Vegetation structure, logging damage and silviculture
in a tropical rain forest
in Suriname

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VEGETATION STRUCTURE, LOGGING DAMAGE AND SILVICULTURE IN A TROPICAL RAIN FOREST IN SURINAME

Proefschrift

ter verkrijging van de graad van
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Abstract

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In the first publication in this series, a polycyclic forest management system was formulated, in which three silvicultural treatments (refinements) were scheduled in a cutting cycle of twenty years. This system, which is referred to as the Celos Silvicultural System, is developed further in this study.

Selective logging is the first action of forest management. Felling limits for most species need to be raised from 35 cm to 50 cm dbh to secure future harvests. If carried out properly, logging does not cause unacceptable damage to the stand. The forest responds to logging with a slow recovery process and a refinement is scheduled one to two years after felling to release commercial species. This treatment consists of cutting lianas and poison-girdling trees without commercial value, which are either larger than 40 cm dbh or 20 – 40 cm dbh and within 10 m of a commercial tree. A second treatment is necessary ten years after the initial harvest and the third one is scheduled a few years before the second cut. These follow-up treatments differ from the first one in the selection of trees to be poison-girdled.

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Stellingen

1. Onder de huidige economische omstandigheden is beheer van tropisch regenbos voor duurzame houtproduktie alleen haalbaar als na een geringe investering per hectare binnen enkele decennia een aantrekkelijke oogst mag worden verwacht.

   Dit proefschrift.

2. Selectieve uitkap van tropisch regenbos leidt niet noodzakelijkerwijs tot een blijvende verarming van het bosecosysteem in enigerlei vorm.

   Dit proefschrift.

3. Het invoeren van op duurzame houtproductie gericht beheer van tropisch regenbos wordt in sterke mate bemoeilijkt indien de houtexploitant geen direct belang heeft bij een dergelijk beheer.

4. De verspreiding van boomsoorten in tropisch regenbos wordt beïnvloed door een veelheid van factoren, en laat zich slechts ten dele verklaren uit tot op heden gepubliceerde wetenschappelijke theoriën.

   Dit proefschrift.

5. De zuidamerikaanse indianen hebben in de loop van duizenden jaren een zeer gedetailleerde kennis van de ecologie van het neotropisch regenwoud opgebouwd, die met hun cultuur dreigt te verdwijnen.

   D.A. Posey, 1983. Indigenous ecological knowledge and development of the Amazon, in E.F. Moran (ed.). The dilemma of Amazonian development. Westview Press, Boulder, USA.
   P. Grenand, 1975. Introduction à l'étude de l'univers Wayãpi. Gestencild rapport, Ecole des Hautes Etudes en Sciences Sociales, Parijs, Frankrijk.

6. Wetenschappelijke informatie over tropisch regenbos dringt onvoldoende door tot tropische landen, mede doordat veel studies of niet of als "grijze" literatuur worden gepubliceerd, hetgeen, in afwijking van wat Grainger (1987) stelt, minder te wijten is aan individuele onderzoekers dan aan hun werkgevers.

   A. Grainger, 1987. Report on the Tiel consultation. (TROPENBOS Information Series 3). TROPENBOS, Ede.

7. De door Poels (1987) gemeten toename van het nutriëntenkapitaal in Surinaams regenbos wijst op een geleidelijke aanwas van de phytomassa en kan dienen als partiële verklaring voor post-glaciale uitbreiding van het regenbosareaal in gebieden met zeer arme bodems.

   R.L.H. Poels, 1987. Soils, water and nutrients in a forest ecosystem in Suriname. (Ecology and management of tropical rain forests in Suriname 2). Landbouwuniversiteit, Wageningen.

8. Wetenschappelijk onderzoek onder primitieve omstandigheden dient niet afhankelijk te zijn van het storingsvrij functioneren van geavanceerde apparatuur.

9. Bij voortzetting van het huidige overheidsbeleid van bezuinigingen in het wetenschappelijk onderwijs en onderzoek dreigen die takken van wetenschap, die zich slecht lenen voor "contract research", te verschrompelen tot weinig meer dan weten op een schap.

10. De besluitvorming bij het verlenen van ontwikkelingshulp vertoont vaak een treffende overeenkomst met een alledaagse opvoedingssituatie, die raak gekarakteriseerd wordt door de kinderuitspraak "als mijn moeder het koud vindt, moet ik een jas aan".

11. Het kunstmatig instandhouden van heidevelden, zandverstuivingen en andere esthetisch fraaie Nederlandse landschappen, die zijn ontstaan als gevolg van ontbossing, wordt ten onrechte beschouwd als natuurbehoud en kan beter omschreven worden als landschapsbescherming.

12. Het opschorten van de Nederlandse ontwikkelingshulp aan Suriname kan gezien worden als een in Nederland weinig omstreden bezuinigingsmaatregel, die althans als zodanig aan zijn doel heeft beantwoord.

Stellingen behorende bij het proefschrift van W.B.J. JONKERS.
Wageningen, 18 november 1987.

Aan Martien, Carolien, Michiel en Wouter

Curriculum vitae

Wybrand Barend John Jonkers werd geboren op 21 oktober 1949 te 's Gravenhage. Van 1962 tot 1968 volgde hij de HBS-B opleiding aan het Grotius Lyceum te 's Gravenhage, waarna hij in 1968 begon met zijn studie in de Bosbouw aan de Landbouwhogeschool te Wageningen, waar hem in 1976 het ingenieursdiploma werd uitgereikt.

Enkele maanden na zijn afstuderen trad hij in dienst van de Voedsel en Landbouw Organisatie van de Verenigde Naties als assistent deskundige. Van 1976 tot eind 1980 was hij als zodanig werkzaam in Maleisië, eerst gedurende twee jaar op het maleise schiereiland en vervolgens in Sarawak, en leverde een bijdrage aan de ontwikkeling van twee methoden om tropisch regenbos op duurzame wijze te beheren. Begin 1981 werd hij aangesteld als wetenschappelijk ambtenaar bij de Landbouwhogeschool om voor de vakgroep Bosteelt onderzoek te verrichten in Suriname in het kader van het project "Antropogene ingrepen in het ecosysteem tropisch regenwoud". Eind 1983 keerde hij terug naar Nederland, en werkte daar aan dit proefschrift, tot augustus 1985 als wetenschappelijk medewerker van de Landbouwhogeschool en later onbezoldigd. Sinds juni 1987 is hij als consultant verbonden aan Tropenbos, een stimuleringsprogramma voor onderzoek in tropisch regenbosgebieden.

CONTENTS

Preface

There is widespread concern in the world today about the future of tropical rain forests, because they are being destroyed with alarming rapidity. There is also a growing awareness that efforts to preserve pristine forests can only be successful if combined with other land utilization types which suit the short-term and long-term economic needs of the people and countries concerned. Action plans have been formulated and policies proposed to save the remaining rain forests, to establish new tree stands, and to halt the deterioration of living conditions in rural areas.

One land utilization type considered is the use of natural forest for sustained timber production. Many tropical countries need hardwoods to feed their own industries and require revenues from lumber export to finance their development. There is an urgent need for management systems which secure an adequate supply in the decades to come. One such system, the Celos Silvicultural System, has been developed in Suriname and is the subject of this report and other publications in the series *Ecology and management of tropical rain forests in Suriname*.

The Celos Silvicultural System is based on ideas formulated in the 1960s and the oldest experiment in which the system was used was established in 1967. Eight years later, the data collected were analysed. Results indicated that polycyclic management is a feasible option. Polycyclic management means that the interval between harvests is short compared with the time trees require to grow to harvestable size and that only part of the stand is felled at one time. It was decided then to test and develop this approach further in a project of the Wageningen Agricultural University and the University of Suriname entitled *Human interference in the tropical rain forest ecosystem* (project LH/UvS01), started in 1978. Links were established with the Man And Biosphere Programme of UNESCO, to whom the project is also known as MAB Project 949.

The first publication in English on the Celos Silvicultural System is by de Graaf (1982), who proposed a sequence of three silvicultural treatments in a cutting cycle of 20 years. A more elaborate description of this concept is found in de Graaf (1986) entitled "A Silvicultural System for Natural Regeneration of Tropical Rain Forest in Suriname". This is the first volume in the series *Ecology and management of tropical rain forests in Suriname*, and contains a detailed discussion on experiments established prior to 1978.

This book is a sequal to de Graaf's thesis. It analyses three experiments initiated between 1978 and 1983 and summarizes the results of two earlier trials. The purpose of this study is to find ways to improve the Celos Silvicultural System. A wide range of topics will be discussed, such as spatial distribution of palm species, volume estimation of timber trees, logging damage, diameter class distributions of timber species, flowering and fruiting of trees, technical aspects of silvicultural treatment and growth of timber trees under various conditions. Each of these topics is of importance for silviculture or forest management in one way or another.

This study suggests some improvements in treatment prescriptions. Further improvements seem possible, but unfortunately, field-work was discontinued by the end of 1983 as result of a political controversy between the Governments of The Netherlands and Suriname. It is my sincere hope that relations between both countries will return to normal and that the work of project LH/UvS01 will be resumed to solve the remaining problems and to strengthen the scientific basis of the Celos Silvicultural System.

I could not have written this study without the help of many people. First of all, I am indebted to Professor R.A.A. Oldeman for his support and his detailed comments on the manuscript and to Dr J.H.A. Boerboom, who made the LH/UvS01 project possible and guided me during my stay in Suriname. Furthermore, I wish to thank Professor L.C.A. Corsten, who gave me valuable advice on matters concerning statistical analysis, and Dr N.R. de Graaf, who selected the site of the MAIN experiment and conducted the logging operation and the initial enumerations.

I am grateful to the successive directors of CELOS and to the CELOS personnel for their technical and administrative assistance. A word of special thanks is due to Mr W. Wolff and his crew for their dedicated and accurate work in the field and also to Mr J. Betlem, field co-ordinator, Mr R. Timpico, foreman at Kabo, and all the others who worked in the forest for project LH/UvS01.

Most of all, I would like to thank my colleagues in the LH/UvS01 team for their co-operation and friendship. I am grateful to Messrs F. de Vet, C. Jelsma and E. Alimoenadi for their assistance in data processing, and to the students who participated in the research work. I also wish to thank the Director of Centraal Bureau Luchtkartering, the Editor of Interciencia and Dr J.P. Schulz for permission to reproduce figures and aerial photographs.

Summary

This study is part of a long-term effort to devise a forest management system for the tropical rain forests of Suriname. Development of its vast, largely untapped forest resources for sustained timber production would benefit the economy of this country, which is heavily dependent on the exploitation of bauxite. A forest management system which requires little labour and capital input per hectare and results in an attractive return on investment is called for.

Investigations carried out in the 1950s and 1960s demonstrated that alleviation of competition in the stand resulted in a substantial increase in the growth of marketable species. However, methods used were considered too expensive and it was not until the 1970s that a more cost-efficient approach was developed. A polycyclic system was formulated, in which three silvicultural treatments (refinements) were scheduled in a felling cycle of 20 years. Each refinement included poison-girdling of all unwanted trees above a specified diameter limit and the cutting of climbers. This system, which is referred to as the Celos Silvicultural System (CSS), has been tested and developed further.

The principal aims of this study were to strengthen the ecological basis of CSS and to achieve further reductions in treatment costs. Data are presented from experiments in a mesophytic rain forest in the Kabo region, 100 km south-west of Paramaribo. The MAIN experiment (148 ha; 1978 – 1983) compared the effects of logging and refinement at three levels each, and was also used for vegetation studies, stem volume estimation, phenological observations and other ecological and silvicultural studies. Poison-girdling techniques were compared in an arboricide trial (7 ha; 1981 – 1983), and relationships between soil and vegetation were investigated in the Van Leeuwen transect (1.32 ha; 1982). Data from earlier investigations in the Mapane region are also included (50 ha; 1967 – 1982).

An extensive analysis of spatial distribution patterns in the forest vegetation revealed that some parts of the study areas had few or no trees of commercial species. This was often due to adverse physical soil properties, and it is preferable not to subject these areas to silvicultural treatment. Large pockets without commercial trees were also found on soils of better quality. The seed dispersal mechanisms of most commercial species appeared to be sufficient to cover these areas. Regenerating such patches by means of a poison-girdling treatment therefore seems possible, but a number of canopy trees should preferably remain to suppress proliferation of weed species. The analysis also indicated that eradication of the larger individuals of

boegroemaka (*Astrocaryum sciophilum*) and other palm species has a benificial effect on stand development. However, as logging already results in a reduction in palm competition, the need for such a treatment may only arise during the second half of the felling cycle.

Timber harvesting is the first action of forest management under CSS. It is shown that selective logging, if properly done, does not inflict unacceptable damage on the stand, even if volumes extracted are twice the average yield currently obtained in commercial operations. However, restrictions with regard to sizes of trees remain necessary and felling limits for many species should be increased from the current level of 35 cm diameter to approximately 50 cm. The forest recovers slowly from disturbance caused by logging, and increment in logged forest is inadequate to produce a next crop within a reasonable period. This means that sustained yield management cannot be achieved without silvicultural treatment. A positive effect of logging is that it creates extensive openings where commercial regeneration can develop. Further stimulation of recruitment through silvicultural treatment does not seem strictly necessary and may even be counterproductive in large gaps. Isolated trees in such openings screen commercial regeneration from excessive light and should preferably not be poison-girdled.

The first refinement is scheduled one to two years after logging. Investigations initiated in the 1960s and 1970s have shown, that a 20 cm diameter limit for refinement leads to attractive growth of commercial trees. This quality of the treatment should not be affected by modifications in prescriptions. Efforts were made to devise a treatment which discriminates between poorly and well stocked parts of the forest. It has been shown that a medium-sized tree without commercial value is unlikely to impede a desirable tree if the distance between both trees is more than 10 m. Hence, a refinement with two diameter limits instead of one is recommended. The lower limit of 20 cm dbh should apply in the vicinity of medium-sized and large desirable trees and the higher limit of 40 cm dbh should apply elsewhere. This study gives a detailed account of the organization of refinement, techniques used and costs involved. Much attention is also given to the ecological implications of the treatment.

The favourable growth rates induced by refinement extend over a period of eight to ten years. A second refinement is necessary ten years after the initial harvest and the third treatment is scheduled a few years before the second cut. These follow-up treatments differ from the first one in the selection of trees to be eliminated. This study concludes with recommendations for these refinements. Although it may be possible in theory to obtain an attractive sustained yield in a felling cycle of 20 years, it is recommended that allowance be made for delays in treatment and other contingencies by planning 25 annual coupes.

Samenvatting

Vegetatiestructuur, exploitatieschade en bosteeltkundige ingrepen in een tropisch regenwoud in Suriname

Sinds de vijftiger jaren wordt in Suriname bosbouwkundig onderzoek verricht in tropisch regenbos, met als doel het ontwikkelen van een beheerssysteem voor duurzame houtproductie. Als ontwikkelingsland met een geringe bevolkingsdruk, hoge werkeloosheid, een groot oppervlak aan bos en een economie die in hoge mate afhankelijk is van één product (bauxiet), heeft Suriname belang bij ecologisch verantwoord bosbeheer, waarbij met een bescheiden investering per hectare een aantrekkelijk rendement kan worden verkregen.

Onderzoek uitgevoerd in de vijftiger en zestiger jaren heeft aangetoond, dat het doden van ongewenste bomen en lianen kan resulteren in een sterke toename van de groei van commercieel belangrijke soorten (Schulz, 1960; Boerboom, 1965), maar de destijds toegepaste methoden werden te duur bevonden. Pogingen om de kosten te verminderen leidden in 1976 tot een polycyclisch systeem (de Graaf and Geerts, 1976; de Graaf, 1982; 1986), waarbij eens in de 20 jaar een deel van de bomen wordt geoogst en waarbij gedurende die 20 jaar drie bosteeltkundige ingrepen worden uitgevoerd. Bij deze behandelingen, die zuiveringen ("refinements") worden genoemd, wordt het aandeel van de commerciële soorten in het bos geleidelijk vergroot. Hiertoe worden lianen gekapt en ongewenste bomen, waarvan de stam dikker is dan een tevoren vastgestelde ondergrens, met arboricide gedood. Dit systeem, dat de naam "Celos Silvicultural System" (CSS) draagt, is sindsdien verder uitgewerkt en getoetst. Dit boek maakt deel uit van een reeks getiteld "Ecology and management of tropical rain forests in Suriname", waarin de resultaten van deze onderzoeksinspanningen worden beschreven.

Het verbeteren van de bosteeltkundige ingrepen is het hoofddoel van deze studie. De nadruk ligt hierbij op ecologische aspecten en het verminderen van de kosten. Drie experimenten werden hiertoe opgezet in tropisch regenbos nabij Kabo, ongeveer 100 km ten zuidwesten van Paramaribo (Fig. 1.1). In het "MAIN experiment" (148 ha; 1978 – 1983) werd de invloed van diverse niveaus van selectieve uitkap en zuivering op de vegetatie bestudeerd. Deze proef werd daarnaast gebruikt voor vegetatiekundig onderzoek en andere ecologische en bosbouwkundige studies. Mogelijkheden om het gebruik van arboriciden bij de zuivering te verminderen werden onderzocht in een "arboricide trial" (7 ha; 1981 – 1983) en de relatie bodem

– vegetatie werd in het "Van Leeuwen transect" (1,32 ha; 1982) geanalyseerd. Verder worden resultaten van oudere proeven in het Mapane gebied (50 ha; 1967 – 1982) besproken.

Uit een analyse van verspreidingspatronen in de bosvegetatie bleek, dat commerciële soorten erg schaars zijn in sommige delen van het "MAIN experiment" en het "Van Leeuwen transect". In een aantal gevallen is dit een gevolg van ongunstige fysische eigenschappen van de bodem. Een zuivering heeft niet het beoogde effect in dergelijke arme bossen en is ongewenst vanuit een ecologische optiek. Op betere bodems werd plaatselijk eveneens bos aangetroffen zonder bomen van commerciële soorten. Omdat de zaadverspreiding geen belemmerende factor bleek te zijn en er op voldoende verjonging van commerciële soorten gerekend kan worden, mag men hier wel gunstige resultaten verwachten van een zuivering, mits een aanzienlijk deel van het kronendak wordt gespaard om wildgroei van secundaire soorten, lianen en andere minder gewenste planten te onderdrukken. Uit het onderzoek bleek verder dat het doden van de grotere individuen van de boegroemaka palm (*Astrocaryum sciophilum*) en andere palmsoorten waarschijnlijk een gunstig effect heeft op de ontwikkeling van de opstand. Een dergelijke ingreep kan noodzakelijk zijn in de tweede helft van de kapcyclus, maar niet eerder, omdat de uitkap ook resulteert in een vermindering van het aantal palmen.

De gevolgen van selectieve uitkap werden onderzocht in het "MAIN experiment". Het bleek dat uitkap, indien met enige zorgvuldigheid uitgevoerd, niet leidt tot onaanvaardbare schade, zelfs niet als het geveld volume per hectare twee maal zo hoog is als gemiddeld in Suriname. Toch is het wenselijk om de bosexploitanten beperkingen op te leggen die verder gaan dan de bestaande wetgeving. De huidige kaplimiet van 35 cm diameter dient voor veel soorten te worden verhoogd tot 50 cm om voldoende verjonging te garanderen en om voldoende bomen over te houden voor een volgende kap. Na uitkap herstelt het bos zich langzaam van de toegebrachte schade. De bomen groeien gemiddeld iets sneller dan in ongestoord bos, maar onvoldoende om duurzaam bosbeheer zonder bosteeltkundige behandeling mogelijk te maken. Verder ontstaan er bij de velling en uitsleep een groot aantal openingen in het kronendak, waaronder de verjonging van commerciële soorten zich goed ontwikkelt. Het is dan ook niet strikt noodzakelijk om de groei van zaailingen en staken verder te stimuleren.

De eerste zuivering dient één tot twee jaar na de uitkap te worden uitgevoerd. Uit eerder onderzoek is reeds gebleken dat een zuivering met een ondergrens van 20 cm dbh leidt tot een aantrekkelijke groei van commerciële soorten (de Graaf, 1986), maar een dergelijke behandeling is te zwaar voor delen van het bos waar deze soorten vrijwel ontbreken. Daarom is gezocht naar een aangepaste behandeling. Het bleek, dat bomen weinig of geen concurrentie ondervinden van kleine en middelgrote exemplaren, die op meer dan 10 m afstand staan. Dit resultaat leidde naar een zuivering met twee diameterlimieten. De ondergrens van 20 cm blijft gelden binnen een straal van 10 m van middelgrote en grote bomen van commerciële soorten, maar elders dient een limiet van 40 cm te worden toegepast. Verder geeft deze studie een gedetailleerd verslag van technische en organisatorische aspecten van de zuivering en wordt uitgebreid aandacht besteed aan het kostenaspect, aan ecologische neveneffecten en aan de groei, mortaliteit en verjonging van commerciële soorten.

Na de eerste zuivering neemt de diametergroei toe en blijft dan acht tot tien jaar op een acceptabel niveau. Tien jaar na de velling is een tweede zuivering nodig om de groei nogmaals te stimuleren en een derde behandeling dient enkele jaren voor de volgende kap te worden uitgevoerd. Bij elke zuivering worden te elimineren bomen geselecteerd volgens andere criteria. In een eerdere publicatie in deze reeks stelt de Graaf (1986) voor om bij de tweede en derde zuivering diameterlimieten toe te passen van 5 à 10 cm. Het gevolg van deze benadering is dat soorten die volgens de huidige normen geen marktwaarde hebben vrijwel worden uitgeroeid. Hiertegen bestaan belangrijke bezwaren van ecologische en economische aard. Dit boek besluit met suggesties om deze bezwaren te ondervangen.

De beschikbare informatie suggereert dat het theoretisch mogelijk is om na 20 jaar een aantrekkelijke oogst te realiseren. In de praktijk moet men echter rekening houden met vertragingen in de uitvoering van de zuiveringen en andere eventualiteiten en daarom is het verstandig te rekenen met een kapcyclus van 25 jaar.

1 Suriname

The Republic of Suriname, only 163 820 km^2 in area, is the smallest independent country on the South American mainland. It is located in the humid equatorial region at 2° – 6° N and 54° – 56° W, between the Atlantic Ocean in the north and Brazil in the south, east of the Republic of Guyana and west of French Guiana (Fig. 1.1).

Most of Suriname's small population (Section 1.4) lives in or near the capital, Paramaribo, and a few other towns along the coast. Most economic activities, such as mining and agriculture, are therefore concentrated in the coastal plain, which comprises about 10% of the land area. The remaining 90% is sparsely populated and mainly covered with untouched tropical rain forest, growing on soils with little potential for permanent land use other than forestry, protection of the environment, and nature conservation. The inaccessibility of this interior region is an important limitation for forestry development, and most activities are presently confined to a relatively narrow zone of easily accessible terrain, the so-called Exploitable Forest Belt or Forestry Belt, which includes most of the Zanderij Formation and the northern fringe of the interior uplands (Fig. 1.1).

The principal objectives of this study and of the studies described in four other publications in the series *Ecology and management of tropical rain forests in Suriname* (de Graaf, 1986; Hendrison, in press; Poels, in press; Schmidt, in press) are to develop and to test methods for sustained timber production both in the Forestry Belt and in other tropical rain forest areas of Suriname which are considered inoperable under current economic conditions, but whose potential may be realised when these conditions change. Research objectives are discussed in more detail in Section 2.3.

