Stenoma catenifer	Stenomidae	Lepidoptera	1	1	10	0
Vertebrates						
none observed						
Post-dispersal						
Invertebrates						
Sternobothrus spp.	Scolytidae	Coleoptera	1,3	1,2	91	58
Myrmica sp.	Myrmicinae	Hymenoptera	1	1	7	0
	Carconophoridae	Dermaptera	1(D)	1,2	<1	0
Nasutitermes sp.	Nasutitermitidae	Isoptera	1(D)	2	<1	0
	Agromyzidae?	Diptera	4	1	0	23
various		Lepidoptera	4	1	0	8
Vertebrates						
various Caviomorphs	Rodentia	1,3	1,2	53	28	

1 Use: 1- seed, 1(D)- dead seed, 2- root, 3 - shoot, 4- leaves.
2 Stages: 1- juvenilel, 2- adult.
3 Data Luis Cervantes, British Museum.

decomposing fungi, which extend their hyphae through the litter layer. An airborne pathogenic specialist fungus also attacks the seeds, but less frequently. When measured in 1992, establishment under parent trees was only 23% due to predation. In the understorey away from parent trees establishment was 40%, while it was 39% in small natural gaps (Hammond & Brown 1993).

By contrast, germination of Clump wallaba is rapid. Germination rate varied from 40 to 60% in gap compared to understorey (Zagt 1994). After germination a fungus is responsible for major mortality (up to 90%). After establishment, the remaining Clump wallaba population is still much larger than any single Greenheart seed crop in the hectare-plots investigated. Mortality after establishment was very low, but severe drought in 1994-1995 caused major loss of seedlings and saplings (Zagt, unpubl. data).

Dispersal versus predation

A large number of Guyana's forest trees are dispersed by terrestrial and arboreal mammals and birds (van Roosmalen 1985, Hammond *et al.* 1993). As mortality of seeds and seedlings is often density dependent (see above) there is a clear advantage of being dispersed away from the parent tree. Several dispersers also act as partial or total predator of seeds. Many species, however, have seeds that are capable of germination even when considerably damaged (Hammond *et al.* 1993). Seeds are obviously not only dispersed by animals. Figure 11 summarizes the results of a study of 190 species (Hammond *et al.* submitted). The average seed size appears to be rather high compared to other neotropical areas (Hammond & Brown 1995). Most timber species have seed fresh weight over 1 g, and are mainly mammal-dispersed. Thus, by selecting large seeded species, logging may cause a shift in the type of resources available (Hammond *et al.*

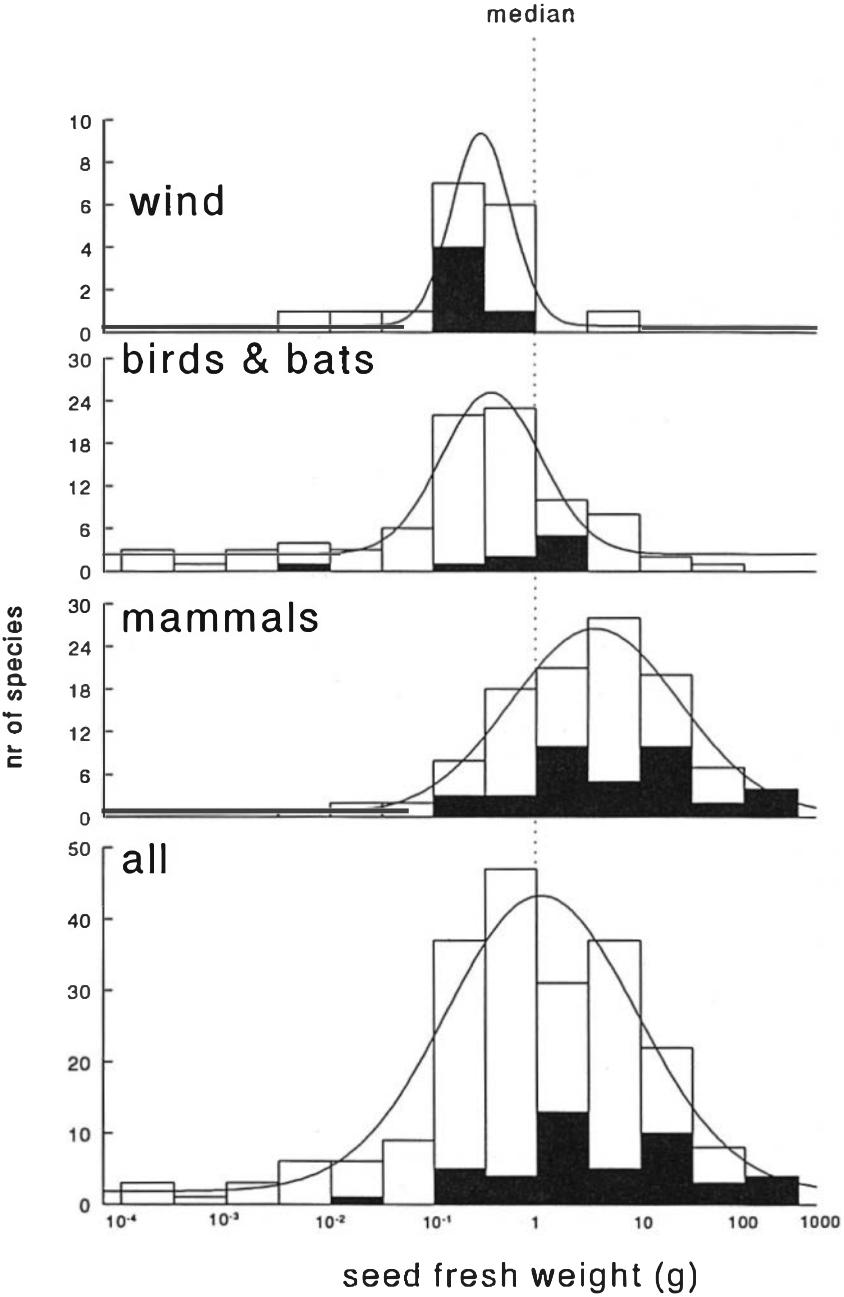


Figure 11. Size class distribution of seed mass for 190 species by dispersal agent. Timber species (black bars) show large seed mass and strong affinity with non-flying mammal dispersal (Hammond *et al.* subm.)

submitted). This justifies further research into animal densities and (feeding-)behaviour, not only from a biological point of view, but also from a management point of view (Chapter 3).

2.4 Growth and productivity in relation to environmental constraints

Gaps and growth of seedlings

In tropical rain forests, canopy openings created by treefalls are important sites for the establishment and growth of canopy trees. Within gaps created in a closed forest, new trees grow up, and a mature canopy will eventually be attained. Therefore, gaps are a critical phase in a forest cycle because what grows up determines the floristic composition of the future stand (see e.g. Whitmore 1990). Understanding the possibilities and limitations of seedlings to cope with the changing light climate and other environmental variables may provide important information for forestry practises.

The question of which species eventually occupies the space in the canopy depends on 1) seeds and or seedlings of tree species present in the understorey at the time of a gap formation and 2) the germination and/or growth response of these species to the environmental changes. To reiterate, the presence of tree seedlings in the understorey depends on: 1) the number and frequency of seeds produced by the adult trees in the stand, 2) their pattern of dispersal, 3) their germination requirements, and 4) the ability of their seedlings to survive in the adverse light conditions of the understorey. Pioneers in the true sense are not present as seedlings in the understorey but lie dormant in the soil contributing to a large seedbank, which can contain up to 200, mainly small, seeds per m^2 (e.g. Holthuijzen & Boerboom 1982).

In high light conditions, seedlings of pioneers show high relative growth rates (RGR) but in the understorey their growth rate is low or even negative (Boot 1994). Climax species rarely contribute to the a seed bank. Their typically large seeds germinate soon after they fall (Garwood 1982, Raich & Gong 1990, ter Steege 1993), Greenheart being a notable exception. Such species often have high survival rates under a closed canopy but low relative growth rates even in high light environments (Boot 1994, in press, ter Steege 1994). Some may even be damaged by high light levels (e.g. Mora and Morabukea, ter Steege unpublished data). In 100% shade there exists indeed a relation between seed size and survival (Boot 1994), but the relation was insignificant in the other light regimes. Thus it appears that under normal forest conditions seed size is a poor estimator of survival and other factors such as herbivory influence the relationship between seed size and mortality (Hammond, unpublished data). Still, seedling size is greatly influenced by initial seed weight (Boot 1994).

A simple model was constructed for evaluating the potential importance of differences of both seedling size and RGR (Boot 1994). The model showed that in large gaps a high RGR is the main feature determining success of a seedling, while in small gaps initial seedling size may be more important. Thus, while seedlings of medium to large seeded climax species establish under a closed canopy, small gaps will favour their final survival and success, and their initial size is of importance in attaining dominance. Large gaps will favour strongly both the establishment and success of pioneers. The former is confirmed by observations in Dipterocarp seedlings, where indeed seedling-size is an important attribute in survival in freshly created gaps (Brown & Whitmore 1992). The latter is supported by a large number of ecological observations (e.g. Hartshorn 1978, Brokaw

1985) and eco-physiological theory (Vazquez-Yanes & Orozco Segovia 1982, 1984, Vazquez-Yanes & Smith 1982).

In general terms on the basis of these considerations, it may thus be postulated that initially the distribution pattern of seedlings is strongly determined by the distribution of adult trees (Hubbell 1979; in Guyana, Zagt 1994), often modified by the action of seed dispersers. In the course of time, however, these initial distribution patterns are influenced by the differential mortality and growth rates imposed by a number of factors like predation, availability of water, nutrients, and light. Usually, the best conditions are found in tree fall gaps, so in time the distribution pattern of seedlings will increasingly reflect the underlying pattern of gaps. Some restrictions apply, however: 1) there will be no seedlings where no seeds are dispersed, 2) other seedlings also perform better in gaps. Thus, it is advantageous to have traits which help the establishment and improved competition in gaps, either a) a large structure, which appears to be the best strategy in small gaps or b) a high relative growth rate, which favours establishment in large gaps. Old and crowded gaps are poor sites for establishment. Such conditions are often found in areas with large seedling banks, such as in the case of Morabukea (*Mora gonggrijpii*) or in large (logging) gaps, dominated by secondary vegetation.

Growth constraints of seedlings

Water availability may limit plant growth. Water potentials are usually high in forest soils (see above) and overall conditions favour the survival of most species. However, differences in soil water retention characteristics may determine to a large extent the vegetation patterns in tropical rain forest (ter Steege 1993, 1994c, and 2.1). Litter decomposition may also be dependant on water status.

Early growth of Morabukea (*Mora gonggrijpii*) is mainly determined by cotyledon storage. Light has little additional effect, but is more important after the cotyledons have been depleted (ter Steege 1994b). Poor drainage conditions, such as occur on poorly drained Laterite have a negative effect on early growth. These effects may be caused by low oxygen levels in the soil or due to toxicity of Aluminium and Iron under acidic, anaerobic conditions.

Mora (*M. excelsa*) and Morabukea (*M. gonggrijpii*) are well segregated along a soil hydrological gradient (1994c), with Mora associated with wet soils and Morabukea associated with dryer uphill soils. Soil water status may thus have an effect on seedling survival. However, in a moderate year, such as 1992 (no flooding, no drought, Jetten 1994a), there was no difference in growth or mortality of either species in either forest type. Extreme conditions do have an effect and seeds of Morabukea are very intolerant to flooding. Germination in this species drops to 50% after only 11 days of flooding, compared to the control treatment. Seeds of Mora float and 80% of the seeds is viable after as much as 50 days of flooding. Artificially submerged seeds of the latter species have an intermediate survival response. Flooding in seedlings results in a halt of growth in both species. Mora appears to be more tolerant to (moderate) flooding. The floating (and survival) of the seeds during flooding periods, which are especially common just after seedfall, is of significance for the dispersal and establishment of this species in riverine forest. Morabukea shows several characteristics (viz; low conductance, high water content), that may enable it to withstand drought more than Mora (ter Steege 1994c). Observations, similar to the above, were made within the genus *Eperua* (ter Steege unpubl.data, Caesar unpubl. data.).

Table 4. Soil characteristics of white and brown sand in Guyana. (Raaimakers 1994). Differences between soils ($p < 0.05$) are indicated with lower case letters.

	unit	White Sand	Brown Sand
soil characteristics			
pH(H_2O)		3.7 a	4.4 b
P (total)	$\mu g\ kg^{-1}$	8 a	55 b
Al	$mg\ kg^{-1}$	1.0 a	4.4 b
Fe[1]	$\mu g\ g^{-1}$	9	106 [1]
Organic matter %	0.3 a	2.0 b	
Bulk density	$kg\ l^{-1}$	2.2 a	2.0 a

[1] one sample only (Eernisse and Brouwer unpubl. data).

The results support the hypothesis that it is not the average climatic/soil conditions that may be important for habitat segregation, but more the extreme conditions that may occur only once in several years (see e.g. Davis & Richards 1933, ter Steege 1993, 1994c).

Nutrient uptake, use and efficiency

The soils in the Mabura Hill area are extremely poor in total nutrients, notably Phosphorus (Table 4). On Iron and Aluminium rich soils most of the Phosphorus is bound to Al-Fe-Sesquioxides and unavailable to plants. As Phosphorus is an essential macro nutrient it must be regarded as (co-)limiting to plant growth under such conditions. Trees growing on these soils are hypothesized to be efficient in nutrient uptake and use, and to minimize losses. Efficiency in uptake can be achieved by long fine roots, root hairs, mycorrhizae or proteoid roots. To minimize losses plants can actively re-allocate Phosphorus from senescing leaves (see 2.3). Phosphorus use efficiency involves several physiological parameters but by comparing Phosphorus content and production or photosynthesis a measure of efficiency in use of Phosphorus can be obtained. Legumes are common in the forest of Guyana and many of them have been reported as nodulating (Norris 1969) and/or showing some type of mycorrhiza (see ter Steege 1990). In natural circumstances, Nitrogen is not limiting, in part due to the nodulating behaviour of several legumes. However, as Nitrogen-fixing species have a high demand for Phosphorus, it poses a further strain in Phosphorus-limited habitats. Roots of seven species have been investigated for the occurrence of mycorrhizal infection. No mycorrhiza was found in the pioneer Duka (*Tapirira marchandii*), endomycorrhiza was present in the pioneer Congo pump (*Cecropia obtusa*), in Charcoal barabara (*Diospyros ierensis*), Imirimiaballi (*Chamaecrista adiantifolia*) and the legume Purpleheart (*Peltogyne venosa*), ectomycorrhiza in Greenheart. Both types were found in the pioneer Kabukalli (*Goupia glabra*) (Raaimakers 1994).

Ectomycorrhizae are linked to low-Phosphorus soils (<5 ppm) and Caesalpinoid legumes in Cameroon (Gartlan *et al.* 1986, Newbery *et al.* 1988). The importance of ectomycorrhiza in South-America has been suggested by St. John & Uhl (1983) and Singer & Araujo (1979) but has lately been questioned by Moyerson (1993) and Béreau & Garbaye (1994).

Given that:

1) ectomycorrhiza are taxonomically linked to certain tribes within the Caesalpinioideae (notably Amherstieae and less Detarieae, Alexander 1989) and members of these tribes (e.g. *Dicymbe* spp. and *Eperua* spp.) dominate in Central Guyana
2) phenology of ectomycorrhizal fungi (Boletes, Amonites and Russulas) is more linked to tree phenology than to high rainfall (Smits 1994) and observations to that extent have been made in Guyana (ter Steege & Zagt pers. obs.)
3) mycorrhizae (both ecto and vescicular-arbuscular) can be of vital importance to tree growth (e.g. Janos 1980)
4) mycorrhizae can be adversely affected by clearing forest (Janos 1980, Smits 1994)

inventories on and experimental studies with mycorrhizae are of great importance both for a better understanding of the forest ecology and dominance of the Guyanese rain forest and the effects of logging thereupon.

Concentrations of Nitrogen and Potassium are not particularly low in seedlings in Guyana. However, Phosphorus concentrations and Phosphorus/Nitrogen ratios in leaves are very low in all species tested (Raaimakers 1994). The most conspicuous differences found among the species are: a high Phosphorus content in the roots of the legumes, which may be related to N-fixation, and a high Phosphorus content in the leaves relative to the roots of the pioneer species which may be related to a high maximum photosynthetic capacity. Leaves from mature trees shows normal Nitrogen values but even lower Phosphorus content than seedlings. The resulting Phosphorus/Nitrogen ratio of both seedlings and adults (0.023-0.056) is extremely low and suggests that most species may be regarded as Phosphorus-deficient.
White Sands are poorer in total nutrient content than Brown Sands (Table 4, Raaimakers *et al.* 1995b in press, Brouwer 1994, van Kekem *et al.* 1995). Contrary to this, plants on White Sand show higher Phosphorus contents than those of Brown Sand (Table 5, Raaimakers *et al.* 1995b in press). This implies higher availability on White Sand and this is confirmed by pot experiments (Raaimakers 1994). Other species studied are efficient in reallocation of nutrients from leaves of mature trees before abscission (see section 2.2)

Photosynthesis of forest species
Large differences in photosynthetic capacity are found between forest species in Guyana. Pioneer species (Congo pump, Kabukalli and Duka) have high photosynthetic rates. Canopy species, capable of regeneration in more shady conditions, have lower rates, particularly Greenheart. All species showed a positive correlation of photosynthetic capacity with light availability on their growing site. This correlation was most pronounced in the pioneer species, but was rather weak in Mora and Greenheart. Potential Photosynthetic Nitrogen Use Efficiencies (PNUE) cover a range similar to data reported for other tree species (Raaimakers *et al.* 1995a). The photosynthetic rate of species from Guyana is comparable to species studied in other tropical areas, but achieved with lower Phosphorus concentrations (Raaimakers *et al.* 1995a). Thus, Guyanese tree species are efficient in using Phosphorus for photosynthesis.

Effects of fertilization

Phosphorus fertilization in a pot experiment, did not increase Phosphorus content in the plants studied (Table 5), except in Congo pump (*Cecropia obtusa*, Raaimakers 1994) and did not increase plant weight significantly (Raaimakers *et al.* 1995b in press). Phosphorus fertilization of seedlings in the forest did increase plant weight of Clump wallaba, but not of Greenheart. Nitrogen fertilization had no effect on the plant weight of Clump wallaba but was lethal for Greenheart (Raaimakers 1994). Even though Phosphorus must be regarded as growth-limiting, the effects of Phosphorus fertilization are small. This may suggest that: 1) addition of Phosphorus (on Brown Sand) did not increase the availability, or 2) while Phosphorus may be limiting, something else is also limiting growth. This might be another limiting (micro-)nutrient, or 3) other toxic effects associated with a low pH (White Sand) may hamper growth (see Table 4). Growth limiting factors associated with low pH (acid soil infertility complex) are high levels of aluminium, manganese, other metal ions, H^+, and deficiency or unavailability of essential elements, particularly Phosphorus, Calcium, Magnesium and Molybdenum (Foy 1984). The addition of litter did not increase Phosphorus content of the plants, but plant weight increased significantly. Possibly, litter increases the pH, thus lessening the effects of soil acidity. Furthermore litter may be of paramount importance for infection with mycorrhiza.

Burslem *et al.* (1995) carried out a similar experiment with species from poor soils in Singapore and also found a strong response to P addition in two pioneer species. They also indicated general pitfalls with translating the results of such pot-experiments into the field. Most important and supported by the Guyanese experiments are the differences in response to fertilizer addition in different species. The observation of the very positive effect of litter, not so much on nutrient content of seedlings, but on the total achieved dry weight, appears to be novel.

Another interesting difference was found between pioneer and climax species. While Congo pump (*Cecropia obtusa*) and Kabukalli (*Goupia glabra*) showed a high efficiency in phosphorus-acquisition coupled to a high RGR, climax species showed low RGR and low efficiency in phosphorus-acquisition. Thus, in disturbed areas, Congo pump is capable of actively incorporating released phosphorus into its biomass. This effect is enhanced by the higher growth rate of this species. Stark (1970) made a similar observation in comparing local secondary species with Caribbean pine in Suriname.

Table 5. Plant total phosphorus content and dry weight in a fertilizer experiment in Guyana (Raaimakers 1994). Differences between treatments are indicated with lowercase letters.

	White Sand	Brown Sand	
P_{tot} (μg)			
on bare soil	584 b	201 a	
with P fertilizer	1505 c	2279 d	[1]
with litter	664 b	818 b	
Dry Weight (g)			
on bare soil	339 b	305 a	
with P fertilizer	344 b	656 c	
with litter	512 c	865 d	

[1] This effect is strongly influenced by the reaction of *Cecropia*. All other species do not react significantly.

3 EFFECTS OF LOGGING

3.1 Logging

Logging involves the felling and extraction of trees. While felling creates a gap much the same way a natural treefall does, there are differences. A tree selected for felling is almost always in the bloom of its life, with fully developed branches and full of leaves. A tree that dies from natural causes usually has a smaller or already decayed crown. Thus, damage by felling trees may be larger. Forest exploitation in Guyana is legally restrained by a felling limit (33 cm dbh) but more so by marketing principles. Greenheart has traditionally contributed up to 70% of the total export (Chapter 1). As Greenheart is often growing gregarious (Chapter 2), felling gaps are mostly produced by cutting more than a single tree. While this may have severe effects on a local scale, the larger scale effects of this 'selective' logging on the forest seem relatively small - much forest, albeit without Greenheart dominance, remains intact. Large scale disturbances, such as hurricanes, earthquakes major forest fires are probably rare in Guyana (Hammond & Brown 1995) and thus gaps formed by logging tend to be larger than natural gaps. Mechanized extraction has no natural equivalent. A skidder compacts the soil as it moves through the forest and is capable of causing excessive damage to seedlings, and small and medium sized trees.

After logging the forest is left with numerous gaps and turned up soil, a mosaic of sites favourable for germination and establishment of pioneers, and untouched patches of forest. This will initially lead to a change in the floristic make-up of the exploited area, which will close up with secondary vegetation dominated by immature Kabukalli (*Goupia glabra*) and *Renialmia orinocense*, and other common genera from secondary vegetation including; *Cecropia*, *Miconia* (and several other Melastomataceae), *Palicourea* (and other Rubiaceae) and *Trema*. Over time a change in floristic composition may be foreseen and some timber species may eventually become more abundant (Rose, unpublished data), dependent on their growth and survival characteristics.

In a lateritic area (Ekuk Compartment, Mabura Hill), logging increased the number of gaps by over 50%, as compared to natural forest. The increase in total gap area due to logging was around 400%, as the size of artificial gaps was larger than the size of natural gaps (Hammond & Brown 1991). Gaps accounted for 12.6% of the area in logged forest compared to less than 3% in natural forest (Hammond & Brown 1992). The size of the gap was largely influenced by the size and number of trees contributing to the opening. Data suggest that the four largest DBH size classes (trees >80cm) accounted for 68% of all felled and otherwise fallen trees. The average crown zone of a 'logging' gap was over 3 times larger than that of a gap produced through natural events. The amount of damage associated with extraction was considerable. On average, to extract a single bole, a basal area equal to the bole was destroyed in the process (two trees of roughly half the basal area of the selected timber tree). The damage on small trees was also considerable, but as pre-harvest data were lacking, no estimate is available for the Ekuk plots.

Exploitation has a number of consequences for the population dynamics of a species, as will be seen below. The initial structure of the population will be altered. In theory, changes in soil properties and microclimate (of which light is most significant), and damage inflicted to the remaining stand will have an effect on birth rate, mortality rate,

and growth rate of the individuals in the population. It is expected that the effects are greatest just after exploitation, and that in time most parameters gradually return to 'normality', except in case of irreparable damage to the population.
The impact of exploitation varies with its intensity, frequency and spatial extent (Waide & Lugo 1992), and also whether the species under consideration is exploited itself, or whether it is simply growing in an area that is exploited for other species.

3.2 Microclimate

Gaps in the canopy structure of the forest allow more radiation to penetrate to the ground, increasing air and soil temperature, and decreasing mid-day air humidity (e.g. Schulz 1960), as well top-soil moisture can be expected (but see below). Size and form as well as specific sampling locations all have influence on the change of these parameters. Changes in these parameters were measured in two artificially created gaps (740 m^2 and 3440 m^2, medium gap and large gap respectively). Increases in radiation were not measured but calculated with hemispherical photographs (ter Steege 1994) and average above-canopy estimates from the meteorological station (Jetten 1993a,b). Average daily radiation above the canopy amounted to 13.2 MJ m^{-2}. Daily radiation in the forest understorey is typically 1-10% of that of above the canopy. Estimated values for the medium and large gap are 7.8 MJ m^{-2} and 10.9 MJ m^{-2} respectively. Mean maximum air temperature was 30.1 °C on the medium gap, 32.4 °C on the large gap, compared to 26.8 °C in the forest understorey (Brouwer 1994). Soil temperatures in the forest rose to just 25 °C during the day but were over 40 °C on skid tracks and values of 50 °C have been observed just below the litter layer in the large gap. Similar differences were found by Schulz (1960). Effects however, are mainly restricted to the litter layer and are almost completely levelled off at 5 cm below soil surface. Whereas the subsoil in general is more moist, the topsoil in the bare zones of the gap is drying out rapidly after a few dry sunny days. Relative air humidity was nearly 100% in the morning on all locations, it decreased to 85% in the understorey, to 75% in the medium gap and to 65% in the large gap. Increases in radiation, temperature and decreases in humidity affect the water balance and mineralisation rates on gaps. They also affect the survival of seedlings, which may either benefit or suffer from the increased radiation levels.

3.3 Soil and water balance

The use of heavy machinery after felling, such as skidders, causes soil compaction (e.g. Hendrison 1990). According to Hendrison (1990), who tested soils in Suriname, comparable to the soils in the Mabura area, the first four passes with a skidder created the largest change in bulk density (from 1.25 to 1.60 g cm^{-3}), after which only slightly more compaction took place. Similar results were obtained by Kamaruzaman (1991) on a clay soil in Malaysia. The initial soil moisture content is important, a wetter soil resulting in more compaction (Dias & Northcliff 1985, Hendrison 1990).
A study of the influence of logging activities on topsoil properties was conducted three months after logging on a White Sand, a loamy and a sandy Brown Sand (Jetten 1994a). Skid trails were compared to undisturbed forest.
In White Sands saturated hydraulic conductivity (Ks) decreased from 3400 cm/day to less than 10% of this value after disturbance. Unsaturated conductivity at field capacity decreased even to 1%. Strange enough, porosity is slightly higher in disturbed top soil,

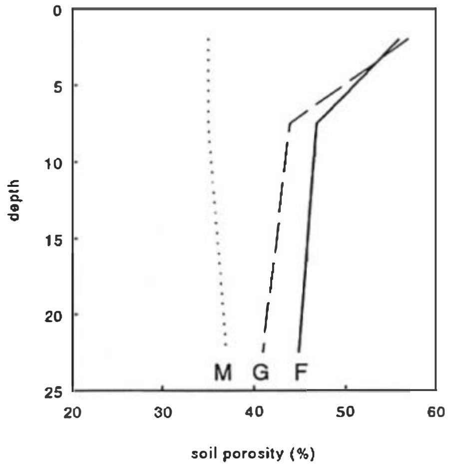


Figure 12. Soil porosity of a loamy Brown Sand at different soil depths for an unlogged forest, a logging gap and a log-market. F=forest, G=gap, M=log-market (Hoefsloot 1991).