1.1 Physical environment

1.1.1 Geomorphology and soils

Suriname can be divided from north to south into three zones, namely the coastal plain, the Zanderij Belt, and the interior uplands (Soe Agnie, 1982). The coastal plain, which is about 40 km wide in the east and 120 km in the west (Fig. 1.1), is almost flat and consists of heavy textured marine clay deposits interchanged with

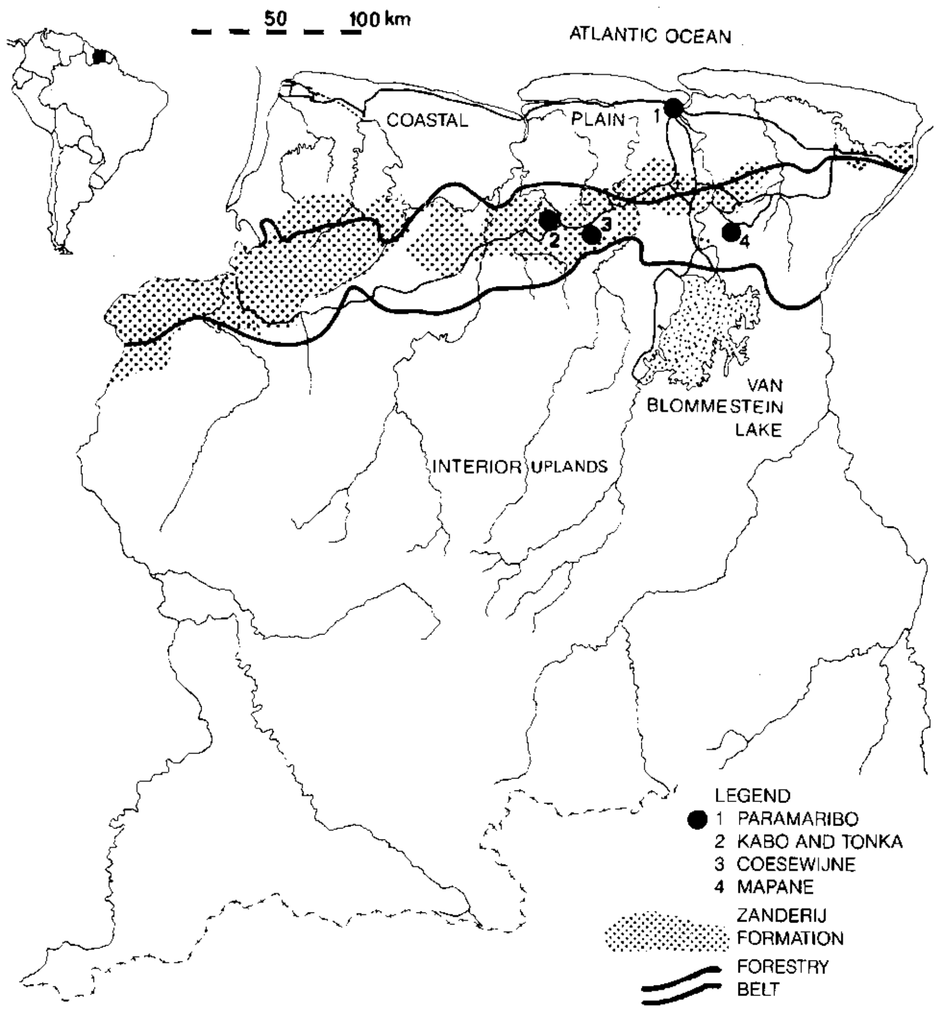


Fig. 1.1 Map of Suriname

sand and shell ridges. Its elevation varies from mean sea level in swampy areas to about 10 m.

The Zanderij Belt is just 5 – 10 km wide in the east, widening to 60 – 70 km in the west (Fig. 1.1), with elevations varying from about 10 m to 50 m. Most forestry activities, including the research discussed in this study, are concentrated in this zone. The Zanderij or Coesewijne Formation was formed during the Tertiary period when alluvial fans were deposited as result of severe erosion of the Guiana Shield (the present interior uplands). In more recent geological eras, the fans in the present coastal plain were covered with marine sediments, while the highest parts remained at the surface and now form the Zanderij Belt. Dendritic creek systems have created an easily accessible, slightly undulating landscape.

The soils of the Zanderij Belt can be divided into two categories, deeply podsolized bleached sandy soils and unbleached loamy textured soils. The transition between them is usually abrupt. The bleached soils are extremely poor in nutrients and have adverse physical properties, making them unsuitable for permanent cultivation (see Goense, 1987). Unbleached soils are slightly less infertile and have a good but fragile structure, which deteriorates rapidly when the soil is used for permanent agriculture (see Boxman, in press).

The interior uplands are part of the Guiana Shield, which consists mainly of deeply weathered rocks of Precambrian age, with a landscape resulting from erosion rather than tectonic activity (Bruijnings et al., 1977). This zone occupies more than 80% of Suriname and includes undulating to steep hilly lowlands as well as mountain ranges with elevations up to 1280 m above sea level. Soils are mostly of low fertility and range in texture from loamy sand to clay.

1.1.2 Climate

Temperature and humidity. Suriname has a warm and humid climate. The relative humidity is high, usually about 80% during the daytime and 95% at night, but slightly lower during long dry spells. Temperature is rather uniform, with an annual mean of 27° C and monthly averages of 26° C to 28° C (Fig. 1.2), but the diurnal

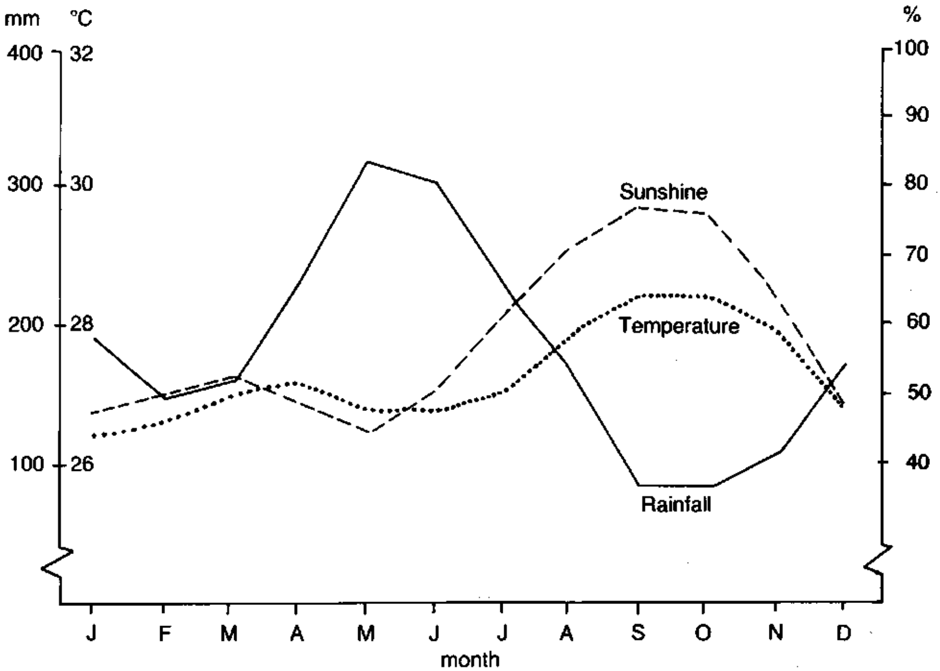


Fig. 1.2 Mean monthly precipitation (mm), temperature (°C) and sunshine (%) in Paramaribo, adapted from Bruijnings et al. (1977)

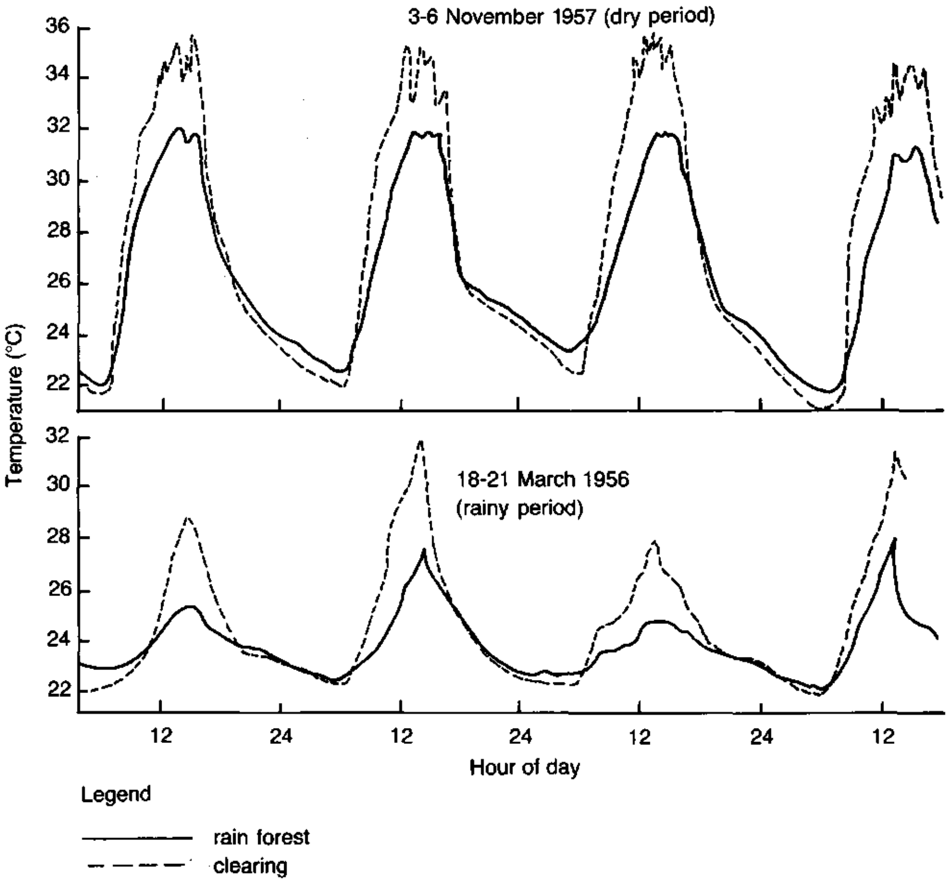


Fig. 1.3 Comparison of daily fluctuations in air temperature in rain forest and a 0.05 ha clearing during selected periods (Source: Schulz, 1960)

range, about 8° C, is considerably larger. The very high temperatures of less humid tropical areas are never experienced.

Precipitation. Annual rainfall varies from 1500 mm in coastal areas to almost 3000 mm in mountain ranges in the interior and occurs in four seasons (Goense, 1987; see also Fig. 1.2):

- short rainy season, 5th of December to 9th of February;
- short dry season, 10th of February to 19th of April;
- long rainy season, 20th of April to 14th of August;
- long dry season, 15th of August to 4th of December.

Based upon this seasonal variation in rainfall, three climatic types are distinguished, following Köppen's classification (Bruijnings et al., 1977):

- permanently wet rain forest (Af) climate, where all months have at least 60 mm precipitation;
- subhumid evergreen rain forest (Am) climate, where one or more months have less than 60 mm rainfall but total annual precipitation is high;
- savannah (Aw) climate, where one or more months have less than 60 mm rainfall and annual precipitation is moderate.

The Af climate is predominant in the coastal plain, the Zanderij Belt and the northern part of the interior uplands. The Aw climate is restricted to a few small areas along the coast and in the interior, and the Am climate predominates in the remaining 70% of the country.

A feature of the rainfall in Suriname is its intensity. A storm generally begins very suddenly, and the intensity of rainfall is high but of short duration. Thunderstorms are uncommon. Storms may be preceeded by short, violent squalls of wind, which

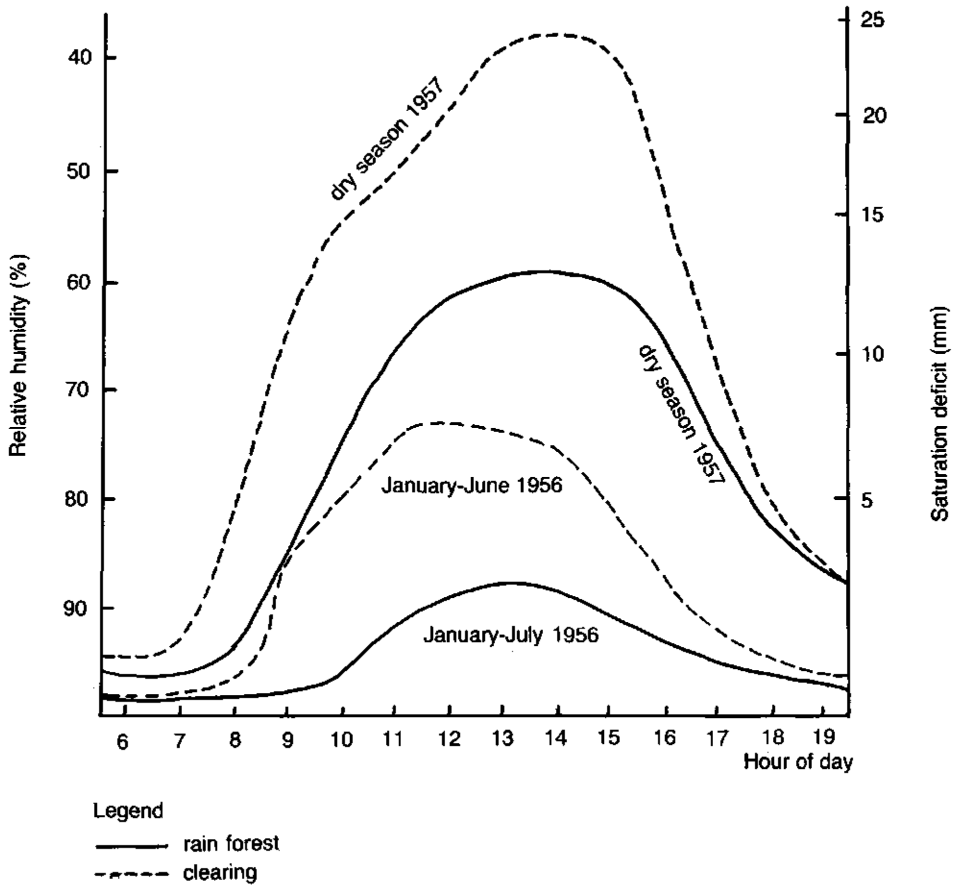


Fig. 1.4 Comparison of average daily fluctuations in atmospheric saturation deficit in rain forest and a 0.05 ha clearing during selected periods (Source: Schulz, 1960)

are important from the point of view of forest ecology because the strong winds sometimes uproot large trees and even destroy stands of several hectares. Schulz (1960) mentioned an area of several *hundred* hectares of wind-blown trees, probably caused by an exceptionally heavy local storm. Heavy rainfall has a similar impact, presumably caused by top-heaviness due to the weight of water adhering to leaves and twigs.

Solar radiation. Suriname is a land of sunshine, and even in the middle of the long rainy season the sun shines a few hours per day. The day-length is almost constant, as in other low latitude areas, varying in Paramaribo from 11 hours 48 minutes to 12 hours 27 minutes. The annual distribution of sunshine is a function of cloudiness and strongly correlated with rainfall, so that September and October tend to be the sunniest months, while mean monthly hours of sunshine are lowest in May and June (Fig. 1.2).

Microclimate on the forest floor. Microclimatic conditions on the floor of undisturbed tropical rain forest are distinctly different from those in the open air. Daily temperature amplitude is only about 2°C and seasonal variation in temperature is also less than in the open field (Fig. 1.3). Only a small proportion (1.5 – 2%) of solar radiation reaches the forest floor and air humidity is higher (Fig. 1.4). Wind velocity is very low, even when heavy gusts occur above the tree crowns. Precipitation is also less than in the open, because virtually all rain is intercepted by the tree crowns and some of it evaporates before reaching the forest floor. Dew starts to fall soon after sunset and may be an important form of precipitation in dry periods. A detailed account of microclimatic conditions is given by Schulz (1960).

1.2 Vegetation

Forest vegetation of some kind covers 92% of Suriname and six broad classes can be distinguished (Lindeman and Moolenaar, 1959):

- mangrove forest (115000 ha), hygrophytic forest in salty and brackish swamps along the coast;
- fresh water swamp forest (725000 ha), mainly in the coastal plain;
- marsh forest (505000 ha), at periodically flooded terrain in the coastal plain and elsewhere;
- savannah forest (150000 ha), xerophytic forest on bleached soils of the Zanderij Belt and locally in the interior uplands;
- mesophytic tropical rain forest (13362000 ha), on unbleached soils in the Zanderij Belt, in the interior uplands and on ridges in the coastal plain.

This study deals almost exclusively with mesophytic forests in the Zanderij Belt, which are rich in species, although not as rich as rain forest ecosystems found in other parts of the world (see Livingstone and van der Hammen, 1978). About 500 tree species have been identified and 100 – 150 species are usually found per hectare (Lindeman and Moolenaar, 1959; Schulz, 1960). Climbers and epiphytes are common and palms tend to be frequent. Floristic composition, canopy height and size class distribution vary considerably from place to place. The average height of taller trees is usually 30 – 50 m, although some emergents may grow to 60 m or more. Diameter class distributions are mostly well balanced and trees of some species may reach diameters of 150 cm. Commercial species tend to be fairly well represented, with some stands containing trees of species on the CELOS commercial species list (49 species, see Appendix I) with diameters at breast height greater than 15 cm, at densities as high as 100 trees per ha.

1.3 Population, land use and economy

Most inhabitants of Suriname are of African, Asian or European descent, with the original population, the Amerindians, forming a small minority of approximately 10000 people. Between 1870 and 1982 the population of Suriname grew from 50000 to 376000, mainly as a result of immigration initially but later due to natural population growth, although the birth rate has declined sharply in recent years. At present, about 25% of the population is under 15 years of age and a further 25% is between 15 and 30 years old.

Suriname has a low population density, 2.3 persons per km^2, and about 80% of the people live in or near Paramaribo. The population elsewhere in the coastal plain accounts for another 10%. Approximately 40000 Amerindians and Bushcreoles, the descendents of escaped African slaves, live in a number of settlements along the main rivers of the interior.

Most economic activities are concentrated within a radius of 30 km of the capital, including bauxite mining and processing, sawmilling, and various industries and agricultural enterprises producing for the local market. Other important economic activities are bauxite mining near Moengo, paddy cultivation near Nickerie, generation of hydro-electric power in the Van Blommenstein Lake, and forest exploitation in the coastal fresh water swamps and the Forestry Belt.

Only a small proportion of Suriname is used for primary production other than timber extraction from natural forest. About 62000 ha, that is 0.4% of the land area, is used for permanent agriculture and animal husbandry (Moerland, 1984) and an estimated 170000 ha is involved in shifting agriculture, about 10% of which is under cultivation at any one time (Vink, 1970). Some 9000 ha are under forest plantations.

Suriname is one of the richer developing countries, although the Gross National Product (GNP), which in 1982 was US$ 8500 per capita, has decreased substantially in the last few years. The economy is dominated by the bauxite industry which produces about one-third of the GNP and three-quarters of the country's export total (Moerland, 1984). The forestry sector is fairly important in Suriname's economy, contributing 1.5% to the GNP and 2.5% to export figures.

Suriname has a working population of 104000 (Moerland, 1984), the largest employer being the government, which provides jobs for 38500 civil servants. Agriculture and industry combined employ only 35000 people and the remaining 31000 work for private companies in the commerce and services sector. The rate of unemployment is high, about 25%, particularly among the young who received no formal education beyond primary school.

There is obviously a large need for diversification of the economy and generation of more jobs. Further development of Suriname's vast forest resources for sustained timber production may well contribute to a better-balanced economic development in the country, and a forest management system which requires little input of labour and capital per unit area and leads to an attractive return on investment is called for.

2 Trends in rain forest silviculture

Commercial timber exploitation has been carried out for centuries in the humid tropics, the oldest record of timber trade in Suriname dating from 1650. In those pre-colonial times, Dutch merchants bought snakewood (letterhout, *Brosimum guianense*) from Amerindian tribes, but organized timber exploitation was not introduced until the 18th century, when "houtplantages" (timber concessions) appeared along navigable parts of Suriname's main rivers. Transport was by water and logging operations were confined to the vicinity of water courses until the 1950s. Logging activities since then have been restricted to dry land forest in the Forestry Belt and swamp forest in the coastal plain. A more detailed history of forest exploitation in Suriname will be included in a later publication in this series (Hendrison, in press).

The history of tropical silviculture is much shorter. In the second half of the 19th century, extensive areas of subhumid teak (*Tectona grandis*) forest were brought under management in the Indian subcontinent, Burma and Indonesia. Experience gained there served as a basis for the first attempts in the early 1900s to develop silvicultural techniques for tropical rain forest, in what is now Peninsular Malaysia. Suriname was among the first countries to apply such methods on an experimental scale, starting in 1904. Many silvicultural systems have been developed since then, mostly in South-East Asia and Africa, but also in Australia and tropical America. Some methods aim at replacing the original vegetation with planted timber trees (artificial regeneration techniques), others aim at stimulating increment of commercial species already present in natural forest (natural regeneration techniques).

A brief history of the origin, development and present status of natural regeneration techniques used in tropical rain forests is given in Sections 2.1 and 2.2, with the emphasis on silvicultural methods which have influenced developments in Suriname. The most recently proposed silvicultural system for Suriname's rain forests (de Graaf, 1986) is briefly reviewed in Section 2.2. The testing and improvement of this system was the principal object of the present study, and Section 2.3 discusses some objections to the system.

2.1 Review of rain forest silviculture, 1900 – 1985

1900 – 1950. The oldest and most widely applied form of tropical rain forest management is a primitive polycyclic system, in which only part of the stand is harvested every 20 to 40 years, often called a "selection system" but more accurately termed a "diameter limit felling system". Using this system, the minimum diameter of trees to be felled is set high to safeguard against overcutting and, in theory at least, leaves forests in a sufficiently viable condition to be exploited again when appropriate silvicultural techniques have been developed.

The first attempts to bring logged tropical rain forest under scientific management date from the beginning of the twentieth century, when silvicultural treatments were devised to stimulate growth of *Palaquium gutta*, then an important latex-producing species in Malaya, the present Peninsular Malaysia (Wyatt-Smith, 1963). These efforts were considered successful and stimulated the development of natural regeneration techniques for Malayan rain forests. In 1926, the Malayan Regeneration Improvement Felling System (RIF) was formulated (Wyatt-Smith, 1963), consisting of a gradual but complete removal of the canopy either by a 7-year sequence of felling operations (Commercial Regeneration Fellings) or by girdling of inferior species, in a series of treatments, followed by final felling (Departmental Regeneration Improvement Fellings). In the 1930s, arsenical poison-girdling was introduced as the action of girdling without poison was considered too slow and erratic. This monocyclic shelterwood system achieved its goal, which was a substantial increase in the recruitment and growth of desirable species.

In the meantime, research into natural regeneration techniques in British colonies in Africa had failed. Methods of artificial regeneration developed in Francophone Africa were more successful, and involved enrichment planting or replacement of the forest by pure plantations (Donis, 1958; Letourneux, 1956).

During the Second World War, a number of foresters with experience in Malaya served in Nigeria, where they helped to formulate and implement the Tropical Shelterwood System (TSS), a technique similar to the Malayan RIF (see Taylor, 1962). TSS has also been applied in a slightly adapted form in Ghana and Trinidad and on an experimental scale in the Ivory Coast (Neil, 1981). A selection system for secondary forest was also developed in Puerto Rico (Wadsworth, 1947; 1952) and experiments were carried out in Queensland, Australia (Baur, 1962), and in Indonesia (van Goor and Kartasubrata, 1982).

1950 – 1965. Around 1950, the introduction of mechanized felling and extraction methods, together with increased demand for a greater range of species, had a considerable influence on rain forest silviculture by resulting in pressure for a single, more profitable harvest operation. Such pressure forced the Forestry Department in Malaya to abandon RIF shortly after the Second World War and to introduce the Malayan Uniform System (MUS). MUS was also a monocyclic system, but exploitable timber was removed in a single felling operation, followed by almost complete eradication of the remaining forest canopy in one poison-girdling treatment. In Malaysia, seedlings of commercial species, most of them Dipterocarpaceae, are generally present in large numbers per hectare. They tend to respond favourably to such a drastic intervention, in spite of infestation by climbers and pioneer species. Follow-up treatments were considered necessary five and ten years after logging, then once every 10 – 15 years, and a second harvest was expected after 60 to 80 years (see Wyatt-Smith, 1963). MUS was also applied in British North Borneo, the present Malaysian state of Sabah.

The MUS sequence of operations included "diagnostic samplings", prior both to felling and to each silvicultural treatment, and human intervention in the forest should have been guided by the results. Most publications on MUS (for example, Wyatt-Smith, 1963) put much emphasis on sampling techniques, although their practical value was questionable, for the following reasons. In practice, the sampling results gave a choice of allowing or postponing a scheduled operation (logging or a standard silvicultural treatment). In Malaysia, however, it proved extremely difficult to postpone logging on silvicultural grounds, and short field inspections were usually adequate to decide upon application of a standard treatment. Moreover, the organization, field-work and analysis involved were so time-consuming that although diagnostic sampling was practised in many MUS silvicultural schemes, it never became a standard routine.

The Philippines was a major timber exporting country in the 1950s and 1960s, but timber resources were rapidly depleted. In the 1950s, a polycyclic system based on Brasnett's "two cycle system" was developed (Reyes, 1968). Prescriptions included a high diameter limit for trees to be felled (80 cm), directional felling aimed at saving groups of valuable trees, and a silvicultural treatment five to ten years after logging, consisting of cutting lianas and ring-barking non-commercial trees. A second harvest was considered possible after 35 years. Although implementation of this system proved difficult, it is still being advocated and modified (see Weidelt and Banaag, 1982).

In Africa, developments followed different lines in various parts of the continent. TSS was frequently revised to reduce treatment costs and was applied with dwindling success in Nigeria and Ghana until the 1970s. In Uganda, a monocyclic system was devised which was intermediate between TSS and MUS in some respects. An important element of this system was that when trees were to be eliminated, harvesting was preferred to poison-girdling, provided that such an operation was economically feasible. Timber trees were felled in one operation. The first silvicultural treatment consisted of cutting climbers and of poison-girdling unwanted trees or felling them for charcoal production. One or two follow-up treatments, preferably commercial thinnings, were scheduled within ten years after logging, and diagnostic sampling was used to determine the intensity and nature of the various treatments. The aim was to retain a crop of about 50 trees per hectare, to be harvested after 60 – 80 years (Dawkins, 1958).

The emphasis in Francophone Africa remained on artificial regeneration, although efforts to develop natural regeneration systems were made in Zaire ("Uniformisation par la haut", see Donis, 1958) and the French colonies in West Africa (Letourneux, 1956; Catinot, 1965). In tropical America, the existing natural regeneration methods in Trinidad and Puerto Rico were improved further and were applied on a modest scale (Neil, 1981). Research into new natural regeneration techniques was carried out in Suriname (see Section 2.2) and a few other countries (Baur, 1962), but most work at that time concentrated on replanting with *Pinus spp.* and some broadleaved species.

1965 – 1975. Interest in natural regeneration techniques in the humid tropics declined in the 1960s for three reasons. Firstly, most tropical countries were facing serious financial problems, and willingness to wait more than half a century for financial return from investments in silviculture was therefore decreasing. Secondly, the demand for tropical timber rose, especially in South-East Asia and West Africa. Governments were under mounting pressure from timber concessionaires to increase annual yields beyond levels acceptable under monocyclic systems, and illegal felling increased sharply. Thirdly, land tenure became a problem in many tropical countries as clearing of rain forest for agricultural purposes increased rapidly (Myers, 1980). Naturally regenerated forest consists mainly of small trees which are easy to clear and it is therefore attractive both to squatters and to large agricultural enterprises.

In Peninsular Malaysia, most forests treated under MUS were converted into oil palm and rubber estates, an obvious setback for the Malaysian Forestry Department. Moreover, timber resources in the Malaysian lowlands dwindled and logging operations moved into the hill forest, which did not respond favourably to MUS. It was not until the late 1970s that a suitable alternative was formulated.

MUS was modified in the Malaysian state of Sabah to meet local conditions (Sabah Forest Department, 1972) to give the Modified Malayan Uniform System (MMUS), which tends towards a polycyclic system. Sound trees of commercial species were retained whenever possible to provide a modest yield after 40 years, that is halfway through the cutting cycle. In the early 1970s, Sabah became the world's largest exporter of tropical timber, and yields per hectare increased dramatically. Application of MMUS was discontinued in 1973 because logging damage had become so severe that poison-girdling was considered no longer useful.

In Indonesia, large-scale logging operations were initiated both in Kalimantan and Sumatra. Two management systems based on natural regeneration were formulated but neither was implemented (Sudiono and Daryadi, 1978). The first was similar to MUS and the second, the Indonesian Selection System, to the Philippine system. In Africa, research into and implementation of natural regeneration techniques came to a complete stop in the early 1970s, but research activities in tropical America and Australia were continued at a modest level.

1975 – 1985. Deforestation and forest degradation became even more serious after 1975. Fortunately, however, interest in conservation and management of tropical rain forest revived. Forest management research became concentrated mainly on the development of polycyclic systems, as monocyclic approaches had proven unrealistic under the prevailing conditions.

Two systems were introduced in Malaysia, namely the Sustained Yield Selective Felling System (SYSF) in Peninsular Malaysia (FAO, 1977b; 1978) and Liberation Thinning in Sarawak (Hutchinson, 1982; 1987; Jonkers, 1982). The SYSF, which is also referred to as the Selective Management System (Schmidt, 1987), is basically a yield regulation method, using inventory data to calculate sustained yields, minimum diameters for trees to be felled, and the length of the cutting cycle. The method of computing diameter limits, which are at least 56 cm for Dipterocarpaceae and 46 cm for other commercial species, is such that at the end of the cutting cycle, a yield similar to the initial one may be expected. The length of the cutting cycle is usually 30 years but may be 25 years in rich stands or more than 30 years in relatively poor forests. Silviculture plays only a minor role in the SYSF system, although tree growth may be promoted by poison-girdling the largest unmarketable trees.

Liberation Thinning is an entirely different approach, in which the emphasis is on silvicultural treatment. The diameter limit for trees to be harvested is fixed at 60 cm and the length of the cutting cycle is 30 years. Those non-commercial trees which either compete for light with commercial species or are expected to become competitors within 30 years are eliminated in one poison-girdling operation, together with all trees larger than 60 cm dbh. Small and medium-sized non-commercial trees, other than actual and potential competitors, are spared and follow-up treatments are not foreseen.

The reason for two systems within one country is economic. Peninsular Malaysia has a large timber industry which processes a broad range of species and assortments both for home consumption and export, so that emphasis in forest management is to avoid overcutting. Logging is considered a silvicultural tool, that is a means to reduce competition in the stand. Sarawak, on the other hand, has virtually no local market for timber products and its forests, although by no means poor, contain less commercial timber than virgin rain forests in many other regions of South-East Asia. Only first quality timber of internationally accepted species is usually felled and there is therefore less need to restrict yields per hectare. Instead, emphasis is on stimulating growth by means of poison-girdling treatment.

Another polycyclic approach was adopted in Queensland, Australia, where selective felling was considered "a means of combining the twin aims of sustaining a supply of timber and minimizing the environmental impact of logging operations" (Queensland Department of Forestry, 1983; p. VII). Management is by means of controlled harvesting operations and no silvicultural treatment is applied, so that increment rates remain rather low and a cutting cycle of 40 – 50 years is required (see Shepherd and Richter, 1985).

Additional large-scale experiments to test polycyclic systems were initiated in many other countries (see Schmidt, 1987), such as Brazil, French Guiana, Suriname (see Section 2.2), Indonesia and the Ivory Coast (see Maitre, 1986; Vooren, in press). The Philippine system also received renewed attention (Weidelt and Banaag, 1983).

Conclusion. In spite of these encouraging developments, this brief history indicates that 85 years of research into rain forest management have, in fact, accomplished little. Only a very small proportion of the remaining forest in the humid tropics is under scientific management (see Lanly, 1982; Schmidt, 1987). Furthermore, the outdated diameter limit system of selective felling described at the beginning of this section is still widely applied throughout the tropics. Even in Malaysia, a country with a long tradition of forest management, many permanent forests are still opened up using this primitive yield regulation system. In spite of growing awareness of the value of tropical rain forest, many still consider it merely an unproductive form of vegetation on land which should be developed for agriculture or some other use, even if conversion does not lead to sustained production. In order to change this attitude, it is necessary to prove beyond doubt that rain forest is a valuable economic asset, not only as a sustained source of timber and other forest products, but also as means of protecting the environment (see also Oldeman and Boerboom, 1982).

2.2 Silviculture in Suriname, 1900 – 1985

1900 – 1950. The history of silviculture in Suriname began in 1904, shortly after the formation of a forestry department. Between 1904 and 1925 experiments in natural and artificial regeneration were established over more than 1000 ha near the present Zanderij airport (Gonggrijp and Burger, 1948). These activities came to an abrupt end when the forestry department was abolished in 1925 and most of the information that had been collected was subsequently lost.

Shortly after World War II, the forestry department was reinstated and study was made of the remains of the Zanderij experiments (Gonggrijp and Burger, 1948; Gonggrijp, 1948). The findings showed that planted indigenous species were capable of reaching heights of approximately 25 m and diameters of about 30 cm within 30 years (see also de Graaf, 1986).

1950–1965. The forestry department (Dienst 's Lands Bosbeheer) made efforts to establish silvicultural systems for logged-over rain forest during this period. A wide range of natural and artificial regeneration techniques was studied. Schulz (1960) initiated the first natural regeneration experiment in 1957, using methods obviously inspired by work in Malaya, Uganda and West Africa (see Section 2.1). Treatments were aimed at converting rain forest into stands composed of relatively few medium and heavy hardwood species suitable for construction purposes (Schulz, 1967). A monocyclic approach with a rotation of 60 – 80 years was adopted (Boerboom, 1965).

In the first experiments, pre-felling treatments were carried out, consisting of cutting lianas and poison-girdling all "undesirable" trees over 5 or 10 cm dbh, that is trees of non-commercial species, and overmature and poorly formed trees of commercial species. This treatment was called refining (Schulz, 1960) or refinement (Boerboom, 1965). The arboricide used was 2,4,5-T butyl ester (2,4,5-trichloro-phenoxypropionic acid, 480 g acid equivalent per litre), applied in a 5% solution in diesel oil. In later experiments, similar treatments were carried out *after* logging.

In practice, all trees above the diameter limit were eliminated except for a few small and medium-sized commercial trees of superior quality. Very soon, however, "it appeared that growth of seedlings and small saplings of commercial species is too slow to allow successful competition with other, more quickly growing primary and secondary forest species" (Schulz, 1960). Proliferation of climbers also was a serious problem, and frequent tending was considered necessary. In order to reduce costs, desirables were liberated in two-metre-wide strips running in an east-west direction. Spacing of the strips depended on the stocking of small-sized commercial regeneration but intervals usually ranged from 10 to 20 m. Weeds within strips were cutlassed or poisoned biannually during the first two or three years, and annually thereafter (Boerboom, 1965).

The growth response of commercial species proved favourable for all size classes. Boerboom (1965) recorded diameter increments of approximately 1 cm/yr, with large trees growing slightly slower than small individuals. However, treatment costs were unacceptable. Inputs required during the first ten years were estimated at 30 man-days and 100 litres of 2,4,5-T solution per hectare (Vink, 1970). Experimental replanting looked more promising and Dienst 's Lands Bosbeheer initiated a programme for establishing plantations, mainly of *Pinus caribaea*.

1965 – 1978. After 1965, natural regeneration research was continued on a modest scale by the Centre for Agricultural Research in Suriname (CELOS), then an institute of Wageningen Agricultural University. Several small-scale experiments were established between 1965 and 1967, in which a large number of treatment schedules was applied, following the recommendations of Boerboom (1965) and Schulz (1967). Possibilities for reducing the tending frequency required by the previous system were investigated. Furthermore, efforts were made to reduce the intensity of refinement, thus diminishing proliferation of competing secondary vegetation and allowing investigation into polycylic management.

Increment data from these experiments were analysed by de Graaf and Geerts (1976) and de Graaf (1982; 1986) and the results indicated that a polycyclic system was preferable to a monocyclic system. De Graaf then formulated a treatment schedule consisting of three refinements, the first shortly after logging, the second eight years later, and the third 16 years after exploitation, with the second harvest foreseen after 20 years. The suggested basal area reductions (de Graaf, 1982) were from 28 to 12 m^2/ha at first refinement, from 20 to 10 m^2/ha at second refinement and from 18 to 15 m^2/ha at third refinement. In de Graaf's approach, diameter limits were based on average stocking and were intended to result in residual basal areas as indicated above, so an inventory had to be carried out before each treatment. In most cases, the diameter limit at first refinement would be about 20 cm and in subsequent refinements approximately 5 cm. De Graaf (1982) named this sequence of operations the Celos Silvicultural System (CSS).

De Graaf's list of operations (1986) included line cutting, sampling of commercial trees and marking, frilling and spraying of trees to be eliminated. He estimated input per hectare for the first refinement to be 40 litres of arboricide and five man-days labour, of which 3.5 man-days were spent on tree marking and poison-girdling (de Graaf, 1982). Expenditure for each subsequent treatment was estimated at 3.3 man-days and 10 – 15 litres of arboricide per hectare. Thus, total expenditure was appraised at 12 man-days and 60 litres of 2,4,5-T solution per hectare during the entire cutting cycle, which is substantially less than the inputs required for the system tried before 1965. This cut in expenditure did not result in a reduction in diameter increment, indicated by growth figures in the order of 1 cm/yr (de Graaf and Geerts, 1976; de Graaf, 1982; 1986; Jonkers and Schmidt, 1984).

In the meantime, growth rates in the older forest plantations decreased to an unattractively low level, probably because of a considerable loss of nutrients from the ecosystem (Boxman, in press). In addition, rising costs for labour, machines and fuel made clearing, planting and maintenance operations too expensive. These developments forced Dienst 's Lands Bosbeheer to terminate its artificial regeneration programme in the late 1970s.

1978 – 1985. De Graaf's encouraging results conduced renewed interest in natural regeneration techniques, so project LH/UvS01, a joint project of Wageningen Agricultural University and the Anton de Kom University of Suriname, was established to test the Celos Silvicultural System thoroughly. Ecological, hydrological, pedological and silvicultural aspects of CSS were studied and an improved logging technique was developed. Furthermore, investigations in secondary succession were carried out and efforts were made to explain the poor increment rate of *Pinus caribaea*. The results of these efforts are published in this study and other publications in the series *Ecology and management of tropical rain forests in Suriname* (Boxman, in press; de Graaf, 1986; Hendrison, in press; Poels, in press; Schmidt, in press; Tjon Lim Sang, in press).

The LH/UvS01 project was terminated prematurely in 1983 as result of a political controversy between the governments of The Netherlands and Suriname, but although all project activities were discontinued, research into CSS did not stop. Recently, Dienst 's Lands Bosbeheer initiated a 500 ha trial applying the Celos Silvicultural System, and it is to be hoped that this will lead to its routine application in the tropical rain forests of Suriname.

2.3 Aims of this study

One of the aims of this study was to test the Celos Silvicultural System. This polycyclic system must result in sufficient timber trees of harvestable size to ensure future harvests comparable or superior to the initial yield, both in quality and in volume. Growth, mortality, recruitment and size class distribution of commercial species determine future yields to a large extent. Information on these subjects, which is still incomplete due to the premature termination of project LH/UvS 01, is presented in Chapters 4, 5 and 6.

The principal aim, however, was to find ways of further improving the Celos Silvicultural System particularly by avoiding ecologically undesirable side-effects and reducing costs. No attempts were made to increase diameter growth beyond the levels achieved in previous experiments, as historical evidence indicated that it was the maximum achievable rate (see Section 2.2).

The following arguments against the Celos Silvicultural System, as it evolved from empirical research in the 1960s and 1970s (see de Graaf, 1986, and Section 2.2), need to be considered:

- logging damage may be too severe to allow sustained yield under polycyclic management;
- polycyclic logging is dysgenic;
- some of the tree species poison-girdled may become marketable in the future;
- the system may result in deterioration of the nutrient status of the ecosystem;
- the arboricide used (2,4,5-T) contaminates the environment and is dangerous for human beings;
- the system results in a substantial reduction in biotic diversity;
- CSS results in a warmer and drier microclimate, thus creating an environment which may be unfavourable for recruitment of shade-tolerant commercial species;
- some critics may find CSS costly or difficult to organize.

Each of these points is briefly discussed below.

Logging damage. Dawkins (1958) was the first to use logging damage as an argument against polycyclic management, stating that logging damage was too severe to allow polycyclic systems on a sustained yield basis. This opinion was based on the extent of felling gaps and skid trails observed in Uganda, rather than on an assessment of actual damage to the tree stand, but Dawkins' arguments seem very convincing and many experienced foresters share his views (Baur, 1962; Wadsworth, 1981). Logging damage in Suriname is discussed in Chapter 5 of this study, where reference is made to Hendrison (in press), who developed a less destructive harvesting technique.

Dysgenic effects. It is recognised that polycyclic logging progressively removes the best seed bearers, while poorly formed and slow growing individuals remain, thus creating a genetically inferior next generation. This effect is hard to quantify, however, as poor form and slow growth are not exclusively determined by undesirable genetic properties. Thinning may prove an effective means to eliminate dysgenic effects and is discussed in Chapter 6.

Market potential of non-commercial species. Silviculturists have always been aware that they are growing timber for posterity, and commercial species lists used in the Celos Silvicultural System (Appendix I) and other natural regeneration systems include not only currently commercial species but also species which produce good quality timber not yet accepted on the market. (For technical information on timbers from Suriname, see Japing and Japing, 1960; Longwood, 1965; Vink, 1977; Chudnoff, 1984).

The timber market tends to be rather conservative, so that several decades may elapse between the discovery of a species' commercial potential and its acceptance (see Freezaillah, 1984; Oldeman, 1982). Hence, it is possible to make a fairly reliable selection of species which may be marketable after one cutting cycle of 20 – 25 years, but making similar predictions for the second and later cutting cycles is more difficult. It may therefore be advisable to avoid poison-girdling trees which would otherwise reach commercial sizes during the second cutting cycle, that is to avoid the low diameter limits proposed by de Graaf (1986) for the second and third refinements. This subject is discussed in Chapter 6.

Reduction in biotic diversity. Applying low diameter limits during refinements will result in a substantial reduction in species diversity. Non-commercial species which do not fruit before they reach 5 cm dbh are likely to become extinct or very rare wherever de Graaf's treatment schedule is applied, meaning that many tree species will disappear. A similar reduction in faunal diversity is to be expected, since many animals depend on these trees for food or in some other way. Reductions in biotic diversity are acceptable in forest managed for timber production, provided that they do not interfere with the ecological functioning of commercial species. Knowledge of tropical rain forest ecology is still too scanty to draw a line between what is acceptable and what is not, so prescriptions for poison-girdling treatments should be conservative. This subject is discussed in Chapter 6.

Nutrient status of the ecosystem. Tropical rain forest is very efficient at taking-up nutrients directly from dead phytomass, before these nutrients reach the mineral soil (Jordan, 1985). This is an important quality of the ecosystem, as the soil is usually very poor and unfit to store substantial quantities of nutrients in exchangeable form (Boxman, in press). After refining, up to 50% of the phytomass dies and large amounts of nutrients become available for the remaining vegetation. The Celos Silvicultural System can only be sustained if not more than a negligible fraction of these nutrients is lost through leaching or fixation in the soil. Published data indicate that leaching of nutrients in refined stands is minimal (Jonkers and Schmidt, 1984; Boxman et al., 1985; Jonkers and Hendrison, 1986). Further studies have been made by Poels (in press) and Schmidt (in press).

However, more substantial losses may occur in parts of the forest poorly stocked with commercial species and a modified treatment differentiating between poor and rich parts of the stand is worth considering. In order to devise such a treatment, spatial species distribution has been studied (Chapters 4 and 6). Leaching and fixation can also be reduced by applying a poison-girdling technique which prolongs the dying process of poison-girdled trees (Chapter 6).

Dangers related to the use of 2,4,5-T. The arboricide 2,4,5-T is an artificial phytohormone. It is decomposed readily by soil micro-organisms and has been applied in forestry and agriculture for more than 30 years. If manufactured properly, 2,4,5-T is moderately toxic for human beings and is one of the safest herbicides, but dubious products may contain small quantities of an extremely toxic impurity called TCDD. Such products were sprayed over large areas during the Vietnam war, causing ailments among the local population and American soldiers. These effects and a tragic accident in a manufacturing plant in Italy led to a ban on the use of 2,4,5-T in many European countries and North America, although its use under permit is now allowed in the USA, Great Britain and West Germany. De Graaf (1986) gives a detailed account of risks involved in the use of 2,4,5-T.

In most silvicultural experiments in Suriname, poison-girdling was done using a 5% solution of 2,4,5-T in diesel oil. Although such a solution is not highly toxic, it should nevertheless be applied with great care at the lowest dose possible. Efforts to reduce 2,4,5-T application are discussed in Chapter 6. Alternative arboricides are available, but they were not tested in the present study.

Impact on microclimate. Schulz (1960), who made an extensive study of the effects of forest disturbance on microclimate and forest regeneration, found that opening up the canopy resulted in higher day-time temperatures and reduced day-time humidity on the forest floor (see also Section 1.1.2). The chances for commercial regeneration in such openings depend on the degree of disturbance. Schulz recorded good growth of existing regeneration of primary species in openings of 0.01 – 0.1 ha, where average daily illumination was 10 – 20 times that in closed forest. Secondary species are better adapted to hot and dry conditions than primary species (see for example Oldeman, 1983), so that in larger gaps, seedlings of primary species are soon suppressed by vigorously growing trees of secondary species, vines and herbs. This suggests that large canopy openings do not favour regeneration of most commercial species and should be avoided. This aspect of silvicultural treatment is discussed in Chapters 4 and 6. Regeneration in felling gaps is discussed in Chapter 5.

Costs and organization. Suriname cannot afford to spend more on silvicultural treatment than is strictly necessary. Its forestry department now employs only ten professional foresters, far too few to manage the country's forest estate (Wood, 1982). Under these conditions, silvicultural operations must be inexpensive, easy to organize and easily understood by technical staff and forest labourers.

De Graaf (1986, p. 47) published an extensive list of operations required for forest management, but most of them are not directly related to silvicultural treatment. Silvicultural operations and costs involved were briefly mentioned in Section 2.2 and possible ways to reduce costs further are discussed in Chapter 6. The treatments proposed by de Graaf are easy to implement, and the modifications should not make organization of silvicultural operations more complex.