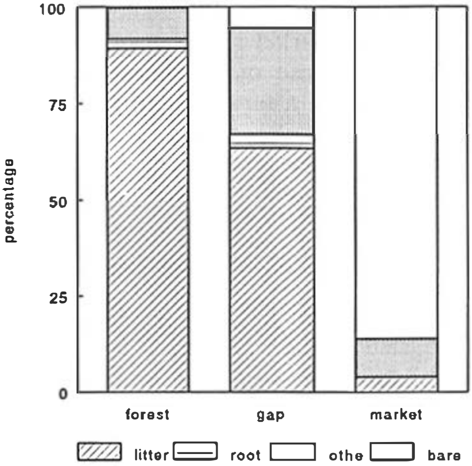


Figure 13. Soil surface cover (litter, roots, other cover or bare) of a loamy Brown Sand for an unlogged forest, a logging gap and a log-market (Hoefsloot 1991).

probably due to mixing of organic matter from the top layer and/or fresh debris. Nevertheless, the White Sand was compacted and the water retention characteristics changed strongly, causing an increase in water holding capacity (expressed as the amount of water stored between field capacity and wilting point). Organic matter, on White Sand usually in the form of small pellets, may concentrate on skid tracks and cause ponding there.

In the sandy Brown Sand Ks decreased to about half of the natural value of 470 cm/day. Both porosity and bulk density increased slightly, indicating not only compaction but a change in the organic matter fraction. Water retention characteristics hardly changed.

Loamy Brown Sands show a high variation of hydrological properties (Jetten *et al.* 1993). Consequently no significant differences were found for Ks, porosity, bulk density and water retention. The stable micro aggregates formed with iron oxides in these Brown Sands apparently remained intact and prevented surface sealing by clay and silt particles. Indeed remarkably little surface sealing was seen in the field after logging. The macro structure in the soils under natural forest was very weakly developed and the effects of logging on soil structure seem limited. However, the high variability of soil hydrological characteristics (Jetten *et al.* 1993) may obscure some of the effects.

One year after logging, compaction was studied on a Brown Sand (Jetten 1994a) The undisturbed forest situation was compared to a large felling-gap and a log-market, i.e. a temporary storage area for logs. Infiltration, saturated hydraulic conductivity, porosity, and moisture retention characteristics appeared to be similar under forest and in the gap but the amount of litter had decreased slightly on the gap. The market, however, showed

significant change in all properties (Figure 12), particularly in the top 25 cm of the soil. This is caused by a loss of soil structure and a decrease in litter surface cover (Figure 13). Water availability decreased in order from forest to gap to market.
Comparison of the two studies indicate that there is a strong temporal effect. When skid trails and market remain bare there will be a rapid decomposition of soil organic matter and a decrease of soil fauna, both of which are elements that keep the soil structure intact. Thus, a further decrease in soil hydraulic conductivity may be expected.

The effects of these changes in soil properties on the hydrological balance were modelled for gaps and skid trails (Jetten 1994a). Results for a gap with 20% skid trails are given in Figure 14. Values for a Brown Sands soils are used, assuming that the disturbance affected the top 20 cm only. Also it was assumed that there is no vegetation left on the gap and skid trails, and no influence from surrounding trees (the gaps are large). The main changes in the hydrological balance are caused by the disappearance of the vegetation; interception and uptake both reduce to zero. Due to changes in soil structure, infiltration and runoff characteristics of skid trails change slightly. As this gap has only 20% skid trails the final effect is negligible. The result of all changes is a decrease of total evapotranspiration (now only evaporation) and an increase of percolation and discharge (changes in microclimate, see above, are also taken into account). Such higher percolation rates potentially lead to higher nutrient leaching rates. In a forest area with 20% logging gaps the total effect will be smaller with a decrease in evapotranspiration from 55% to 51% of total precipitation, and an increase in discharge from 45% to 49%. This is well within the error of measurements of these fluxes. In the wet season soil moisture was not different in gaps and forest understorey (Brouwer 1994, Jetten 1994a). However, during dry periods soil moisture in the forest is lower than in gaps. Increased evaporation (see above), apparently does not dry out the subsoil more than pF 2 (pF = -log (H_2O pressure)), compared to transpiration of the trees in the forest, which lowered moisture levels to almost pF 3. This result is confirmed by experiments with two gaps in Costa Rica (500 and 2500 m^2, Parker 1985).

When gaps recover with forest tree seedlings and secondary vegetation, interception and uptake will increase. Jetten (1994a) estimated that Leaf Area Index (LAI) will increase to 2.2 m^2 m^{-2} in one year. This would bring evapotranspiration back to 75% of the original value. Sites near San Carlos de Rio Negro recovered to LAI of 2.3 in one year and to a LAI of 6 m^2 m^{-2}, comparable to natural forest, in 10-20 years (Saldarriaga & Luxmoore 1991, Saldarriaga 1994). With the limited effects on soil hydrological properties measured, the hydrological cycle would then be more or less equal to mature forest - note that the same conclusion does not necessarily hold for forest composition.
Because of the sandy nature of the soils and the small extent of the skidtrails, the 'Experimental-Catchment' as a whole was not be affected much by low intensity logging. In the absence of vegetation immediately after logging the drainage to the groundwater will increase but if plant cover restores, the balance will probably be regained. The shape of the catchment is typical for the area and plays an important role in this. The water divides are wide and flat with steep slopes towards the creeks. A small flat floodplain (often a swamp) is usually present at the lower parts but is small in the log-catchment. Thus logging took place on the water divide and upper slopes. If increased surface runoff in such a situation occurs (which is not likely) the water will infiltrate on the mid and lower parts of the slopes before it reaches the creek. Thus a change in peak flow is not

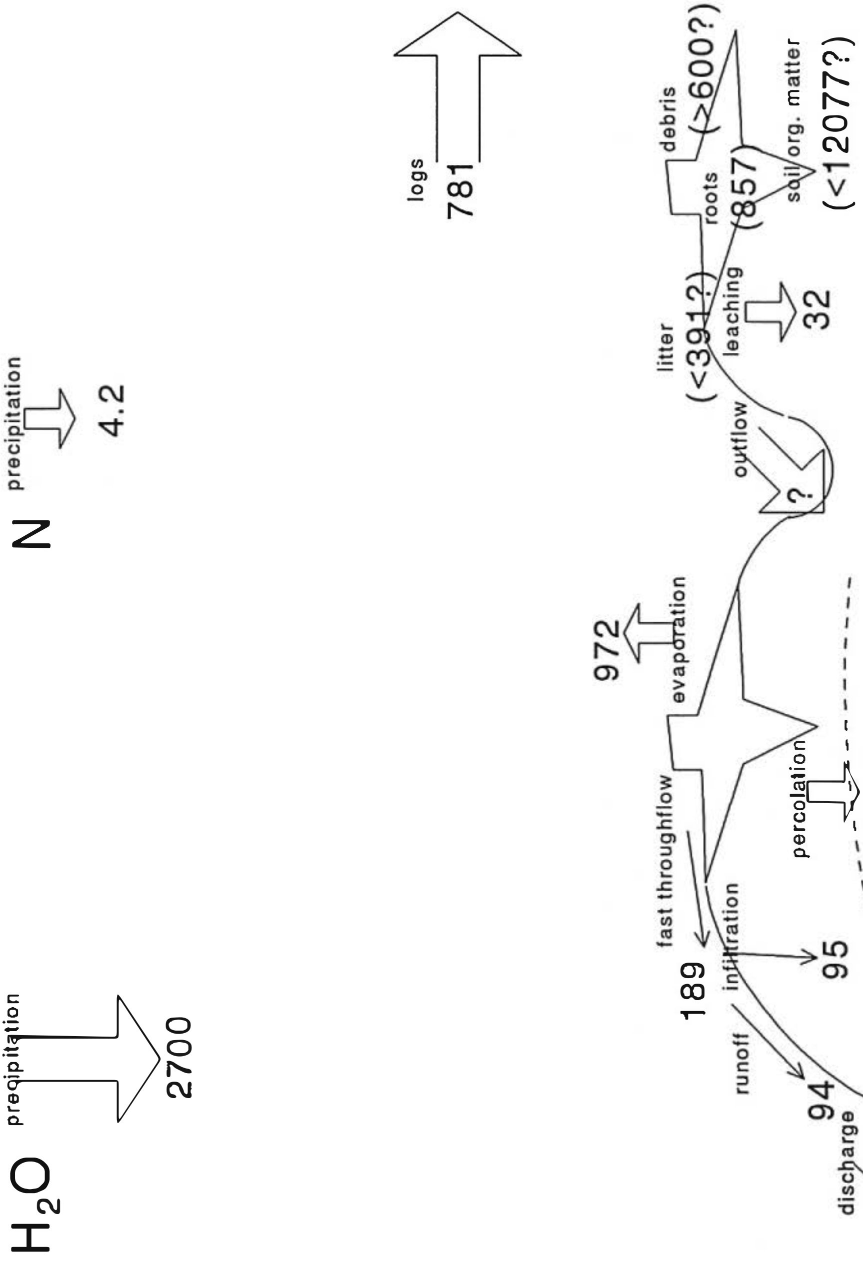


Figure 14. Water balance and Nitrogen budget for a large gap in mixed rain forest on a Brown Sand in Guyana. Left: water balance, water movements in mm year^{-1} (Jetten 1994a). Right: Nitrogen budget, in parentheses. Nitrogen standing stocks in kg ha^{-1} (Suriname, Poels 1987), Nitrogen fluxes in kg ha^{-1} year^{-1}, except logs which is in kg ha^{-1} (one single logging action, Brouwer 1994).

Figure 15. Nitrate concentration in groundwater at 1.20m in an undisturbed forest and large gap skid trail ▸ (Brouwer 1995).

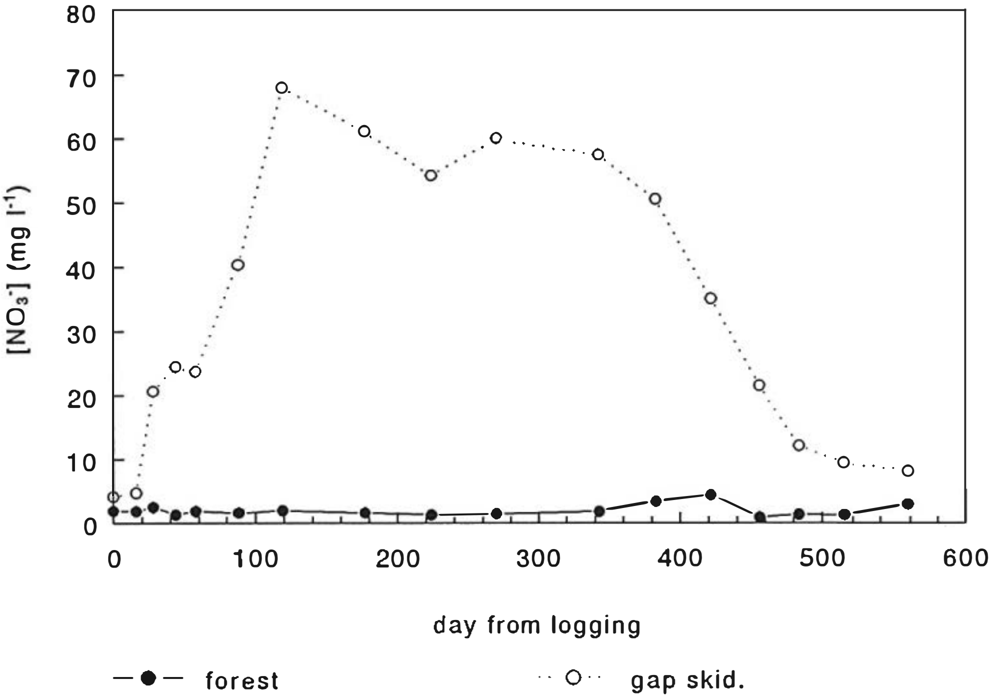
expected and discharge analysis results indicate that this is the case. The only changes on a catchment scale will be in groundwater levels and base flow, which increase and fluctuate more. These changes are small, however, and fall within the sampling error in the measurements on the 'Experimental Catchment'.
Due to high infiltration rates and limited logging in the vicinities of creeks siltation as a result of logging is probably low. Observations indicate that siltation does occur, mainly as a result of erosion of road surfaces, as is the case in many tropical timber areas (Bruijnzeel & Critchley 1993).

It should be noted that these results are valid for the sandy soils only. The research did not comprise the lateritic soils that cover a large part of the concession. Although these soils have not been studied extensively a few remarks can be made with regard to logging. An entirely different reaction to logging can be expected on these soils as they have a high clay content and can be very impermeable, depending on how much gravel is present. However, erosion also takes place under natural forest as the erosivity of throughfall can be equal or even higher than that of rainfall. It has been observed that the suspended sediment load of Laterite creeks increases strongly during a rainstorm. Surface sealing of the clayey soils will take place because of skidding activity and also by the impact of raindrops if the soil is left bare after logging. Thus increased runoff and erosion can be expected. Obviously this will change the groundwater fluctuation and discharge of the area. How this is affected by different logging intensities is not clear.

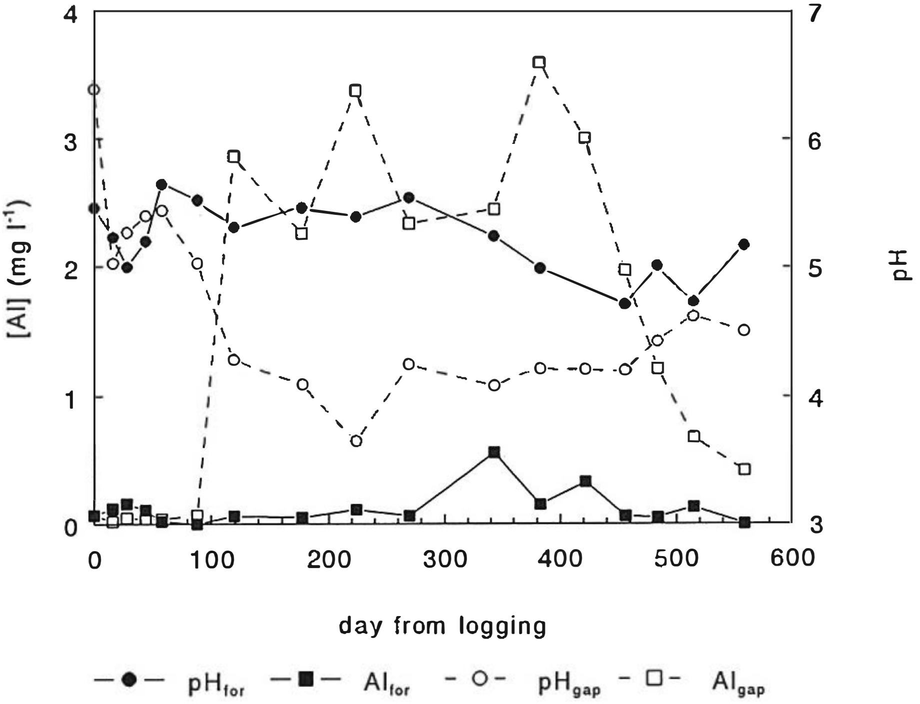
3.4 Nutrient balance

The effects of exploitation on changes in nutrient and associated water fluxes were studied in two gaps of different size (see above), created using logging methods and equipment commonly used in Guyana. The gaps were divided into three different zones reflecting degree of soil damage, amount of decomposable biomass and degree of disturbance of vegetation. In each of these zones, and in an undisturbed forest plot, drainage and soil solution chemistry were monitored. Additionally leaf litter decomposition tests and micro-climatological measurements (see above) were carried out. Extracted timber volumes were estimated and wood samples taken for analysis of nutrient contents.
Timber extraction was a major loss in nutrients on a gap (Figure 14). On the large gap 781 kg/ha of Nitrogen was removed in the form of logs. This is equal to almost all Nitrogen contained in stems in natural forest (data from Poels 1987) and was a result of the almost clear felling on the gap. Losses of other elements were also considerable (see Table 2, Chapter 2). Soil nutrient leaching increased considerably after felling, especially for Nitrogen (Figure 15). This was due to both higher concentrations of nitrate (ammonium being insignificant compared to nitrate) in drainage water and to increased drainage amounts in gaps (see above). Leaching losses seem mainly related to the vicinity of undisturbed vegetation as well as soil damage and the amount of decomposing biomass. In the skidder zone concentrations of Potassium and Magnesium start to rise sharply (10

Figure 16. Aluminium concentration and pH in groundwater at 1.20 m in an undisturbed forest and large ▸ gap skid trail (Brouwer 1995).



[NO$_3^-$] (mg l^{-1})
0
10
20
30
40
50
60
70
80
0
100
200
300
400
500
600
day from logging
—●— forest
··○·· gap skid.



[Al] (mg l^{-1})
0
1
2
3
4
pH
3
4
5
6
7
0
100
200
300
400
500
600
day from logging
—●— pH$_{for}$
—■— Al$_{for}$
- ○ - pH$_{gap}$
- □ - Al$_{gap}$

times background levels) after three months of logging. Fifteen months after logging Potassium levels seem to have returned to background levels, Magnesium remains slightly higher in the exploited zone. Concentrations of Nitrogen, which rose sharply after logging, declined fairly rapidly after 15 months of logging. However, they failed to reach background levels, even after 2.5 years after logging. At that time Nitrate concentrations are still 5 to 10 times higher than background concentrations.

In terms of percentages logging takes away 5.2% of the total Nitrogen in localized areas of the forest system. When leaching approaches (relatively) to background levels in about 1.5 years, an additional 0.3% has leached away. Initial leaching losses are thus small compared to the log output, but continue. Losses of potassium, Calcium and Magnesium due to logging are, 2.8%, 1.7% and 4.5% respectively. Leaching losses (1.5y) are, in the same order, 1.8%, 1.7%, 5.0%. Therefore cation-leaching is far more important than Nitrogen-leaching. In total, 10% of the Magnesium will disappear due to logging. Whether Magnesium (and other nutrient) capitals can build up to original levels between cutting cycles of 20-25 years is unknown yet.

A drop in pH occurred approximately five months after logging (Figure 16), probably as a result of conversion of Ammonium into Nitrate (nitrification). As a reaction the levels of soluble aluminium in the groundwater rose steeply (Figure 16). Soluble Aluminium level declined to near background levels in approximately 550 days.

Decomposition of fresh and shed leaves was monitored for a period of almost one year. Decomposition was slow in the open areas in the gaps, which may serve as a nutrient conserving mechanism. While nitrification rates increase (above, Montagnini & Buschbacher 1989), decomposition may slow down in gaps (Brouwer 1994) due to more extreme temperatures (see above) and/or lower (micro-) biological activity (e.g. Alexander *et al.* 1992, Burghouts *et al.* 1992). However, decomposition was high in the crown zone of trees, which is consistent with the higher leaching levels found there, and this may contribute substantially to leaching. All of these processes will be lessened by a small-as-possible gap size.

At catchment level ('Log Catchment') no changes in creek discharge were measurable (Jetten 1994a, see above). As observed in the 'Gap Experiment', leaching was also observed in the 'Log Catchment' at the logging sites (N, Ca, K; Brouwer 1994). The concentrations of these important ions did not change significantly in the creek water and thus at catchment level overall changes are small. However, levels of sodium in creek water increased though being irregular. It is possible that the vegetation at the slopes (where no logging took place) absorbed these important nutrients (Brouwer 1994). A similar suggestion was made by Poels (1990). Nitrogen has leaching levels as high as sodium in the 'Gap Experiment'. As such, higher levels were expected in creek water. Apart from absorbtion by slope vegetation Nitrogen may also have been lost by de-nitrification which is usually more pronounced the wet anaerobic soils such as those along the creek.

3.5 Population structure, growth of adults

Extraction rates, measured in 4 hectare-size plots, in Ekuk amounted to 57-102 m^3 ha^{-1} (Zagt 1994). Between 38-71% of all Greenheart adults (>30 cm DBH) were logged. Most striking was that the larger part of the sub-adult (<30 cm DBH) population had also disappeared. Observations in the plots suggests that logging intensity, especially

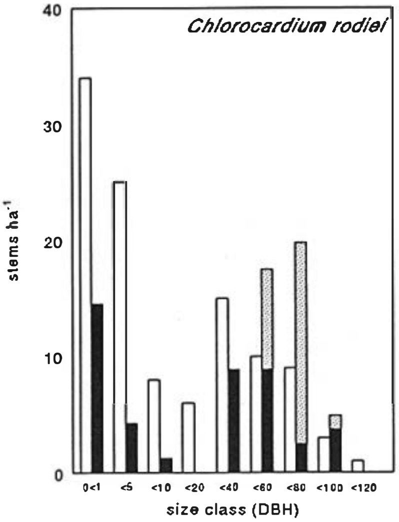


Figure 17. Population structures of Greenheart in natural (□) and logged (■) forest. Hatched bars indicate standing trees, white bars in the case of Greenheart in logged forest are logged individuals (Zagt 1994).

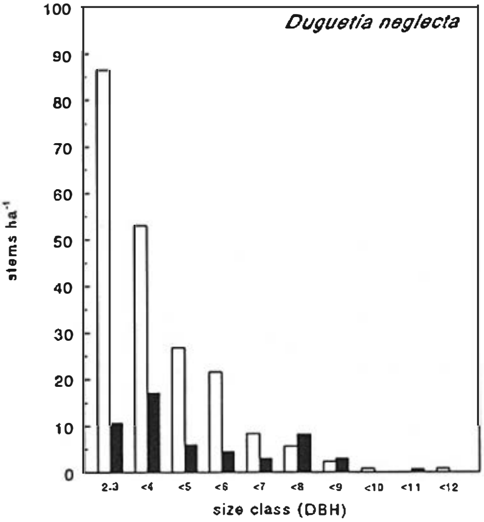


Figure 18. Population structure of Yarri yarri in natural (□) and logged (■) forest (Zagt 1994).

skidding impact, may have been the main cause for the loss of the smaller individuals. This observation is supported by observations in the experimental 'Log-catchment', where logging and skidding intensity were far less (35 m^3 ha^{-1}) and winching was used in preference of skidding, with the result that damage to the remaining stand was limited. Obviously, other species are affected as well by logging. Figures 17 and 18 show the Greenheart and Yarri yarri (*Duguetia neglecta*) populations in an unlogged 'Greenheart forest' plot compared with a logged 'Greenheart forest' plot (Zagt 1994). In the logged plot felling was mainly directed at individuals of 60 cm and larger. Assuming that the population structure of the two plots would have been comparable, it appears that a large part of the sub-adult population is killed as well, similar to the Ekuk plots (see above). In the case of Yarri yarri, which is not logged, the effect is even more pronounced.

Although these results represent the structure of various populations at one moment in time, and do not give insight in the dynamic properties of these populations, two tentative conclusions may follow from these data. First, the exploitation of Greenheart also affects populations of other species. Furthermore, the absence of sub-adult trees in this particular Greenheart population indicates that a rotation cycle of twenty years is too short to provide for a new population of exploitable trees in this plot.

Growth of both Greenheart (Figure 19) and Clump wallaba (Zagt 1994) seems to be higher for most classes in the exploited plot compared to the natural plot, but sample size for the exploited plot is small (due to incomplete first enumeration). On average, growth rates for Greenheart > 11.4 cm in the exploited plot are slightly less than double compared to the natural plot, whereas Clump wallaba grows more than twice as fast as Greenheart in both cases. These favourable figures for Greenheart are reverted when total annual volume increment is calculated (disregarding the fact that some trees may be hollow). Due to the poor condition of the remaining stand, and to the small size of it, volume increment in the natural plot exceeds that of the exploited plot (Zagt 1994).

Comparison of the distribution of growth rates is also instructive, as it gives a good impression of the variability of growth. Greenheart growth rates never exceed 0.6 cm/yr even in the exploited plot; and more than 40% of the trees in the natural plot does not show any significant growth at all. The range in growth rates is much wider in Clump wallaba, with even in the natural plot a number of very fast growing trees (> 1 cm/yr). In the exploited plot more than 25% of the trees have that growth rate (Zagt 1994).

The growth rates for Greenheart in the natural plot are generally somewhat below the values obtained in increment plots elsewhere in Guyana (Figure 19). The results for the exploited plot seem to agree well with those given there for exploited but untreated forest. The reported values for trees in treated forest are never attained in the exploited plot (see Chapter 3.7).

Comparison with growth rates cited in Jonkers 1987 (table 5.5, p. 97) for trees measured during development of the CELOS system in Suriname reveals that Greenheart ranks among the slower growing species in the region, both in natural forest and in exploited forest. (The exploited forests in Suriname had different exploitation levels than in this study; all of them lower). Clump wallaba grows as fast as the fastest growers in Suriname in the natural plot, and tops all of them in the exploited forest.

3.6 Flowering, germination, survival and growth of seedlings and saplings

Flowering activity of Greenheart increased after logging. A larger percentage of the trees flower and they flower more abundantly. However, the higher reproductivity cannot compensate for the loss of adult individuals. Thus overall reproductivity decreases and this is also the case in Clump wallaba (Zagt 1994).

Seed production of Greenheart occurs over a long period of time (Chapter 2), and so does germination (it starts around June but can be prolonged or maintained to more than a year after seedfall). Limitations to logging operations during seedfall will, thus, only marginally increase the number of seedlings in the population. Two studies have addressed the germination of Greenheart seeds. Ter Steege *et al.* (1994) found, in an eight week period, that germination declined from a closed canopy environment to more open environments. In large gaps germination was nil and mortality near 100%, due to drying out and subsequent fungal attack. Hammond & Brown (1993) found a low germination success (20%) in large gaps after 14 months. Highest germination occurred in the crown zone of natural gaps (65%).

Seedlings of Greenheart were thought to be shade resistant (e.g. Fanshawe 1947) but it was assumed that a series of small gaps was necessary for establishment in the canopy. In ideal circumstances, such as in the above mentioned experiment with shade treatments Greenheart proved to be very shade resistant, with no mortality in any (including the 0%) shade treatment (Boot 1994). Growth of such seedlings and of those in the understorey is negative and seedlings use a strategy of slow depletion of the cotyledon reserves. Once these reserves have been depleted the seedlings will most probably die (ter Steege *et al.* 1994). Predation of the cotyledons in the forest should therefore be considered of great importance in the mortality of Greenheart seedlings. This is confirmed by the high mortality of seedlings under parent trees, as a result of cotyledon damage (Hammond & Brown 1993, see below) and low survival in understorey conditions after cotyledon removal (ter Steege *et al.* 1994). In a pot experiment, survival was indeed higher in large gaps (ter Steege *et al.* 1994). However, in a field study Hammond & Brown (1993) found that establishment of seedlings was lowest in large gaps (5%), followed by locations under the parent trees (19%, density dependent mortality, see above). Best establishment (40-50%) was found in the understorey >30 m away from parent trees and in the crown zone of natural gaps.

Seedlings of Greenheart respond favourably to increased canopy openness as a result of logging (ter Steege *et al.* 1994). Seedlings in large gaps were larger and had more biomass than those of small gaps and those of the forest understorey. Estimated relative growth rate declined over a continuum from large gaps to forest understorey and was negative in most small gaps and the understorey. In such cases leaf turn over was high and the plants never had more than a few leaves. It was hypothesised that under such dark conditions Greenheart seedlings could not maintain a positive carbon balance. Greenheart seedlings were also more numerous and larger in the Exploited Plot compared to the Natural Plot. This is caused by the fact that the seedlings in the Exploited plot are older and have experienced better growth conditions (more light). The seedlings in the exploited plot showed lower mortality than those of the natural plot. However, seedlings of the exploited plot may have been more vigorous in the past and are now gradually losing leaves (Zagt, unpubl. data). Death comes after a long time of decreasing vigour and most seedlings in the exploited plot are still in the declining phase. Thus it appears that the initial vigorous growth after exploitation comes to a halt when seedlings are overtopped by individuals of faster growing species, such as Kabukalli (*Goupia glabra*) and Clump wallaba and seedlings are left with a large physical structure not suitable for the current conditions. This, added to the fact that overall reproductive capacity declined in the exploited plot, implies that former reports of favourable seedling development after exploitation (e.g. Clarke 1956), have to be interpreted with caution.

Litter decreases locally in gaps during logging, especially with use of heavy machinery. As has been shown above, litter may improve plant growth, either by lessening some of the toxic properties in the soil or by providing a substrate for mycorrhizae. Concentrations of some potentially toxic elements, notably aluminium raise steeply in large open areas. This too may have great consequences on species behaviour in large gaps. Both processes may thus greatly influence the future species composition of gaps.

3.7 Animal seed dispersers

Logging

In general, extensive information on the effects of logging on any animal group is sorely lacking. However, a 5-month pilot study examining the differences between logged and unlogged stands of mixed forest on laterite suggests at least that population densities of Red rumped agouti (*Dasyprocta agouti*) in logged forest are not substantially different from those in unexploited forest expressing similar resource and domicile availabilities. Primates, however, were not sighted as frequently in the logged plot during the same sampling period, possibly due to the effects of logging on their movement within the canopy (Hammond *et al.* 1992). Bird diversity in similar forest in French Guiana was strongly affected by selective logging (Thiollay 1992). Most affected were birds associated with the understorey and forest floor. Densities of primates on Borneo, however, did not correlate well with forest age since logging or logging intensity (Johns 1992). Information concerning invertebrate responses to logging is unavailable, but it is hoped that this will soon be rectified.

Forest access roads

Roads used during the forest operation represent distinct, spatially defined disruptions in the forest. The impact of road types on large (>0.5 kg) mammals in central Guyana was evaluated using a quantitative road cruise technique (Hammond, submitted). Results suggest that roads can have a negative impact on many large mammals which are forced to cross roads in order to access needed resources and subsequently killed by oncoming traffic. In particular, species not adapted for rapid movement on the ground across open space are vulnerable (e.g. Sloth [*Bradypus*], Tamandua [*Tamandua*], Kinkajou [*Potos*]). Many other arboreal species are hesitant in descending to the ground and would benefit if the distance between consecutive canopy corridors along a road was kept at a minimum. Large cats, peccaries and tapir actively use small roads for travelling and basking. These roads should be kept free from unnecessary traffic and should under no means be used for vehicle-based hunters.

Seed dispersal agents

At present no concrete information is available on 'Keystone species', those trees that produce large fruit crops during periods of resource scarcity and are heavily relied upon by the resident fruit and seed-eating animals. However, several tree species found in the area are known to fruit primarily during months when most trees do not (June-Sept.). These species are listed in Table 6. At least until their role as keystone species can be confirmed or denied, these species should be selectively preserved during forest exploitation. The harvesting of potential keystone species which yield commercial timber (e.g. Aromata [*Clathrotropis brachypetala*]) should be planned while bearing in mind the important role they may play in maintaining animals which disperse seeds of other timber species. A failure to disperse seed due to inadequate visitation by suitable dispersers can

Table 6. Some potential keystone species for the forestry belt in Guyana as indicated by the % of fruiting records of a species in the general off-fruiting season, June-Sept (data from ter Steege & Persaud 1991).

Species	family	% rec. June-Sept.	comm. timber	main disp. agent
Maho (*Sterculia pruriens)*	Sterculiaceae	76	yes	arboreal mammals, large birds.
Kokorittiballi (*Pouteria egregia*)	Sapotaceae	74	no	primates
Duru (*Apeiba petoumo*)	Tiliaceae	64	yes	primates
Pasture tree (*Trymatococcus paraensis*)	Moraceae	59	no	birds
Sawari nut (*Caryocar nuciferum*)	Caryocaraceae	54	no	rodents
Aromata (*Clathrotropis brachypetala*)	Leguminosae	53	yes	rodents
Hog plum (*Spondias mombin*)	Anacardiaceae	48	no	primates, rodents
Akuyuru (*Astrocaryum aculeatum*)	Palmae	43	no	primates, rodents

quickly lead to a collapse in regeneration should the species be heavily attacked by density-dependent vertebrate, invertebrate and/or pathogenic predators (Hammond *et al.* 1992, Hammond *et al.* submitted). In addition, long term dispersal should increase crossing between closely related offspring, causing further inbreeding depression within the population and reducing the general quality of the timber resource.

Seed predators

Seed predators can have a substantial impact on species regeneration since they determine the number of seeds from which the next set of trees will come from. Invertebrate pre-dispersal seed predators can heavily attack seed crops of many timber trees (e.g. Purpleheart [*Peltogyne* spp.], Locust [*Hymenaea* spp.], Shibadan [*Aspidosperma* spp.]) even before these seeds have a chance to be dispersed. Many other species are often selectively targeted for by arboreal mammals, especially Bearded sakis (*Chiropotes satanus*), which feed on immature seeds and fruits. For many tree species this may be one of the main reasons of their relatively low abundances in Guyanan forests. Harvesting plans should take into account the fact that many timber trees are not able to produce large quantities of viable seeds due to pre-dispersal attack by insects. Adequately spaced seed trees need to be selectively preserved in order to optimise the opportunities for natural reseeding of depleted areas.

Hunting and live animal trade

Hunting can have the most devastating effect on the forest animal community within the shortest period of time. Many mammal species have extremely low and inconsistent reproductive rates. The loss of a fraction of the population of these animals to hunting can readily result in a precipitous decline in populations as reproduction drops off. The collection of reptiles, amphibians and mammals for sale in the live trade produces a similar effect to hunting in that typically it is the healthy, reproductive mature individuals which are caught and removed from the area. Because accessibility is so much increased after logging, both practices, hunting and live trapping, should be restricted within logging concessions and this restriction should be vigorously enforced.

The effect of logging on animal populations may in turn have an effect on the seed dispersal and the seedling establishments. In Crabwood (*Carapa procera*), dispersal uphill by Acouchi may increase establishment by a factor of 10 (Hammond *et al.* 1993). The rareness of Acouchi in logged areas may decrease the influx of Crabwood seeds in potentially good sites. In Locust (*Hymenaea courbaril*) seeds under the parent tree suffer high mortality from beetles (Bruchidae) and weevils (Curculionidae). Seeds dispersed by primate regurgitation, probably suffer less mortality (cf. density dependent mortality in Greenheart). Limited dispersal and low success under parent trees probably explain to a large extent the rareness of this species. The inaccessibility of logged forest for primates may severely limit the re-establishment of Locust in these areas (Hammond *et al.* 1993). In Greenheart the main dispersal type appears to be gravity, though rodent removal in times of food resource scarcity may be large as well. Seeds and seedlings under parent trees are infested by a number of invertebrates (see above). In logged over areas increased levels of Agouti, due to increased slash cover, lead to 50% removal of seeds. Seedlings also appear more frequently browsed by terrestrial fauna. If patterns of rodent foraging keep consistently biased towards areas, previously logged throughout the building phase, then recruitment could be seriously impeded (Hammond *et al.* 1993). Road construction also potentially decreases accessibility for arboreal animals (Hammond in prep). Climbing animals, such as sloths, will not be able to cross distances in excess of 1 m, jumping mammals, such as Primates, may cross 5 m or more. Measurement of distances between locations where canopy at different sides of the road allows for crossing (Inter Canopy Corridor Distance, ICCD) along 61 km of main trail, showed that such distances were often much more than 1 km away from each other. This means that home ranges of several arboreal mammal species may not include canopy crossings.

3.8 Rain forest management based on natural regeneration

What is natural regeneration?

In silviculture, natural regeneration is a silvicultural system which uses the naturally available components in the forest; i.e. seeds, seedlings, saplings, advance growth to grow the future crop. Natural regeneration is the opposite to artificial regeneration in which seeds or seedlings are introduced to grow the next crop (plantation forestry).

Why natural regeneration?

When faced with a worked-out forest area the forest manager can select roughly between four options:

- Leave the forest to regenerate by itself;
- Convert the natural forest to a forest plantation;
- Apply silvicultural treatment to enhance growth of and reduce competition for remaining commercial stems;
- Apply silvicultural treatment to induce regeneration of commercial species.

The last two options both fall under the heading natural regeneration.
To compare natural regeneration (NR) to artificial regeneration (AR) we will look into the advantages and constraints of natural regeneration.

Advantages:

- NR maintains the natural forest environment while AR is usually accompanied by total clearing which involves a high cost;
- NR always keeps the soil sheltered except for roads, log markets, etc. Chances that the site would suffer nutrient losses or soil erosion are much less;
- Although a forest that is regenerated by NR differs from primary forest and the species richness is reduced the future forest is still more varied and richer in species than a forest plantation;
- NR is based on species and provenances that are selected by the natural environment. With plantation forest this is usually not the case which brings along several risks;
- It has not been proved yet that soil fertility is affected with NR. Such proof exists in the case of AR;
- Also there are few examples known of the occurrence of pests and diseases as opposed to case of AR;

- NR offers the opportunity to grow various species which apparently cannot be grown in monocultures. Reasons for failure can be various, such as unsuited microclimate, high soil temperature, soil degradation, diseases, lack of mycorrhizae;
- With NR the natural environment is maintained to certain extent providing a sustained opportunity to produce non-timber products simultaneously;
- A naturally regenerated stand tolerates neglect much better than a plantation. This is an especially valuable characteristic in case of uncertain future funding. If by reduced funds a plantation is neglected (postponing thinning or weeding) the plantation may collapse;
- A naturally regenerated forest is a better option to preserve the forest's regulatory functions (climate regulation, regulation of hydrological balance), carrier functions (habitat for indigenous people, areas for recreation, nature reserves), information functions (spiritual and religious information, scientific information) besides the production function.

Disadvantages and Constraints:

- Biological constraints. In managing the natural forest major problems are to be expected in relation to:
    - * the low density of seedlings / saplings of desired species or the difficulty to let them grow or induce them.
    - * the strong variation in the forest environment in space and in time with varying light environment and the difficulty to manipulate the environment in a way that optimal circumstances for growth and regeneration circumstances for the desired species are created at different points in time;
- Management constraints. At which species management should focus its attention. Different commercial species have different ecological requirements. Which species has the best economic perspective? Is this a fast or a slow growing species? What is the market value? How will the timber market develop?
- The naturally regenerated forest is a mosaic containing many tree species with varying ecological requirements and many woody climbers occur that could be potential "pests" to the future crop trees. Such a system is difficult to manipulate. Therefore the development of a silvicultural system demands much knowledge on and experience with several species. Once a satisfying system is conceived this usually means that the "domesticated" forest has different components than the original (logged/primary) forest. When in future one is considering to regenerate the same stand after the second harvest one cannot follow the same system indiscriminately;
- It is unknown what the long-term consequences are of the quite radical chances in structure and composition that occur with logging and even more so with logging followed by silvicultural treatment. Not only can many species be decimated, some might even disappear completely. Also certain ecological niches may disappear like large, hollow trees and there will be an increase of light on the forest floor level in general;
- The harvesting of trees will be an important link in the silvicultural system. The trees removed during logging are usually the best trees (the ones with no or minor defects). This brings along the risk of negative selection. Harvest and treatment

directives can meet these objections partly (e.g. leave a proportion of sound/without defect trees);

- Most rain forest trees have a large crown which contributes to heavy felling damage. Therefore directives should be introduced and enforced to minimise felling damage. The margin for improvement is small however especially compared to natural tree fall gaps where usually senescent, partly decayed trees fall who already have lost part of their crown if not all of it;
- NR demands more specialist knowledge from forest workers: species identification, some insight in ecological requirements of different tree species, some insight in the effect of drastic canopy opening, etc;
- To reduce competition to desirable stems other forest components are eliminated or devitalised. In case of trees this is usually done with arboricide. This has drawbacks from a hygienic, biological and practical nature. Sodiumarsenite has been used in the past as a very effective arboricide. It is not biodegradable and highly poisonous to plants, animals and mankind. 2,4,5-T (artificial plant hormone) has proven quite effective, is biodegradable, and harmless to animals and mankind. However it always has impurities of the highly poisonous dioxin. Both herbicides have been withdrawn from most markets. Herbicides that are accepted and effective at present are mainly artificial plant hormones; i.e. glyfosate, 2,4-D and triclopyr. A possibility to avoid the use of arboricide may be the application of double ring-barking. More time is needed for trees to die. In an experiment in Suriname 70% of the trees had died after two years (Jonkers 1987). Only a couple of species were able to restore their *sapstream* and recuperate from the treatment;
- Productivity in terms of volume of harvestable timber per area unit is low. 1 - 3 m^3/ha/year. This figure contrasts sharply with figures sometimes mentioned in plantation forestry, with in extreme cases, volume increments of up to 40 m^3/ha/year. It must be noted however that:
    - * such production is only achieved in exceptional circumstances and with large investments;
    - * such production is usually only maintained during the first years after establishment;
    - * risks of such a system are high;
    - * quality of the product is much lower;
    - * experience is restricted to a few, mainly fast growing, species - e.g. Pine (*Pinus*), Eucalypt (*Eucalyptus*), *Albizzia*, *Acacia*, and *Gmelina*. Experiments with slower growing species have not been very successful. Cost of maintenance of plantations of slow growing species is high;
    - * sustainability of high producing artificial systems is questionable especially in the humid tropics with infertile, fragile soils.

The conclusion should be that under the prevailing circumstances in worked-out forests on soils in the Berbice formation (brown and white sands) artificial regeneration should not be considered the most appropriate option for management of these forests.

Plantation work carried out in Guyana

Most plantation trials in Guyana were performed with Caribbean pine (*Pinus caribbaea*). In most cases the trials were abandoned due to high mortality mainly caused by Leaf

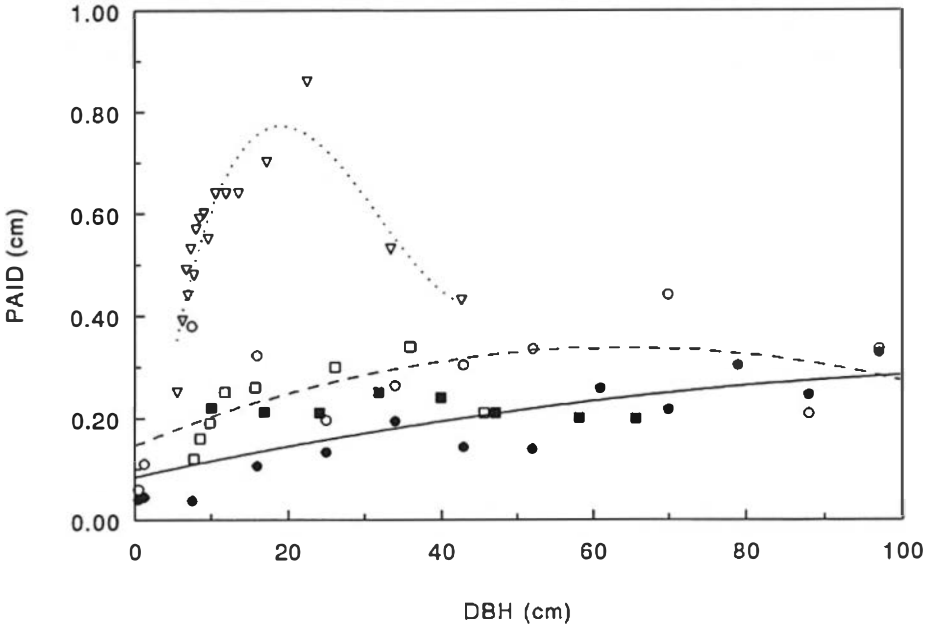


Figure 19. Periodic annual increment in diameter (PAID) of Greenheart in logged and treated forest (▽ Prince 1971b), logged and untreated forest (○ Prince 1971b, □ Zagt 1994) and natural forest (● ter Steege 1990, ■ Zagt 1994).

cutting ants (*Atta cephalotes*), high cost of maintenance, and lack of market opportunities. Caribbean Pine is much less capable of concentrating nutrients after clearing than are the local pioneer species (Stark 1970) and it must be expected that especially on the sandy soils (where Pine is mostly planted) large losses of nutrients will occur. Other local species have been tried (Crabwood [*Carapa* spp.], Red cedar [*Cedrela odorata*], Baromalli [*Catostemma* spp.], Dalli [*Virola* spp.], Tatabu [*Diplotropis purpurea*], Simarupa [*Simarouba amara*]). Most plantations were abandoned after several years of neglect (Prince 1971c). To reiterate, on sandy soils, with their low CEC, large clear felling will certainly lead to unacceptable losses of nutrients, which can only be supplemented at a high cost.

Silvicultural treatments previously carried out in Guyana
Most silvicultural work in Guyana has concentrated on Greenheart. They can be divided in four main groups, three of which are mentioned here:

Moraballi Creek (1938-1959): The reserve was heavily logged in 1930 and improvement treatments started in 1938. In 1957 three important observations were made (1) The regeneration of Greenheart is unevenly distributed and, even after silvicultural treatment, does not achieve uniform distribution. A similar observation was made by Aalders & Klopstra (1990) in another area. (2) heavy opening of the canopy stimulated secondary growth, which in most cases suppressed the regeneration of Greenheart. This is in agreement with the observations of the low to negative growth of Greenheart in shade and recent observations in exploited plots (Zagt 1994). (3) Although the regeneration of Greenheart and Determa (*Nectandra rubra*) was disappointing, there was adequate stocking of other merchantable species. The area was treated again in 1958 and results obtained in 1970 resulted in rotation estimates of 135 years (Prince 1971a).

Research Plot Ess (Essequibo) 1/61: This plot was established in 1961 in logged forest to investigate the behaviour of valuable species to four different post-harvest treatments. Dominant trees were followed from 1961 to 1976. Results of 12 years of diameter growth showed that commercial species reacted well to post harvest treatments (ter Steege 1990), comparable to results obtained in Surinam (e.g. Jonkers 1987).

Tree Increment Plots (TIP) Ess 3/63, 5/63 and 7/64: The first two plots were established in logged forests and one received silvicultural treatment. The third was laid out in unlogged forest. Prince (1971b, 1973) reported on the results of the first two plots. Only the results for the fast growing individuals were published in 1973 and this may lead to erroneously optimistic rotation times. Compared with natural forest (ter Steege 1990) the trees in the logged but untreated forest showed little sign of improved diameter growth, as appears to be a general case (van der Hout 1992). Trees in the logged and treated forest had considerably higher diameter increments (Figure 19). There was also a considerable effect on early regeneration and stand frequency diagrams showed very positive curves (see Prince 1971b).

Based on the optimistic results of the treatments Prince (1971b) suggests rotation times of 60 years. This rotation time, however, is based upon growth of the best trees only and projected on semi-natural stands instead of the treated plots itself. The estimates of 50 m^3 per ha each 60 years seem exaggerated (ter Steege 1990). With a simple growth model ter Steege (1990) estimated growth for Plot Ess 5/63 to be only 0.19 m^3 ha^{-1} y^{-1}. Similarly low regrowth figures of Greenheart were obtained in other traditionally logged 'Greenheart forests' (ter Steege 1990).

3.9 Silviculture in related forests

Trinidad, Mora forest

Logging in Trinidad has concentrated partially on forests dominated by Mora. While formerly logging consisted of clear felling and replanting with Caribbean Pine and Teak, Bell (1969) developed a system that allowed a timber regrowth of 2.2 m^3 ha^{-1} y^{-1}. Five trees per ha are harvested per rotation and these trees should be chosen as evenly spaced as possible. The system has been updated numerous times (e.g. Clubbe & Jhilmit 1992). Sustained production based on the one dominant species proves possible because Mora attains strong dominance and has a very positive population structure. Based on the results of the above mentioned research in Trinidad sustainable systems may be easy to construct for forests dominated by one of both Mora and Morabukea. However, logging in Mora forest may be restricted to dry season, for logistical reasons and protection. Furthermore, as the results show that Morabukea is not well adapted to decreased soil aeration, soil compaction should be kept at minimum. The latter species is also vulnerable to high irradiation loads (ter Steege 1993), which limits the gaps sizes that can be created during logging.

Suriname, mixed mesophytic forest, The CELOS Management System
The CELOS Management System (CMS) consists of the CELOS Harvesting System (CHS) and CELOS Silvicultural System (CSS). The system was developed when it became clear that plantation forestry (e.g. Pine), monocyclic systems, enrichment planting and systems based on natural regeneration without human interference were either not sustainable or economically undesirable (Hendrison 1990). The system is described in a number of publications notably de Graaf (1986), Boxman *et al.* (1987), Jonkers (1987) and Hendrison (1990). A provisional manual was prepared by van Bodegom (undated).
The CHS aims to provide a cost-effective harvesting scheme, while at the same time reducing damage to the remaining stand by controlled felling and skidding. A full enumeration of commercial trees, mapping of tree and terrain data and the planning of a skid trail work prior to harvesting, directional felling and log winching are necessary ingredients of this system. On experimental scale CHS proved to be cheaper than conventional logging, due to reduced skidding cost. Furthermore controlled logging reduced damage to the remaining stand by almost 50% (Hendrison 1990).
The CSS comes into operation shortly after logging has taken place. First all commercial trees are inventoried and a schedule is defined to reduce competition by non-commercial trees. This is necessary to overcome the relative depletion of the commercial stock due to harvesting and to compensate for the often lower growth rates of these commercial species. Three refinements are scheduled. The first refinement in the first year after logging aims to reduce the basal area to 12 m^2/ha. It is expected (but not proven as yet!) that a rotation of 20-25 years will allow a second harvest of 20 m^3/ha.

3.10 Harvesting as a tool in silviculture

It must be understood that the silvicultural systems developed elsewhere reflect its time and place of origin. Silvicultural systems should not be regarded as if they were packages to be applied indiscriminately to forests about which little is known. To reduce the risks of misleading and costly results from such a limited approach it is suggested that silvicultural investigations start by obtaining the results of individual silvicultural operations. Once the consequences of an operation are sufficiently well known, different operations may be pieced together to form a tentative "silvicultural system" which then may be applied and tested as a unit.

A silvicultural system is made up of a series of individual operations each of which contribute towards the objectives of the system. Harvesting is one of them and should fit into the silvicultural concept and may be used as a silvicultural tool. If harvesting is well planned and executed it may help to provide conditions for increased growth and for successful regeneration.

From a silvicultural point of view the current logging practice in Guyana could be improved considerably if the principle of the CELOS harvesting system developed by Hendrison (1990) for Suriname would be introduced. The CHS has two objectives:

- to minimise damage caused by felling and skidding to the remaining stand and the soil.
- to carry out the harvesting operation as a whole as cost-effectively as possible.

As to the first objective the experiments in Suriname showed that it was possible to reduce logging damage. At a felling intensity of 8-10 trees per hectare approximately 13% of the area was damaged by felling gaps in a traditional operation compared to 7% of the area in controlled felling. In controlled skidding damage was restricted to 7% of the remaining forest, whereas in traditional skidding the affected area was 15%. Application of winching techniques reduced the area damaged by skidding even more to 5% of the total area.
As to the second objective, the CHS proved to be cheaper than traditional operations. Total logging cost were reduced by 16%. The higher cost in CHS because of the introduction of new activities such as prospecting and planning appeared to be more than compensated by a much more efficient use of the skidder.

In order to achieve the objectives the following elements were introduced:

- 100%-enumeration and mapping of all harvestable trees before any activity is started.
- detailed planning of harvesting operation, including:
    * identification and demarcation of logging blocks with sufficient stock to harvest;
    * planning of the skidtrail network in accordance with topography and enumeration data;
    * elimination of woody climbers one year before felling.
- logging methods which aim at minimal damage to the remaining stand:
    * directional felling
    * winching
- Registration of felled trees, skidded and trucked logs to trace rejected and overlooked logs and in general to reduce wastage.

3.11 Directional Felling

Directional felling means predetermining the direction of the lie of the tree on the ground. The direction of the lie should be in an angle of 30°-45° to the adjacent trail (135° - 150° to the direction of travel of the loaded skidder) with the butt end of the log towards the trail (herring bone felling). In this way logs are positioned for smooth extraction and skidding damage to the remaining stand is minimised. It is not considered to be an adequate strategy to protect future crop trees during felling, because this would distort the herringbone pattern. The damage caused by excessive undesirable movements of the skidder is usually greater than the felling damage. As said above, felling damage can be considerably reduced by cutting woody climbers which should be seen as the major cause to large felling gaps. On the other hand some diverging (up to 15° either side) is allowed and future crop trees within this range can be spared. It should be realised that a perfect herring bone pattern is not feasible for practical reasons: avoid cross felling, avoid felling across depressions, avoid felling on forks or large branches, all to avoid splitting or breaking of the log. Furthermore directions that would cause a obvious hang-up in a neighbouring tree should be avoided.

Although there are some restrictions it appears to be very well possible to direct the falling direction. Hendrison (1990) found that 80% of the trees that were felled followed the predetermined lie plus or minus a deviation up to 45 degrees on either side. Current Tropenbos research (van der Hout, unpubl. data) shows that the deviation can be reduced to 20 degrees.

3.12 Winching

Winching is pulling logs over some distance while the machine on which the winch is mounted remains stationary. The aim of winching is to avoid travelling from the skidtrail to the stump area. More manual labour is needed to pull out a winch line to the stump. It is obviously more convenient for the assistants if the skidder drives up to the stump.

To make the work more attractive the weight of the winch line should be reduced. This can be achieved by equipping it with choker bells instead of the conventional hook. This not only reduces weight and will expand the winch line's lifetime, it also makes setting the line to the log much easier.

The only way to get forest workers to employ both directional felling as winching techniques is paying them special incentives to ensure quality work instead of having them working on a piece rate system. Using piece rate systems that aim at increasing a worker's productivity can be quite deceptive. As mentioned before the additional cost of damage prevention and producing quality work is more than compensated by the overall improvement of logging efficiency: less machine hours, less damage to logs, less overlooked logs; and by reducing logging damage create more productive forest stands.

3.12 Logging intensity

The next step in designing silvicultural systems for Guyana's forests is to investigate logging intensity. As already mentioned the harvesting operation should be considered a silvicultural operation and as such the interest should focus on the stand that will remain after the logging operation.