The only complication in de Graaf's list is an inventory scheduled between logging and first refinement, to determine the diameter limit for silvicultural treatment (Section 2.2). Inventory data have to be collected and analysed quickly to avoid delays in treatment, but the shortage of qualified personnel will probably force the forestry department to neglect this activity, as has happened previously even in countries with a better-staffed forest service such as Malaysia (Section 2.1). Moreover, the need for such an inventory is questionable, because stand composition is very variable (Chapter 4), and averages for a whole logging compartment are poor indicators of growth conditions within the stand. Treatment prescriptions should preferably not depend on the outcome of an inventory which takes no account of spatial variation in the stand, even if average stocking figures are collected for other purposes. Efforts to find an alternative are discussed in Chapter 6.

Conclusion. There is an obvious need to reconsider which vegetation components should be eliminated in silvicultural operations. The basis for such selections should be a study of the forest and an examination of changes in the stand as result of logging and silvicultural treatment. Ecological aspects need to be considered, together with the costs of treatment and the response of the commercial stand. In addition, improvements in the technique of refinement need to be pursued and regulations with regard to the harvest need to be considered.

3 Methods and analyses

When project LH/UvS01 started in 1978, two research areas, Kabo and Tonka, were selected in pristine rain forest in the Zanderij Belt. Both areas are located in the uninhabited Kabo region, approximately 100 km south-west of Paramaribo (Fig. 1.1). Data presented in the following chapters were obtained from four experiments in the Tonka research area, and are supplemented with results from nutrient cycling and phytomass studies in the Kabo research area, which will be discussed in detail in a later publication in this series (Schmidt, in press), and also with diameter increment data from two older trials in the Mapane region (Fig. 1.1).

The Tonka experiments investigated distribution patterns in the vegetation, the effects of logging and refinement on the forest, modifications in silvicultural prescriptions, and organization, efficiency and costs of refinement. The most important was called "Experiment 78/5, Mortality, Natural Regeneration and Increment" when established in 1978, but is referred to as the MAIN experiment for convenience. A range of enumerations and surveys was carried out in this 148 ha silvicultural trial to test the Celos Silvicultural System, to detect shortcomings of CSS, and to improve it. Data collected were adequate for a detailed study of many aspects of the system, but the recording period was too short for an in-depth analysis of stand growth, one of the principal objectives of the experiment (Jonkers, 1984). Methods and analyses used are discussed in Section 3.1.

Two other Tonka experiments, an arboricide trial and a vegetation study, were more modest in size and objectives. The arboricide trial (Experiment 81/36) was approximately 7 ha in area and was established in 1981 to study ways to reduce 2,4,5-T application. Methods used are discussed in Section 3.2. The 1.32 ha Van Leeuwen transect (Experiment 82/15) was established in 1982 to investigate commercial stocking in relation to site factors and other relationships between soil and vegetation. Methods and analyses used are discussed in Section 3.3.

Costs and practical aspects of silvicultural treatment were studied not only in the MAIN experiment and the arboricide trial, but also in a large-scale hydrological experiment (Experiment 78/35) which was established in the Tonka research area in 1978 to study the impact of refinement on the leaching of nutrients. The arboricide trial and major parts of the two other experiments, totalling about 200 ha in area, were treated silviculturally during the long dry season of 1981. Records were kept of the number of man-days and the amount of arboricide used during this refinement operation, and an effort was made to organize the treatment as efficiently as possible.

Field organization and costs are discussed in Section 6.3, but aspects of forest hydrology are beyond the scope of this study, and will be discussed in another publication in this series which also provides a detailed description of Experiment 78/35 (Poels, in press).

The Mapane experiments (Experiments 67/9A and 67/9B) were much older. Experiment 67/9A, which was 25 ha in area, was established in 1967 to test as many as 16 different treatment schedules. The experiment consisted of 25 plots. Assessment plots were 80×80 m (0.64 ha) in area and were surrounded by a 10 m wide buffer zone. Growth, recruitment and mortality of commercial species in size classes exceeding 3 cm dbh were recorded between 1967 and 1982. Only the results from untreated plots and two treatment schedules comparable with CSS are discussed in this study (Section 6.5.2).

Experiment 67/9B, which was also 25 ha in area, was established in 1975. It consisted of one 16 ha assessment plot surrounded by a 50 m wide buffer zone. A refinement with a diameter limit of 20 cm was applied throughout the plot. Growth, recruitment and mortality of commercial species were recorded between 1976 and 1982. Commercial trees larger than 15 cm dbh were assessed over the whole 16 ha plot, smaller individuals were recorded in a 20% sample. Results are summarized in Section 6.5.2. The Mapane experiments have been described in detail by de Graaf (1986) and will not be discussed further in this chapter.

3.1 The MAIN experiment

The original objective of the MAIN experiment was to determine which combination of logging intensity and silvicultural treatment would result in optimal development of the commercial stand. Hence, only trees of commercial species were enumerated initially. The scheduled silvicultural treatments were two varieties of CSS and a control treatment, and the logging treatments were three levels of semi-controlled selective felling.

In 1981, about one year after felling had been completed, it was realised that the experiment would be of much greater value if the focus was not on trees of commercial species only. A study incorporating other forest components, such as non-commercial trees, palms, lianas, seedlings and saplings would be more likely to reveal possible improvements of CSS. In order to allow such a change in approach, both experimental lay-out and enumeration technique had to be altered to include new elements alongside the original ones.

3.1.1 Experimental design

The multi-purpose MAIN experiment was a complete factorial block experiment with two factors, logging and silvicultural treatment, at three levels (Fig. 3.1). The experiment originally consisted of three randomized blocks (replications), each of

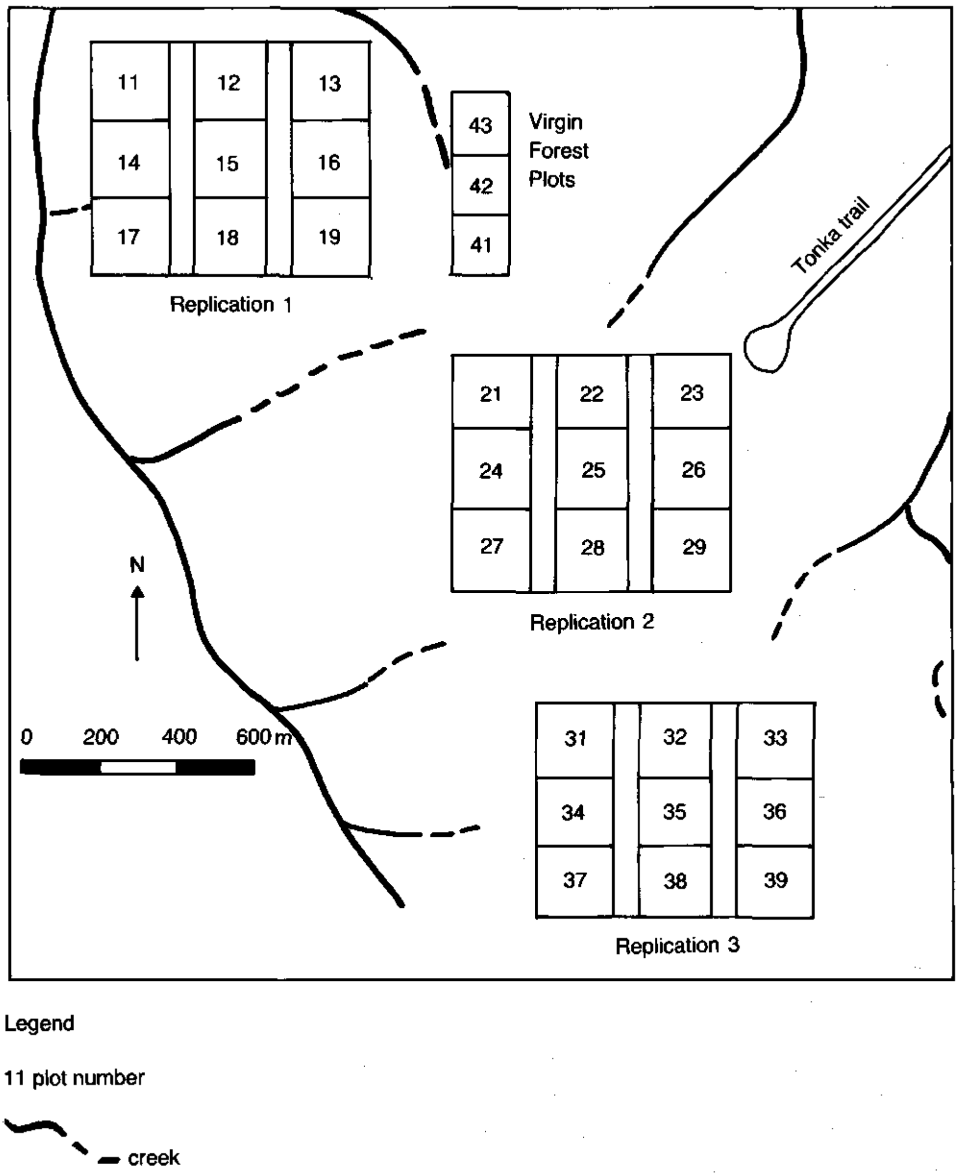


Fig. 3.1 Lay-out of the MAIN experiment

nine treatment plots, but three virgin forest plots were added in 1981. In this study, each treatment plot or compartment was identified by a two digit code number. The first digit was the replication number (1, 2 or 3), and the second digit was the plot number within the replication (1,2,. . . ,8,9). The code numbers used for virgin forest plots were 41, 42 and 43.

The lay-out of individual compartments (Fig. 3.2) became more complicated since the experiment began. Originally, each compartment consisted of a 150×150 m

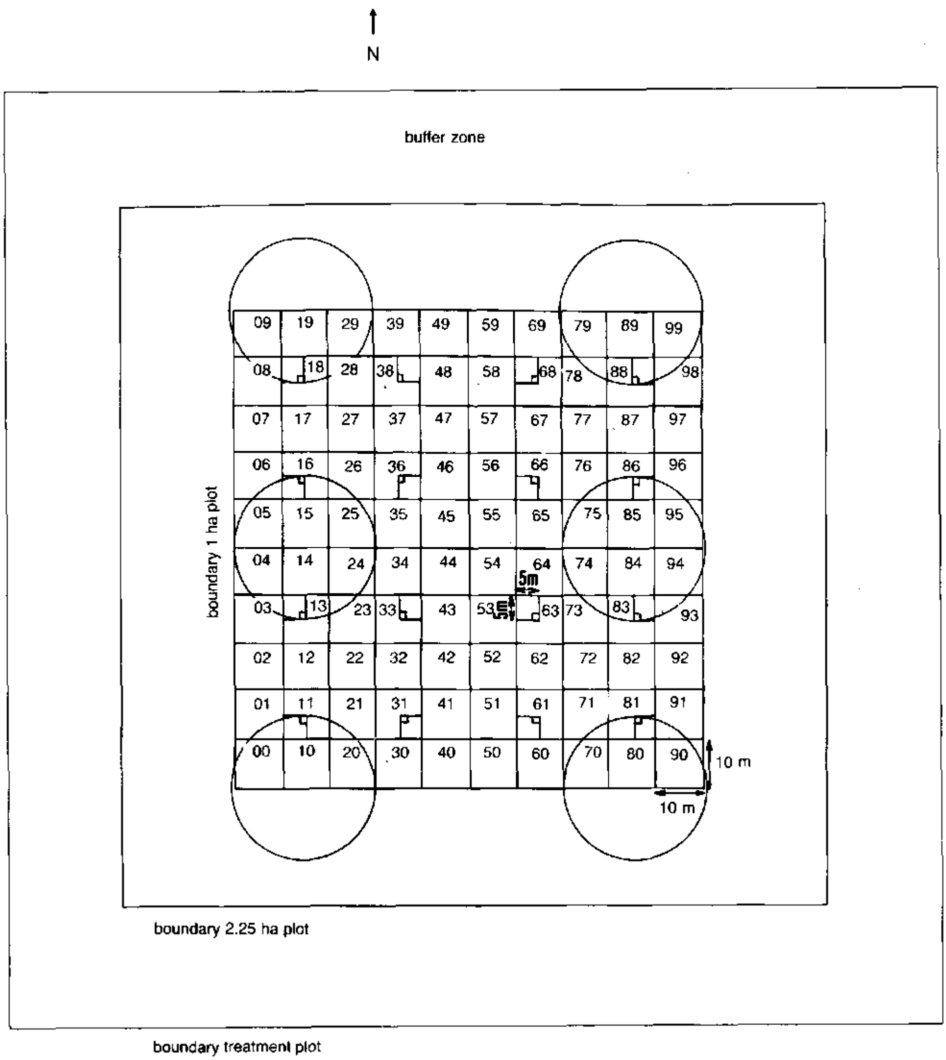


Fig. 3.2 MAIN experiment: lay-out of a treatment plot

assessment plot, surrounded by a 25 m wide buffer zone. Six circular sub-plots, each of 750 m^2 with a radius of 15.45 m, were located systematically within each assessment plot. Commercial species over 15 cm dbh were assessed in the 150×150 m plots, and commercial trees larger than 5 cm dbh were enumerated in the circular sub-plots.

This lay-out was considered inadequate for the multi-purpose approach adopted in 1981 and assessment plots measuring 100×100 m were therefore established centrally within each compartment. Each plot consisted of 100 quadrats measuring 10×10 m, as advocated by Synnott (1979), and was intended mainly to enumerate both commercial and non-commercial trees with diameters larger than 15 cm dbh.

Smaller individuals of all tree species were assessed in systematic sub-samples in all compartments of replications 1 and 2 only. Trees of less than 15 cm dbh but exceeding 2 m in height were tallied in 16 sapling sub-plots, each measuring 5×5 m (Fig. 3.2). Seedlings, that is regeneration of tree species less than 2 m in height, were tallied in a sub-sample consisting of 16 quadrats per compartment, each measuring 2×2 m and located within a sapling sub-plot.

3.1.2 Treatments

Logging. CSS can be classified as a Stratified Uniform System sensu Dawkins (1958). Dawkins did not favour such a polycyclic system for Uganda, arguing that logging damage was too severe and would not leave enough sound trees to guarantee a sustained yield in the future. On the other hand, logging is used as a silvicultural tool in recently developed polycyclic systems in Malaysia and Queensland (see Section 2.1). Determination of the actual effects of exploitation is therefore of paramount importance when testing a polycyclic system for tropical rain forest, and the outcomes of silvicultural treatment have to be assessed at various logging intensities.

The MAIN experiment was selectively logged in 1979 and 1980, shortly after the first enumeration. Three levels of exploitation were applied, namely removing basal areas of 1, 2 and 4 m^2/ha (Table 3.1), which amounted to yields of 15, 23 and 46 m^3/ha when expressed in volume terms. These yield figures are reflected in the treatment codes used in this study (E 15, E 23 and E 46).

Logging operations in Suriname are usually poorly organized (see Jonkers and Schmidt, 1984; Jonkers and Hendrison, 1986; Hendrison, in press). No advance inventory is made and the trees to be harvested are selected by the tree feller, whose only instruction is to fell a daily quota of stems meeting certain specifications regarding species, size and defects. Skidding is done without the aid of a map. Such an operation is not suitable for experimental purposes, so a more sophisticated, semi-controlled harvest technique was employed instead. Trees to be felled were selected in such a way that a fairly even distribution over a compartment was achieved. Felling was done by the project's tree feller using a chain saw, without the application of directional felling or other techniques likely to result in less damage than the traditional haphazard method. Extraction was carried out by a contractor using wheeled skidders which were allowed to enter each compartment at six points, three on the western side and three on the eastern side. A map indicating the locations of felled trees was used to find the shortest routes to the logs, and the operators had to remove all logs including defective logs, but apart from these restrictions, the contractor was free to chose his own extraction technique.

Silviculture. Three levels of silvicultural treatment were applied, namely a control treatment (code S 0), a relatively light refinement (diameter limit 30 cm, code SR 18) and a relatively heavy refinement (diameter limit 20 cm, code SR 14). Each treatment

TABLE 3.1. MAIN experiment: treatment schedule

Silvicultural treatment*	Replication	Compartment numbers per exploitation level**		
		E 15	E 23	E 46
S 0	1	19	14	12
	2	28	26	22
	3	34	38	32
SR 18	1	13	15	17
	2	23	27	25
	3	35	36	31
SR 14	1	11	18	16
	2	29	21	24
	3	37	33	39

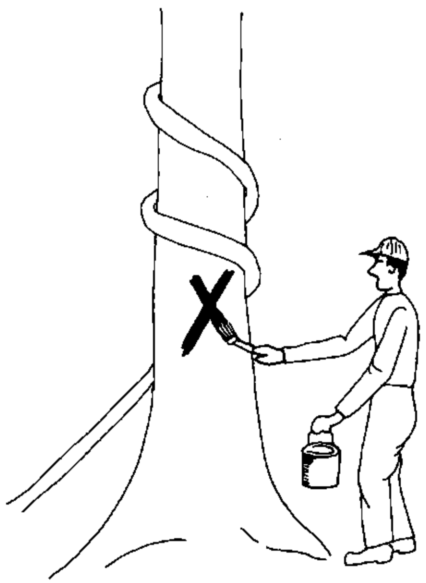
* S 0: control treatment
SR 18: refinement with 30 cm dbh limit
SR 14: refinement with 20 cm dbh limit
** E 15: basal area felled approximately 1 m^2/ha
E 23: basal area felled approximately 2 m^2/ha
E 46: basal area felled approximately 4 m^2/ha

level was applied in three plots per replication (see Table 3.1) and prescriptions included climber cutting and poison-girdling of non-desirable trees of diameters above the limits specified. Non-desirable trees in this context include all trees of non-commercial species and all trees of commercial species with very serious defects (no crown, hollow or split trunk, or extensive stem decay). Operations started in September 1981 and were completed in June 1982.

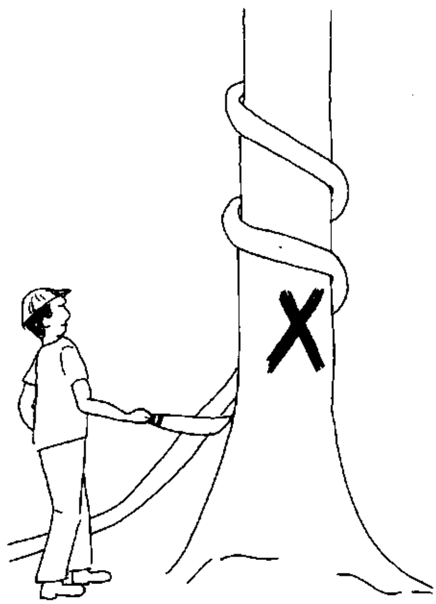
Prescriptions for refinement must be straightforward, as they have to be understood by unskilled labourers. In the MAIN experiment, the first refinement was carried out in four steps (Fig. 3.3). Firstly, trees above the diameter limit were identified by a tree spotter and those to be poison-girdled were marked with blue paint. The tree spotter was accompanied by a labourer who cut all lianas of more than 2 cm in diameter with a machete (step 2).

These two men were followed by the poison-girdling gang, who frill-girdled marked trees at a convenient height with a light, short-handled axe (step 3). Frill-girdling is done by making overlapping cuts over the whole circumference of the tree, forming a kind of channel. The cuts should extend just into the sapwood making an angle with the vertical of about 45°. However, sections of fluted or buttressed stems which could not be reached with the axe were not cut.

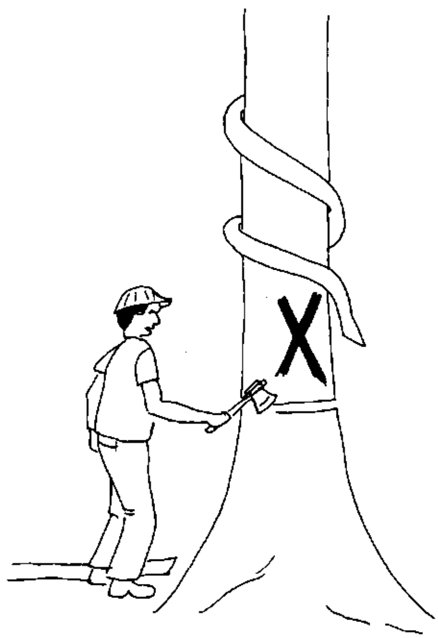
After completion of the frill-girdle, a 5% solution of 2,4,5 Esteron O.S. (2,4,5-T) in diesel oil was administered (step 4) with a low-pressure knapsack sprayer. This was modified by removing a small rotating component of the sprayer nozzle, so that the arboricide was applied as a jet rather than a spray. The frill-girdle was filled carefully



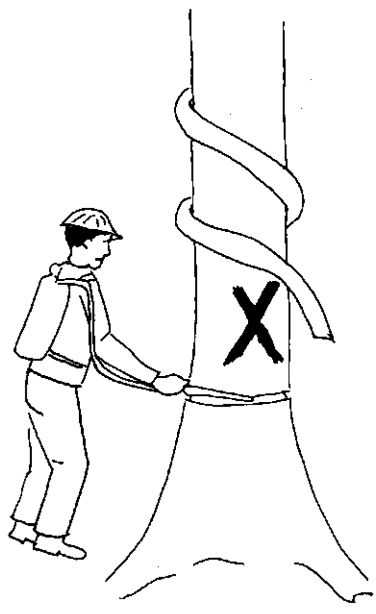
Step 1: The trees to be poison-girdled are marked



Step 2: Lianas are cut



Step 3: The frill-girdle is made



Step 4: The arboricide is administered

Fig. 3.3 Refinement technique (Source: Jonkers and Schmidt, 1984) and 10 cm of bark immediately above it was then coated with a film of arboricide. If the stem had been incompletely frill-girdled, uncut sections were treated to a height of at least 40 cm above the frill-girdle. Care was taken that the frill-girdle did not overflow, and that no arboricide was spilled on the forest floor. These prescriptions will be discussed further in Chapter 6.

3.1.3 Enumerations, surveys and observations

Information collected in the MAIN experiment included various types of enumerations, a soil survey, phenological observations, a contour map and aerial photographs. The enumerations were of four types:

- tree enumerations of commercial species;
- tree enumerations of all species;
- enumerations of seedlings and saplings;
- enumerations of other forest components, such as palms and lianas.

All surveys and enumerations were described in detail in the experiment plan (Jonkers, 1984). A brief description, including all aspects relevant to this study, is given below.

Tree enumerations of commercial species. The trees of commercial species have been enumerated four times: in 1978 – 1979 (prior to logging); in 1980 (shortly after logging); in 1981 – 1982 (shortly before silvicultural treatment); and in 1982 – 1983 (about one year after silvicultural treatment). Virgin forest plots were only assessed twice, in 1981 and 1983. Enumerations included all commercial species above specified diameter limits (15 cm in 2.25 ha plots and 5 cm in circular sub-plots). The ten different measurements and classifications used to describe individual trees are discussed briefly below and commercial species are listed in Appendix I.

The two most important pieces of information for each tree were its species and its trunk diameter at reference height (dbh). Species were identified by two of the most experienced tree spotters in Suriname, Jan and Rudolf Elburg. Most vernacular names used are monospecific, but some represent two or more botanically related species. Diameters were measured at fixed heights, usually at the standard height of 1.3 m (breast height), or one metre above the buttresses.