According to the forest act of Guyana any tree may be cut if its diameter exceeds 33 cm. In the Greenheart forests felling as much as possible of the desired species may produce logging intensities of more than 20 stems per hectare (or more than 50 m^3/ha).

In one of the CELOS experiments in Suriname logging damage at different logging intensities was studied. Following Jonkers' (1987) figures felling of 20 stems per hectare might lead to near total destruction of the forest; i.e. clear felling.

4 SUMMARY, CONCLUSIONS, AND RECOMMENDATIONS

Four years of research in the Mabura Hill area have generated a substantial amount of results. Research concentrated on patterns and processes in natural and logged forest. Information has become available on the hydrological balance, nutrient balance, patterns of fruit production, and seedling growth characteristics, to name a few. Apart from these several projects of general value were carried out. A soil map of an area of 250,000 ha has been completed (van Kekem *et al.* 1995) and will be used to construct a vegetation/plant diversity map. A field guide for the 100 most promising commercial timber species was made (Polak 1992). For the same 100 species a handlens key (identification of logs at the mill site) has been prepared (Brunner *et al.* 1994) and microscopical key (identification of sawn and manufactured timber, Détiene & Gérard in prep), as well as a book on the timber characteristics (Miller 1995 in prep.) are nearly completed. It is envisaged that such information will make a more balanced use of the forest resource in Guyana possible. In this chapter some conclusions and recommendations will be made based on the information given in Chapter 2 (the natural forest) and chapter 3 (the effects of logging) and some information already available, ranging from recommendations for research on how these projects could be carried out to recommendations for forest management.

4.1 Mapping and modelling

The forest in central Guyana consists of a small-scale mosaic superimposed on a larger mosaic. The larger mosaic coincides with four physiographic units (Laterite, Brown Sands, White Sands, alluvial floodplains) distributed over four major landforms (hills, plateaus, dissected plains, swamps and floodplains), each with a characteristic set of forest associations. A further distinction in different forest types may be possible but it could not be mapped adequately. Within these forest types there exists a gradient from the wet to dry sites. It appears that soil hydrology is a main determinant of spatial distribution of tree species. Within forest types a spatial variation in light exists due to gaps of different sizes. This variation is of importance for regeneration of pioneers and a majority of canopy tree species.

> Soil type and hydrology are major determinants of forest composition in central Guyana. The resulting mosaic of forest types has a fine scale pattern.

The major forest types found agree more or less with the typification made by UNDP and FAO in the late 60's (e.g. de Milde & de Groot 1970). However, within-group variation in mixed forest associations, as found in our studies, is of a very fine scale and thus largely absent at the scale of the maps prepared by the UNDP/FAO reports. Such maps are good tools for national forest planning (reconnaissance level), but are not recommended for management planning. With the large variation within mixed forest any map based on air-photo interpretation will include high variation within mixed forest types. In the process of map making, the objectives of the map should be clear and the level of field sampling has to be adjusted to those objectives. In the case of mixed forest stands this includes either a large sampling effort or acceptance of high variation. This is equally true for vegetation maps for scientific purposes or for forest maps for management purposes.

Radar remote sensing offers several advantages to visible light imagery, as it is immune to cloud cover. It shows good potential for large scale mapping of existing roads and geomorphology. So far, however, the methods has not been able to provide any greater detail of forest composition that rendered using conventional airphoto interpretation. In a multi-temporal approach, logging activities can be made visible with airborne radar data.

The three major physiographic units (Laterite, Brown Sands, White Sands) are well defined on the basis of soil hydrological characteristics, each having a different combination of soil properties that explains the differences in infiltration and sorptivity. However, variation of these properties may be large within a soil type. Most characteristics show a scale of variation of a few hundred meters. A proper level of variance of several soil characteristics has not been established. Similarly data on variation in canopy structure, biomass and root densities distribution are completely lacking for any forest type. It is even questionable if it is possible to establish the levels of variance of both soil and forest characteristics for the different soil and forest types. This limits the use of semi-detailed soil maps for GIS based hydrological models for large areas, unless a large variation is accepted. On a small scale, e.g. gap level, a hydrological model, as developed, works satisfactorily and coupling to nutrient fluxes will be possible. As the number of sample points to describe the spatial structure of soil and vegetation structure adequately is prohibitive, the best method is random sampling, to ensure that the values are good representatives of the aereal mean and variance (Jetten 1994). As evapotranspiration dominates the water balance in all forest types investigated, this may be fully justified for modelling water balance at a larger scale.

> As the number of sample points required to describe the spatial structure of soil and vegetation structure adequately is prohibitive, the best method is random sampling, to ensure that the values are good representatives of the aereal mean and variance.

4.2 Forest structure and population dynamics

Conventional selective extraction of Greenheart currently leads to a large amount of damage. For each Greenheart tree felled many more trees are killed but mostly smaller ones. Individuals killed include Greenheart sub-adults (which are the individuals for the next harvest) and other species as well.

Damage can be reduced by liana cutting prior to felling and directional felling. The latter can be used as a tool to decrease damage to the remaining stand or to reduce skidding activities (herring-bone felling). Directional felling appears best to be used to decrease skidding distances as skidding is the main cause of damage. Some felling damage is inevitable and avoiding damage to individual trees will disrupt the herring bone patters and consequently lead to increased logging damage. Such a system is currently under development in the Tropenbos-Guyana Programme (Van der Hout 1995). Communication between felling crews and skid crews, preferably with maps, is also necessary to decrease search time and search distance. Winching from skid tracks may also reduce skid distance significantly and thus further reduce damage. Less skidding activity will also lead to less soil compaction and finally, also prove to be more cost efficient (Hendrison 1990, van der Hout, unpubl. data).

> Skidding is a main cause for damage to the remaining stand. Skidding activities should be as little as possible. Directional (herring bone) felling should be used as a tool to reach this goal. Controlled skidding will also lead to a decrease in total logging costs, especially if employed together with winching and choker straps.

4.3 Hydrological and nutrient balance

Hydrological balance

The sandy soils in central Guyana are characterized by high infiltration rates. Therefore, runoff is a relatively unimportant process on these soils. This is not likely to change much after logging. Although some compaction is noticeable after logging, the effects on soil properties are relatively small, except on log markets. In addition logging mainly takes place on the flat tops and top slopes of watersheds and not on steep slopes. After logging, processes of interception and transpiration disappear with the vegetation in gaps and are replaced by soil evaporation. This results in an increase in percolation from the root zone of 43% to 75% and a decrease in evapotranspiration from 40% to 25% on the gap itself. This has consequences for nutrient leaching and the rate of chemical reactions. However, depending on the size of the area converted from forest to gap, the effects on a catchment scale appear to be small. Evapotranspiration stabilizes after 1 year of logging at about 76% of the original forest value. It is expected that evaporation will be equal to that of natural forest in about 10 to 20 years. Discharge of the experimental catchment has not increased after low intensity logging and the increased percolation is buffered by the groundwater body. Thus the effects of low intensity logging are mainly confined to the areas where the actual damage is done.

If logging occurs mainly uphill, infiltration of additional runoff will take place at mid slopes. As a consequence, siltation due to logging is of little importance in such areas. To keep siltation insignificant, forest around creeks should preferably be protected. Such stream reserves could also act as refuges for forest animals. Siltation due to road erosion is commonplace in central Guyana. If siltation due to road erosion is a major problem (this has not been inventoried as yet), it is advisable to study if alternative road construction methods exist, with less effect on siltation (e.g. smaller roads with more forest cover overhead), which may also have a positive effect on populations of arboreal mammals.

> Low intensity logging has little effect on the hydrological cycle in sandy areas.
>
> To avoid erosion and siltation, logging should not occur in a buffer strip along creeks. Logging should also not occur on steep hills for the same reasons.

Runoff is a far more important process on Laterite and clayey soils. Moreover, infiltration characteristics are more likely to change as a result of logging. The limited effect of logging on the hydrological cycle in sandy areas cannot be extrapolated to such other areas.

Nutrient balance

The main pools of nutrients in intact forest systems are the standing biomass and soil organic matter. Logging takes away 5.2% of the total Nitrogen in localized areas of the forest system. Leaching has not decreased to background levels in about 1.5 years, after which an additional 0.3% has leached away. Leaching losses for Nitrogen are thus small compared to the log removal. Losses of Potassium, Calcium and Magnesium due to log removal are, 2.8%, 1.7% and 4.5%, respectively. Leaching losses (1.5y) are, in the same order, 1.8%, 1.7%, 5.0%. Therefore cation-leaching is far more important than nitrogen-leaching, relative to the total nutrient element pools of the ecosystem. A total of 10% of the magnesium will disappear due to logging. Atmospheric inputs are small and are almost equalled by outputs through discharge. If gaps are small input in the form of litter from the surrounding forest may help to restore the nutrient balance faster. The overall effect of logging on the nutrient balance of a partially logged forest in central Guyana is yet unknown. As log output is a main drain from the system, output should be kept at minimum. Even in the case of liberation treatments the killed individuals should be left to decompose, instead of converting them to fuel wood. This should not be considered as a loss of valuable wood.

Whether Magnesium (and other nutrient) stocks can build up to original levels between cutting cycles of 20-25 years is unknown yet. In a large gap, without buffering effects from surrounding vegetation, it can be calculated that even if all nutrients that enter by rain will be captured by the system (which is highly improbable) it would take between 40 to 50 years for cations to reach pre-harvesting levels. For Nitrogen it would take more than 200 years, assuming no additional losses. In a series of small gaps surrounded by forest, litterfall from surrounding vegetation will enter the gap and root from the surrounding vegetation will take up some of the released nutrients. In such a case, it would take at least 5 years to rebuild previous cation levels, but depending on the efficiency of the vegetation in capturing released nutrients, it may take some more time. To be able to make more reliable predictions, further monitoring of nutrient accumulation is highly recommended.

> In a sustainable management system it is important to limit skid trails (and other soil damage) since in these areas leaching losses are largest.
>
> Gap size should be kept as small as possible, as surrounding vegetation may be able to decrease the amount of leaching (by root activity) and buffer nutrient losses through litter input.

On White Sand soil nutrient content is less than on Brown Sand. Leaching losses on these low CEC soils may be larger, after logging. As logging of Wallaba (*Eperua* spp.). may increase, studies of the nutrient budget before and after logging on White Sand are necessary.

4.4 Seedling establishment

Germination and growth of pioneers is strongly enhanced by large gaps. In large uncrowded gaps, the high relative growth rate of these species more than compensates for their low seed mass. A few timber species such as Kabukalli, Futui (*Jacaranda copaia*), Simaroupa (*Simarouba amara*), Kereti (*Ocotea oblonga*) and Ulu (*Trattinickia* sp.) are true pioneers in the juvenile stage. Germination of Greenheart is not favoured by large gaps. Establishment of seedlings is best in small natural gaps, which are mostly single tree fall gaps. Seedlings can survive in the understorey with intact cotyledons. Without cotyledons, they cannot maintain a positive carbon balance in the understorey and slowly die. Greenheart is probably best described as a small gap species. Optimum gap size is unknown as yet and depends on both survival characteristics of timber species and pioneer species in relation to gap size. Large gaps may also be difficult sites for Greenheart to establish naturally as dispersal is limited.

> To ensure optimum regeneration of slow growing commercial species, gap size should be kept small, preferably no larger than a 'single tree fall gap'. Such gaps should be spaced evenly over the exploited areas.
>
> Other commercial species, such as Kabukalli or Futui, are favoured by larger gaps. As such, gap size will influence the future composition of the forest.

4.5 Growth constraints

The soils in the Mabura Hill area are among the poorest known. White Sands are poorer in total nutrient content, especially phosphorus. However, phosphorus is better available on White Sands, as on Brown Sands it is immobilized. Plants growing on these poor soils exhibit low phosphorus content but not a low maximum photosynthesis, thus they are highly efficient. Internal recycling also contributes to high Phosphorus efficiency. Much of the nutrients is stored in biomass but a large organic soil pool is present. However, only a few percent of soil phosphorus is readily available to plants.

Even though phosphorus concentrations in both soil and plants are low and must be considered limiting, fertilizer experiments including phosphorus were not conclusive with regard to limitations to growth. Among other factors, the low pH and related problems with toxicities, of among others Aluminium, may be causal. The increasing acidity (probably due to de-nitrification) and rising aluminium levels after logging are a cause for concern in this respect. Climax species have a high efficiency in using phosphorus for growth (largely because they conserve nutrients in long-lived leaves and roots). In contrast to climax species, Congo pump (*Cecropia*), a pioneer, has a high efficiency in capturing nutrients (but with higher turn-over). Thus in large gaps establishment of Congo Pump may decrease leaching losses.

As fertilization with Nitrogen and Phosphorus has very limited effect on plant growth, fertilization is not yet advisable. Nitrogen fertilization with Urea is considered unwise as it will lower the pH even more. This will limit the possibilities of agriculture and plantations on sandy soils. The low CEC on White Sands will be a further constraint in fertilization effectiveness, as most nutrients will leach quickly.

Litter has a stimulating effect on plant growth, more than fertilization. Litter may improve mycorrhizal infection or decrease toxicity. Litter is thus also of paramount importance to plants growing in gaps.

Increased light levels may limit growth of species in gaps. Morabukea has been shown to be intolerant of high radiation regimes. Drought induced mortality has been noted in Morabukea (Davis & Richards 1933) and Greenheart (Richards (1952) and may play a role in large gaps.

Nutrient capitals, CEC, and fertilizer efficiency are (too) low on sandy soils. Forestry with low levels of exploitation appears to be the best land use option.

4.6 Animals

After logging numbers of large rodents (Agouti) did not change substantially. Primates may have decreased in numbers. Bird diversity in a similar forest in French Guiana was also strongly affected by selective logging. Protected zones within logging areas are potential sites where such animals may retreat. As shown by Johns (1992) strips along streams (to protect water quality, see also above) and other non-commercial stands, amounting to 5% of a concession area could contain populations of most species regarded as intolerant to logging. The use of such buffers is highly recommended. Arboreal mammals will be less hampered by small roads where it is possible to cross via the canopy. In order to reduce the Inter-Canopy Corridor Distance it is recommended to keep the width of roads at a minimum.

To protect mammal populations:
1) hunting should be limited in newly opened areas
2) the amount of vegetation removed should be small
3) road size should be kept small

At present no hard information is available on so-called keystone species, trees that produce large fruit crops in times when other fruit food sources are scarce (Whitmore 1990, Johns 1992). In Chapter 3 a few potential key-stone species were identified. Key-stone species are of paramount importance for the survival of large frugivores and should be spared in logging and liberation practices. The identification of such species is important, especially if liberation treatment will be established as a management tool.

Hunting increases after logging, due to greater accessibility of the area. It is unknown if over-hunting occurs in central Guyana and this matter may need some attention. Killing of large cats for protection of forest camps seems unnecessary and should be discouraged.

4.7 Optimum gap size

The size (and orientation) of a gap determines to a large extent the changes in microclimate, compared to the forest understorey. Increases in radiation, air temperature, soil temperature and decreases in humidity and soil water content are all inter-related (Figure 20). Leaching, pH and aluminium concentration, as well as re-introduction of seeds (e.g. of Greenheart), are also affected by gap size. However, not all factors increase or decrease at similar rates with increase in gap size. Germination, growth and survival of seedlings are affected by changes in the overall gap climate. In general pioneers will be favoured by large gap conditions and climax species, to which many but not all timber species belong, conditions found in small gaps. As we deal with many species and their interactions the final species composition in a gap, which may determine forest structure for several decades is complex and to a large extent unknown. Studies in gaps of different sizes is thus highly recommended and will lead to a better understanding of relevant processes after gap creation, including differences in response of species to different growth conditions in gaps as caused by gap size.

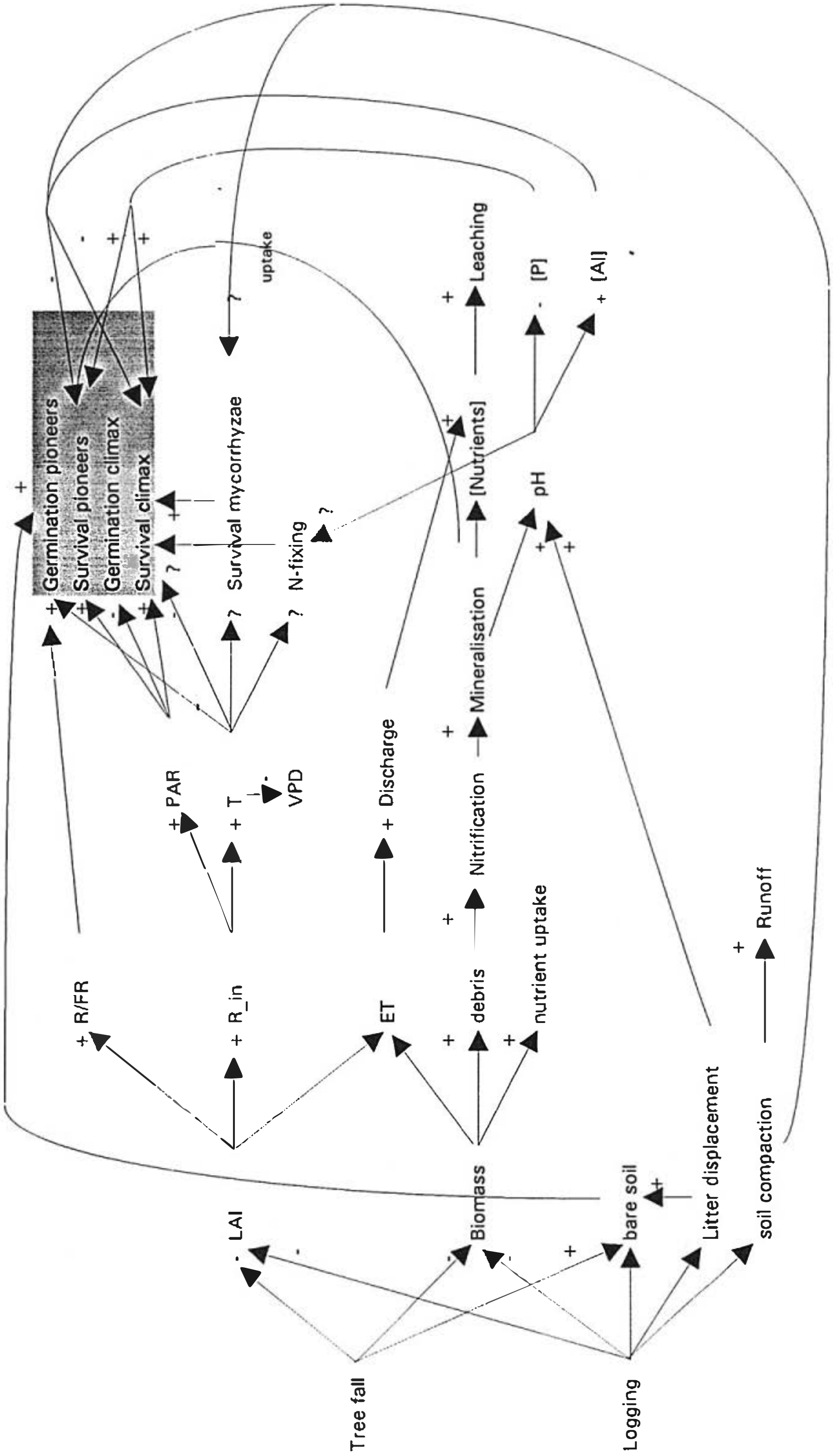
Gap size and orientation has an influence on almost all processes (biotic and abiotic). A small gap size is to be preferred from the point of view of nutrient losses and unwanted growth of secondary vegetation. The actual optimum size is unknown, but a single tree fall gap is to be preferred over multiple tree fall gaps.

4.8 Silvicultural treatments

In general silvicultural treatments are necessary to overcome the relative depleteion of commercial tree species due to logging and to compensate for the slow growth rate. As shown in Chapter 3, growth figures of logged, but untreated forest do not differ from unlgged forest. Only after liberation species like Greenheart will increase growth.

There are two further constraints for developing a sustainable management system based mainly on Greenheart.

1) The lack of individuals in the lower adult size classes does not allow a second harvest in a relatively short time. With emphasis on Greenheart only, rotation times of over 60 year should be expected. Inclusion faster growing species in themanagementsystem and/or species with larger sub-adult size classes may allow for shorter rotation periods.
2) The low growth rate of Greenheart gives the species a disadvantage in comparison to many other species, especially true pioneers and long-lived pioneers.


Tree fall
Logging
LAI
Biomass
bare soil
Litter displacement
soil compaction
R/FR
R_in
ET
debris
nutrient uptake
Runoff
PAR
T
VPD
Discharge
Nitrification
Mineralisation
[Nutrients]
Leaching
pH
[P]
[Al]
Germination pioneers
Survival pioneers
Germination climax
Survival climax
Survival mycorrhyzae
N-fixing
uptake
?
+
-

Even with careful planning and execution of harvest and treatments, logging inevitably leads to a shift in species composition. It must be determined what deviation is acceptable both from an ecological and management point of view. It is preferable to set aside conservation areas of intact examples of (all commercial?) forests. A figure of roughly 5% per concession (as is done in other countries) could be used as a starting point but hard data to make such decision are lacking.

> The lack of individuals in the lower adult size classes of Greenheart does not allow a second harvest in a relatively short time.
>
> To compensate for low growth rate and proportional decline after harvest silvicultural treatments are necessary to ensure future commercial potential of the forest.

4.9 Conditions to be fulfilled to achieve sustained timber production in the natural forest

Before we can address the technical aspects of rain forest management we first have to pay attention to the conditions that must be fulfilled at the organisational level.

At the national level
At the national level the following guidelines are important (ITTO 1990):

- There should be a strong political commitment at the highest level for sustainable forest management to succeed.
- There should be a national forest policy forming an integral part of the national land use policy, supported by appropriate legislation, and being revisable in the light of new circumstances.
- A national forest inventory should establish the importance of all forests;
- There should be a strong and committed forest service.
- Certain categories of land need to be kept under permanent forest cover. Furthermore, there should be a clear plan for the permanent forest estate with regard to land tenure, including forests set aside for conversion, forest for sustainable management, (forest for use of small products) and forest to be reserved (natural parks and nature reserves). All these forests should have a legal title.
- A general management model for the main forests to be managed should be adopted. Such a model should include matters such as: local inventories, yield regulation, annual allowable cut, harvesting rules (waste reduction, damage

◂ **Figure 20.** Effects of natural and man made gap creation on a number of abiotic and biotic parameters with consequences for regrowth. Abbreviations: LAI = leaf area index, R/FR = red farred ratio, R_in = radiation in, ET = evapotranspiration, PAR = photosynthetic active radiation, T = temperature, VPD = Vapour Pressure Deficit.

control), silvicultural treatments, growth modelling, monitoring, environmental impact assessment.

All these points need serious attention. The forest law needs updating. There has been a national reconnaissance inventory, but no firm land use plan was developed on its basis. There is only one small National Park and no other firm plans for Nature Reserves.

Land allocation for timber production

- It should be realised that a private commercial enterprise based on allocated forest land will only have a vested interest in the regeneration of the remaining stand after logging if he has to do so to stay in business. Therefore concessions should have long-term agreements that last at least for two cutting cycles; or, better, renewable on condition. This forces them to invest in forest management and to apply proper harvesting methods and appropriate silvicultural techniques.

At the concession level

At the concession level preparation of a management plan is important (long-term (>10 years), medium long-term (5 years) and short-term (2-5 years). The management plan should include:

- identification of forest types;
- forest inventory;
- based on the results of these two activities: identification of forest-use types - production forest, non-productive forest, protection forest, nature reserves;
- part of the production forest should be allocated as forest-for-zero-management.
  In that part no logging or silvicultural work should take place. It is necessary to preserve parts of the production forest in the original structure and composition to serve as:
  - * a point of reference for the future; to evaluate the effects of logging and treatments;
  - * a source of species diversity in general;
  - * more in particular, a refuge for seed-dispersing and pollinating animals, such as monkeys, birds, bats, insects, etc.

Annual cut

The concession should be divided into compartments. These compartments serve as forest management units. One compartment should have at least the size of an annual coupe. The annual coupe depends on the size of the operation (mill demand, available felling crews, available forest machinery).

After the harvest a compartment should be closed down and left to regenerate (aided by silvicultural treatment). The importance of restricting relogging cannot be stressed enough. Re-entering of a compartment should not be allowed until it is silviculturally advised to do so.

It is also unwise to set a fixed cutting cycle for the compartments. The forest is quite variable in structure and composition by nature and will be even more variable after logging has taken place. This has consequences for the growth one can expect. Growth as well will be quite variable in place and in time.

Therefore it is recommended to carry out diagnostic sampling to determine when a compartment will be ready for a second harvest. In addition permanent sample plots must be established in each compartment for the monitoring of the forest's reactions to forest exploitation and treatments.

In terms of institutional strength and infrastructure, both very weak in Guyana, it is not possible to jump from low management levels to fully controlled, intensive management. Institutional strengthening and building of technical capabilities are on the increase through the National Forestry Action Plan.

4.10 Where to go?

From the above it may be clear that six years of research in the natural forest and the effects of logging on the forest in Guyana has led to a better understanding of the forest and the magnitude of the disturbances on some of the forest processes. Based on these findings directions have been given for management. However, they do not lead as yet to a fully documented management system. Problems exist in translation of detailed scientific results into clearly understandable management practices. Even if such efforts are made they need not necessarily lead to general use. For instance, the Celos Management System as developed in neighbouring Suriname, showed good prospects of both economic as well as some ecological sustainability. However, no company is currently using the system.[2] Furthermore, sustainability implies a full understanding of long term processes, which cannot be easily gathered in a short while.

Reality dictates that the forests are and will be used; and that, apart from setting aside large blocks of forest in conservation areas, forests may only be retained if they are given an economic value. Guyana has a large forest resource and an expanding timber industry. The current government stresses the need to use this resource for the development of the population. To safeguard the forests for future protection and production, Guyana is in urgent need of a management system. It is encouraging to note that the Guyana Forestry Commission has taken a first step in developing a code of practice for forest management, which is now under discussion within the forestry sector in Guyana. Secondly, Guyana has set aside a large tract of primary forest for conservation and for applied and basic research (Hawkes & Wall 1993, Kerr 1993). This area (360,000 ha) is large enough to enable a practical scale test of sound forest management.

The most realistic approach for forest management in Guyana is to concentrate on stands with high stocking of commercial species (e.g., Greenheart [*C. rodiei*], Wallaba [*Eperua* spp.], Crabwood [*Carapa* spp.], Kabukalli [*Goupia glabra*], Purpleheart [*Peltogyne* spp.], Tatabu [*Diplotropis purpurea*], Mora and Morabukea [*Mora* spp]), and applying cheap and simple treatments (van der Hout 1992). Treatments are necessary as growth in logged forests is only marginally faster than in natural forest and would not be sufficient to secure sustained timber production (de Graaf 1987, Jonkers 1987, van der Hout 1992). Such silvicultural work is currently undertaken in the Tropenbos-Guyana Programme. Increased utilization of lesser known species rather than poisoning them may be part of the solution. However, the danger exists that this may lead to increased logging intensity. Furthermore, lesser known species are not readily marketable and possibly unknown to

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[2] At present the Government of Suriname insists that all new concessions apply the CELOS system.

forest workers. A handbook on timber characteristics (projected for 1995) may help in finding uses for such lesser known species. Identification is aided by the field guide for the major timber trees in Guyana (Polak 1992), a checklist with vernacular names (Mennega *et al.* 1988), a hand lens key (Brunner *et al.* 1994) and a microscopical key (projected for 1995).

In general it would appear that applied research may give fast results in an often 'quick and dirty' approach. Basic research, if directed at the right forest processes may provide answers when the 'quick and dirty' approach does not fulfil its objectives. As such they are complementary. In tropical forest management we cannot wait until basic research provides all answers leading to proper forest management; a combination of both would provide us with the necessary answers in the long term.

4.11 Major conclusions for forest management

1 Nutrient levels, CEC and fertilizer efficiency are very low on sandy soils. Forestry with low intensity of exploitation appears to be the best land use option.

2 Low intensity logging of 20 -25 m^3/ha on sandy soils appears to have fairly little impact on the hydrological and nutrient cycle at catchment level

3 To avoid erosion and siltation, logging should not occur in a buffer strip along creeks. Logging should also not occur on steep slopes for the same reasons, but this may depend on soil type.

4 The lack of individuals in the lower adult size classes of Greenheart does not allow a second harvest after 20-25 years.

5 To compensate for low growth rate and decline in populations of commercial species relative to non-commercial species, after harvest, silvicultural treatments are necessary to ensure future commercial potential of the forest.

6 Uncontrolled skidding is a main cause for damage to the ecosystem because of:

- destruction of seedlings, saplings and treelets;
- soil compaction on the skid trails;
- leaching losses, which are largest on skid trails;
- unfavourable growth conditions due to high Aluminium concentration and high acidity on trails.

7 Directional felling (herring-bone felling) should thus be used as a tool to reduce skidding impact on the forest ecosystem.

8 Gap size should be kept small:

- changes in microclimate will be less;
- establishment of most commercial climax species is likely to be best on such gaps;
- surrounding forest may buffer losses in nutrients and water by root absorption;
- surrounding forest may buffer shortages in nutrients at a later stage by litter input.

9 Gaps should be as evenly spaced over the exploited areas as possible.

10 Some commercial species, such as Kabukalli or Futui, and many non-commercial species are favoured by larger gaps. As such, gap size will influence the future composition of the forest.

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APPENDIX 1 Study sites

Site map with main study areas. Permanent sample plots (PSPs) are identified as with *.

R **Ecological Reserve**. 900 hectare with a buffer zone of approximately equal size, established in the framework of the 'Forest Project Mabura Hill' in 1988. The reserve is dissected by the Maiko creek. The western half consists of an area with mainly sandy soils. Forests in this part are characterised by Wallabas (*Eperua falcata, Eperua grandiflora*) on White Sands and by Clump wallaba (*Dicymbe altsonii*), Greenheart (*Chlorocardium rodiei*), Morabukea (*Mora gonggrijpii*), and Black kakaralli (*Eschweilera sagotiana*) on Brown Sands. In the creek heads Palm-Swamp forest on peaty soil is found. The eastern part of the reserve is formed by a dolerite dyke with mainly lateritic soils. Mixed forest on this hill is characterised by presence of Greenheart, Morabukea, Black kakaralli and Sarebebeballi (*Vouacapoua americana*). On shallow soils a xeric low forest with dominance of Myrtaceae is found. Along the main creek, forest dominated by Mora (*Mora excelsa*) with abundance of Watafa (*Eperua rubiginosa*) and Trysil (*Pentaclethra macroloba*) is found.

Several sites are located near or in the Ecological Reserve:

Fs **Field Station**. Situated in a large clearing near to the Maiko creek, at the southern side of the Reserve. One main building for working and cooking (kitchen, toilet and shower), a second dormitory with space for 6 to 8 persons (two rooms). Rain and creek water are collected in tanks. Solar and generator power present. Two nurseries, several small field sites (seedling growth) nearby.

1 **Meteorological station**. Situated in a large gap at the northern side of the reserve. Automatically measures incoming and outgoing radiation, air temperature, air humidity, wind speed, and rain fall.

2 **Control Catchment**, 6 ha, Runoff plots. The plot was meant as one of a 'paired catchment study' with the 'Experimental catchment'. A dam with v-notch was installed but due to several logistical reasons hydrological data collection was too incomplete to be used.

3 **Wallaba plot**. I hectare, located in dry evergreen forest on white sand in the Reserve. Used for litterfall, litter decomposition, and throughfall studies.

4* **'Natural Plot'**. 2.5 hectares located in Greenheart forest in the Reserve. Used for population studies (Greenheart, Clump wallaba, Yarri yarri [*Duguetia neglecta*]), litter fall, throughfall, stemflow, and botanical diversity studies.

5* **'Exploited plot'**. 4 hectares, located in exploited Greenheart forest just west of the Ecological Reserve. Logged in 1988 with an extraction rate of 57 m^3 ha^{-1}. Used for population studies (Greenheart, Clump wallaba, Yarri yarri, Kabukalli [*Goupia* *glabra*], and Congo pump [*Cecropia obtusifolia*]) and botanical diversity studies.

6* **Gap experiment**, nutrient loss studies. Two gaps (730 m^2, the medium gap and 3440 m^2, the large gap) were created in Greenheart bearing mixed forests on brown sand in 1992. Microclimate changes after gap creation and nutrient losses due to felling and leaching are being determined in these two gaps and compared to the understorey of adjacent natural forest.

7* **Experimental catchment.** 6.18 ha. Monitored for one year prior to logging and two years thereafter. Felling took place in 1992 at a rate of 21m^3 ha^{-1} and was well distributed with no gaps larger than 50m^2, no felling on steep slopes and in the stream buffer zone. Used for litterfall, leaching, creek outflow (dam with v-notch), population studies (Greenheart, Clump wallaba, Yarri yarri). Plots destroyed by accidental re-logging in 1994.

8 **Greenheart-Morabukea plots** in natural forest in the eastern part of the Ecological Reserve. 5 ha. Used for plant-animal interaction studies (dispersal, herbivory, seed predation, pre-dispersal seed attack), animal density studies.

W **Waraputa Inventory Watershed.** 480 ha, 252 plots of 0.05 ha were sampled to describe forest types. Regeneration studies on Greenheart and logging damage studies took place. At present a part of the area is used for botanical diversity studies.

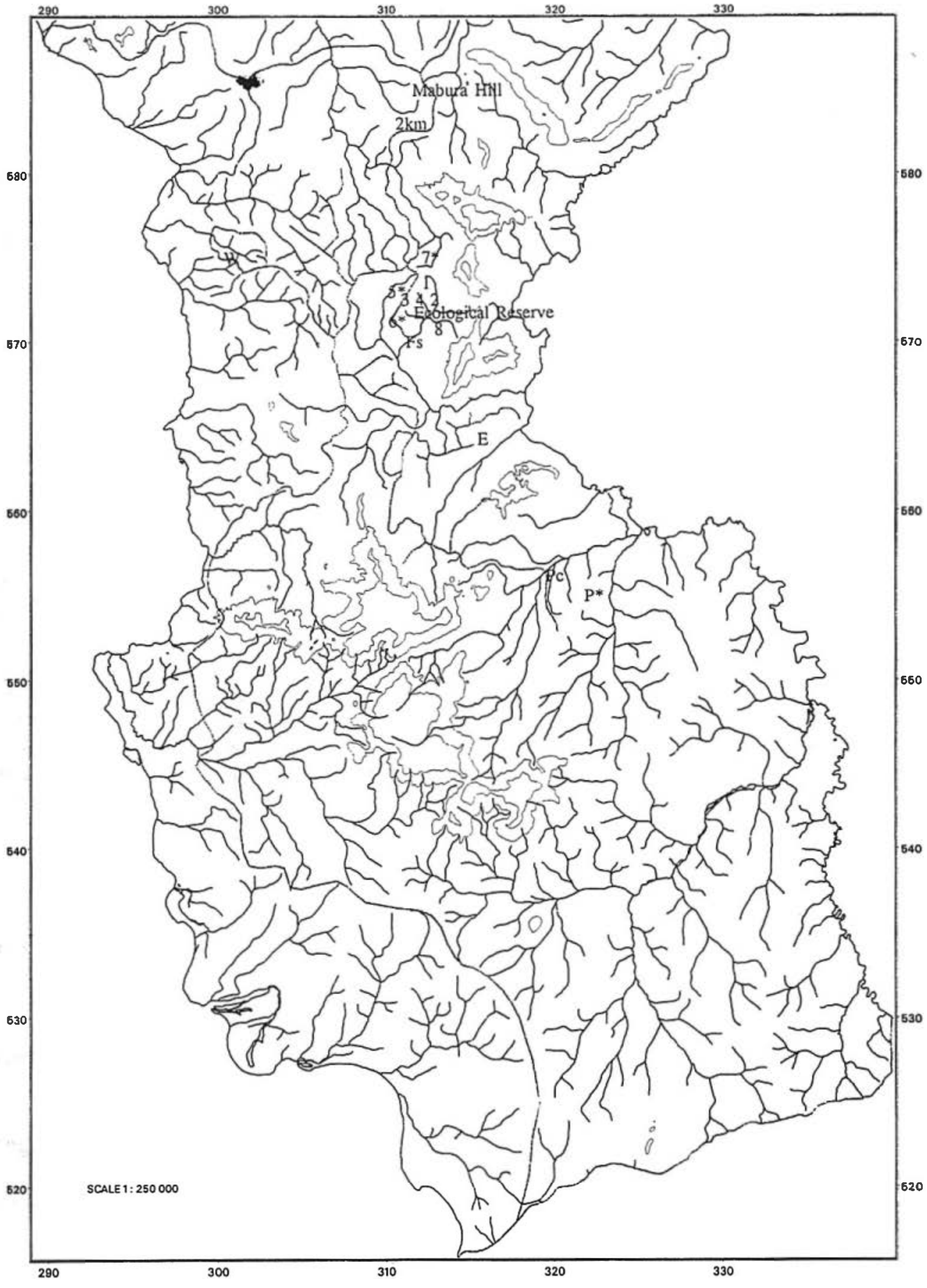
E **Ekuk compartment plots.** On 15 ha plot in exploited forest on lateritic soils, logged in 1990 at an average rate of 37 m^3 ha^{-1}. The plots are situated in forest with overstorey trees such as Greenheart, Morabukea, and Black kakaralli and understorey trees such as Yarri yarri and Karishiri (*Oxandra asbeckii*). Population studies, plant animal interaction studies (dispersal, herbivory, seed predation, pre-dispersal seed attack), animal density studies.

P* **West Pibiri Management** Trial, 15 plots of 2 ha with 2 ha buffer zone. Directional Felling studies, controlled skidder extraction. Plots received extraction rates of 0, 4, 8, 8 and 16 trees per ha (three replicates), one set of 8 trees per ha will receive post-harvest treatment. The area is also being used for botanical diversity studies (effect of logging) and is earmarked for further studies in phase 2.

Pc **Pibiri camp site.** Range house with accommodation for 12 persons, kitchen and working area. Solar and generator power, rain water collection, overhead tank.

2km **DTL tree spotter trail.** Patch of undisturbed forest near Mabura Hill (2 Km sign) with good species representation. Large trees are tagged and used to train tree spotters by DTL's tree spotter 'sensei' Mr. Sam Robberts. Surrounding area logged in 1985/1986 and used for botanical diversity studies.

Figure 21. Map of study locations. Abbreviations in text. ▸


290
300
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320
330
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530
520
Mabura Hill
2km
W
7*
1
5*
3
4
2
Ecological Reserve
6*
8
Fs
E
Pc
P*
SCALE 1 : 250 000

APPENDIX 2 Checklist of vascular plants of Mabura Hill and surroundings

The area covered is approximately 10,000 ha. Plants collectors in the area are in chronological order: Jenman, 1881-1898, several trips; Abraham, 1919; Hohenkerk, 1909-1923; Becket, 1906; Forest Department 1935; Paul Maas *et al.* 1981, 1988; Ton Stoffers *et al.* 1982, Hans ter Steege *et al.* 1985-1992; John Pipoly *et al.* 1986-1987; Claude Persaud, 1987; Marion Jansen-Jacobs *et al.* 1989; Bill Hahn, 1989; Marcel Polak *et al.* 1990-1992; Renske Ek, 1993-present; Eric Christensen and Carol Kellof 1994.
Richard and Robert Schomburgk also collected extensively along the Essequibo river in the area. However, these collections are not numbered in chronological order and often have no locality other than Essequibo. Consequently they could not be included.
In addition to these collections species enumerated in research have been added. These lists include: Great Falls Inventory, ter Steege *et al.*, 1992 Waraputa compartment and Peter van der Hout and Renske Ek, 1994 and continuing.
Most families appear relatively well collected. Due to the bias of some major collectors in the area Orchidaceae may be over-represented in the check list. Palmae are probably under-collected, as some other understorey groups may be. The total species list amounts to 1323 species (June 1995).

ANTHOPHYTA

ACANTHACEAE (6)
Beloperone violaceae Planch & Linden
Mendoncia squamuligera Nees
Odontonema schomburgkianum (Nees) Kuntze
Ruellia rubra Aublet
Teliostachya alopecuroidea (Vahl) Nees
Acanthaceae indet

ALISMATACEAE (1)
Echinodorus subalatus (Mar.) Griseb. subsp. ?

AMARANTHACEAE (1)
Cyathula prostrata (L.) Blume

ANACARDIACEAE (4)
Anacardium occidentale L.
Loxopterigium sagotii J.D. Hook *
Tapirira guianensis Aublet
Tapirira obtusa syn. nov. ined.

ANNONACEAE (33)
Anaxagorea dolichocarpa Sprague & Sandw.
Annona haematantha Miq.
Annona sericea Dunal
Annona symphyocarpa Sandw.
Annona sp.
Bocageopsis multiflora (Mart.) R.E. Fries
Cymbopetalum brasiliense (Vell.) Benth. ex Baill.
Duguetia cadaverica Huber
Duguetia calycina Benoist
Duguetia inconspicua Sagot
Duguetia neglecta Sandw.
Duguetia pycnastera Sandw.
Duguetia sp.
Ephedranthus guianensis R.E. Fries
Fusaea longifolia (Aublet) Safford
Guatteria punctata (Aublet) R.A. Howard
Guatteria schomburgkiana Mart.
Guatteria sp.
Oxandra asbeckii (Pulle) R.E. Fries
Oxandra guianensis R.E. Fries
Oxandra sp.
Rollinia exsucca (Dunal ex DC.) A. DC.
Trigynaea guianensis R.E. Fries
Trigynaea sp.
Unonopsis glaucopetala R.E. Fries
Unonopsis guatterioides (A. DC.) R.E. Fries
Unonopsis perrottetii (A. DC.) R.E. Fries
Unonopsis rufescens (Baill.) R.E. Fries
Unonopsis stipitata Diels
Xylopia aromatica (Lam.) Mart.
Xylopia benthamii R.E. Fries
Xylopia nitida Dunal
Annonaceae indet

APOCYNACEAE (32)
Allamanda cathartica L.
Ambelania acida Aubl.
Anartia meyeri (G.Mey. ex G. Don) Miers
Aspidosperma album (Vahl) Benoist ex Pichon
Aspidosperma cruentum Woodson
Aspidosperma excelsum Benth.
Aspidosperma sandwithianum Markgr.
Aspidosperma vargasii A. DC.
Aspidosperma sp.
Forsteronia acouci (Aubl.) A. DC.
Forsteronia cf. *schomburgkii* A. DC.
Forsteronia gracilis (Benth.) Muell. Arg.
Forsteronia guyanensis Muell. Arg.
Forsteronia sp.
Geissospermum sericeum (Sagot) Benth. & J.D. Hook.
Himatanthus articulatus (Vahl) Woodson
Himatanthus articulatus x *bracteatus*
Himatanthus sucuuba (Spruce ex Muell. Arg.) Woodson
Lacmellea utilis (Arnott) Markgraf
Macoubea guianensis Aubl. var. *guianensis*
Malouetia gracilis (Benth.) A. DC.
Malouetia tamaquarina (Aubl.) A. DC.
Odontadenia geminata (Roem. & Schult.) Muell. Arg.
Odontadenia macrantha (Roem. et Schult.) Markgr.
Odontadenia perrottetii (A. DC.) Woodson
Odontadenia puncticulosa (A. Rich.) Pulle
Parahancornia fasciculata (Poir.) Benoist ex Pichon

Prestonia surinamensis Muell. Arg.
Tabernaemontana cerea (Woodson) Leeuwenberg
Tabernaemontana disticha DC.
Tabernaemontana undulata Vahl
Apocynaceae indet

AQUIFOLIACEAE (2)
Ilex martiana D. Don.
Ilex sp.

ARACEAE (21)
Anthurium gracile (Rudge) Lindl.
Anthurium hookeri Kunth
Anthurium jenmanii Engl.
Anthurium scolopendrinum (Hem.) Kunth
Anthurium trinerve Miq.
Anthurium sp.
Dieffenbachia paludicola N.E. Brown ex Gleason
Heteropsis flexuosa (Kunth) G.S. Bunting
Montrichardia arborescens (L.) Schott *
Philodendron callosum Krause
Philodendron ecordatum Schott
Philodendron linnaei Kunth
Philodendron pedatum (Hook.) Kunth
Philodendron rudgeanum Schott
Philodendron scandens C. Koch & Sello
Philodendron squamiferum Poepp.
Philodendron sp.
Rhodospatha sp.
Spathiphyllum sp.
Stenospermation maguirei Jonker & A.M.E. Jonker
Urospatha sagittifolia (Rudge) Schott
Araceae indet

ARALIACEAE (3)
Dendropanax sp.
Schefflera decaphylla (Seemann) Harms
Araliaceae indet.

ARISTOLOCHIACEAE (2)
Aristolochia daemoninioxia Mast.
Aristolochia sp.

ASCLEPIADACEAE (5)
Blepharodon nitidus (Vell.) Macbr.
Matelea palustris Aubl.
Matelea stenopetala Sandw.
Tassadia propinqua Decne.
Asclepiadaceae indet

BEGONIACEAE (1)
Begonia humilis Dryander

BIGNONIACEAE (34)
Anemopaegma foetidum Bureau & K. Schum.
Anemopaegma oligoneuron (Sprague & Sandw.) A. Gentry
Anemopaegma parkeri Sprague
Arrabidea candicans (L.C. Rich.) DC.
Arrabidea mollis (Vahl) Bureau ex K. Schum.
Arrabidea patellifera (Schl.) Sandw.
Callichlamys latifolia (L.C. Rich.) K. Schum.
Clytostoma binatum (Thunb.) Sandw.
Clytostoma sciuripabulum Bur. & K. Schum.
Cydista aequinoctialis (L.) Miers
Cydista sp.
Distictella elongata (Vahl) Urb.
Distictella magnoliifolia (Kunth) Sandw.
Distictella parkeri (DC.) Sprague & Sandw.
Jacaranda copaia (Aublet) D. Don ssp. *copaia*
Lundia erionema DC.
Martinella obovata (Kunth) Bureau & K. Schum.
Memora alba (Aubl.) Miers
Memora flaviflora (Miq.) Pulle
Memora racemosa A. Gentry
Memora schomburgkii (DC.) Miers
Memora sp.
Mussatia prieurii (DC.) Bureau ex K. Schum.
Paragonia pyramidata (L.C. Rich.) Bureau
Phryganocydia corymbosa (Vent.) Bur. ex K. Schum.
Pleonotoma clematis (Kunth) Miers
Pleonotoma echitidea Sprague & Sandw.
Pleonotoma sp.
Potamoganos microcalyx (G.F.W. Mey.) Sandw.
Roentgenia sordida (Bureau & K. Schum.) Sprague & Sandw.
Schlegelia violacea (Aublet) Griseb.
Tabebuia insignis (Miq.) Sandw. var. *monophylla* Sandw.
Tabebuia serratifolia (Vahl) Nichols
Bignoniaceae indet

BOMBACACEAE (3)
Catostemma commune Sandw.
Catostemma fragrans Benth.
Rhodognaphalopsis flaviflora (Pulle) A. Robyns var. *flaviflora* *

BORAGINACEAE (10)
Cordia bicolor A. DC.
Cordia exaltata Lam. var. *melanoneura* (Klotzsch) I.M. Johnston
Cordia fallax I.M. Johnston
Cordia nervosa Lam.
Cordia nodosa Lam.
Cordia sagotii J.M. Johnston
Cordia schomburgkii DC.
Cordia sp.
Heliotropium filiforme Lehm.
Tournefortia ulei Vaupel

BROMELIACEAE (18)
Aechmea bromeliifolia (Rudge) Baker
Aechmea melinonii Hook.
Aechmea mertensii (Meyer) Schult.f.
Aechmea tillandsoides (Mart. ex Schult.f.) Baker
Ananas sp. *
Bromelia plumieri (Griseb.) Mez
Catopsis berteroniana (Schult.f.) Mez
Guzmania lingulata (L.) Mez
Guzmania roezlii (E. Morren) Mez
Pitcairnia caricifolia Mart. ex Schult.f.
Tillandsia anceps Lodd.
Tillandsia bulbosa Hook.
Tillandsia spiculosa Griseb. var. *spiculosa*
Tillandsia tenuifolia L
Tillandsia sp.
Vriesea gladioliflora (Wendl.) Antoine
Vriesea rubra (Ruiz & Pav¢n) Beer
Bromeliaceae indet

BURMANNIACEAE (6)
Campylosiphon purpurascens Benth.
Dictyostega orobanchoides (Hook.) Miers spp *parviflora* (Benth.) Snelders & Maas
Gymnosiphon breviflorus Gleason
Gymnosiphon divaricatus (Benth.) Benth. & Hook.f.
Gymnosiphon guianensis Gleason
Hexapterella gentianoides Urban

BURSERACEAE (9)
Protium aracouchini (Aublet) Marchall
Protium decandrum (Aublet) Marchall
Protium demerarense Swart
Protium guianense (Aubl.) March. var. *guianense*
Protium heptaphyllum (Aublet) Marchall
Protium sp.
Tetragastris altissima (Aublet) Swart
Trattinickia burserifolia Mart.
Trattinickia sp.

CACTACEAE (2)
Epiphyllum sp.
Rhipsalis sp.

CAPPARIDACEAE (1)
Capparis maroniensis Benoist

CARYOCARACEAE (1)
Caryocar nuciferum L.

CECROPIACEAE (5)
Cacropia angulata J.W. Bailey
Cacropia obtusa Trèc.
Cecropia sp.
Coussapoa microcephala Trèc.
Pourouma guianensis Aubl. ssp. *guianensis*

CELASTRACEAE (2)
Goupia glabra Aublet
Maytenus myrsinoides Reissek

CHRYSOBALANACEAE (37)
Couepia bracteosa Benth.
Couepia cognata (Steudel) Fritsch
Couepia comosa Benth.
Couepia exflexa Fanshawe & Maguire
Couepia parillo A.P. DC.
Couepia sp.
Hirtella racemosa Lam var. *haxandra* (Willd. ex R. & S.) Prance
Hirtella silicea Griseb.
Licania alba (Bern.) Cuatr.
Licania boyanii Tutin
Licania buxifolia Sandw.
Licania canescens Benoist
Licania caudata Prance
Licania coriacea Benth.
Licania cuprea Sandw.
Licania densiflora Kleinh.
Licania fanshawei Prance
Licania guianensis (Aub.) Griseb.
Licania heteromorpha Benth. var. *heteromorpha*
Licania heteromorpha Benth. var. *perplexans* Sandw.
Licania hypolauca Benth.
Licania incana Aubl.
Licania intrapetiolaris Spruce ex J.D. Hook.
Licania laevigata Prance
Licania laxiflora Fritsch
Licania leptostachya Benth.
Licania majuscula Sagot
Licania membranacea Sagot ex Laness.
Licania micrantha Miq.
Licania persaudii Fanshawe & Maguire
Licania piresii Prance
Licania sp.
Parinari campestris Aublet
Parinari excelsa Sabine
Parinari parvifolia Sandw.
Parinari rodolphii Huber
Parinari sp.

COMBRETACEAE (7)
Buchenavia fanshawei Exell & Maguire
Buchenavia grandis Ducke
Combretum laxum Jacq.
Combretum rotundifolium L.C. Rich.
Terminalia amazonica (J.F. Gmelin) Exell
Terminalia cf. *guyanensis* Eichl.
Terminalia dichotoma G. Mey.

COMMELINACEAE (2)
Commelina erecta L.
Commelina virginica L.

COMPOSITAE (20)
Acanthospermum australe (Loefl.) Kuntze
Bidens cynapiifolia Kunth
Calea caleoides (DC.) H. Robinson
Chromolaena odorata (L.) R. King & H. Robinson
Clibadium sylvestre (Aubl.) Baill.
Conyza bonariensis (L.) Cronq.
Emilia coccinea (Sims) Swert
Emilia sonchifolia (L.) DC. ex Wight
Erechtites hieracifolia (L.) Raf. ex DC.
Lepidaploa gracilis (Kunth) H. Robinson
Lepidaploa remotiflora (L.C. Rich.) H. Robinson
Mikania hookeriana DC.
Mikania psilostachya DC.
Porophyllum ruderale (Jacq.) Cass.
Unxia camphorata L.f.
Vernonia cinerea (L.) Less.
Vernonia cyanthillium (L.) H. Robinson
Vernonia remotiflora L.C. Rich.
Wulffia baccata (L.f.) Kuntze
Compositae indet

CONNARACEAE (12)
Cnestidium guianense (Schellenb.) Schellenb.
Connarus coriaceus Schellenb.
Connarus erianthus Benth. ex Baker var. *stipitatus* Forero
Connarus megacarpus S.F. Blake
Connarus perrottetii (DC.) Planch. var. *perrottetii*
Connarus perrottetii (DC.) Planch. var. *rufus* Forero
Connarus sp.
Rourea cf. *kappleri* Lanj.
Rourea frutescens Aublet
Rourea induta Planch. var. *induta*
Rourea pubescens (DC.) Radlk. var. *spadicea* (Radlk.) Forero
Connaraceae indet

CONVOLVULACEAE (7)
Dicranostyles guianensis A.M.W. Mennega
Ipomoea tiliacea (Willd.) Choisy
Ipomoea phillomega (Vell.) House
Jacquemontia tamnifolia (L.) Griseb.
Lysiostyles scandens Benth.
Maripa scandens Aublet
Merremia umbellata (L.) H. Hallier

CUCURBITACEAE (14)
Cayaponia ophthalmica R.E. Schultes
Cayaponia racamosa (Mill.) Cogn.
Cayaponia selysioides C. Jeffrey
Citrullus lanatus (Thunb.) Matsumura & Nakai
Cucurbita moschata (Duch. ex Lam.) Duch. ex Poir.
Gurania acuminata Cogn.
Gurania bignoniacea (Poepp. & Endl.) C. Jeffrey
Gurania spinulosa (Poepp. & Endl.) Cogn.
Gurania subumbellata (Miq.) Cogn.
Gurania sp.
Lagenaria siceraria (Molina) Standl.
Momordica charantia L.
Psiguria triphylla (Miq.) C. Jeffrey
Psiguria sp.