Stem class, silviculture code, crown and stem injury, crown form and crown illumination were also recorded to describe the condition of individual trees. Stem class and silviculture code were assessed for both living and dead trees. The stem class of a living tree indicates whether its stem has potential for future use. It is termed "excellent", "adequate" or "poor", depending on the stem form and possible stem defects, but regardless of the species of the tree and the condition of its crown. Dead stems were classified as felled, fallen (uprooted or snapped off below reference height), broken (no crown left) or complete (standing, with a crown). Felled and fallen trees were considered dead even if they were still physiologically active. The silviculture code determines whether a tree has been poison-girdled and if so, how much the tree has been affected. This classification is similar to that applied in the arboricide trial (see Section 3.2).

In this study, injury is defined as damage observed on a living tree and caused by a physical force but frill-girdles made on poison-girdled trees were not considered as injury. As many as six stem damage and four crown injury classes were distinguished in the field (see Jonkers, 1984), but in the analyses a comprehensive classification of four categories was used:

- very severe injury: the whole crown has broken off, the trunk has split, or the tree has been partially unprooted;
- severe injury: extensive injury on stem or crown, or visible injury on both stem and crown (extensive stem injury means that the bark has been ripped off over a length of at least two metres or over at least 20 cm of the stem circumference or, if the tree is small, over at least one-third of the stem circumference; extensive crown injury means that at least half of the crown has broken off);
- minor injury: any visible not qualifying as severe or very severe injury;
- no injury.

Crown form and crown illumination were classified according to Synnott's Manual of Permanent Plot Procedures (1979). Five crown form and five crown illumination classes were distinguished, ranging from excellent to very poor. These classifications proved inconsistent, however, and were rarely used in this study.

Trunk height and diameter at crown point were recorded on a limited number of trees for volume estimation purposes. Volumes of felled logs were measured while logging was in progress, and bole volumes of all commercial trees within the 100×100 m plots were assessed during the 1982 – 1983 enumeration.

Tree enumerations of all species. These enumerations were carried out shortly before and about one year after refinement in replications 1, 2 and 3, both times in conjunction with commercial tree enumerations, and once during 1983 in the virgin forest plots. All trees exceeding 15 cm dbh and all stumps of felled trees were assessed in 100 quadrats of 10×10 m per compartment, using the same measurements and observations as in the commercial tree enumerations, also forest class and measurements to determine the exact location of stems and cut stumps.

Forest class was introduced to quantify quickly any areas damaged or disturbed as result of logging, refinement or natural causes. During the enumerations, a forest class was assigned to each 10×10 m quadrat. If the undergrowth had been destroyed over at least half the area of a quadrat, this quadrat was classified as gap, or, if the area under skid trails exceeded the area under fallen stems and crowns, as skid trail. Quadrats which did not meet this criterion were classified as residual forest. This method was adapted from Hutchinson (1982) and has been applied previously in Sarawak (Jonkers, 1982).

Additional measurements were carried out in compartments 32, 34 and 38 during the most recent enumeration to determine trunk height, total tree height and crown radii in the four main compass directions. These extra parameters were used in a simulation study into light conditions after various intensities of refinement (Section 6.1).

Seedling and sapling enumerations. Seedlings and saplings were enumerated shortly after silvicultural treatment in May and June 1982, before refinement had become effective. Individuals of all tree species were tallied per species and per size class in replications 1 and 2. Size classes used were 0.2 – 2 m height, more than 2 m height but less than 5 cm dbh, 5 – 10 cm dbh, 10 – 15 cm dbh and larger than 15 cm dbh. The smallest size class was assessed in quadrats measuring 2×2 m, while the other size classes were tallied in sub-plots of 5×5 m (see also Section 3.1.1). The forest class was also determined for each 5×5 m quadrat, using the principles described above.

Other enumerations. Shortly before refinement, all palms exceeding 1.5 m in total height were tallied by species in 100 quadrats measuring 10×10 m per compartment. A tally of lianas was made after refinement in 1982. Lianas greater than 5 cm in diameter were counted by 5 cm diameter class in a sub-sample of 20 quadrats measuring 10×10 m per compartment. Neither enumeration was extended to the virgin forest plots.

Phenological observations. Flushing, flowering and fruiting of all trees larger than 15 cm dbh were recorded in two blocks measuring 50×50 m in replication 2 (compartments 21 and 22). Compartment 21 had received the SR 14 poison-girdling treatment nine months before the first observations in August 1982, but compartment 22 had not been treated silviculturally. Observations were discontinued after September 1983.

The principal aim of this exercise was to study impacts of refinement on shoot elongation and seed production. Monthly recordings were made by carefully observing tree crowns with binoculars. If flushing was restricted to part of a crown, usually one or two reiterations, a single (+) was recorded. New leaves over the whole crown circumference were indicated as (+ +). Some species tend to shed all leaves simultaneously, replacing them almost immediately, and this phenomenon was encoded as (+ + +). Flowering and fruiting were recorded in a similar fashion.

Maps, surveys and aerial photographs. Two sets of aerial photographs of Tonka research area were available. The first set (scale 1 : 30000) was made for photogrammetic purposes in 1971, long before the MAIN experiment was created. The second set (scale 1 : 10000) was taken for the LH/UvS01 project in September 1982.

Field-work for a contour map and a soil survey were carried out in 1983, shortly before termination of the LH/UvS01 project. Altitudes above a reference point of approximately 12.5 m above sea level, the lowest point in the Tonka research area, were measured at each corner of the 150×150 m assessment plots. The same locations were used for soil augerings, but the soil survey could not be completed before termination of the project. No augerings were made in the central part of replication 2 and no samples were taken for chemical and physical analyses. However, additional information is available from a soil pit in the centre of replication 2, described in full by Poels and de Fretes in 1978. The physiography and soils of the Tonka research area are discussed in Section 4.1 and Appendix II.

3.1.4 Analysis of vegetation data

Knowledge of spatial arrangements and size class distributions of rain forest species is essential for understanding the impacts of logging and silvicultural treatment (see Section 2.3). Efforts were therefore made to describe the forest in the MAIN experiment in quantitative terms. Quantitative analysis of rain forest data has received considerable attention from plant ecologists in recent years (see Gauch, 1983; Golley, 1983; Greig-Smith, 1983; Leigh et al., 1982; UNESCO, 1978; Rollet, 1974), resulting in a bewildering multitude of stochastic techniques. Methods used in this study were selected because they best suited its objectives (see Section 2.3) and the data from the MAIN experiment. The analyses were purposely simple and understandable and only used advanced stochastic techniques where necessary.

Diameter class distributions. An important prerequisite for polycyclic management is that sufficient small and medium-sized trees of commercial species are available to secure adequate yields in the second and third felling cycles. Hence, the diameter class distribution of the commercial stand was studied, using separate analyses for each replication to illustrate differences within the experimental area. Furthermore, size class distributions were computed for individual commercial species. This information was used to illustrate long-term fluctuations in species composition and to propose diameter limits for trees to be felled. The results are discussed in Section 4.3.2.

Variation in species composition. An ordination technique was used to analyse differences in species composition between plots. The usual objective of ordinating sets of vegetation data is to generate hypotheses about relationships between species composition and environmental or other factors which determine it (Greig-Smith, 1983). In this study, however, ordination was used mainly to investigate vegetational variation in itself.

Many techniques have been developed in the last decades (see Gauch, 1983; Greig-Smith, 1983). In this study a multivariate approach advocated by Corsten (1976) for contingency tables was used and although it was not specially devised for vegetation studies, it proved satisfactory. For a good understanding of the results, a concise description of the computation procedure is given below to explain the basic principles of multivariate analysis. More detailed accounts of multivariate techniques are available in the publications cited.

Assume that there is a set of plots numbered 1,2,...,*m* in which *n* species called (a), (b), (c), etc. are found. It is then possible to create *n* orthogonal (perpendicular) "species axes", with the co-ordinate of plot *i* on the first axis being the number of trees of species (a) in plot *i*, the co-ordinate of plot *i* on the second axis being the number of individuals of species (b) in plot *i*, etc. The result is that the plots are represented by *m* "plot points" in an *n*-dimensional space.

It is then possible to perform a multivariate analysis on raw data, but more meaningful information is usually generated if the data are transformed by moving the origin of the "species axes" to the centroid of the set of "plot points" (centring), and/or applying some form of standardization.

The next step is the multivariate analysis itself. The (transformed) "species axes" are replaced by another set of *n* orthogonal axes, using a least-square method. Both sets share the same origin. In this connection, the term orthogonal regression can also be used, as the new axes are somewhat analogous to regression lines. The projections of the "plot points" on these ordination axes are the new co-ordinates of the *m* plots. For these calculations, recourse has to be made to a matrix approach.

The ordination in itself does not produce any reduction in dimensionality. Its value is that in changing the species axes into a new orthogonal set it concentrates the variability in the successive axes derived, so that relevant information is likely to be accounted for by the first new axes and the later ones may be ignored. In non-centred ordinations, however, the first axis is uninformative, indicating the degree of heterogeneity of the vegetation only.

The ordination described above is an ordination of plots, but the same data set can be used to perform an ordination of species, following the same principles. Interchanging the words "species" and "plot" each time these words appear in the explanation will give a description of a species ordination.

The technique applied in this study is non-centred and standardized. Standardization is by species total and by plot total, that is the frequency of species (j) in plot *i* is divided by the square root of the number of trees of species (j) in the whole data set (species total), and by the square root of total number of trees in plot *i* (plot total). The data thus derived are arranged in a matrix and subjected to a multivariate technique called Singular Value Decomposition, which results in an ordination of plots and an ordination of species (for a theoretical description, see Lawson and Hanson, 1974). The new co-ordinates of plot *i* are then adjusted by multiplication with the square root of the plot total.

In Corsten's theory, species co-ordinates should also be adjusted by multiplying by the square root of the species total and the "eigenvalues" to obtain a balanced species ordination. A species ordination is meaningful if individual plots represent distinctly different ecological conditions. Such differences between plots in the MAIN experiment were small, and it was preferred to present unadjusted data, which provide a better illustration of the impacts of individual species on the ordination of plots than adjusted values.

Two ordinations were carried out, the first based on pre-felling frequencies of commercial species, and the second based on a post-harvest enumeration of all species. The results are discussed in Section 4.3.3.

Spatial arrangement of trees. Small-scale patterns in the spatial distribution of certain tree categories (for example, a single species, all non-commercial species combined, all commercial species within a specified diameter range) were studied in the 100×100 m assessment plots. Of the many pattern analysis techniques documented (see Bartlett, 1975; Greig-Smith, 1983; Hubbell and Foster, 1983; Rollet, 1974), Greig-Smith's χ^2 nested type test was selected as the most suitable (Greig-Smith, 1952; 1983).

The test procedure is such that patterns of different scales can be tested simultaneously. The central 96×96 m area of each plot was divided into 64 blocks of 12×12 m. These basic units were then arranged in 16 blocks of 24×24 m, and finally into 4 blocks of 48×48 m. The basic block size of 12×12 m is too small for analyses based on relatively small numbers of trees, such as in tests for individual species, and in those cases, the 24×24 m blocks were used as the basic units. Numbers of trees were computed per block and tested with one of the schedules presented in

TABLE 3.2. MAIN experiment: pattern analysis, using Greig-Smith's χ^2 nested type test

PART I: Schedule of computations

Item	df	Sum of squares (SS)*	Mean square (MS)
for 8×8 blocks			
within 4s	48	$(\Sigma x_1^2 - \Sigma x_4^2/4)64/\Sigma x$	SS/48
between 4s within 16s	12	$(\Sigma x_4^2 - \Sigma x_{16}^2/4)16/\Sigma x$	SS/12
between 16s	3	$(\Sigma x_{16}^2 - \Sigma x_{64}^2/4)4/\Sigma x$	SS/3
total	63	$(\Sigma x_1^2 - \Sigma x_{64}^2/64)64/\Sigma x$	SS/63
for 4×4 blocks			
within 4s	12	$(\Sigma x_4^2 - \Sigma x_{16}^2/4)16/\Sigma x$	SS/12
between 4s	3	$(\Sigma x_{16}^2 - \Sigma x_{64}^2/4)4/\Sigma x$	SS/3
total	15	$(\Sigma x_4^2 - \Sigma x_{64}^2/16)16/\Sigma x$	SS/15

PART II: 95% confidence limits for random distribution (MS values)

Degrees of freedom (df)	3	12	15	48	63
Lower limit	0.07	0.35	0.42	0.64	0.68
Upper limit	3.12	1.94	1.80	1.44	1.38

* Σx_1^2 = sum of squares of numbers in 12×12 m blocks
Σx_4^2 = sum of squares of numbers in 24×24 m blocks
Σx_{16}^2 = sum of squares of numbers in 48×48 m blocks
Σx_{64}^2 = square of number of trees in 96×96 m block
Σx = total number of trees in the test

Table 3.2. Tests based on less than 16 trees were rejected.

This analysis of variance is a two-tailed test with a Poissonian random distribution. When the arrangement of trees is perfectly random, the mean square (MS) will be unity for all block sizes, but if MS is significantly greater than unity for one or more block sizes, the arrangement can be considered patchy. A regular distribution is indicated if MS values for all block sizes are significantly less than unity. The results are discussed in Section 4.3.4.

Spatial distribution of seedlings and saplings. The distances between seedlings and the nearest potential seed source were analysed, and species composition of recruitment in gaps, on skid trails and under residual forest was studied. Recruitment is mainly of importance where logging and refinement have created relatively large openings in the canopy and the aim was to indicate the chances for natural regeneration in such areas. Both analyses were carried out for commercial species only. Some information on spatial distribution of non-commercial recruitment is included in Section 4.3.5.

Distances between seedlings and the nearest potential mother tree provide information on seed dispersal strategies of individual species. The term "ineffective dispersal strategy" is used for species whose seedlings tend to be clumped under the mother tree, and are therefore ineffective in colonizing man-made openings in the forest, whereas an "effective dispersal strategy" is marked by a wider distribution of seedlings. A simple approach was adopted, in which seedlings were assumed to be located in the centres of the 2×2 m quadrats, and seedling to seed source distances were classified as small (seedling less than 5 m from the tree trunk), medium (5 – 15 m) or large (more than 15 m). Note that crown radii of canopy trees are usually less than 5 m. Frequencies per distance class were computed for individual species and a comparison was made, the results of which are discussed in Section 4.3.5.

The analysis of seedling and sapling stocking per forest class (gaps, skid trails and residual forest) was equally simple. Each seedling sub-plot was assumed to be of the same forest class as the sapling sub-plot in which it was located. Frequencies per forest class were estimated for individual species and converted into numbers per unit area. A comparison between commercial species was then made and the results are discussed in Section 5.5.

Spatial distribution of palms and lianas. The frequencies of palms and lianas in individual compartments were tabulated and compared. Furthermore, small-scale distribution patterns of individual palm species were studied in the central 80×80 m area of each compartment. The procedure was identical to that already described for trees (Table 3.2, test for 8×8 blocks), except that block sizes were 10×10 m, 20×20 m and 40×40 m. The results are discussed in Section 4.3.6.

3.1.5 Analysis of forestry data

Efforts were made to find accurate estimates for trunk volumes of commercial species, to estimate the impacts of logging and refinement on the residual stand, and to formulate improvements in refinement technique.

Estimation of trunk volume. The trunk volume of each commercial tree in the 100×100 m assessment plots was estimated using Smalian's equation (Equation 3.1).

$$V = [(d_{1.3})^2 + (d_t)^2]\pi h_s/8 \qquad (3.1)$$

where:
V = trunk volume (m^3).
$d_{1.3}$ = diameter at reference height (m).
d_t = diameter at crown point (m).
h_s = trunk length (m).

Linear regression analysis (LRA) was used to identify relationships between basal area and stand volume, and between diameter at reference height and stem volume. The results are discussed in Appendix VI.

Effects of logging. Damage to the residual stand caused by logging was studied and the impact on increment and recruitment of commercial species. For this purpose, each replication was divided into three smaller replications, each consisting of three

TABLE 3.3. MAIN experiment: replications used in analysis of logging effects (ANOVA tests)

Replication	Compartment numbers per exploitation level*		
	E 15	E 23	E 46
1A	11	14	12
1B	13	15	16
1C	19	18	17
2A	23	21	22
2B	28	27	24
2C	29	26	25
3A	34	38	31
3B	35	33	32
3C	37	36	39

* E 15: basal area felled approximately 1 m^2/ha
E 23: basal area felled approximately 2 m^2/ha
E 46: basal area felled approximately 4 m^2/ha

treatment plots which had received different logging treatments (Table 3.3). Analyses were straightforward, using stochastic techniques described in most statistical textbooks (for example, Steel and Torrie, 1981) and the results are discussed in Chapter 5.

To analyse logging damage, trees of commercial species were classified into six damage categories using stem classes and injury classes defined in Section 3.1.3, namely "felled", "destroyed" (stem classes "fallen" and "broken"), "very severe injury", "severe injury", "minor injury" and "no damage". Analysis of variance (ANOVA) and linear regression analysis (LRA) were used to study relationships between logging intensity and basal areas in these categories. The same stochastic techniques were used to investigate areas under gaps, skid trails and standing forest (for definitions, see Section 3.1.3). As non-commercial trees had not been assessed in the pre-felling enumeration, it was not possible to include these species in the statistical analysis. Damage to non-commercial components of the stand was therefore estimated by assuming similar rates of destruction per diameter class as for commercial species.

Efforts were made to estimate reductions in phytomass (dry weight of the vegetation) caused by exploitation, using Equations 3.2, 3.3 and 3.4.

$$W_s = \{10^{(-3.4853 + 2.5132 \log d)}\}1.1184 \quad (3.2)$$
$$W_b = \{10^{(-4.8516 + 2.8368 \log d)}\}1.4428 \quad (3.3)$$
$$W_l = \{10^{(-3.7644 + 1.9961 \log d)}\}1.2602 \quad (3.4)$$

where:
W_s = dry weight of the tree trunk (kg).
W_b = dry weight of the branches (kg).
W_l = dry weight of the leaves (kg).
d = diameter at reference height (mm).

These empirical equations, which were adapted from Schmidt (in press), estimate the dry weights of individual trees. They are based on ecological studies in "Fytomassabos", a stand comparable to the MAIN experiment in terms of stocking and species composition, which is located in the Kabo research area (Fig. 1.1).

Analysis of the impact of exploitation on increment and recruitment was equally uncomplicated, using ANOVA to test the effect on diameter increment of commercial species. Growth of small trees (5 – 15 cm dbh) and of larger individuals were analysed separately. Seedling and sapling populations were studied in relation to forest class (see Section 3.1.4).

Refinement and stand development. The aims of refining are to stimulate growth and recruitment of commercial species, to keep their mortality low and to increase timber production, by eliminating much of the other flora of the forest (see Section 3.1.2). Efforts were made to quantify the treatments applied by estimating the number, basal area and phytomass of poison-girdled trees and the number of lianas cut, and to assess the impact of refinement on stand development. Equations 3.2, 3.3 and 3.4 were used in phytomass calculations.

The period between refinement and the last enumeration was too short to estimate growth and mortality rates over the whole cutting cycle, but it was nonetheless considered useful to test the impact of refinement on diameter growth with ANOVA. Separate tests were carried out for small (5 – 15 cm dbh) and larger commercial trees. Data on growth and mortality from older experiments in the Mapane region (Fig. 1.1) are used to illustrate developments over longer periods.

The effect of refinement on recruitment received relatively little attention. Frequencies and abundances of flushing, flowering and fruiting were studied by comparing phenological observations in refined and untreated stands (see also Section 3.1.3), but other data on recruitment in refined forest are not available. The results are discussed in Sections 6.3, 6.4 and 6.5.

Improvements in refinement technique. Efforts were made to improve prescriptions for refinement (see also Section 3.2), either by improving the implementation of refinement without affecting the nature of the treatment, or by reducing the number of trees poison-girdled without reducing the growth response of the remaining trees. No efforts were made to stimulate diameter increment of commercial species beyond the levels obtained in the Mapane experiments, because this had been investigated by de Graaf (1986).

A comparison between actual and prescribed treatments was made to identify shortcomings in field instructions. Trees poison-girdled mistakenly, thick lianas not cut and non-desirable trees not eliminated were counted by size class. The results are discussed in Section 6.3.2.

Reducing the number of trees poison-girdled may lead to reductions in costs as well as being ecologically desirable (see Section 2.3). This may be achieved by applying higher diameter limits for trees to be eliminated, by poison-girdling only those non-desirable trees obviously competing for light with commercial individuals of specified sizes and qualities, and by restricting refinement to areas within a specified distance from the nearest tree to be liberated. One or more of these modifications may be combined.

A simulation study was carried out to estimate the impact of such modifications on light conditions and availability of nutrients in the residual stand. The following 14 treatments were simulated in plots 32, 34 and 38, each measuring 100×100 m:

- a refinement identical to treatment SR 14, consisting of poison-girdling all non-desirable trees exceeding 20 cm in diameter (see Section 3.1.2);
- four treatments analogous to treatment SR 14, but in which poison-girdling was restricted to areas within a specified distance (7,8,9 or 10 m) from commercial stems of at least 20 cm dbh;
- a fifth modification of treatment SR 14, in which poison-girdling was restricted to non-desirable trees overtopping or shading at least one commercial tree of 20 cm dbh or more;

- six treatments analogous to those listed above, but using diameter limits of 30 cm dbh for trees to be eliminated and commercial species to be liberated;
- two treatments included for comparison only, namely a control treatment and a treatment consisting of poison-girdling all non-desirable trees of 15 cm dbh or more.

Phytomass killed in each treatment was estimated using Equations 3.2, 3.3 and 3.4. Simulating light conditions was more difficult as there is insufficient knowledge about extinction coefficients of tree crowns and various other factors determining quantities of light available for photosynthesis. Literature on light in tropical rain forest (for example, Brinkmann, 1971; Oldeman, 1974; Schulz, 1960; Richards, 1952; Heuveldop 1977; 1979) does not provide information relevant for this purpose. Development of a sophisticated model would require substantial research efforts, so a simple approach was therefore adopted, based on the work of van Leersum (1984). Separate simulations were carried out for each treatment in each plot.

The method simulates interception of sunlight as it passes through a geometrical model of a stand. As the tallest tree in the study areas was 48 m high, every one-hectare plot was represented by $100 \times 100 \times 48 = 480000$ units, each of 1 m^3, thus creating a three-dimensional model. In this context, the terms "crown space" and "commercial crown space" are used, indicating the amount of space occupied by all crowns, and by all crowns of commercial species respectively. Crown sizes were estimated using parameters described in Section 3.1.3 in Equation 3.5.

$$S_C = (r_N + r_S)(r_E + r_W)(h_T - h_B) \quad (3.5)$$

where:
S_C = crown size (m^3).
r_N = crown radius in north direction (m).
r_S = crown radius in south direction (m).
r_E = crown radius in east direction (m).
r_W = crown radius in west direction (m).
h_T = total tree height (m).
h_B = trunk height (m).

Light was assumed to come from seven directions only, namely from straight above and obliquely from the east and west at angles of 15°, 30° and 45° to the vertical. Extinction rates were estimated per direction for each cubic metre of commercial crown space, using the provisional Equation 3.6.

$$E = \{\log (X + 1)\}/\log 8 \quad (3.6)$$

where:
E = extinction rate.
X = crown space the light has passed through (number of cubic metre units).

Extinction is supposedly complete when X = 7. For the sake of economy, extinction rates were computed in sub-samples, consisting of 17 equidistant, east-west cross-sections per plot of dimensions $80 \times 1 \times 48$ m. Mean extinction rates (E_M) per plot were then calculated for each treatment, that is the sum of extinction rates divided by the number of directions (7) and by the commercial crown space in the sub-sample. E_M is considered to be a measure of light interception which is suitable for comparing effects of different treatments simulated in the same stands. In addition, the relationship between diameter at reference point (dbh) and crown diameter was analysed with LRA. The results are discussed in Sections 6.1 and 6.4.2.