CYCLANTHACEAE (4)
Cyclanthus bipartitus Poit.
Evodianthus funifer (Poit.) Lindm. spp. *trailanus* (Drude) Harling
Evodianthus funifar (Poit.) Lindm.
Thoracarpus bissectus (Vell.) Harding

CYPERACEAE (26)
Becquerelia cymosa Brongn.
Calyptrocarya glomerulata (Brogn.) Urb. var. *glomerulata*
Cyperus ligularis L.
Cyperus luzulae (L.) Retz.
Cyperus simplex Kunth
Cyperus sphacelatus Rottb.
Cyperus surinamensis Rottb.
Diplasia karataefolia L.C. Rich.
Fimbristylis annua (All.) Roem. & Schult.
Fimbristylis littoralis Gaud.
Fimbristylis miliacea (L.) Vahl
Hypolytrum amplum Poepp. & Kunth. ex Kunth.
Hypolytrum jenmanii C.B. Clarke
Kyllinga odorata Vahl
Kyllinga sp.
Lagenocarpus verticillatus (Spreng.) T. Koyama & Maguire
Mapania sylvatica Aublet ssp. *sylvatica*
Mariscus ligularis (L.) Urb.

Pycreus polystachyos (Rottb.) Beauv.
Rhynchospora cephalotes (L.) Vahl
Rhynchospora holoschoenoides (L.C. Rich.) Herter
Rhynchospora pubera (Vahl) Boeck.
Rhynchospora watsonii (Britt.) Davidse
Scleria pterota Presl.
Scleria stipularis Nees
Scleria sp.

DICHAPETALACEAE (2)
Tapura capitulifera Baill.
Tapura guianensis Aublet

DILLENIACEAE (9)
Davilla kunthii St.Hil.
Doliocarpus brevipedicellatus Garcke ssp. *brevipedicellatus*
Doliocarpus guianensis (Aublet) Gilg.
Doliocarpus major J.F. Gmelin ssp. *major*
Doliocarpus spraguei Cheesm.
Tetracera asperula Miq. ssp. *asperula*
Tetracera tigarea DC.
Tatracera volubilis L. ssp. *volubilis*
Dilleniaceae indet

DIOSCOREACEAE (6)
Dioscorea amazonicum Mart. ex Griseb.
Dioscorea crotalariifolia Uline
Dioscorea dodecaneura Vell.
Dioscorea pilosiuscula Bert. ex Spreng.
Dioscorea samydea Mart. ex Griseb.
Dioscorea sp.

EBENACEAE (5)
Diospyros dichroa Sandw.
Diospyros guianensis Guerke subsp. *guianensis*
Diospyros ierensis Britton *
Diospyros virginiana L.
Diospyros sp.

ELAEOCARPACEAE (4)
Sloanea aff. *laurifolia* (Benth.) Benth.
Sloanea grandiflora J.E. Smith
Sloanea guianensis (Aubl.) Benth. *
Sloanea sp.

ERIOCAULACEAE (3)
Eriocaulon heterodoxum Moldenke
Paepalanthus bifidus (Schrad.) Kunth
Eriocaulaceae indet

ERYTHROXYLACEAE (3)
Erythroxylum citrifolium St.Hil.
Erythroxylum macrophyllum Cav.
Erythroxylum squamatum Sw.

EUPHORBIACEAE (28)
Alchorneopsis floribunda (Benth.) Muell. Arg.
Aparisthmium cordatum (Adr.Juss.) Baill.
Chaetocarpus schomburgkianus (Kuntze) Pax & K. Hoffm.
Chamaesyce serpens (Kunth) Small var. *serpens*
Conceveiba guianensis Aubl.
Croton trinitatis Millsp
Croton sp. nov.?
Croton sp.
Dalechampia parvibracteolata Lanj.
Euphorbia hirta L.
Euphorbia thymifolia L.
Glycydendron amazonicum Ducke
Hevea pauciflora (Spruce ex Benth.) Müll. Arg. var coriacea Ducke
Hyeronima alchorneoides Allemao var. *alchorneoides*
Hyeronima oblonga (Tul.) Muell. Arg.
Mabea speciosa Muell. Arg. ssp. *concolor* (Muell. Arg) Den Hollander
Mabea sp.
Maprounea guianensis Aublet
Micrandra elata (Didrichs) Muell. Arg.
Pera bicolor (Klotzsch) Muell. Arg.
Pera sp. *
Phyllanthus stipulatus (Raf.) Webster
Plukenetia volubilis L.
Sandwithia guyanensis Lanj.
Sandwithia lessertiana (Baill.) Muell. Arg.
Sebastiania corniculata (Vahl) Pax
Tragia lessertiana (Baill.) Muell.
Euphorbiaceae indet

FLACOURTIACEAE (11)
Carpotroche surinamensis Uitt.
Casearia combaymensis Tul.
Casearia commersoniana Camb.
Casearia javitensis Kunth
Casearia pitumba Sleumer
Casearia sp.
Homalium guianense (Aubl.) Oken
Homalium racemosum Jacq.
Lacistema aggregatum (Bergius) Rusby
Laetia procera (Poepp.) Eichl.
Ryania speciosa Vahl var. *tomentosa* (Miq.) Monachino
Flacourtiaceae indet

GENTIANACEAE (10)
Coutoubea ramosa Aublet
Irlbachia alata (Aublet) Maas ssp. *alata*
Irlbachia purpurascens (Aublet) Maas
Voyria aphylla (Jacq.) Pers.
Voyria caerulea Aublet
Voyria cf. *tenuiflora* Griseb.
Voyria clavata Splitg.
Voyria corymbosa Splitg ssp. *corymbosa*
Voyria rosea Aublet
Voyriella parviflora (Miq.) Miq.

GESNERIACEAE (9)
Alloplectus coccineus (Aublet) Mart.
Besleria laxiflora Benth.
Besleria verecunda C. Morton
Chrysothemis pulchella (Donn ex Sims) Decne.
Codonanthe calcarata (Miq.) Hanst.
Codonanthe crassifolia (Focke) C.V. Morton
Nautilocalyx pictus (Hook.) Sprague
Paradrymonia densa (C.H. Wright) Wiehler
Gesneriaceae indet

GRAMINEAE (71)
Andropogon bicornis L.
Andropogon leuchostachyus Kunth
Andropogon selloanus (Hack.) Hack.
Axonopus capillaris (Lam.) Chase
Cenchrus echinatus L.
Digitaria lanuginosa (Nees) Henr.
Eragrostis maypurensis (Kunth) Steud.
Eragrostis sp.
Gymnopogon foliosus (Willd.) Nees
Gynerium sagittatum (Aubl.) P. Bureav.
Homolepis isocalycia (G. Mey.) Chase
Ichnanthus nemoralis (Schrad.) Hitchc. & Chase
Ichnanthus pallens (Sw.) Munro ex Benth.
Lasiacis ligulata Hitchc. & Chase
Olyra micrantha Kunth
Orthoclada laxa (Rich.) P. Bureav.
Panicum pilosum Sw.
Panicum stoleniferum Poir.
Paspalum decumbens Swartz
Paspalum melanospermum Desv. ex Poir.
Gramineae indet

GUTTIFERAE (29)
Calophyllum brasiliense Camb.
Clusia cuneata Benth.

Clusia fockeana Miq.
Clusia grandiflora Splitg.
Clusia jenmanii Engl.
Clusia myriandra (Benth.) Planch. & Triana
Clusia nemorosa G. Mey.
Clusia palmicida L.C. Rich.
Clusia pana-panari (Aublet) Choisy
Clusia schomburgkiana (Planch. & Triana) Benth. ex Engl.
Clusia sp.
Clusiella elegans Planch. & Triana
Garcinea sp.
Havetiopsis flavida (Benth.) Planch. & Triana
Platonia insignis Mart.
Quayapoya bracteolata Sandw.
Quayapoya? sp.
Rheedia sp.
Symphonia globulifera L.f.
Tovomita brevistaminea Engl.
Tovomita calodictyos Sandw.
Tovomita cephalostigma Vesque
Tovomita tenuiflora Benth.
Tovomita sp.
Vismia guianensis (Aublet) Choisy
Vismia macrophylla Kunth
Vismia sessilifolia (Aublet) Choisy
Vismia sp.

HIPPOCRATEACEAE (15)

Cheiloclinium cognatum (Miers) A.C. Smith
Cheiloclinium diffusiflorum (Peyr.) A.C. Smith
Cheiloclinium hippocrateoides (Peyr.) A.C. Smith
Cheiloclinium sp.
Hippocratea volubilis L.
Peritassa compta Miers
Prionostemma aspera (Lam.) Miers
Salacia maburensis A.M.W. Mennega
Tontelea attenuata Miers
Tontelea coriacea A.C. Smith
Tontelea nectandrifolia (A.C. Smith) A.C. Smith
Tontelea ovalifolia (Miers) A.C. Smith
Tontelea sandwithii A.C. Smith
Tontelea sp.
Hippocrateaceae indet

HUMIRIACEAE (4)

Humiria balsamifera (Aublet) A. St.Hil. var. *balsamifera*
Humiria balsamifera (Aublet) A. St.Hil. var. *guianensis* (Benth.) Cuatr. *
Humiriastrum obovatum (Benth.) Cuatr.
Sacoglottis guianensis Benth. var. *guianensis*

ICACINACEAE (4)

Discophora guianensis Miers
Emmotum fagifolium Desv. ex Hamilton
Hyptis atrorubens Poit.
Pleurisanthes flava Sandw.

LACISTEMACEAE (2)

Lacistema aggregatum (Bergius) Rusby
Lacistema sp.

LAURACEAE (27)

Aiouea guianensis Aublet
Aniba canelilla (Kunth) Mez
Aniba citrifolia (Nees) Mez
Aniba hypoglauca Sandw.
Aniba panurensis (Meisner) Mez
Aniba riparia (Nees) Mez
Aniba cf. rosaedora Ducke
Chlorocardium rodiei (Schomb.) Rohwer, Richter & v.d. Werff
Endlicheria multiflora (Miq.) MezAllen
Endlicheria punctulata (Mez) C.K.
Licaria cannella (Meisner) Kosterm.
Nectandra amazonum Nees
Nectandra sp.
Ocotea aciphylla (Nees) Mez
Ocotea aff. *caudata* (Nees) Mez
Ocotea canaliculata (L.C. Rich.) Mez
Ocotea cf. *discrepens* C.K. Allen
Ocotea cymbarum Kunth
Ocotea floribunda (Swartz) Mez
Ocotea glomerata (Nees) Mez
Ocotea guianensis Aublet
Ocotea pauciflora (Nees) Mez
Ocotea rubra Mez *
Ocotea schomburgkiana (Nees) Mez
Ocotea sp.
Ocotea sp. nov.
Lauraceae indet

LECYTHIDACEAE (19)

Couratari gloriosa Sandw.
Couratari guianensis Aublet
Eschweilera alata A.C. Smith
Eschweilera coriacea (A. DC.) Mori
Eschweilera decolorans Sandw.
Eschweilera micrantha (Berg) Miers
Eschweilera parviflora (Aubl.) Miers
Eschweilera pedicellata (Rich.) Mori
Eschweilera potaroensis Sandw.
Eschweilera sagotiana Miers
Eschweilera subglandulosa (Steud. ex Berg) Miers
Eschweilera wachenheimii (Benoist) Sandw.
Eschweilera sp.
Gustavia angusta L.
Lecythis confertiflora (A.C. Smith) Mori
Lecythis corrugata Poit. ssp. *corrugata*
Lecythis holcogyne (Sandw.) Mori
Lecythis zabucajo Aublet
Lecythidaceae indet

LEGUMINOSAE (Caesalpinioideae) (54)

Bauhinia guianensis Aubl. var. *guianensis*
Bauhinia siqueiraei Ducke
Bauhinia surinamensis Amsh.
Bauhinia sp.
Campsiandra comosa Benth. var. *comosa*
Cassia cowanii Irwin & Barneby var. *guianensis* (Sandw.) Irwin & Barneby
Cassia sp.
Chamaecrista adiantifolia (Benth.) Irwin & Barneby var *pteridophylla* (Sandw.) Irwin & Barneby
Chamaecrista apoucouita (Aublet) Irwin & Barneby
Crudia glaberrima (Steud.) Macbr.
Dicymbe altsonii Sandw.
Dimorphendra conjugata (Splitg.) Sandw.
Dimorphandra polyandra Benoist
Elizabetha coccinea M.R. Schomb. ex Benth. var *oxyphylla* (Harms) Cowan
Elizabetha durissima Ducke
Eperua falcata Aublet
Eperua grandiflora (Aublet) Benth. ssp. *guyanensis* Cowan
Eperua jenmanii Oliver ssp *sandwithii* Cowan
Eperua rubiginosa Miq.
Eperua schomburgkiana Benth.
Hymenaea courbaril L. var. *courbaril*
Macrolobium bifolium (Aubl.) Pers.
Macrolobium jenmanii (Gleason) Sandw.
Macrolobium montanum Ducke var. *potaroanum* Cowan
Macrolobium sp.
Mora excelsa Benth.
Mora gonggrijpii (Kleinh.) Sandw.
Paloue riparia Pulle
Peltogyne paniculata Benth. ssp. *pubescens* (Benth.) M.F. da Silva
Peltogyne venosa (Vahl) Benth. ssp. *densiflora* (Spruce ex Benth.) M.F. da Silva
Peltogyne venosa (Vahl) Benth. ssp. *venosa*
Peltogyne sp.
Sclerolobium guianense Benth. var. *guianense*

Senna latifolia (G.F.W. Mey.) Irwin & Barneby
Senna quinquangulata (L.C. Rich.) Irwin & Barneby
Swartzia benthamiana Miq. var. *benthamiana*
Swartzia cf. *polyphylla* DC.
Swartzia grandifolia Bong. ex Benth.
Swartzia guianensis (Aubl.) Urb.
Swartzia jenmanii Sandw.
Swartzia laevicarpa Amsh.
Swartzia leiocalycina Benth.
Swartzia leiogyne (Sandw.) Cowan
Swartzia longipedicellata Sandw.
Swartzia oblanceolata Sandw.
Swartzia schomburgkii Benth. var. *schomburgkii*
Swartzia sprucei Benth. var. *tessellata* Cowan
Swartzia xanthopetala Sandw.
Swartzia sp.
Swartzia sp. nov.
Tachigali cf. *rusbyi* Harms
Tachigali sp.
Vouacapoua americana Aublet
Vouacapoua macropetala Sandw.

LEGUMINOSAE (Mimosoideae) (27)

Aberema jupunba (Willd.) Britton & Killip var. *trapezifolia* (Vahl) Berneby & Grimes comb nov.
Acacia paraensis Ducke
Balizia pedicellaris (DC.) Barneby & Grimes gen & comb. nov. ined.
Enterolobium cf. *cyclocarpum* (Jacq.) Griseb.
Enterolobium sp.
Inga alba (Sw.) Willd.
Inga disticha Benth.
Inga huberi Ducke
Inga lateriflora Miq.
Inga meissneriana Miq.
Inga nobilis Willd.
Inga rhynchocalyx Sandw.
Inga sertulifera DC.
Inga stipularis DC.
Inga thibaudiana DC.
Inga sp.
Macrosamanea discolor (Humb. & Bonpl.) Britton & Rose ex Britton & Killip
Mimosa myriadenia (Benth.) Benth. var. *myriadenia*
Mimosa sp.
Newtonia suaveolens (Miq.) Brenan
Parkia nitida Miq.
Parkia pendula (Willd.) Benth. ex Walpers
Parkia ulei (Harms) Kuhlmann var. *surinamensis* Kleinh.
Pentaclethra macroloba (Willd.) Kuntze
Pseudopiptadenia suaveolans (Miq.) Grimes
Zygia latifolia (L.) Fawcett & Rendle
Zygia racemosa (Ducke) Barneby & Grimes, comb. nov. ined.

LEGUMINOSAE (Papilionoideae) (47)

Acosmium nitens (Vogel) Yakovlev
Acosmium praeclarum (Sandw.) Yakovlev
Aeschynomene sensitiva L.
Alexa imperatricis (Schomb.) Baill.
Alexa leiopetala Sandw.
Alexa sp.
Calopogonium mucunoides Desv.
Centrosema latissimum Ducke
Centrosema triquetrum Spruce ex Benth.
Clathrotropis brachypetala (Tul.) Kleinh.
Clathrotropis macrocarpa Ducke
Clitoria sagotii Fantz var. *canaliculata* Fantz
Clitoria leptostachya Benth.
Dalbergia ecastophyllum (L.) Taubert
Dalbergia riedelii (Radlk.) Sandw.
Derris sp.
Desmodium adscendens (Sw.) DC.
Desmodium axillare (Swartz) DC.
Desmodium barbatum (L.) Benth. & Oerst.
Dioclea elliptica Maxwell
Dioclea scabra (Rich.) Maxwell var. *scabra*
Dioclea sp.
Diplotropis purpurea (Rich.) Amsh. var. *purpurea*
Dipteryx odorata (Aubl.) Willd.
Hymenolobium cf. *davisii?*
Hymenolobium sp.
Hymenolobium sp. nov.
Machaerium ferox (Mart. ex Benth.) Ducke
Machaerium madeirense Pittier
Machaerium myrianthum Spruce ex Benth.
Machaerium cf. *oblongifolium* Vogel
Machaerium quinatum (Aublet) Sandw. var. *parviflorum* (Benth.) Rudd
Machaerium sp.
Mucuna sp.
Ormosia cf. *amazonica*
Ormosia coccinea (Aubl.) Jackson
Ormosia costulata (Miq.) Kleinh.
Ormosia coutinhoi Ducke
Ormosia paraensis Ducke
Poecilanthe hostmannii (Benth.) Amsh.
Pterocarpus rohrii Vahl
Pterocarpus santalinoides L'Her. ex DC.
Vatairea guianensis Aublet
Vigna luteola (Jacq.) Benth.
Zornia latifolia J.E. Smith var. *latifolia*
Leguminosae (Papilionoideae) indet
Leguminosae indet

LENTIBULARIACEAE (1)

Utricularia pusilla Vahl

LILIACEAE (2)

Crinum erubescens L.F. ex Solander
Hippeastrum puniceum (Lam.) Baker

LINACEAE (2)

Hebepetalum humiriifolium (Planch.) Benth.
Roucheria schomburgkii Planch.

LISSOCARPACEAE (2)

Lissocarpa guianensis Gleason
Lissocarpa sp.

LOGANIACEAE (10)

Spigelia humilis Benth.
Spigelia multispica Steud.
Strychnos bredemeyeri (Schult.) Sprague et Sandw.
Strychnos diaboli Sandw.
Strychnos guianensis (Aubl.) Mart.
Strychnos hirsuta Spruce ex Benth.
Strychnos melinoniana Baill.
Strychnos mitscherlichii Rich. Schomb. var. *mitscherlichii*
Strychnos tomentosa Benth.
Strychnos sp.

LORANTHACEAE (13)

Oryctanthus florulentus (L.C. Rich.) Urb.
Phoradendron crassifolium (Pohl ex DC.) Eichl.
Phoradendron dimidiatum (Miq.) Eichl.
Phoradendron piperoides (Kunth) Trel.
Phoradendron racemosum (Aublet) Krug. & Urb.
Phoradendron sp.
Phthirusa dissectifolia (Rizzini) Kuijt
Phthirusa guyanensis Eichl.
Phthirusa rufa (Mart.) Eichl.
Phthirusa stelis (L.) Kuijt [comb. ined.!]
Phthirusa sp.
Struthanthus sp.

MALPIGHIACEAE (21)
Banisteriopsis martiniana (A. Juss.) Cuatr. var. *martiniana*
Burdachia sphaerocarpa Adr. Juss.
Byrsonima crassifolia (L.) Kunth
Byrsonima aerugo Sagot
Byrsonima eugeniifolia Sandw.
Byrsonima gymnocalycina A. Juss.
Byrsonima stipulacea A. Juss.
Heteropterys macradena (DC.) W.R. Anderson
Heteropterys macrostachya Adr. Juss.
Heteropterys multiflora (DC.) Hochr.
Heteropterys nervosa Adr. Juss. in St. Hil.
Hiraea faginea (Sw.) Nied.
Mascagnia guianensis W.R. Anderson
Mascagnia sepium (A. Juss.) Griseb.
Mezia includens (Benth.) Cuatr.
Stigmaphyllon sinuatum (DC.) A. Juss.
Tetrapterys acutifolia Cav.
Tetrapterys calophylla Adr. Juss.
Tetrapterys fimbripetala Adr. Juss.
Tetrapterys mucronata Cav.
Malpighiaceae indet

MALVACEAE (4)
Abutilon indicum (L.) Sweet
Hibiscus sabdariffa L.
Sida glomerata Cav.
Urena lobata L.

MARANTACEAE (5)
Ischnosiphon foliosus Gleason
Ischnosiphon obliquus (Rudge) Körn.
Marcgravia parviflora Rich. ex Wittm.
Ischnosiphon puberulus Loes. var. *scaber* (Petersen) L. Andersson
Monotagma spicatum (Aublet) Macbr.

MARCGRAVIACEAE (5)
Marcgravia coriacea Vahl
Marcgravia parviflora Rich ex Wittm.
Norantea guianensis Aublet
Norantea sp.
Souroubea guianensis Aublet ssp. guianensis

MELASTOMATACEAE (39)
Aciotis circaeifolia (Bonpl.) Triana
Aciotis fragilis (DC.) Cogn.
Aciotis indecora (Bonpl.) Triana sensu Mathies
Aciotis laxa (DC.) Cogn. var. *C*
Aciotis laxa (DC.) Cogn. var. *keppleriana* (Naud.) Cogn.
Aciotis ornata (Miq.) Gleason
Aciotis purpurascens (Aublet) Triana
Aciotis viscosa (Naud.) Triana
Bellucia grossularioides (L.) Triana
Clidemia bullosa DC.
Clidemia conglomerata DC.
Clidemia involucrata DC.
Clidemia minutiflora (Triana) Cogn.
Clidemia aff. saülensis Wurdack
Comolia sp.?
Henriettea multiflora Naud.
Henriettea ramiflora (Swartz) DC.
Leandra divaricata (Naudin) Cogn.
Leandra purpurea Gleason
Loreya mespilioides Miq.
Macrocentrum cristatum (DC.) Triana var. *parviflorum* (DC.) Cogn.
Miconia argyrophylla DC. ssp. *argyrophylla*
Miconia argyrophylla DC. ssp. *gracilis* Wurdack
Miconia bracteata (DC.) Triana
Miconia ceramicarpa (DC.) Cogn. var. *ceramicarpa*
Miconia gratissima Benth. ex Triana
Miconia hypoleuca (Benth.) Triana
Miconia mirabilis (Aublet) L.O. Williams
Miconia nervosa (Sm.) Triana
Miconia prasina (aff.) (Swartz) DC.
Miconia punctata (Desr.) D. Don
Miconia rubiginosa (Bonpl.) DC.
Mouriri acutiflora Naud.
Mouriri sp.
Tibouchina aspera Aublet var. *asperrima* Cogn.
Tococa acuminata Benth.
Tococa aristata Benth.
Tococa sp.
Melastomataceae indet

MELIACEAE (7)
Carapa guianensis Aublet
Carapa procera A. DC.
Cedrela odorata L. *
Guarea kunthiana Adr. Juss.
Guarea pubescens (L.C. Rich.) Adr.Juss. ssp. *pubescens*
Trichilia sp.
Meliaceae indet

MENISPERMACEAE (17)
Abuta barbata Miers
Abuta bullata Mold.
Abuta candollei Triana & Planch.
Abuta cf. *grandifolia* (Mart.) Sandw.
Abuta obovata Diels
Abuta rufescens Aublet
Abuta sp.
Anomospermum sp.
Cissampelos andromorpha DC.
Curarea candicans (L.C. Rich.) Barneby & Krukoff
Odontocarya tamoides (DC.) Miers
Sciadotenia cayennensis Benth.
Sciadotenia sagotiana (Eichl.) Diels
Telitoxicum inopinatum Mold.
Telitoxicum krukovii Mold.
Telitoxicum sp.
Menispermaceae indet

MONIMIACEAE (3)
Siparuna decipiens (Tul.) A. DC.
Siparuna guianansis Aublet
Siparuna sp.

MORACEAE (15)
Bagassa guianensis Aublet
Brosimum guianense (Aubl.) Huber
Brosimum rubescens Taub.
Clarisia ilicifolia (Spreng.) Lanj. & Rossberg
Coussapoa latifolia Aubl.
Ficus gomelleira Kunth & Bouch
Ficus guianensis Desv.
Ficus mathewsii (Miq.) Miq. / *F. amazonica* (Miq.) Miq.
Ficus obtusifolia Kunth
Ficus paludica Standl.
Ficus panurensis Standl.
Ficus paraensis (Miq.) Miq.
Ficus sp.
Helicostylis tomentosa (Poepp. & Endl.) Rusby
Naucleopsis guianensis (Mildbr.) C.C. Berg
Trymatococcus paraensis Ducke

MUSACEAE (5)
Heliconia acuminata L.C. Rich.
Heliconia cf. *bihai* (L.) L.
Heliconia chartacea Lane ex Barreiross
Heliconia densiflora Verlot ssp. *angustifolia* L. Andersson
Heliconia sp.

MYRISTICACEAE (6)
Iryanthera lancifolia Ducke
Otoba? sp.
Virola elongata (Benth.) Warb.
Virola michelii Heckel
Virola sebifera Aublet
Virola surinamensis (Rol. ex Rottb.) Warb.

MYRSINACEAE (9)
Cybianthus fulvopulverulenta Mez subsp. ?
Cybianthus gracillimus Mez
Cybianthus guianensis (A. DC.) Miq. ssp. *pseudoicacoreus* (A. DC.) Agostini

Cybianthus multipunctatus A.Dc.
Cybianthus prieurii A. DC.
Cybianthus surinamensis (Spreng.f.) Agostini
Cybianthus venezuelanus Mez
Stylogyne schomburgkiana (DC.) Mez
Myrsinaceae indet

MYRTACEAE (25)
Calycolpus goetheanus (Mart. ex DC.) O. Berg
Calycolpus ravolutus (Schauer) O. Berg
Calyptranthes forstari O. Berg
Calyptranthes sp.
Eugenia aff. *cucullata* Amsh.
Eugenia coffeifolia DC. vel aff.
Eugenia conjuncta Amshoff
Eugenia excelsa O. Berg
Eugenia patrisii Vahl
Eugenia tapacumensis O. Berg
Eugenia trinervia Vahl
Eugenia sp.
Marlieraa montana (Aubl.) Amsh. / *Eugenia patrisii* Vahl
Marlieria schomburgkiana O. Berg.
Myrcia fallax (L.C. Rich.) DC.
Myrcia subobliqua (Benth.) Nied.
Myrcia sylvatica (G. Mey.) DC.
Myrcia sp.
Myrcia sp. [sect. Aulomyrcia]
Myrciaria floribunda (West ex Willd.) O. Berg
Myrciaria vismeifolia (Benth.) O. Berg
Psidium guajava L.
Psidium parsoonii McVaugh
Psidium striatulum DC.
Myrtaceae indet

NYCTAGINACEAE (6)
Guapira fragrans (Dum.-Cours.)Little
Guapira sp.
Neea constricta Spruce ex Schmidt
Neea sp.
Pisonia glabra Heimerl
Nyctaginaceae indet

OCHNACEAE (5)
Ouratea aff. *cardiosperma* (Lam.) Engler
Ouratea leblondi (Tiegh.) Lem e
Ouratea vs. *guianensis* Aublet
Ouratea sp.
Sauvaugesia erecta L.