3.2 The arboricide trial

The main objective of the arboricide trial was to reduce the amounts of 2,4,5-T used in silvicultural treatments. The experiment was located directly east of replication 3 of the MAIN experiment (Fig. 3.4) and consisted of five parallel 100 m-wide strips in which five treatments were applied. The trial was not replicated.

Treatments. The first treatment (treatment T-1) was identical to the most intensive refinement applied in the MAIN experiment, in which unwanted trees of diameters exceeding 20 cm dbh were frill-girdled and poisoned with a 5% solution of 2,4,5-T in diesel oil. The arboricide was poured into the frill-girdle and applied on the bark immediately above it (see Section 3.1.2).

Treatment T-2 was a modification of treatment T-1. The arboricide was applied in the frill, but application on the bark was restricted to unfrilled stem sections. Treatments T-3 and T-4 were identical to treatments T-1 and T-2 respectively, except that the concentration of 2,4,5-T used was 2.5% instead of 5%.

Treatment T-5 attempted to kill trees without arboricide. Trees with regular stem form were ring-barked twice (treatment T-5a), but most fluted stems and buttressed trees had to be poison-girdled according to the prescriptions of treatment T-3 (treatment T-5b).

Data collection and analysis. Each treatment was applied to 100 trees shortly after they had been identified and their girths measured. The condition of individual trees was assessed four times, namely a few days, six months, fifteen months, and two years after treatment, using five classification categories:

- dead or leafless: the tree had no living leaves and was dead or dying;
- almost leafless: the tree had few green leaves left and was apparently dying;
- no phloem contact: phloem contact between crown and roots was interrupted completely as the bark was dead or missing over the whole circumference of the trunk;
- some phloem contact: transport of assimilates was partly restored or had never been interrupted fully; the bark was dead or missing over almost the whole

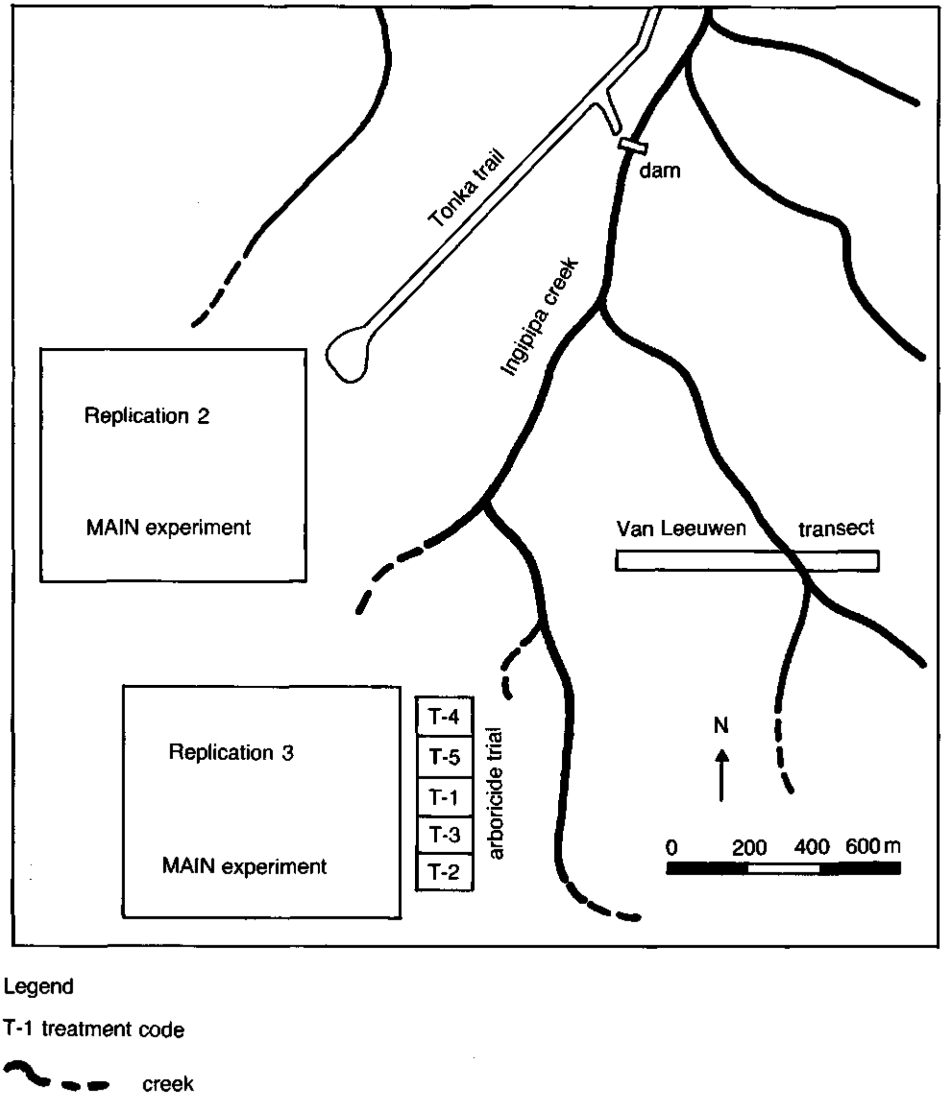


Fig. 3.4 Locations of the arboricide trial and the Van Leeuwen transect. See Section 3.2 for explanation of treatment codes

circumference of the stem;

- recovered: phloem contact seemed restored almost completely; a major part of the frill-girdle was overgrown by callus tissue.

Frequencies per category were used to estimate the effectiveness of each treatment and to study the relationship between rate of mortality and the time elapsed since treatment. The results are discussed in Section 6.2.2.

3.3 The Van Leeuwen transect

The impacts of soil qualities on vegetation were investigated in a 600×22 m transect located in the Ingipipa creek catchment area (Fig. 3.4). The transect was more or less perpendicular to the contour lines and crossed a plateau, a slope and a valley. The western part of the catchment area, in which 150 m of the transect was located, had been subject to refinement shortly before the study was carried out. Field-work and a major part of the analysis was done by van Leeuwen (1983). The principal objective of this study was to investigate the hypothesis that differences in species composition between mature forest stands on different soil types are distinct and that such differences are reflected in forest structure.

Data collection. All trees over 5 cm dbh, including those poison-girdled, were enumerated and an architectural forest profile diagram of the whole transect was drawn, following Oldeman's method (Hallé et al., 1978). Furthermore, a detailed soil survey was carried out with Edelman augerings at intervals of 50 m, two deep augerings to depths of 6.0 and 7.5 m and three profile pits. Soils were described according to standard procedures (FAO, 1977a) and soil samples were taken from the profile pits for chemical and physical analysis.

Data analysis. The forest profile diagram was used to identify areas homogenous in forest structure (vegetation units), and units of similar forest structure were then grouped into forest types. Vegetation units of the chablis forest type (gaps and forest in an early growing phase) were disregarded in further analysis. Soils were classified according to USDA Soil Taxonomy (USDA, 1975) and boundaries of forest types and soil types were compared. The results are discussed in Sections 4.1.2 and 4.2.

Differences in species composition between vegetation units were analysed with a simple ordination technique, developed by Orloci and Austin (Orloci, 1966), which is quite different from the multivariate approach described in Section 3.1.4 although the objective is the same. Spatial positions of individual vegetation units are defined relative to one another, without making a direct reference to species scores, and the ordination is reduced to a simple arithmetic operation on the basis of the Pythagorean theorem.

Firstly, differences in species composition between pairs of units are expressed as "distances", using Equation 3.7.

$$D_{jk} = \{\Sigma_{i=1}^{N} (x_{ij} - x_{ik})^2\}^{1/2} \qquad (3.7)$$

where:

D_{jk} = distance between vegetation units j and k.
x_{ij} = number of trees per hectare of species i in unit j.
x_{ik} = number of trees per hectare of species i in unit k.
N = total number of species in units j and k.

The two most distinct units (highest distance value) are selected as reference points, R_1 and R_2, for the first axis. Co-ordinates of the vegetation units are then computed by Equation 3.8.

$$X_j = \{(D_{1j})^2 + (D_{12})^2 - (D_{2j})^2\}/2D_{12} \tag{3.8}$$

where:

X_j = co-ordinate of unit j on the first axis, measured from R_1.
D_{1j} = distance between units R_1 and j.
D_{12} = distance between units R_1 and R_2 (= length of the first axis).
D_{2j} = distance between units R_2 and j.

The distance h_j of unit j from the first axis is then given by Equation 3.9.

$$h_j = \{(D_{1j})^2 - (X_j)^2\}^{1/2} \tag{3.9}$$

The unit furthest from the first axis is the third reference point R_3. Co-ordinates on the second axis are then calculated, using Equation 3.10.

$$Y_j = \{(h_j)^2 + (X_j - X_3)^2 + (h_3)^2 - (D_{3j})^2\}/2h_3 \tag{3.10}$$

where:

Y_j = co-ordinate of unit j on the second axis.
X_3 = co-ordinate of unit R_3 on the first axis.
h_3 = distance between unit R_3 and the first axis (= length of the second axis).
D_{3j} = distance between units R_3 and j.

If a two-dimensional representation does not provide all the information required, co-ordinates on subsequent axes may be computed following the same principles. The results are discussed in Section 4.2.2.

4 Distribution patterns in rain forest vegetation

De Graaf (1986) showed that the Celos Silvicultural System (CSS) worked well in stands adequately stocked in all size classes, but the possibility that it might be too drastic locally, that is, where commercial stocking is poor, was not taken into account (see Sections 2.2 and 2.3). This chapter therefore includes an analysis of the spatial variation of forest vegetation to investigate this possibility. Horizontal distribution patterns and size class distributions were studied in the MAIN experiment and the Van Leeuwen transect, using methods described in Sections 3.1.4 and 3.3. Vertical distribution patterns will be discussed in a later publication in this series (Schmidt, in press).

In recent years, many studies have been made of spatial distributions of species and size class distributions in tropical rain forests in various parts of the world. They have generated a wide variety of hypotheses about the origin and nature of the patterns found (see Golley, 1983 and UNESCO, 1978 for detailed reviews). Some of these studies indicate that spatial distribution of species in tropical rain forests is at least partially influenced by topography-related factors such as water availability (see Bourgeron, 1983), and by other soil factors such as availability of phosphorus (for example Austin et al., 1972; Lescure and Boulet, 1985).

Hallé et al. (1978) and Oldeman (1974; 1978; 1983), on the other hand, have described the forest as a dynamic, ever-changing mosaic of successional phases determined by a process called sylvigenesis. According to this theory, transition from one successional phase to another is triggered by the formation of a chablis (an open space created by one or more fallen trees and covered with their debris) or other less drastic disturbances to the forest canopy. A large chablis may lead to a complete regression to the pioneer phase while a smaller chablis may result in partial regression, or the beginnings of a later phase, depending on a number of factors including the chablis size. According to Hallé et al. (1978), the chronology of early successional phases is well understood, but is completely hypothetical for subsequent phases. Chablis formation has been demonstrated to be more frequent on slopes and river banks than on flat or undulating land (Oldeman, 1978), thus resulting in differences in the frequency of various successional phases between sites differing in physiography.

These theories are complementary rather than contradictory (see Bourgeron, 1983; Oldeman, 1983). Each partially explains species distribution patterns and should be considered in the design of a silvicultural system based on natural regeneration, such as CSS. However, each theory has different implications. If an undesirable species composition is the result of sylvigenesis or other ecological interactions, a carefully designed natural regeneration treatment may be beneficial. However, if poor stocking is the result of adverse physical conditions a substantial improvement from such a treatment cannot be expected. Size class distribution is also determined to some extent by sylvigenesis and soil-related factors. Canopy trees are usually smaller on soils with adverse physical characteristics, and in areas of high chablis frequency.

4.1. The physical setting

The MAIN experiment and the Van Leeuwen transect were both located in the Tonka research area, only a few hundred metres apart (Fig. 3.4). Geologically, the Tonka research area is part of the Zanderij formation and parent material usually consists of several metres of Pliocene sediments of the Coesewijne series over weathered basement rock of the Guiana Shield. In places, residual parent material is at or near the surface and such a ferrite outcrop of Precambrian age is present in the north-west corner of replication 1 of the MAIN experiment (Fig. 4.2).

4.1.1 The MAIN experiment

The replications of the MAIN experiment were located on two plateaus and adjacent slopes (Fig. 4.1). The southern plateau, which is the site of replications 2 and 3, is one of the largest in the region. Landscape in this part of the experiment is exceptionally uniform, with no gullies or other distinctive features. Topography is gently undulating with altitudes of 12 to 23 m above a reference point in the Ingipipa Creek (about 25 – 36 m above sea level, see Fig. 4.1). The landscape of replication 1 and the virgin forest plots is more uneven, with slightly steeper slopes and altitudes of 2 to 18 m above the reference point (about 15 – 31 m above sea level). Topography is undulating except for a steep slope between the ferrite cap and a small, low area in the extreme north-west of replication 1. A shallow gully is present in the south-western part of this replication.

The experiment area is almost homogeneous in soil type (Fig. 4.2). All soils encountered in the soil survey were classified as Haplorthox according to Soil Taxonomy (USDA, 1975), and were usually well drained, tending towards moderately well drained in relatively low-lying edges. Imperfectly drained soils were found only in replication 1 along the gully and in the extreme north-west.

Soil texture was found to vary from sand to sandy loam in the upper 10 cm, and the clay content increased with depth. Sandy clay loam texture was usually reached within 60 cm below the surface, but sandy clay was seldom recorded within 120 cm. Imperfectly drained soils tended to be lighter in texture, and the heaviest soils were found in the northernmost virgin forest plot (plot 43) where sandy clay was present within 60 cm. A description of a representative soil profile in the centre of replication

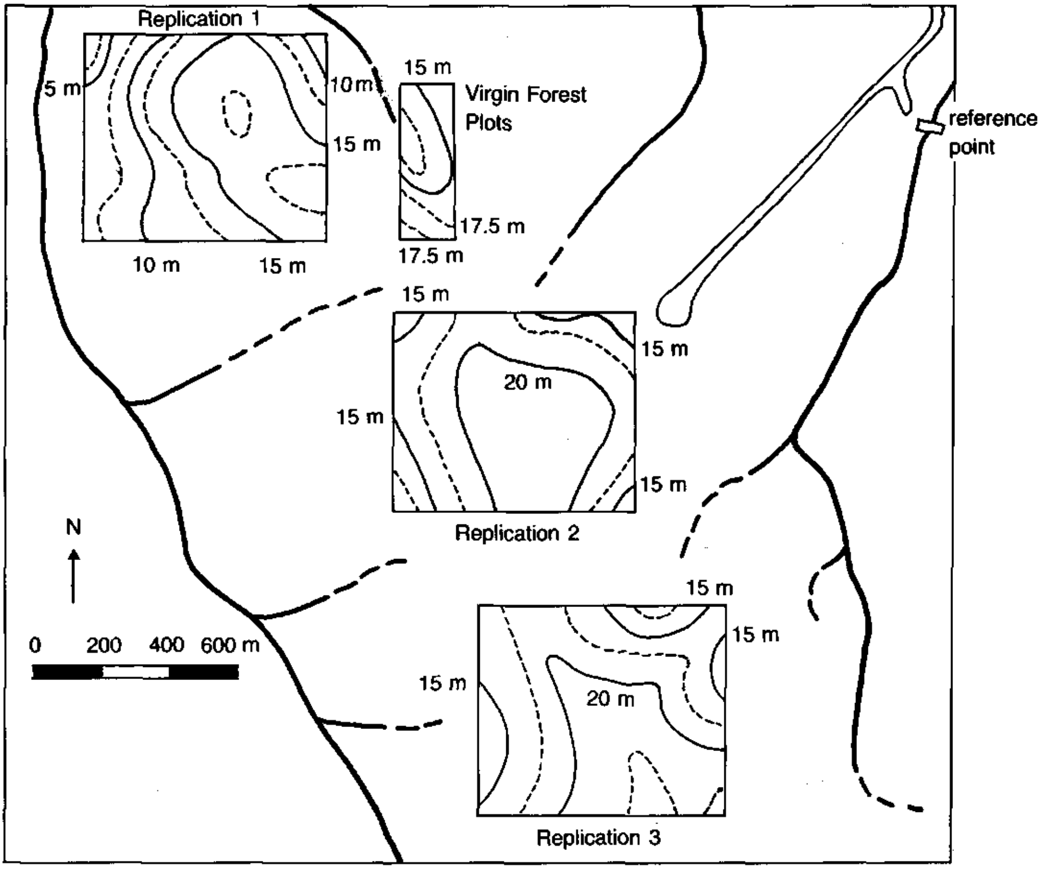


Fig. 4.1 MAIN experiment: contour map

2 is included in Appendix II.

Chemical analyses of samples taken from this soil pit showed that these soils were acid and very poor in nutrients (Table II.1). Cation exchange capacity (CEC) at soil pH did not exceed 2 me/100 g soil throughout the profile. Aluminium saturation was high (about 70%), leaving little room for calcium, magnesium and potassium at the adsorption complex. Available phosphorus (P Bray I) was also extremely low, ranging from 6 to 7 ppm in the topsoil to about 1 ppm in the B horizon. Amounts of nutrients in non-exchangeable form were probably considerably higher, but these figures are not available. Boxman (in press) measured P-total values of 60 – 70 ppm and K-total values of about 0.3 me/100 g soil for similar soils in the Kabo research area, and these values seemed to vary little with depth.

Physical analyses of the soil pit showed that the soil structure was good (Table II.2). Available moisture, that is the water content at field capacity (pF 2) minus the water content at permanent wilting point (pF 4.2), decreased from 12% (volume) in the topsoil to less than 8% in the B horizon. Available moisture within 180 cm below the surface was 155 mm, which was equivalent to about 7% of the annual rainfall.

Poels (in press) made an extensive study on soils and hydrology in the Tonka research area and calculated that the available moisture within 4 m of the surface was insufficient to compensate for rainfall deficits in an average long dry season. Trees apparently need access to groundwater to secure their water supply, and Poels (in press) found that the groundwater at one location in the strip between replications 2 and 3 was more than 7 m below the surface, all the year round, indicating that the

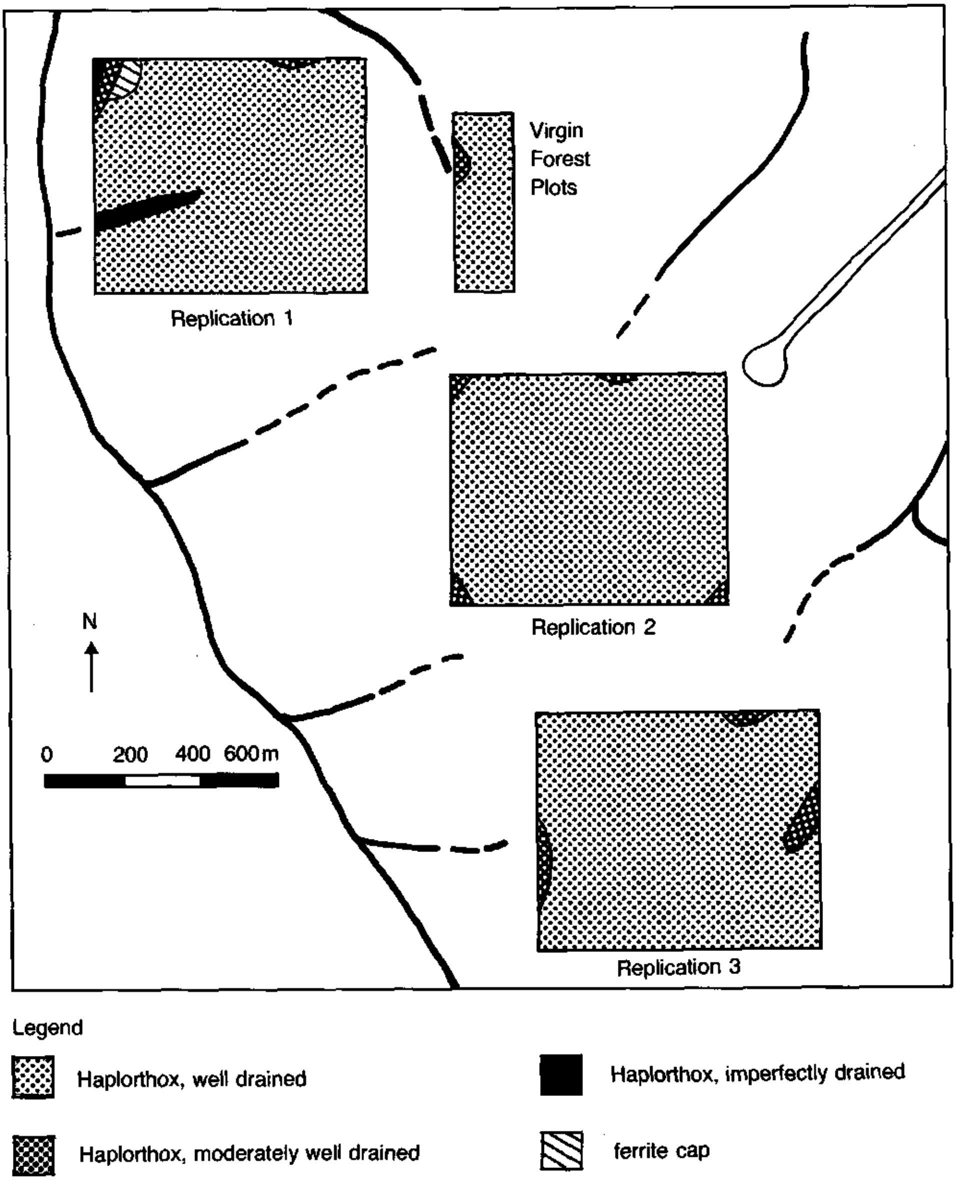


Fig. 4.2 MAIN experiment: provisional soil map

tree roots need to penetrate deeply into the soil. Circumstantial evidence, such as the presence of a gully and lower elevation above creek level, suggests that groundwater tables in the relatively low-lying replication 1 and virgin forest plots were closer to the surface than in replications 2 and 3.

4.1.2 The Van Leeuwen transect

The 1.32 ha Van Leeuwen transect was more variable in landscape and soil than the MAIN experiment (Fig. 4.3). Altitudes ranged from 5.5 to 17.5 m above the reference point (about 18 – 30 m above sea level), and topography was undulating. The transect was more or less perpendicular to the contour lines and, from west to east, crossed a small plateau, a gentle slope, a swampy valley bottom and the footslope on the eastern bank of the creek.

Five soil types were distinguished in the transect (van Leeuwen, 1983). Soils on the plateau and upper slope were classified as Ultic Haplorthox and were comparable to well drained soils in the MAIN experiment. The groundwater table was more than 7 m below the surface for most of the year, and the layer of Zanderij sediments was only a few metres thick, with a sharp transition to the underlying Guiana Shield, marked by a laterite stone layer. This stone layer was encountered at a depth of 2.5 m near the water divide, but it was closer to the surface at lower altitudes.

Soils on the mid-slope were moderately well to somewhat imperfectly drained sandy clays, with a sandy or sandy loam topsoil, and were classified as Plinthic Paleudult. The groundwater table was deep, and remained at least a few metres below the surface in the long rainy season. These soils were almost as poor in nutrients as the Haplorthox described in Section 4.1.1. A laterite stone layer, which probably originated from indurated plinthite, was present at depths of 70 – 90 cm. An argillic horizon had developed above this layer, and the soil material at greater depth was predominantly residual and of sandy clay texture.

Sandy soils were present on the footslopes on both sides of the creek (Fig. 4.3). On the western side, imperfectly to poorly drained conditions prevailed, and land close to the swampy valley bottom was sometimes flooded for short periods after exceptionally heavy storms. Drainage was lateral through a light grey horizon in the subsoil which approached the surface in the valley bottom, and laterite was absent. These soils were poorer in nutrients than those elsewhere in the transect, and were classified as Aquic Quartzipsamment. Similar soils were found on the eastern bank of the creek, but the grey horizon was absent there.

Better drained sandy soils were found even further east at slightly higher altitudes (Fig. 4.3). These somewhat imperfectly to moderately well drained soils, with no evidence of lateral water transport, were classified as Orthoxic Quartzipsamment. The fifth soil type was restricted to the swamp alongside the Ingipipa creek, where the land was waterlogged for about ten months per year. The topsoil consisted of decomposing organic material and the subsoil was sandy. This very poorly drained soil was classified as Histic Tropaquept.

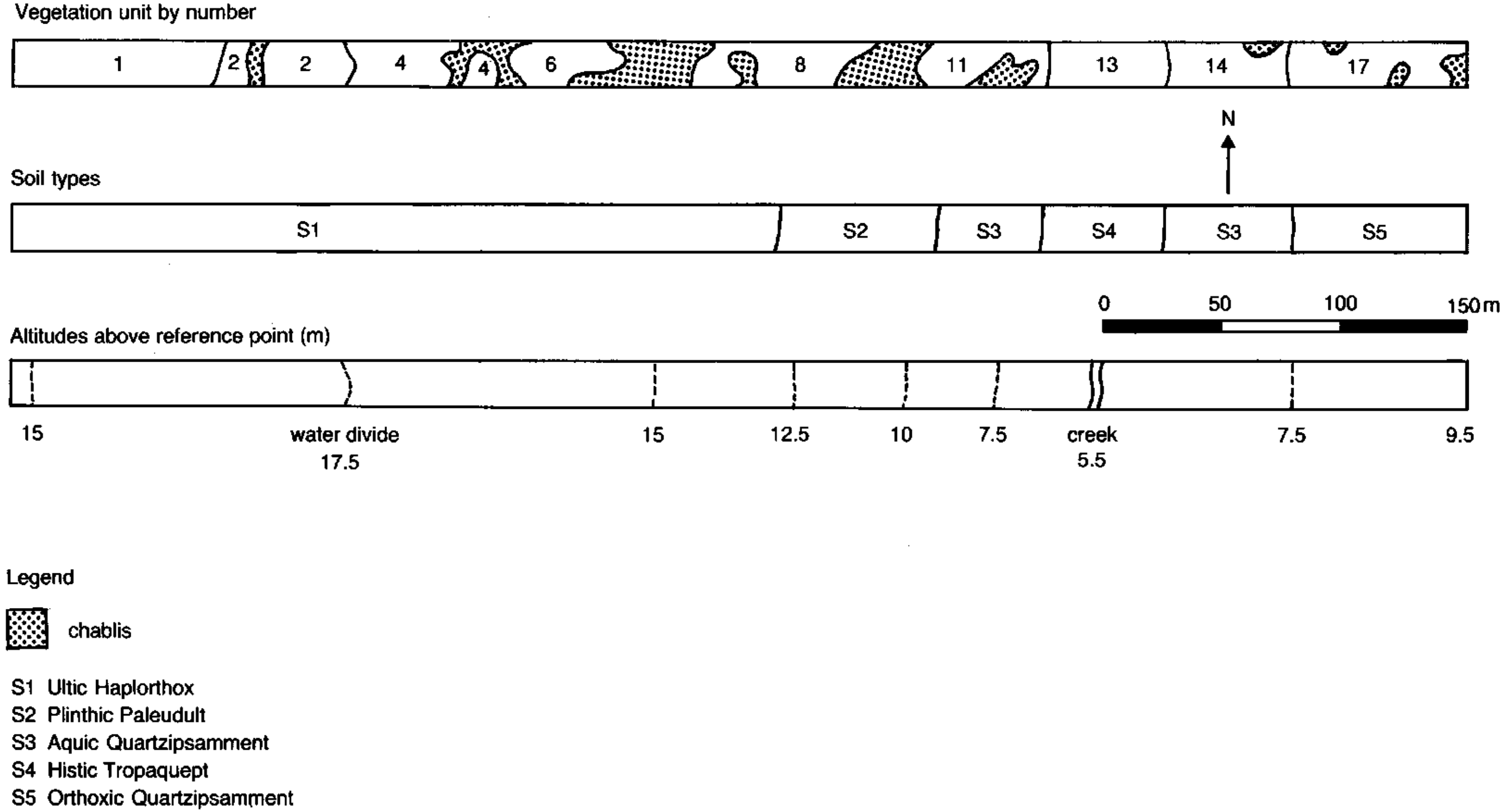


Fig. 4.3 Van Leeuwen transect: vegetation units, soil types and altitudes

4.2 Vegetation in the Van Leeuwen transect

4.2.1 Description of forest types

The Van Leeuwen transect was established to develop hypotheses about relationships between forest structure, species composition and soil type (for methodology, see Section 3.3). Forest structure is a rather loose term, used in this study to refer to all features which can be visualized in a forest profile diagram, such as forest architecture, height of the canopy and density of the vegetation. Van Leeuwen (1983) used forest structure to distinguish eight forest types. One of these, the chablis type, represented recent gaps and young forest, where the vegetation consisted mainly of seedlings and saplings. These plants were not enumerated (see Section 3.3), so including the chablis type in the analysis was not meaningful. The remaining seven types were:

- poorly developed, refined, plateau forest in vegetation unit 1;
- well developed, refined, plateau forest in vegetation unit 2;
- well developed, virgin, plateau forest in vegetation units 4 and 6;
- virgin "ingipipa-boegroemaka" slope forest in vegetation unit 8;
- virgin footslope forest in vegetation units 11 and 14;
- virgin swamp forest in vegetation unit 13; and
- virgin "walaba-pakiratiki" slope forest in vegetation unit 17.

Forest types on clay loam soils. The forest west of the water divide (Fig. 4.3) was

TABLE 4.1. Van Leeuwen transect: frequencies and basal areas of commercial and all trees > 5 cm dbh per vegetation unit, including all poison-girdled trees but excluding chablis

Vegetation unit	Area (m^2)	Frequency (n/ha)		Basal area (m^2/ha)	
		All species	Commercial species	All species	Commercial species
on clay loam soils					
1	1602	499	94	23.3	10.7
2	1188	606	160	35.1	13.6
4	1307	566	122	39.6	21.3
6	819	476	98	23.9	15.4
8	1055	644	133	51.6	19.0
on sandy soils					
11	892	807	157	27.9	2.2
13	1147	689	148	33.8	12.5
14	739	650	81	20.6	3.1
17	1433	1151	167	43.1	12.8
all units	10182	684	131	33.9	12.8

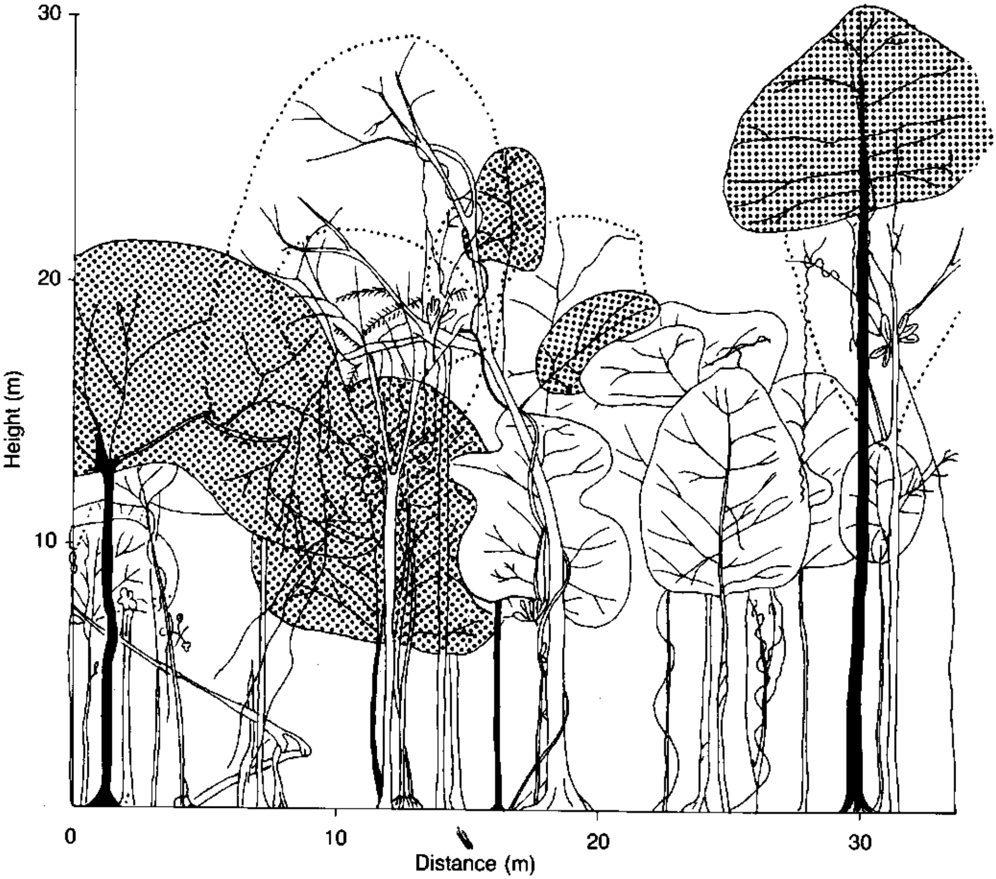


Fig. 4.4 Van Leeuwen transect: profile diagram, showing trees larger than 10 m total height in poorly developed plateau forest, vegetation unit 1, adapted from van Leeuwen (1983). Commercial species are shaded, dotted lines indicate crowns of poison-girdled trees

refined one year before the forest profile diagram was drawn. This altered the forest, but the original structure was still discernible, and two forest types were identified. Unit 1 contained poorly developed plateau forest, with evidence of repeated chablis formation 20 – 40 years before the transect was drawn (Fig. 4.4). The pioneer species bospapaja (*Cecropia spp.*) and boskoeswé (*Sloanea cf. gracilis*), a species believed to germinate on decaying fallen stems, were present. Many trees showed signs of severe damage in the past, and stems were generally short or poorly formed and incapable of growing taller. Tree heights seldom exceeded 30 m, the basal area was low (Table 4.1), and although commercial species were not uncommon, most trees were of inferior quality. Unit 2, which was on the same type of soil, contained well developed plateau forest. Before refinement, this unit was probably comparable in structure to the forest directly east of the water divide (unit 4).

The forest in vegetation unit 4 was well developed, reaching heights of 50 m and more (Fig. 4.5). The two largest individuals in Fig. 4.5 belonged to the commercial

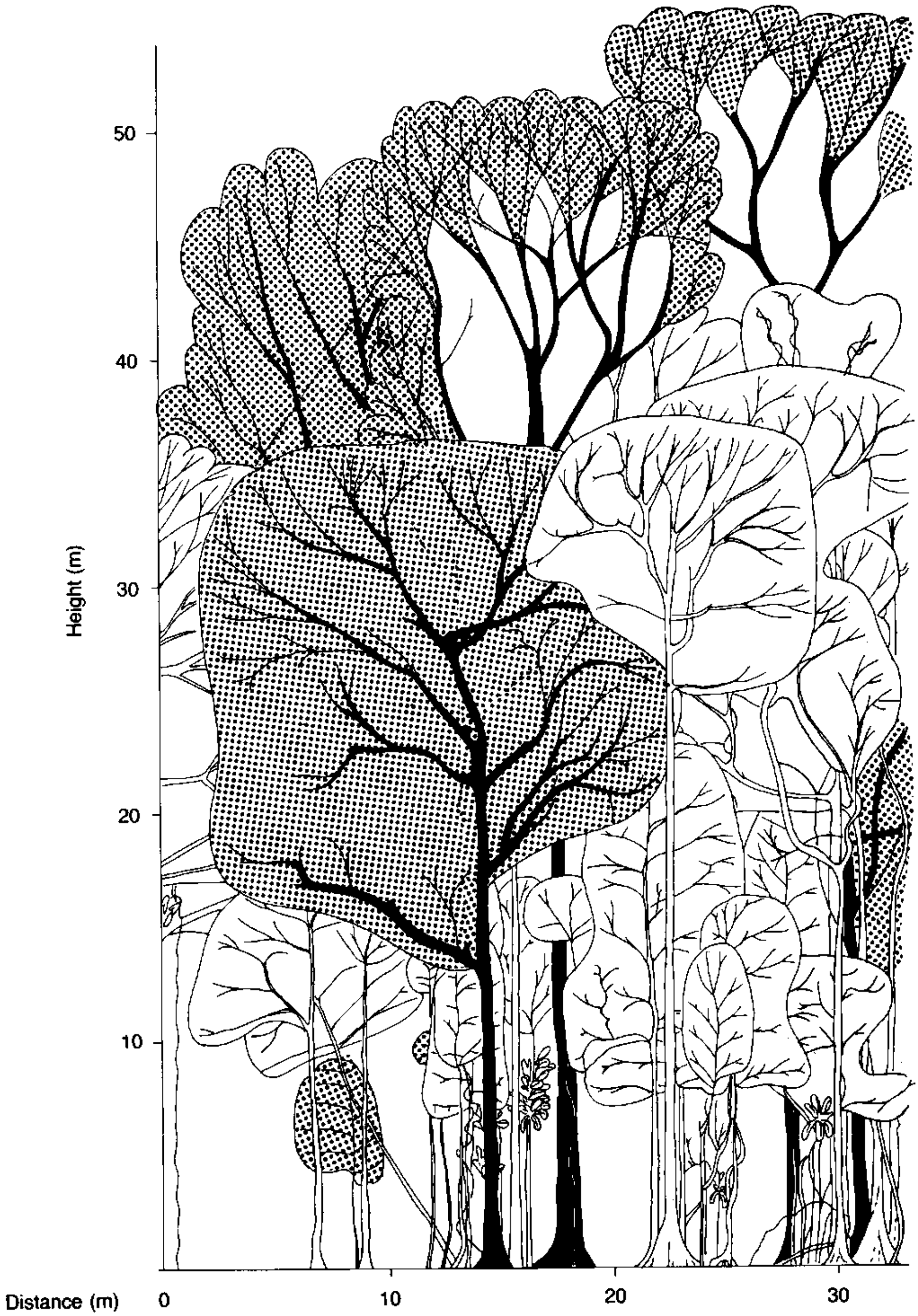


Fig. 4.5 Van Leeuwen transect: profile diagram, showing trees larger than 10 m total height in well developed plateau forest, vegetation unit 4, adapted from van Leeuwen (1983). Commercial species are shaded

species bergi gronfoeloe (*Qualea rosea*), which was well represented among emergent trees in this unit and in most other plateau forests in Tonka research area. The incidence of commercial species proved rather high, especially in the larger diameter classes, and the basal area was well above average (Table 4.1). Unit 6 was considered

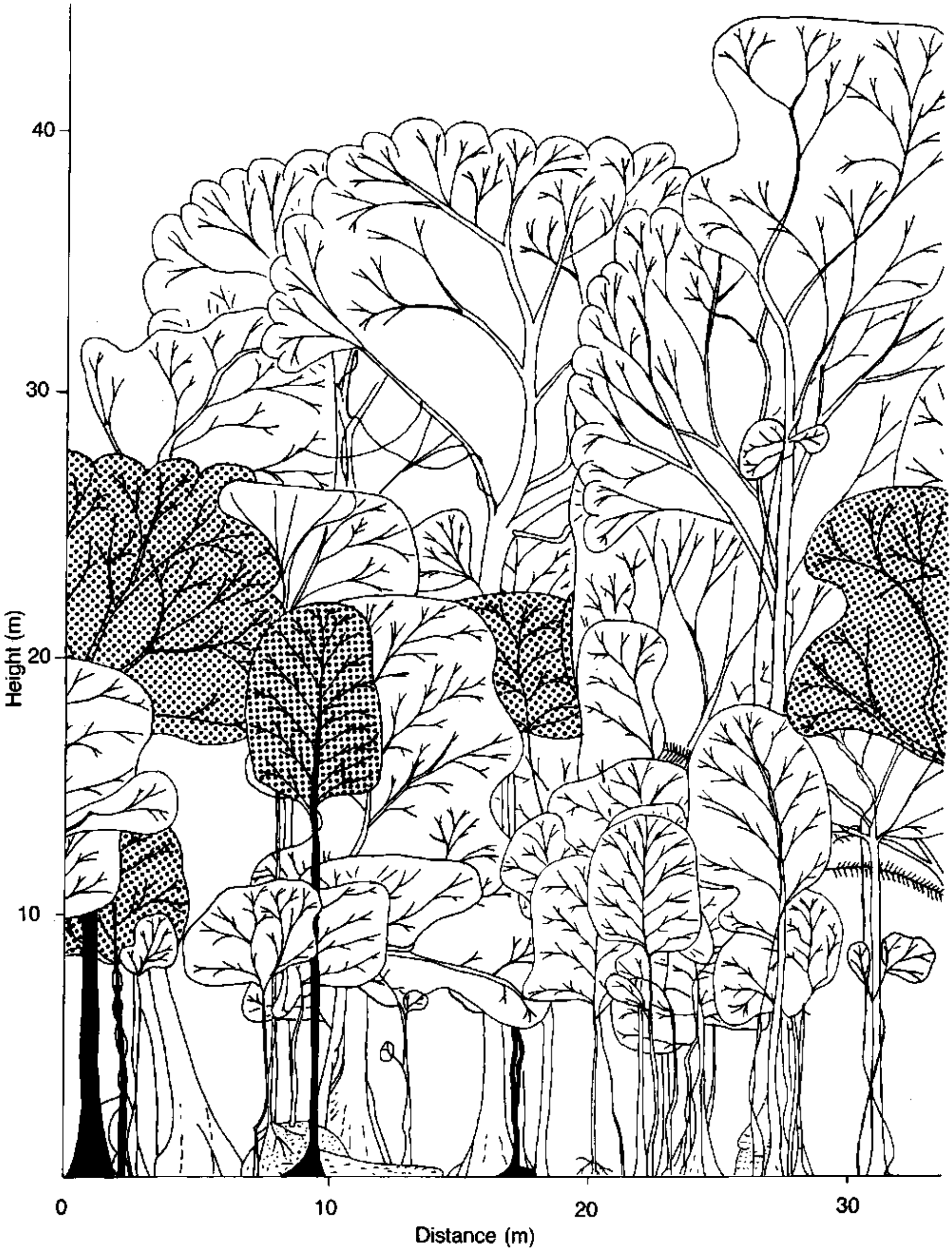


Fig. 4.6 Van Leeuwen transect: profile diagram, showing trees larger than 10 m total height in well developed slope forest, vegetation unit 8, adapted from van Leeuwen (1983). Commercial species are shaded

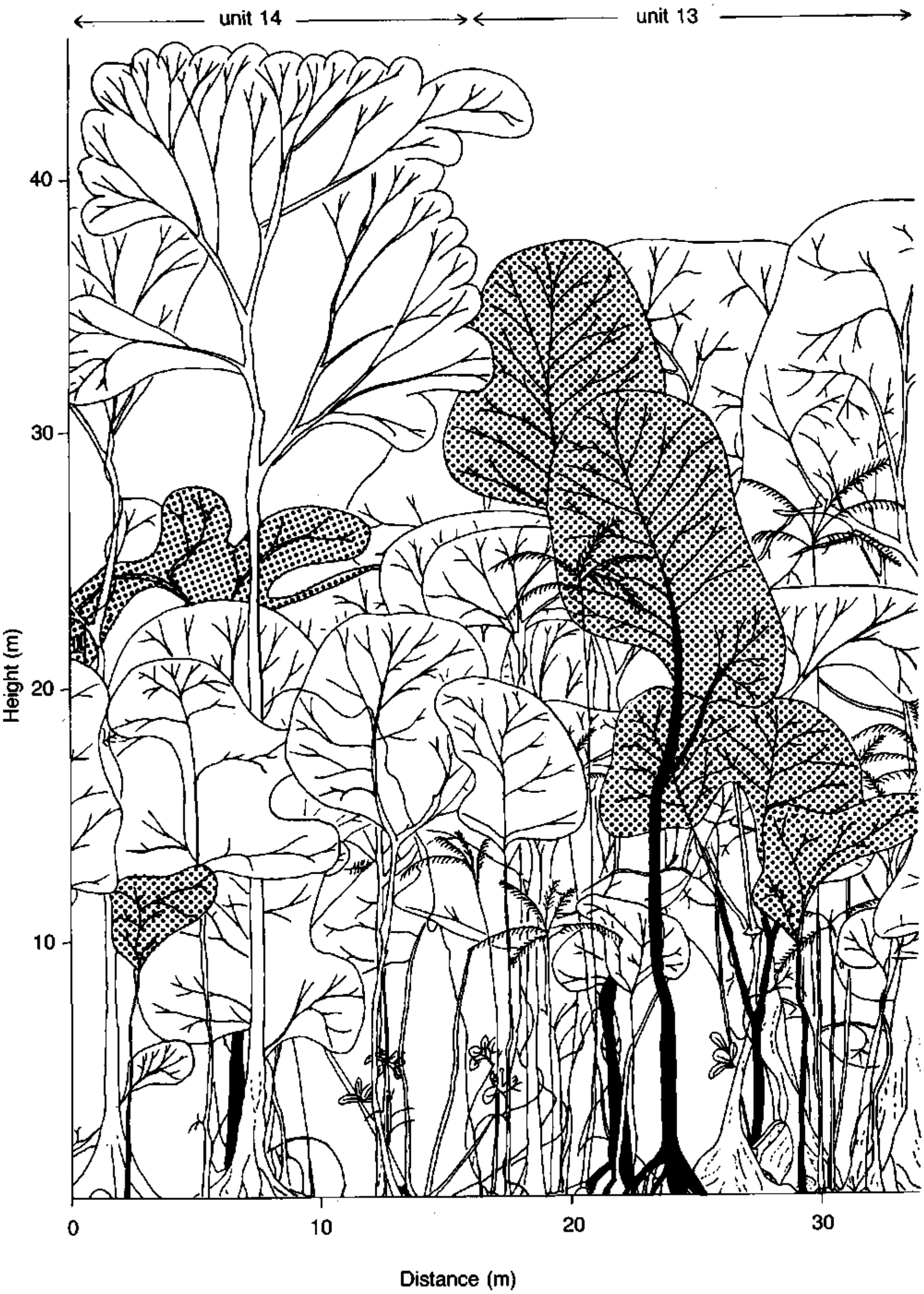


Fig. 4.7 Van Leeuwen transect: profile diagram, showing trees larger than 10 m total height in swamp forest, vegetation unit 13, and in forest on imperfectly drained sandy soils, vegetation unit 14, adapted from van Leeuwen (1983). Commercial species are shaded

similar in forest structure to unit 4, but the basal area and incidence of emergent trees were lower, because of recent tree falls.