OlACACEAE (4)
Dulacia guianensis (Engler) Kuntze
Heisteria cauliflora J.E. Smith
Maburea trinervis Maas
Minquartia guianensis Aubl. *

ONAGRACEAE (3)
Ludwigia decurrens Walter
Ludwigia erecta (L.) Hara
Ludwigia hyssopifolia (G. Don) Exell

OPILIACEAE (2)
Agonandra silvatica Ducke
Opiliaceae indet

ORCHIDACEAE (117)
Batemannia colleyi Lindl.
Bifrenaria longicornis Lindl. *
Brassavola martiana Lindl.
Brassia verrucosa Lindl. (= *B. bidens* Lindl.?)
Brassia wageneri Rchb.f.
Campylocentrum fasciola (Lindl.) Cogn.
Campylocentrum micranthum (Lindl.) Rolfe
Catasetum barbatum (Lindl.) Lindl. var. *barbatum*
Catasetum discolor (Lindl.) Lindl.
Caulhartron bicornutum (Hook.) Raf.
Cheiradenia imthurnii Cogn.
Coryanthes sp.
Dichaea muricata (Sw.) Lindl.
Dichaea picta Rchb.f.
Dichaea sp.
Dimerandra elegans (Focke) E. Siegerist
Elleanthus graminifolius (Barb. Rodr.) Lojtnant
Encyclia calamaria (Lindl.) Pabst
Encyclia diurna (Jacq.) Schltr.
Encyclia fragrans (Sw.) Dressler
Encyclia oncioides (Lindl.) Schlechter
Encyclia pygmaea (Hook.) Dressler
Encyclia selligera (Batem. ex Lindl.) Schltr. *
Encyclia vespa (Vell.) Dressler
Epidendrum anceps Jacq.
Epidendrum carpophorum Barb. Rodr.? *
Epidendrum compressum Griseb.
Epidendrum difforme Jacq.
Epidendrum diffusum Sw.
Epidendrum latifolium (Lindl.) Garay & Sweet *
Epidendrum microphyllum Lindl.
Epidendrum nocturnum Jacq.
Epidendrum purpurascens Focke
Epidendrum rigidum Jacq.
Epidendrum schlechterianum Ames
Epidendrum sculptum Rchb.f. *
Epidendrum strobiliferum Rchb.f.
Epidendrum sp.
Gongora atropurpurea W.J. Hook.
Gongora quinquenervis Ruiz & Pav. *
Jacquiniella globosa (Jacq.) Schltr.
Koellensteinia carraoensis Garay & Dunsterv. *
Koellenstainia graminea (Lindl.) Rchb.f.
Lepanthes helicocephala Rchb.f.
Macroclinium mirabile (Schweinf.) Dodson
Maxillaria alba (Hook.) Lindl.
Maxillaria caespitifica Rchb.f.
Maxillaria camaridii Rchb.f
Maxillaria discolor Rchb.f.
Maxillaria imbricata (Lodd. ex Lindl.) Barb. Rodr.
Maxillaria parkeri Hook.
Maxillaria rufescens Lindl.
Maxillaria splendens Poepp. & Endl.
Maxillaria superflua Rchb.f.
Maxillaria trinitatis Ames
Maxillaria uncata Lindl.
Maxillaria violaceopunctate Rchb.f.
Maxillaria sp.
Notylia sagittifera (Kunth) Linn., Klotzsch & Otto
Notylia wullschlaegeliana Focke
Octomeria brevifolia Cogn.
Octomeria deltoglossa Garay
Octomeria grandiflora Lindl.
Octomeria minor Schweinf.
Octomeria sp.
Oncidium lanceana Lindl. *
Oncidium orthostates Ridl. *
Ornithocephalus bicornis Lindl.
Palmorchis pubescens Barb. Rodr.
Palmorchis sp.
Platystele ovalifolia (Focke) Garay & Dunsterv.
Plectrophora iridifolia Focke
Pleurothellis barbulata Lindl.
Pleurothallis biglandulosa Schltr.
Pleurothallis bravipes Focke
Pleurothallis braviscapa Schweinf.
Pleurothallis cf. *aristata* W.J. Hook.
Pleurothallis determannii Luer
Pleurothallis ephemera Lindl. in Hook.
Pleurothallis glandulosa Ames
Pleurothallis minima Schweinf.
Pleurothallis miqueliana (Focke) Lindl.
Pleurothallis monophylla (W.J. Hook.) Fawc. & Rendle
Pleurothallis picta Lindl.
Pleurothallis polygonoides Griseb.
Pleurothallis pruinosa Lindl.
Pleurothallis semperflorens Lindl.
Pleurothallis sariata Lindl.
Pleurothallis spiculifera Lindl.
Pleurothallis vitarrifolia Schultr.
Pleurothallis sp.
Polystachya flavescens (Bl.) J.J. Smith

Polystachya foliosa (Hook.) Rchb.f.
Polystachya stenophylla Schltr.
Quekettia microscopice Lindl.
Quekettia vermeuleniana Determann
Reichenbachantus reflexus (Lindl.) Brade
Rodriguezia candida (Lindl.) Christenson
Rodriguezia lanceolata Ruiz & Pav.
Rudolfiella aurantiaca (Lindl.) Hoehne *
Scaphyglottis amethystina (Rchb.f.) Schltr.
Scaphyglottis modasta (Rchb.f.) Schltr.
Scaphyglottis prolifera Cogn.
Scaphyglottis sickii Pabst
Scaphyglottis violacea Lindl.
Scaphyglottis sp.
Selenipedium palmifolium (Lindl.) Rchb.f.
Stalis argantata Lindl.
Stelis sp.
Trichosalpinx memor (Rchb.f.) Luer
Trichosalpinx orbicularis (Lindl.) Luer
Trigonidium acuminatum Batem.
Trigonidium obtusum Lindl.
Vanilla cf. *cristato-callosa* Hoehne
Vanilla sp.
Wullschlaegelia calcarata Benth.
Xarorchis sp.

OXALIDACEAE (1)

Oxalis frutescens L.

PALMAE (15)

Astrocaryum munbaca Mart.
Attalea regia (C. Mart.) W. Boer
Bactris balanophora Spruce
Bactris humilis (Wallace) Burrat
Bactris oligoclada Burret
Bactris ptariana Steyerm.
Bactris sp.
Desmoncus polyacanthos Mart.
Euterpe oleracea Mart. *
Geonoma maxima (Poit.) Kunth
Geonoma sp.
Jessenia bataua (Mart.) Burret *
Maurtitia flexuosa L.f. *
Oenocarpus bacaba Mart.
Palmae indet

PASSIFLORACEAE (10)

Passiflora auriculata H.B.K.
Passiflora cirrhiflora Juss.
Passiflora coccinea Aublet
Passiflora fuchsiiflora Hemsley
Passiflora garckei Mast.
Passiflora glandulosa Cav.
Passiflora laurifolia L.
Passiflora misera Kunth
Passiflora vespertilio L.
Passiflora sp.

PHYTOLACCACEAE (1)

Phytolacca rivinoides Kunth & Bouch

PIPERACEAE (16)

Peperomia macrostachya (Vahl) A. Dietr. var. *macrostachya*
Peperomia maguirei Yunck.
Peperomia obtusifolia (L.) A. Dietr.
Peperomia ouabianae C. DC.
Peperomia pellucida (L.) Kunth
Peperomia quadrangularis (Thomps.) A. Dietr.
Peperomia rotundifolia (L.) Kunth
Peperomia sp.
Piper arboreum Aublet
Piper bartlingianum (Miq.) C. DC.
Piper demeraranum (Miq.) C. DC.
Piper hostmannianum (Miq.) C. DC.
Piper insipiens Trel. & Yun.
Piper nigrispicum C. DC.
Piper trichoneuron (Miq.) C. DC.
Piper sp.

POLYGALACEAE (3)

Bredemeyera densiflora Benn. var. *glabra* Benn.
Moutabea guianensis Aublet
Securidaca spinifex Sandw.

POLYGONACEAE (5)

Coccoloba cf. *lucidula* Benth.
Coccoloba gymnorrachis Sandw.
Coccoloba marginata Benth.
Coccoloba parimensis Benth.
Coccoloba sp.

PORTULACACEAE (1)

Talinum fruticosum (L.) Juss.

QUIINACEAE (3)

Quiina guianensis Aublet
Quiina indigofera Sandw.
Quiina sp.

RAPATEACEAE (1)

Rapatea paludosa Aublet

RHABDODENDRACEAE (1)

Rhabdodendron amazonicum (Spruce ex Benth.) Huber

RHAMNACEAE (1)

Gouania blanchetiana Miq.

RHIZOPHORACEAE (2)

Cassipourea guianensis Aubl.
Cassipourea lasiocalyx Alston

ROSACEAE (1)

Prunus myrtifolia (L.) Urb. *

RUBIACEAE (65)

Amaioua guianensis Aublet var. *guianensis*
Borreria capitata (Ruiz & Pav.) DC.
Coccocypselum guianense (Aublet) K. Schum.
Cosmibuena grandiflora (Ruiz & Pav.) Rusby var. *grandiflora*
Diodia ocimifolia (Willd. ex Roem. & Schult.) Bremek.
Duroia amapana Steyerm.
Duroia cf. *hirsuta* (Poepp. & Endl.) K. Schum.
Duroia eriopila L.f.
Duroia sp.
Faremea occidentelis (L.) A. Rich. ssp. *occidentalis*
Feramea quadricostata Bremek.
Faramea sessilifolia (HBK) DC.
Ferdinandusa goudotiana K. Schum. var. ?
Genipa americana L.
Geophila cordifolia Miq. var. *cordifolia*
Gonzalagunia dicocca Cham. & Schlecht.
Hemidiodia ocimifolia (Willd.) K. Schum.
Hillia illustris (Vell.) K. Schum.
Isertia hypoleuca Benth.
Ixora aluminicola Steyerm.
Ixora davisii Sandw.
Ixora floribunda (Rich.) Griseb.
Ixora graciliflora Benth.
Ixora intrapilosa Steyerm.
Malanea hypoleuca Steyerm.
Malanea macrophylla Bartling ex Griseb. var. *macrophylla*
Malanea sarmentosa Aublet
Morinda brachycalyx (Bremek.) Steyerm.
Morinda debilis (Sandw.) Steyerm.
Morinda tenuiflora (Benth.) Standl.
Oldenlandia corymbosa L.
Pagamea guianensis Aublet
Palicourea crocea (Sw.) R. & S.
Palicourea croceoides Hamilton
Palicourea guianensis Aubl. ssp. *guianenisis*
Palicourea guianensis Aublet ssp. *occidentalis* Steyerm.
Palicourea riparia Benth.
Palicourea sp.
Posoqueria latifolia (Rudge) Roem. et Schult.
Psychotria anceps Kunth
Psychotria apoda Steyerm.
Psychotria bahiensis DC. var. *bahiensis*
Psychotria capitata Ruiz & Pav. ssp. *inundata* (Benth.) Steyerm.
Psychotria cuspidata Bredem. ex Roem. & Schult.
Psychotria cf. *irwinii* Steyerm.

Psychotria mapourioides DC. var. *chionantha* (DC.) Steyerm.
Psychotria deflexa DC.
Psychotria glomerulata (Donn. Sm.) Steyerm.
Psychotria hoffmannseggiana (Willd. ex Roem. & Schult.) Mull. Arg.
Psychotria lupulina Benth. ssp. *lupulinum*
Psychotria officinalis (Aublet) Sandw. ssp. *officinalis*
Psychotria puberulenta Steyerm.
Psychotria rosea (Benth.) Muel. Arg.
Psychotria uliginosa Swartz
Psychotria sp.
Rudgea cornigera Bremek.
Rudgea hostmanniana Benth. ssp. *hostmanniana*
Sabicea aspera Aublet
Sabicea glabrescens Benth.
Sipanea biflora (L.f.) Cham. & Schlechtend.
Sipanea pratensis Aublet
Spermacoce capitata Ruiz & Pav.
Rubiaceae indet

RUTACEAE (4)

Angostura toxicaria (Engl.) Albug.
Hortia regia Sandw.
Ticorea pedicellata DC.
Rutaceae indet

SAPINDACEAE (26)

Cupania hirsuta Radlk.
Cupania scrobiculata L.C. Rich.
Cupania sp.
Matayba arborescens (Aublet) Radlk.
Matayba camptoneura Radlk.
Matayba inelegans Spruce ex Radlk.
Matayba laevigata (Miq.) Radlk.
Matayba macrostylis Radlk.
Matayba opaca Radlk.
Matayba sp.
Paullinia bernhardi Uittien
Paullinia capreolata (Aubl.) Radlk.
Paullinia grandifolia Benth. ex Radlk.
Paullinia pinnata L.
Paullinia rufescens L.C. Rich. ex Juss.
Paullinia sp.
Serjania paucidentata DC.
Talisia elephantipes Sandw.
Talisia furfuracea Sandw. *
Talisia microphylla Uitt.
Talisia squarrosa Radlk.
Talisia *sp.*
Toulicia elliptica Radlk.
Toulicia guianensis Aublet
Toulicia pulvinata Radlk.
Sapindaceae indet

SAPOTACEAE (28)

Chrysophyllum pomiferum (Eyma) Penn.
Chrysophyllum sparsiflorum Klotzsch ex Miq.
Ecclinusa psilophylla Sandw.
Manilkara bidentata (A. DC.) Chev. ssp. *surinamensis* (Miq.) Penn.
Micropholis venulosa (Mart. & Eichl.) Pierre
Micropholis sp.
Pouteria ambeloniifolia (Sandw.) Penn.
Pouteria caimito (Ruiz & Pav.) Radlk.
Pouteria cladantha Sandw.
Pouteria coriacea (Pierre) Pierre
Pouteria cuspidata (A. DC.) Baehni ssp. *dura* (Eyma) Penn.
Pouteria durlandii (Standl.) Baehni
Pouteria egregia Sandw. / P. reticulata (Engl.) Eyma ssp. *surinamensis* Pennington
Pouteria engleri Eyma
Pouteria filipes Eyma *
Pouteria fimbriata Baehni
Pouteria guianensis Aublet
Pouteria hispida Eyma
Pouteria speciosa (Ducke) Baehni
Pouteria surumuensis Baehni
Pouteria torta (Mart.) Radlk. ssp. *glabra* Penn.
Pouteria venosa (Mart.) Baehni subsp. *amazonica* Pennington
Pouteria sp.
Pradosia schomburgkiana (DC.) Cronq.
Pradosia surinamensis (Eyma) Pennington
Sapotaceae indet

SCROPHULARIACEAE (4)

Bacopa aquatica Aubl.
Lindernia crustacea (L.) F. Muell.
Lindernia diffusa (L.) Wettst.
Scoparia dulcis L.

SIMAROUBACEAE (6)

Picramnia guianensis (Aublet) Jansen-Jacobs
Simaba cedron Planch.
Simaba guianensis Aublet
Simaba multiflora Adr. Juss.
Simaouba amara Aubl. *
Simaroubaceae indet

SMILACACEAE (8)

Smilax cf. *poeppigii*
Smilax lasseri Steyerm.
Smilax latipes Gleason
Smilax santaremensis DC.
Smilax schomburgkiana Kunth
Smilax syphilitica Willd.
Smilax sp.
Smilax sp. (aff. *kunthii*)

SOLANACEAE (13)

Markea coccinea L.C. Rich.
Markea porphyrobaphes Sandw.
Markea sp.
Solanum coriaceum Dunal
Solanum crinitum Lam.
Solanum leucocarpon L.C. Rich. ex Dunal
Solanum paludosum Moric.
Solanum rubiginosum Vahl
Solanum rugosum Dunal
Solanum stramonifolium Jacq.
Solanum subinerme Jacq.
Solanum sp.
Solanaceae indet

STERCULIACEAE (5)

Sterculia guianensis Sandw.
Sterculia pruriens (Aubl.) K. Schum. var. *glabrescens*/ var. *pruriens*
Sterculia rugosa R. Brown
Sterculia sp.
Waltheria indica L.

THEACEAE (1)

Theaceae indet

THURNIACEAE (1)

Thurnia sphaerocephala (Rudge) J.D. Hooker

TILIACEAE (5)

Apeiba petoumo Aublet
Lueheopsis rosea (Ducke) Burret
Lueheopsis rugosa (Pulle) Burret
Mollia lepidota Spruce ex Benth. ssp. *sphaerocarpa* (Gleason) Meijer
Vasivaea alchorneoides Baill.

TRIGONIACEAE (3)

Trigonia laevis Aublet var. *laevis*
Trigonia laevis Aublet var. *microcarpa* (Sagot ex Warm.) Sagot
Trigonia spruceana Benth. ex. Warm.

TRIURIDACEAE (3)

Peltophyllum luteum Gardner
Sciaphila albescens Benth.
Triuris hyalina Miers

TURNERACEAE (2)

Turnera aurantiaca Benth.
Turnera rupestris Aubl. var *frutescens* (Aubl.) Urb.

ULMACEAE (1)

Trema micrantha (L.) Blume

URTICACEAE (1)

Laportea aestuans (L.) Chew

VERBENACEAE (6)

Aegiphila macrantha Ducke

Aegiphila villosa (Aubl.) J.F. Gmelin
Petrea macrostachya Benth.
Petrea sp.
Stachytarpheta jamaicensis (L.) Vahl
Vitex stahelii Mold.

VIOLACEAE (10)
Amphirrhox longifolia (St. Hil.) Spreng.
Paypayrola guianensis Aublet
Paypayrola longifolia Tul.
Paypayrola sp.
Rinorea brevipes (Benth.) Blake
Rinorea endotricha Sandw.
Rinorea flavescens (Aublet) Kuntze
Rinorea guianensis Aubl.
Rinorea riana Kuntze
Violaceae indet

VITACEAE (2)
Cissus erosa L.C. Rich.
Cissus sicyoides L.

VOCHYSIACEAE (3)
Ruizterania albiflora (Warm.) Marcano Berti
Vochysia schomburgkii Warm.
Vochysia surinamensis Stafleu var. *surinamensis*

ZINGIBERACEAE (2)
Costus claviger Benoist
Renealmia orinocensis Rusby

GYMNOSPERMAE

GNETACEAE (3)
Gnetum nodiflorum Brongn.
Gnetum urens (Aublet) Blume
Gnetum sp.

PTERIDOPHYTA

ADIANTACEAE (1)
Adiantum sp.

ASPLENIACEAE (2)
Asplenium angustum Sw.
Asplenium serratum L.

BLECHNACEAE (1)
Blechnum serrulatum L.C. Rich.

CYATHEACEAE (1)
Cyathea sp.

DENNSTAEDTIACEAE (6)
Lindsaea divaricata Klotzsch
Lindsaea lancea (L.) Bedd. var. *falcata* (Dryand.) Ros.
Lindsaea sagittata (Aublet) Dryand.
Lindsaea schomburgkii Klotzsch
Lindsaea ulei Hieron.
Lindsaea sp.

DRYOPTERIDACEAE (3)
Cyclodium inerme (Fee) A.R. Smith
Cyclodium meniscioides (Willd.) K. Presl var. *meniscioides*
Dryopteridaceae indet

GRAMMITIDACEAE (3)
Cochlidium furcatum (Hook. ex Grev.) C. Chr.
Cochlidium serrulatum (Swartz) L.E. Bishop
Grammitis flabelliformis (Poir.) C.V. Morton

HYMENOPHYLLACEAE (10)
Hymenophyllum sp.
Trichomanes ankersii Parker ex Hook. & Grev.
Trichomanes arbuscula Desv.
Trichomanes cf. *crispum* L.
Trichomanes diaphanum Kunth
Trichomanes kapplerianum J.W. Sturm
Trichomanes martiusii Presl
Trichomanes pedicellatum Desv.
Trichomanes pinnatum Hedw.
Trichomanes sp.

LOMARIOPSIDACEAE (3)
Elaphoglossum glabellum J. Smith
Elaphoglossum luridum (Fee) Crist.
Elaphoglossum sp.

LOMARIOPSIDACEAE (1)
Lomariopsidaceae indet

LYGODIACEAE (1)
Lygodium volubile Swartz

METAXYACEAE (1)
Metaxya rostrata (Kunth) K. Presl

OLEANDRACEAE (1)
Nephrolepis biserrata (Sw.) Schott

POLYPODIACEAE (7)
Dicranoglossum desvauxii (Klotzsch) Proctor
Microgramma ciliata (Willd.) Alston
Microgramma lycopodioides (L.) Copel.
Microgramma reptans (Cav.) A.R. Smith
Pleopeltis percussa (Cav.) Hook. & Grev.
Polypodium sp.

PTERIDACEAE (2)
Pityrogramma calomelanos (L.) Link
Pteris sp.

SCHIZAEACEAE (3)
Actinostachys pennula (Sw.) Hook.
Schizaea fluminensis Miers ex Sturm.
Schizaea incurvata Schkuhr

TECTARIACEAE (3)
Cyclopeltis semicordata (Sw.) J. Sm.
Tectaria plantaginea (Jacq.) Maxon var. *macrocarpa* (Fe) Morton
Triplophyllum acutilobum Holttum

THELYPTERIDACEAE (1)
Thelypteris sp.

VITTARIACEAE (5)
Anthrophyum guyanense Hieron.
Anthrophyum sp.
Hecistopteris pumila (Spreng.) J.E. Smith
Vittaria costata Kunze
Vittaria lineata (L.) J.E. Smith

LYCOPODIACEAE (3)
Huperzia dichotoma (Jacq.) Trevis.
Lycopodiella cernua (L.) Pic.-Ser.
Lycopodium sp.

SELAGINELLACEAE (3)
Selaginella parkeri (Hook. & Grev.) Spring
Selaginella producta Baker
Selaginella sp.

APPENDIX 3 Checklist of the mammals from Mabura Hill and surroundings

Animals sighted in the area south of Mabura. Names in the list follow Emmons & Feer (1990). Included are sightings from David Hammond, Hans ter Steege, Roderick Zagt, Renske Ek, Peter van der Hout and Leo Brouwer. Bats were net-trapped by Zoologists of the Royal Ontario Museum, who also trapped rodents (Mark Engstrom and Burton Lim, unpublished data).
At present 75 species of mammals have been observed in the area.

MARSUPIALIA (6)	**MARSUPIALS**
Didelphidae (6)	**Opossums**
Didelphis marsupialis	Common opossum
Philander opossum	Common gray four-eyed opossum
Micoureus demerarae	Hairy-tailed mouse opossum
Micoureus cinereus	Woolly mouse opossum
Marmosa murina	Murine mouse opossum
Monodelphis brevicaudata	Red-legged short-tailed opossum
XENARTHRA (5)	**ANTEATERS, SLOTHS, ARMADILLOS**
Myrmecophagidae (3)	**Anteaters**
Cyclopes didactylus	Pygmy anteater
Myrmecophaga tridactyla	Giant anteater
Tamandua tetradactyla	Southern tamandua
Bradipodidae (1)	**Sloths**
Bradypus tridactylus	Pale-throated three-toed sloth
Dasipodidae (1)	**Armadillos**
Dasypus septemcinctus	Seven-banded armadillo
CHIROPTERA (27)	**BATS**
Phyllostomidae (21)	**Leaf-nosed or fruit eating bats**
Artibeus obscurus	Sooty fruit bat
Artibeus planirostris	Grey fruit bat
Artibeus lituratus	Giant fruit bat
Artibeus gnomus	Yellow dwarf fruit bat
Artibeus concolor	Unlined fruit bat
Uroderma bilobatum	Tent-making bat
Vampyressa sp.	Yellow-eared bat
Desmodus rotundus	Common vampire bat
Phyllostomus elongtus	Common spear-nosed bat
Micronycteris nicefori	Grey little big-eared bat
Mimon crenulatum	Hairy nosed bat
Chrotopterus auritus	Wooly false vampire bat
Tonatia silvicola	Large round-eared bat
Tonatia bidens	Striped round-eared bat
Trachops cirrhosus	Frog-eating bat
Sturnira tildae	Hairy-legged fruit bat
Glossophaga soricina	Common nectar feeding bat
Lonchophylla thomasi	Thomas' nectar feeding bat
Carollia brevicauda	Small short-tailed fruit bat
Carollia perspicillata	Common short-tailed fruit bat
Rhinophylla pumilio	Little fruit bat
Mormoopidae (1)	**Leaf-chinned bats**
Pteronotus parnellii	large leaf-chinned bat
Emballonuridae (3)	**Sac-winged bats**
Saccopteryx bilineata	White-lined sac-winged bat
Saccopteryx leptura	Brown sac-winged bat
Cormura brevirostris	Chestnut sac-winged bat
Molossidae (1)	**Free-tailed bats**
Molossus molossus	Small house bat
Vespertilionidae (1)	**Vespertilionid bats**
Myotis nigricans	Black myotis bat
PRIMATES (8)	**MONKEYS**
Callitrichidae (1)	**Marmosets & Tamarins**
Saguinus midas	Golden-handed tamarin
Cebidae (7)	**(New world) Monkeys**
Chiropotes satanus	Brown-bearded saki
Pithecia pithecia	White-faced (Guianan) saki
Cebus apella	Brown capuchin monkey
Cebus olivaceus	Weeping capuchin monkey
Saimiri sciureus	Common squirrel monkey
Alouatta seniculus	Red howler monkey
Ateles paniscus	Black spider monkey

CARNIVORA (15)	**CARNIVORES**
Canidae (2)	**Bush-dogs, Foxes**
Speothos vaneticus	Bush dog
Urocyon cinaraoerganteus	Gray fox
Procyonidae (3)	**Racoon family**
Nesue nesue	South american coati
Potos flavus	Kinkajou
Procyon cancrivorous	Crab-eating raccoon
Mustelidae (4)	**Weasel family**
Eira barbera	Tayra
Galictis vittata	Grison or Huron
Lutra longicaudis	Southern river otter
Pteronura brasiliensis	Giant otter
Felidae (6)	**Cats**
Felis tigrina	Little spotted cat
Felis pardalis	Ocelot
Felis wiedii	Margay
Felis yagouaroundi	Jaguarundi
Puma concolor	Puma
Panthera onca	Jaguar
PERISSODACTYLA (1)	**TAPIRS**
Tapiridea (1)	**Tapirs**
Tapirus terrestris	Brazilian tapir
ARTIODACTYLA (5)	**PECCARIES, DEER**
Tayassuidae (2)	**Peccaries**
Tayassu pecari	White-lipped peccary
Tayassu tajacu	Collared peccary
Cervidae (3)	**Deer**
Odocoileus virginianus	White-tailed deer
Mazama americana	Red brocket deer
Mazama gouazoubira	Gray brocket deer
RODENTIA (9)	**RODENTS**
Sciuridae (1)	**Squirrels**
Sciurus aestuans	Guianan squirrel
Muridae (2)	**Typical Rats and Mice**
Oecomys concolor	Reddish climbing mouse
Oecomys bicolor	Bicolored climbing mouse
Erethizontidae (1)	**New world Porcupines**
Coendou prehensilis	Brazilian porcupine
Agoutidae (1)	**Pacas**
Agouti pace	Paca or Labba
Dasyproctidae (2)	**Agoutis**
Dasyprocta egouti	Red-rumped agouti
Myoprocta acouchy	Red acouchy
Echimyidae (2)	**Spiny rats**
Proechimys guyannensis	Guianan spiny rat
Proechimys cuvieri	Cuvier's spiny rat

APPENDIX 4 Checklist of birds from Mabura Hill and surroundings

Family affinities in the checklist follow Ridgeley and Tudor (1989, 1994) for Passeriformes; Meyer de Schauensee (1978) for remaining Orders. For authorities the reader is referred to those publications. The list is largely based on the field sightings of Roderick Zagt 1990-1995, with additional information from Cornelissen & ter Steege, 1985; Bob Brown, 1989, 1990 (including mist-net trapping); Hein Prinsen, 1990; Terry Maxwell, 1994 (mist-net trapping).
At present 302 birds species have been observed in the area.

TINAMIDAE (3)	**TINAMOUS**
Tinamus major	great tinamou
Crypturellus variegatus	variegated tinamou
Crypturellus erythropus	red-footed tinamou
PHALACROCORACIDAE (1)	**CORMORANTS**
Phalacrocorax olivaceous	olivaceous cormorant
ANHINGIDAE (1)	**DARTERS**
Anhinga anhinga	anhinga
ARDEIDAE (7)	**HERONS and EGRETS**
Ardea cocoi	white-necked heron
Casmerodius albus	great egret
Butorides striatus	striated heron
Agamia agami	chestnut-bellied heron
Bubulcus ibis	cattle egret
Pilherodius pileatus	capped heron
Tigrisoma lineatum	rufescent tiger-heron
COCHLEARIIDAE (1)	**BOAT-BILLED HERONS**
Cochlearius cochlearius	boat-billed heron
THRESKIORNITHIDAE (1)	**IBISES**
Mesembrinibis cayennensis	green ibis
ANATIDAE (1)	**DUCKS, GEESE and SWANS**
Cairina moschata	muscovy duck
CATHARTIDAE (3)	**AMERICAN VULTURES**
Sarcoramphus papa	king vulture
Cathartes burrovianus	lesser yellow-headed vulture
Cathartes melambrotus	greater yellow-headed vulture
ACCIPITRIDAE (17)	**HAWKS and EAGLES**
Gampsonyx swainsonii	pearl kite
Elanoides forficatus	swallow-tailed kite
Chondrohierax uncinatus	hook-billed kite
Leptodon cayanensis	gray-headed kite
Harpagus bidentatus	double-toothed kite
Ictinia plumbea	plumbeous kite
Rostrhamus sociabilis	snail kite
Accipiter superciliosus	tiny hawk
Buteo platypterus	broad-winged hawk
Buteo magnirostris	roadside hawk
Buteo brachyurus	short-tailed hawk
Buteo nitidus	gray hawk
Leucopternis albicollis	white hawk
Heterospizias meridionalis	savanna hawk
Buteogallus urubitinga	great black eagle
Harpia harpyja	harpy eagle
Spizastur melanoleucus	black-and-white hawk-eagle
PANDIONIDAE (1)	**OSPREYS**
Pandion haliaetus	osprey
FALCONIDAE (5)	**FALCONS and CARACARAS**
Micrastur semitorquatus	collared forest-falcon
Micrastur gilvicollis	lined forest-falcon
Daptrius ater	black caracara
Daptrius americanus	red-throated caracara
Falco rufigularis	bat falcon
CRACIDAE (3)	**CHACHALACAS, GUANS and CURASSOWS**
Ortalis motmot	little chachalaca
Penelope marail	marail guan
Crax alector	black curassow
PHASIANIDAE (1)	**QUAILS and PARTRIDGES**
Odontophorus gujanensis	marbled woodquail
PSOPHIIDAE (1)	**TRUMPETERS**
Psophia crepitans	gray-winged trumpeter
RALLIDAE (1)	**RAILS, GALLINULES and COOTS**
Aramides cajanea	gray-necked wood-rail
EURIPYGIDAE (1)	**SUNBITTERNS**
Eurypyga helias	sunbittern
CHARADRIIDAE (3)	**PLOVERS and LAPWINGS**
Hoploxypterus cayanus	pied lapwing
Pluvialis dominica	lesser golden plover
Charadrius collaris	collared plover
SCOLOPIDAE (2)	**SANDPIPERS and SNIPES**
Actitis macularia	spotted sandpiper

Gallinago gallinago	common snipe
LARIDAE (2)	**GULLS and TERNS**
Phaetusa simplex	large-billed tern
Sterna superciliaris	yellow-billed tern
RYNCHOPIDAE (1)	**SKIMMERS**
Rynchops niger	black skimmer
COLUMBIDAE (8)	**PIGEONS and DOVES**
Columba speciosa	scaled pigeon
Columba plumbea (subvinacea)	plumbeous (incl. ruddy) pigeon
Columbina passerina	common ground-dove
Columbina minuta	plain-breasted ground-dove
Columbina talpacoti	ruddy ground-dove
Leptotila verreauxi	white-tipped dove
Leptotila rufaxilla	gray-fronted dove
Geotrygon montana	ruddy quail-dove
PSITTACIDAE (17)	**MACAWS, PARROTS and PARAKEETS**
Ara ararauna	blue-and yellow macaw
Ara chloroptera	red-and-green macaw
Ara nobilis	red-shouldered macaw
Forpus passerinus	green-rumped parrotlet
Brotogeris chrysopterus	golden-winged parakeet
Touit batavica	lilac-tailed parrotlet
Touit purpurata	sapphire-rumped parrotlet
Pionites melanocephala	black-headed parrot
Pionopsitta caica	caica parrot
Pionus menstruus	blue-headed parrot
Pionus fuscus	dusky parrot
Amazona dufresniana	blue-cheeked parrot
Amazona festiva	festive parrot
Amazona ochrocephala	yellow-headed parrot
Amazona amazonica	orange-winged parrot
Amazona farinosa	mealy parrot
Deroptyus accipitrinus	red-fan parrot
CUCULIDAE (4)	**CUCKOOS**
Coccyzus melacoryphus	dark-billed cuckoo
Piaya cayana	squirrel cuckoo
Piaya melanogastar	black-bellied cuckoo
Crotophaga ani	smooth-billed ani
STRIGIDAE (2)	**OWLS**
Pulsatrix perspicillata	spectacled owl
Glaucidium brasilianum	ferruginous pygmy-owl
NYCTIBIIDAE (1)	**POTOOS**
Nyctibius griseus	common potoo
CAPRUMULGIDAE (3)	**NIGHTHAWKS and NIGHTJARS**
Nyctidromus albicollis	pauraque
Caprimulgus maculicaudus	spot-tailed nightjar
Caprimulgus nigrescens	blackish nightjar
APODIDAE (2)	**SWIFTS**
Streptoprocne zonaris	white-collared swift
Chaetura spinicauda	band-rumped swift
TROCHILIDAE (12)	**HUMMINGBIRDS**
Phaethornis superciliosus	long-tailed hermit
Phaethornis ruber	reddish hermit
Phaethornis longuemareus	little hermit
Campylopterus largipennis	gray-breasted sabrewing
Florisuga mellivora	white-necked jacobin
Discosura longicauda	racket-tailed coquette
Chlorestes notatus	blue-chinned sapphire
Thaluranea furcata	fork-tailed wood-nymph
Hylocharis sapphirina	rufous-throated sapphire
Amazilia fimbriata	glittering-throated emerald
Topaza pella	crimson topaz
Heliothryx aurita	black-eared fairy
TROGONIDAE (4)	**TROGONS**
Trogon melanurus	black-tailed trogon
Trogon viridis	white-tailed trogon
Trogon rufus	black-throated trogon
Trogon violaceus	violaceous trogon
ALCEDINIDAE (5)	**KINGFISHERS**
Ceryle torquata	ringed kingfisher
Chloroceryle amazona	amazon kingfisher
Chloroceryle americana	green kingfisher
Chloroceryle inda	green-and-rufous kingfisher
Chloroceryle aenea	pygmy kingfisher
MOMOTIDAE (1)	**MOTMOTS**
Momotus momota	blue-crowned motmot
GALBULIDAE (4)	**JACAMARS**
Galbula albirostris	yellow-billed jacamar
Galbula dea	paradise jacamar
Galbula leucogastra	bronzy jacamar
Jacamerops aurea	great jacamar
BUCCONIDAE (7)	**PUFFBIRDS**
Notharchus macrorhynchus	white-necked puffbird
Notharchus tectus	pied puffbird
Bucco tamatia	spotted puffbird
Bucco capensis	collared puffbird
Malacoptila fusca	white-chested puffbird
Monasa atra	black nunbird
Chelidoptera tenebrosa	swallow-wing
CAPITONIDAE (1)	**BARBETS**
Capito niger	black-spotted barbet
RAMPHASTIDAE (5)	**TOUCANS and ARACARIS**
Pteroglossus aracari	black-necked aracari
Pteroglossus viridis	green toucanet

Selenidera culik	guianan toucanet
Ramphastos vitellinus	channel-billed toucan
Ramphastos tucanus	red-billed toucan
PICIDAE (8)	**WOODPECKERS and PICULETS**
Piculus flavigula	yellow-throated woodpecker
Piculus rubiginosus	golden-olive woodpecker
Celeus undatus	waved woodpecker
Celeus elegans	chestnut woodpecker
Dryocopus lineatus	lineated woodpecker
Melanerpes cruentatus	yellow-tufted woodpecker
Veniliornis cassini	golden-collared woodpecker
Campephilus rubricollis	red-necked woodpecker
FURNARIIDAE (20)	**OVENBIRDS and WOODCREEPERS**
FURNARIINAE (10)	**OVENBIRDS**
Synallaxis gujanensis	plain-crowned spinetail
Philydor pyrrhodes	cinnamon-rumped foliage-gleaner
Philydor ruficaudatus	rufous-tailed foliage-gleaner
Automolus infuscatus	olive-backed foliage-gleaner
Automolus ochralaemus	buff-throated foliage-gleaner
Automolus rufipileatus	chestnut-crowned foliage-gleaner
Xenops minutus	plain xenops
Sclerurus mexicanus	tawny-throated leaftosser
Sclerurus rufigularis	short-billed leaftosser
Sclerurus caudacutus	black-tailed leaftosser
DENDROCOLAPTINAE (10)	**WOODCREEPERS**
Dendrocincla fuliginosa	plain-brown woodcreeper
Dendrocincla merula	white-chinned woodcreeper
Deconychura longicauda	long-tailed woodcreeper
Glyphorynchus spirurus	wedge-billed woodcreeper
Hylexetastes perotii	red-billed woodcreeper
Dendrocolaptes certhia	barred woodcreeper
Xiphorhynchus pardalotus	chestnut-rumped woodcreeper
Xiphorhynchus guttatus	buff-throated woodcreeper
Lepidocolaptes souleyetii	streak-headed woodcreeper
Campylorhamphus procurvoides	curve-billed scythebill
THAMNOPHILIDAE (27)	**TYPICAL ANTBIRDS**
Cymbilaimus lineatus	fasciated antshrike
Thamnophilus murinus	mouse-colored antshrike
Thamnophilus punctatus	slaty antshrike
Thamnophilus schistaceus	plain-winged antshrike
Thamnophilus amazonicus	amazonian antshrika
Thamnomanus ardesiacus	dusky-throated antshrike
Thamnomanus caesius	cinereous antshrike
Myrmotherula surinamensis	streaked antwren
Myrmotherula guttata	rufous-bellied antwren
Myrmotherula gutturalis	brown-bellied antwren
Myrmotherula axillaris	white-flanked antwren
Myrmotherula longipennis	long-winged antwren
Myrmotherula menetriesii	gray antwren
Terenura spodioptila	ash-winged antwren
Cercomacra tyrannina	dusky antbird
Herpsilochmus strictocephalus	todd's antwren
Herpsilochmus (stricturus)	spot-tailed antwren
Hypocnemis cantator	warbling antbird
Hypocnemoides melanopogon	black-chinned antbird
Percnostola rufifrons	black-headed antbird
Percnostola leucostigma	spot-winged antbird
Mymaciza ferruginea	ferruginous-backed antbird
Myrmeciza atrothorax	black-throated antbird
Pithys albifrons	white-plumed antbird
Gymnopithys rufigula	rufous-throated antbird
Hylophylax naevia	spot-backed antbird
Hylophylax poecilonota	scale-backed antbird
FORMICARIIDAE (6)	**GROUND ANTBIRDS**
Myrmornis torquata	wing-banded antpitta
Formicarius colma	rufous-capped antthrush
Formicarius analis	black-faced antthrush
Hypolezus macularius	spotted antpitta
Myrmothera campanisona	thrush-like antpitta
Grallaricula ferrugineipectus	rusty-breasted antpitta
CONOPHAGIDAE (1)	**GNATEATERS**
Conophagus aunta	chestnut-belted gnateater
TYRANNIDAE (50)	**TYRANT-FLYCATCHERS and ALLIES**
TYRANNINAE (35)	**TYRANT-FLYCATCHERS**
Tyrannus savanna	fork-tailed flycatcher
Tyrannus melancholicus	tropical kingbird
Tyrannus dominicensis	gray kingbird
Empidonomus varius	variegated flycatcher
Legatus leucophaius	piratic flycatcher
Coryphotriccus albophaius	white-ringed flycatcher
Myiodynastes maculatus	streaked flycatcher
Myiozetetes cayanensis	rusty-margined flycatcher
Laniocara hypopyrrha	cinereous mourner
Rhytipterna simplex	grayish mourner

Myiarchus ferox	short-crested flycatcher
Myiarchus tyrannulus	brown-crested flycatcher
Myiarchus tuberculifer	dusky-capped flycatcher
Terenotriccus erythrurus	ruddy-tailed flycatcher
Myiobius barbatus	sulphur-rumped flycatcher
Onychorhynchus coronatus	royal flycatcher
Hirundinea ferruginea	cliff flycatcher
Platyrinchus platyrhynchos	white-crested spadebill
Platyrinchus coronatus	golden-crowned spadebill
Platyrinchus saturatus	cinnamon-crested spadebill
Tolmomyias poliocephalus	gray-crowned flycatcher
Rhynchocyclus olivaceous	olivaceous flatbill
Rhamphotrigon ruficauda	rufous-tailed flatbill
Lophotriccus vitiosus	double-banded pygmy-tyrant
Colopteryx galeatus	helmeted pygmy-tyrant
Myiornis ecadatus	short-tailed pygmy-tyrant
Elaenia parvirostris	small-billed elaenia
Myiopagis gaimardii	forest elaenia
Camptostoma obsoletum	southern beardless tyrannulet
Mionectes oleaginea	ochre-bellied flycatcher
Mionectes macconnelli	McConnels flycatcher
Pachyramphus polychopterus	white-winged becard
Platypsaris minor	pink-throated becard
Tityra cayana	black-tailed tityra
Tityra inquisitor	black-crowned tityra
PIPRINAE (6)	**MANAKINS**
Pipra erythrocephala	golden-headed manakin
Pipra pipra	white-crowned manakin
Corapipo gutturalis	white-throated manakin
Manacus manacus	white-bearded manakin
Xenopipo atronitens	black manakin
Neopipo cinnamomea	cinnamon tyrantmanakin
Tyraneutes virescens	tyni tyrantmanakin
Schiffornis turdinus	thrush-like mourner
COTINGINAE (7)	**COTINGAS**
Cotinga cayana	spangled cotinga
Xipholena punicea	pompadour cotinga
Iodopleura fusca	dusky purpletuft
Lipaugus vociferans	screaming piha
Querula purpurata	purple-throated fruitcrow
Perissocephalus tricolor	capuchinbird
Procnias alba	white bellbird
Phoenicircus carnifex	guianan red-cotinga
HIRUNDINIDAE (9)	**SWALLOWS and MARTINS**
Tachycineta albiventer	white-winged swallow
Phaeoprogne tapera	brown-chested martin
Progne subis	gray-breasted martin
Progne dominicencis	carribean martin
Atticora faciata	white-banded swallow
Atticora melanoleuca	black-collared swallow
Stelgidopteryx ruficollis	rough-winged swallow
Riparia riparia	bank swallow
Hirundo rustica	barn swallow
TROGLODYTIDAE (3)	**WRENS**
Thryothorus coraya	coraya wren
Microcerculus bambla	wing-banded wren
Cyphorhinus arada	musician wren
SYLVIIDAE (3)	**GNATCATCHERS and GNATWRENS**
Ramphocaenus melenurus	long-billed gnatwren
Polioptila plumbea	tropical gnatcatcher
Polioptila guianensis	guianan gnatcatcher
TURDIDAE (1)	**THRUSHES and SOLITAIRES**
Turdus albicollis	white-necked thrush
VIREONIDAE (2)	**VIREOS and PEPPERSHRIKES**
Vireo olivaceus	red-eyed vireo
Hylophilus ochraceiceps	tawny crowned greenlet
EMBERZIDAE (39)	**TANAGERS, FINCHES and ALLIES**
PARULINAE (2)	**WOOD-WARBLERS**
Dendroica striata	blackpoll warbler
Basileuterus rivularis	river warbler
THRAUPINAE (21)	**TANAGERS**
Cyanerpes caeruleus	purple honeycreeper
Cyanerpes cyaneus	red-legged honeycreeper
Chlorophanes spiza	green honeycreeper
Dacnis cayana	blue dacnis
Euphonia minuta	white-vented euphonia
Euphonia chlorotica	purple-throated euphonia
Euphonia violacea	violaceous euphonia
Euphonia cayennensis	golden-sided euphonia
Euphonia plumbea	plumbeous euphonia
Tangara velia	opal-rumped tanager
Tangara punctata	spotted tanager
Tangara mexicana	turquoise tanager
Tangara gyrola	bay-headed tanager
Thraupis episcopus	blue-gray tanager
Thraupis palmarum	palm tanager
Ramphocelus carbo	silver-beaked tanager

Lanio fulvus	fulvous shrike-tanager
Tachyphonus rufus	white-lined tanager
Tachyphonus cristatus	flame-crested tanager
Tachyphonus surinamus	fulvous-crested tanager
Hemithraupis flavicollis	yellow-backed tanager
COEREBINAE (1)	**BANANAQUITS**
Coereba flaveola	bananaquit
ICTERINAE (6)	**AMERICAN ORIOLES and BLACKBIRDS**
Scaphidura oryzivora	giant cowbird
Psarocolius decumanus	crested oropendola
Psarocolius viridis	green oropendola
Cacicus cela	yellow-rumped cacique
Cacicus haemorrhous	red-rumped cacique
Icterus chrysocephalus	moriche oriole
CARDINALINAE (6)	**CARDINALS, GROSBEAKS and ALLIES**
Saltator maximus	buff-throated saltator
Caryothraustes canadensis	yellow-green grosbeak
Periporphyrus erythromelas	red-and-black grosbeak
Pitylus grossus	slate-colored grosbeak
Paroaria gularis	red-capped cardinal
Cyanocompsa cyanoides	blue-black grosbeak
EMBERIZINAE (3)	**EMBERIZINE FINCHES**
Sporophila lineola	lined seedeater
Sporophila nigricollis	yellow-bellied seedeater
Sporophila castaneiventris	chestnut-bellied seedeater

Wallaba forest is characterised by a very smooth canopy.

In creek heads in white sand areas palm swamp forest on peaty soil is often found.

Dakama forest and muri scrub is commonly found on the most excessively drained white sands.

Mora forest, as found along creeks and rivers has a very irregular canopy.

White Sand soil (Albic Arenosol), as found under Wallaba forest.

Brown Sand Soil (Ferralic Arenosol) under a mixed Greenheart forest.

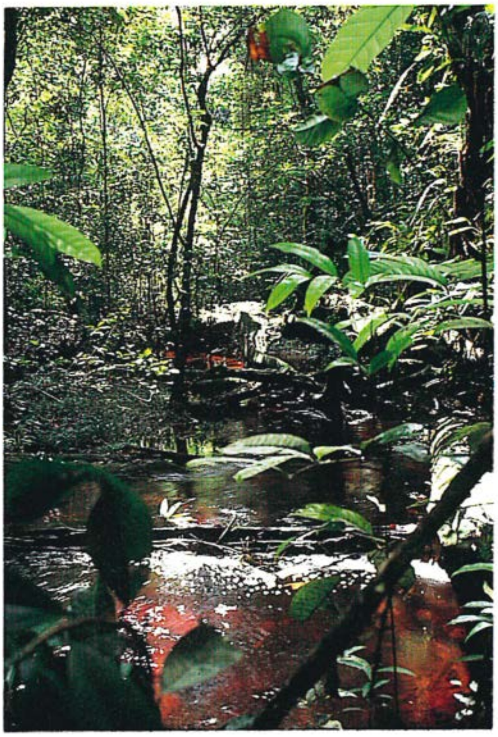
High water table in a floodplain soil (Dystric Fluvisol) under Mora forest.

Auguring in a White Sand soil.

Due to its open canopy, epiphytes can flourish near ground level in Wallaba forest.

In the dark Morabukea forest, dense seedling banks of Morabukea develop.

In Mora forest along creeks, buttresses are a common phenomenon.



White sand areas are mostly drained by 'black water creeks'.

A feller at work at a Greenheart.

Watching as it goes down. Techniques are being developed to accurately determine the falling direction to minimize damage.

Skidding is cause for a lot of damage, especially of smaller trees. Such damage can be reduced by planning operations carefully.

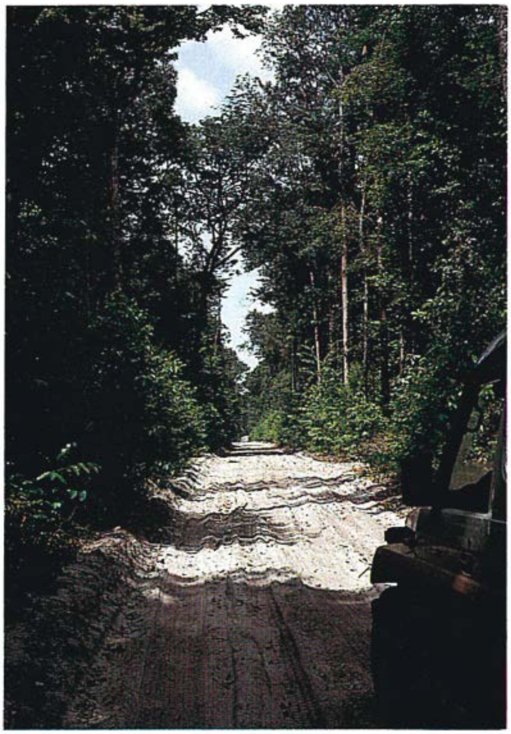
Because of the clumped occurrence of Greenheart trees, local damage can be substantial.

Canopy photograph of a small single tree gap.

Canopy photograph: a medium size gap of 730 m².

Canopy photograph: a large gap of 3440 m².

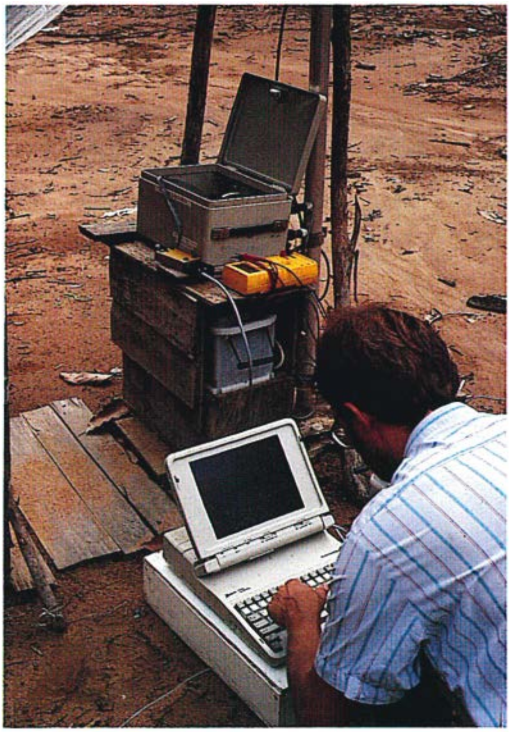
In large gaps pioneers, such as this newly germinated Congo pump (*Cecropia obtusa*) flourish.



A small white sand road on top of a watershed is cause for little erosion problems.

Very occasionally, e.g. on steep lateritic terrain, erosion and siltation may be serious.

Calibration of a dam with V-notch in the experimental catchment.



Downloading data from the 'meteo station' in a large gap.

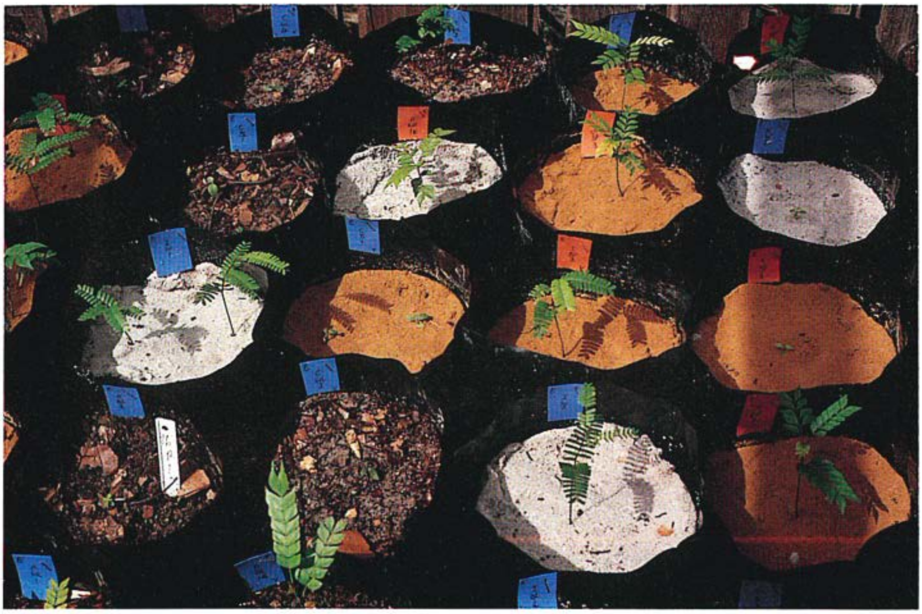
Marking a Greenheart tree for diameter growth measurements.

Monitoring height growth of seedlings.

Burying litter bags for litter decomposition studies.

Measurements of photosynthesis in the field.

The Field Station at the Ecological Reserve has been the base for much research in the first phase. Some of the nurseries are visible in the background.



A plant growth experiment on different soil substrates.

Seedlings in one of the shade boxes used to investigate the effect of shade on survival and growth of seedlings.

Attempting to catch seed dispersers is not always successful. Toads and insect-eating mammals, such as this opossum, may also pay a visit to the traps.