Unit 8, which was located on the upper and mid-slope (Fig. 4.3), was slightly different in forest structure from units 4 and 6. The forest was well developed, reaching heights of more than 40 m (Fig. 4.6), and the basal area was exceptionally high (Table 4.1). Ingipipa (*Couratari spp.*) was predominant among emergent trees. Large ingipipas were common on slopes throughout the Tonka research area, but were rarely seen on plateaus and in valleys. The stocking rates of commercial species in small and medium size classes (5 – 50 cm dbh) were similar to values found in well developed plateau forest (units 2, 4 and 6), but stocking rates for the exploitable size classes were considerably lower. The boegroemaka palm (*Astrocaryum sciophilum*), which was present in all vegetation units except unit 13 (swamp forest), was most abundant in unit 8, where it formed a discontinuous canopy in the understorey.

Forest types on sandy soils. The poorest stands of the transect were found on imperfectly drained sandy soils in units 11 and 14 (Fig. 4.3 and Table 4.1). Their forest structure was distinctive (Fig. 4.7). Small trees were numerous and medium-sized and large individuals were rare. The basal area was well below average and the canopy was rather low, with very few emergent trees over 40 m total height. Walaba (*Eperua falcata*), a species with a distinct preference for sandy soils (Appendix III), was present but not in abundance. Commercial species were well represented in the small diameter classes, but individuals of more than 20 cm dbh were rare. Commercial trees were mostly in poor condition and held little promise for the future.

The forest on well drained sandy soils in unit 17 was of better quality (Fig. 4.3 and Table 4.1). An exceptionally high number of small-sized stems was recorded and larger size classes were fairly well represented. The basal area was well above average and the 40 m high canopy was almost continuous (Fig. 4.8). A striking feature was the abundance of walaba, of which 188 trees larger than 5 cm dbh per hectare were recorded. Understorey species such as pakiratiki (*Tapura guianensis*) and merkitiki (*Tabernaemontana undulata*) were also present in large numbers (Appendix III). Commercial stocking was acceptable, with nearly all commercial trees of more than 30 cm dbh belonging to the species basralokus (*Dicorynia guianensis*). Bergi gronfoeloe (*Qualea rosea*) and a few other commercial species were common in the understorey, but did not seem likely to reach timber size in this environment. Throughout the Tonka research area, mature bergi gronfoeloe trees were almost confined to well drained clay loam plateau soils.

The structure of the swamp forest in unit 13 was distinctive (Fig. 4.7). The dense canopy was almost 40 m high, and trees greater than 30 m total height belonged to three typical swamp species not found elsewhere in the transect: watra bebe (*Pterocarpus officinalis*), which can be recognized in Fig. 4.7 by its impressive buttresses, and the commercial species mataki (*Symphonia globulifera*) and laagland baboen (*Virola surinamensis*). Pina (*Euterpe oleracea*), a slender palm which is characteristic of swamp forest and may reach heights of 25 m, was abundant in unit 13. The typical structure of swamp forest was not reflected in frequencies and basal area values summarized in Table 4.1, however, which were about average. Most species present in swamp forest occurred in other forest types as well, and even pina was not strictly confined to swampy areas. A pina clump was seen in unit 1 and the species was also recorded in various plots of the MAIN experiment.

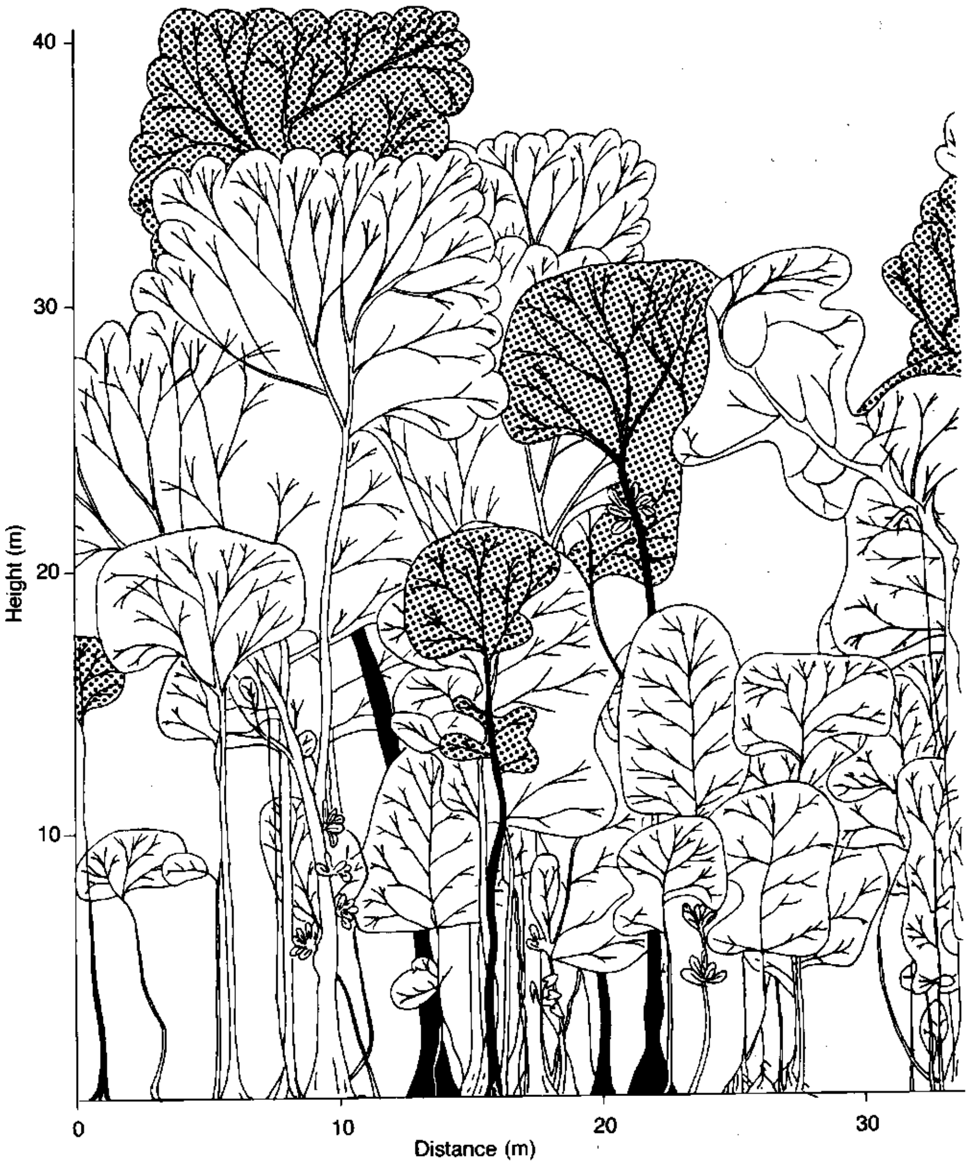


Fig. 4.8 Van Leeuwen transect: profile diagram, showing trees larger than 10 m total height in forest on well-drained sandy soils, vegetation unit 17, adapted from van Leeuwen (1983). Commercial species are shaded

Conclusion. Forest structure does seem to be dependent on physiography and soil type, but the exact nature of this relationship could not be determined in this small transect (see also Section 4.2.2). A study made in Venezuela by Brünig and co-workers (Brünig et al., 1979; Brünig, 1983) indicates that such a relationship may also be expected in a toposequence from "mesic" (well drained) sites to "xeric" (excessively drained) spodosols.

The presence of small areas which are poor in good quality commercial trees (units 1, 11 and 14) in a matrix of well-stocked forest is important from a silvicultural point of view. Such areas require a different silvicultural treatment than that applied to the surrounding forest. Of equal interest is that some commercial species seem capable of establishing themselves in a sub-optimal physical environment, although they do not grow to commercial timber size there. Silvicultural treatment will probably not overcome such physical limitations.

4.2.2 Spatial variation in species composition

The Van Leeuwen transect was rich in tree species, with as many as 138 vernacular names recorded among 775 trees larger than 5 cm dbh. The most common species were walaba (*Eperua falcata*, 51 trees) and hoogland oemanbarklak (*Lecythis corrugata*, 49 trees). There were 152 trees of 29 commercial species, basralokus (*Dicorynia guianensis*, 16 trees) being the most common.

Twenty-two species were recorded ten or more times and although none were restricted to one forest type, strong site preferences were apparent for at least 16 of them (Appendix III). Seven species, including the commercial species rode sali (*Tetragastris altissima*), hoogland baboen (*Virola melinonii*) and goebaja (*Jacaranda copaia*), were found almost exclusively on clay loam soils. Two species, walaba and boskoffie (*Coussarea paniculata*), seemed to prefer sandy soils, the former's preference having been noted in many studies since the 1930s (see Richards, 1952; Schulz, 1960). Boskoffie, a typical understorey species, was common on the imperfectly to moderately well drained sandy soils of vegetation units 11 and 17, and almost absent elsewhere on the transect. Five species, including basralokus and bergi gronfoeloe (*Qualea rosea*) were found frequently on well drained soils of both light and heavy texture, but bergi gronfoeloe seemed to develop poorly on sandy soils. Site preferences of some other species were mentioned in Section 4.2.1.

A simple ordination technique was used to analyse differences in species composition between vegetation units (Section 3.3), and the results show that the classification into forest types corresponds fairly well with the ordinated arrangement of vegetation units (Fig. 4.9). Vegetation units on clay loam soils are clearly separated from units on sandy soils, indicating that species composition is at least partly determined by soil texture, and there is also a distinct relationship between soil drainage and floristic composition (Fig. 4.9).

Units 2, 4, 6 and 8, all of them on clay loam soils, all come close together in the ordinated arrangement, indicating a similarity in species composition. The similarity

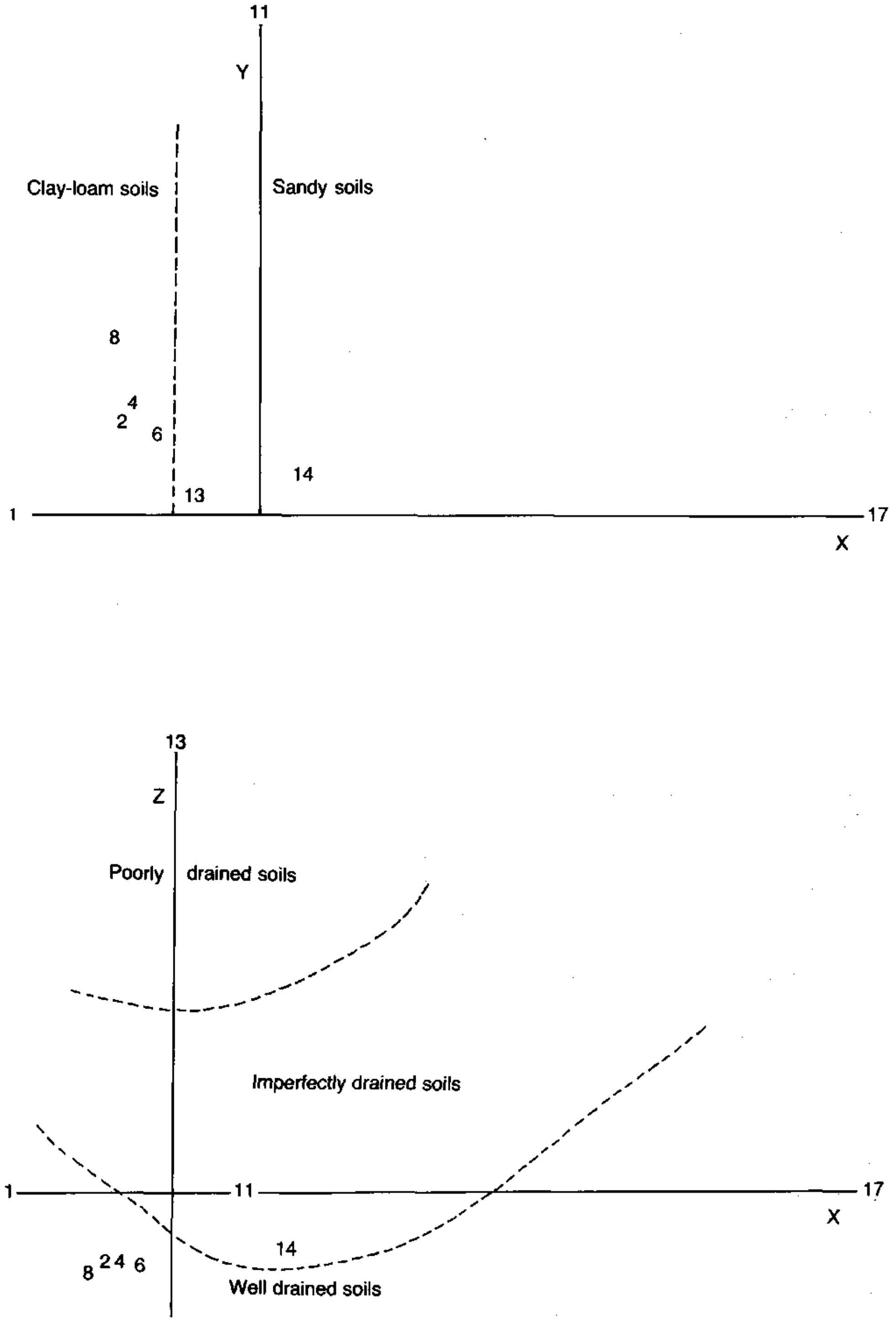


Fig. 4.9 Van Leeuwen transect: ordinated arrangement of vegetation units

between most units on well drained plateau soils (2, 4 and 6) is very strong, and the deviant position of unit 1 on the same soil type seems to be a result of severe disturbance in the past (see Section 4.2.1). The vegetation in unit 8 on the upper slope seems only slightly different from well developed plateau forest.

The floristic variation between the units on sandy soils was greater. The swamp forest in unit 13 had relatively few species in common with other forest types, and this is reflected in the ordination (Fig. 4.9). Interpretation of the divergent position of unit 17 is more difficult. Unit 17 was located on the better drained sandy soils and had many species in common with other vegetation units in the transect (Appendix III). The forest in this unit had an exceptionally high number of trees per hectare (Table 4.1), and with the ordination technique used, this characteristic results in large "distances" between unit 17 and all other units, in spite of obvious similarities (see Section 3.3).

Affinity between units on imperfectly drained sandy soils (11 and 14) was rather loose, and differences in soil and physiography are considered too small to serve as an explanation (see Section 4.1.2). It is more likely that species composition was strongly influenced by adjacent forest. Many species seemed incapable of growing into mature trees in this environment (see Section 4.2.1) and probably originated from seed sources on less restrictive soils. Species composition was therefore dependent on the availability of such seed trees in the immediate vicinity.

4.3 Vegetation in the MAIN experiment

The location of the MAIN experiment was selected in 1978 because of relative homogeneity in site characteristics and vegetation. The forest was untouched and has since been logged and treated silviculturally. Unfortunately, non-commercial species were not assessed in the pre-felling enumeration and the description of the vegetation is therefore partially based on data collected after logging had been completed.

The pristine forest was similar to well developed plateau forest in the Van Leeuwen transect (Section 4.2.1 and Fig. 4.5). The tree stand included some 250 trees per hectare with diameters larger than 15 cm dbh. Basal area and above-ground phytomass were about 27 m^2/ha and 440 t/ha respectively, comparable to pan-tropical averages for tropical rain forest (see Rollet, 1978). The stock of commercial species was more than adequate, about 100 trees larger than 15 cm dbh per hectare, and they contributed approximately 60% to the basal area and phytomass of the virgin stand.

The experimental area was fairly rich in species and 193 vernacular names were recorded among trees larger than 15 cm dbh, including 37 commercial species. The most common species were basralokus (*Dicorynia guianensis*), bergi gronfoeloe (*Qualea rosea*) and the non-commercial species rode jakanta (*Dendrobangia boliviana*).

Some aspects of forest structure can be identified on aerial photographs (scale

1 : 30000) taken eight years before exploitation (Fig. 4.10). Emergent trees reaching heights up to 50 m are common, and many chablis and pockets of young aggrading forest can be seen. Differences in structure within the experiment are manifest. The canopy is comparatively open in replication 1 and the virgin forest plots, where numerous tiny openings suggest a scarcity of small trees and a dense palm layer in the understorey. The canopy in replications 2 and 3 is denser and openings other than those resulting from gap regeneration processes are rare. Two very large openings in replication 3 are a striking feature.

4.3.1 Variation in commercial stocking

One of the characteristics of tropical rain forest is its heterogeneity. There was considerable variation in vegetation even in the MAIN experiment, where physical site conditions were exceptionally uniform (Section 4.1.1), and this is reflected in the commercial stocking figures presented in Table 4.2. Excellent stands were found on the southern plateau, especially in replication 2, but the forest in the northern area was distinctly poorer. Pre-felling stocking of commercial species in replication 1 was

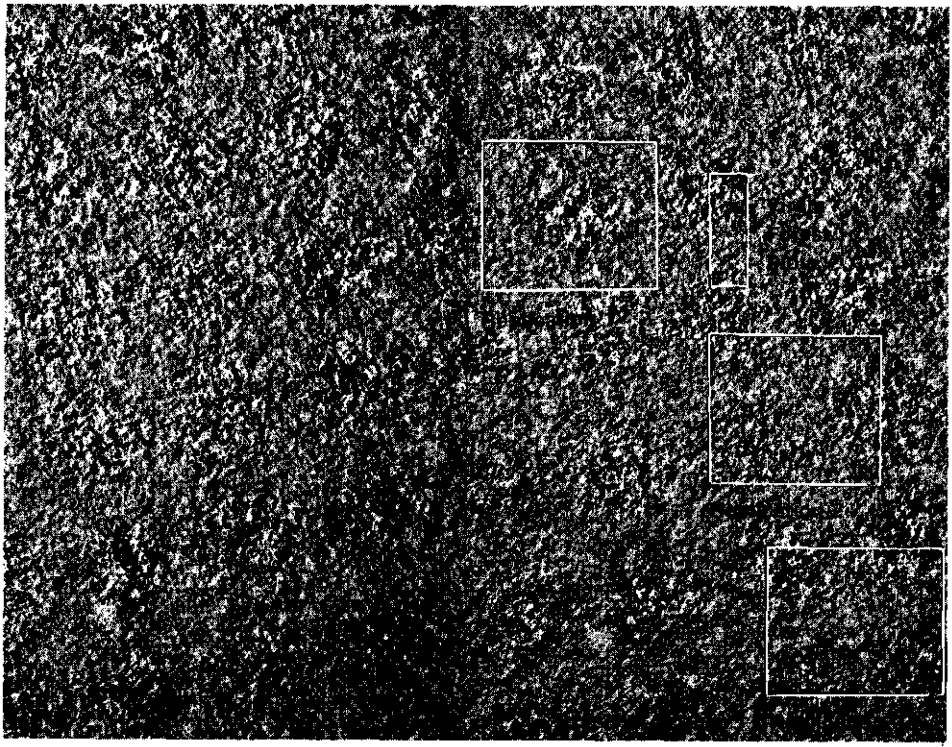


Fig. 4.10 MAIN experiment: aerial photographs, taken in 1973. Scale: approximately 1:30000. Courtesy of Centraal Bureau Luchtkartering, Paramaribo

TABLE 4.2. MAIN experiment: the commercial stand of trees > 5 cm dbh prior to logging, using numbers of trees (n/ha) and basal areas (m^2/ha) per plot*

Replication 1			Replication 2			Replication 3			Virgin forest plots		
Plot	n/ha	m^2/ha	Plot	n/ha	m^2/ha	Plot	n/ha	m^2/ha	Plot	n/ha	m^2/ha
11	154	14.2	21	271	17.5	31	192	14.1	41	179	14.6
12	116	12.3	22	206	14.7	32	227	15.5	42	132	12.2
13	101	13.6	23	270	22.0	33	227	15.3	43	72	8.9
14	161	14.1	24	277	17.6	34	204	12.6			
15	135	14.6	25	257	19.5	35	231	16.6			
16	133	13.8	26	180	15.5	36	211	16.4			
17	106	12.3	27	268	19.6	37	260	14.6			
18	99	12.3	28	266	17.9	38	149	11.8			
19	92	10.5	29	160	15.1	39	125	12.2			
mean	122	13.1	mean	239	17.7	mean	203	14.3	mean	127	11.9

* Including trees overlooked in pre-felling enumeration, sample areas of 2.25 ha (trees > 15 cm dbh) and 0.45 ha (trees 5 – 15 cm dbh) per plot

estimated at 122 trees larger than 5 cm dbh per hectare, whereas almost twice as many were found in replication 2. Differences in the basal area of commercial species, which proved strongly correlated with trunk volume (Equation VI.1, Appendix VI), were less spectacular. The standing volumes in replications 1, 2 and 3 were estimated at 172 m^3/ha, 243 m^3/ha and 190 m^3/ha respectively.

Variation within replications was relatively small, although each replication included a distinctly poorer part in the south-east corner (Table 4.2). The virgin forest plots, on the other hand, differed markedly from one another. The forest in plot 41, located on the edge of the southern plateau (Fig. 4.1), was rich in commercial species, plot 42 was similar to replication 1, and plot 43 had the poorest stand in the experiment.

4.3.2 Patterns in diameter class distributions

Numbers of trees per diameter class decrease almost geometrically with increasing tree size in tropical rain forest (Rollet, 1978), a phenomenon which has inspired scientists to search for mathematical models. Rollet (1974) published the results of an extensive study of diameter class distributions in East Venezuela (Venezuelan Guyana) together with a review of research in other tropical rain forest areas. He proposed an exponential curve for all of humid tropical America in which succeeding 10 cm diameter classes contain about half as many trees, that is to say numbers per class decrease from about 80 trees/ha in the 20 – 30 cm class to approximately one tree per hectare in the 90 – 100 cm class. This rule does not apply for size classes below 20 cm dbh (Rollet, 1978). It is probable that the pre-felling size class distribution in the MAIN experiment corresponded fairly closely with Rollet's pan-neotropical curve (see Table 6.1), but this cannot be verified because non-commercial trees were not measured.

Patterns in the commercial stand. Patterns in size class distribution of the commercial stand are most important from a forester's point of view. In the MAIN experiment, numbers per diameter class were found to decrease gradually with tree size, although the distribution does not appear to fit a simple geometrical model (Table 4.3). Differences in size class distributions between replications were small for classes larger than 30 cm dbh, but distinct for the smaller size classes. Stocking of small commercial trees (5 – 30 cm dbh) was more than adequate in replications 2 and 3, and marginal in replication 1 (Table 4.3).

Size class distributions are such that polycyclic management on a sustained yield basis is possible. Application of the Celos Silvicultural System would probably result in diameter growth rates for medium-sized and large trees of approximately 1 cm/yr, and an annual mortality rate of about 2% (Jonkers and Schmidt, 1984). At least 15 trees/ha would therefore reach a diameter of 50 cm during each 20 year cutting cycle, provided that logging damage is kept within reasonable limits (see Chapter 5). Even if, for example, 50% of the trees proved to be defective or poorly formed, attractive sustained yields could still be achieved through application of CSS. Similar results were obtained in other parts of Suriname by de Graaf (1986) and Hendrison (in press).

Distributions of individual species. Size class distribution patterns of tree species are mostly determined by intrinsic physiological and ecological characteristics. Rollet

TABLE 4.3. MAIN experiment: pre-felling frequencies (n/ha) of commercial trees per diameter class and per replication*

Dbh class (cm)	Frequencies (n/ha) per replication			
	Replication 1	Replication 2	Replication 3	Mean
5 – 10	18.6	84.0	54.0	52.2
10 – 15	16.2	42.5	35.8	31.5
15 – 20	16.6	28.5	30.8	25.3
20 – 30	19.3	27.9	30.4	25.9
30 – 40	16.7	17.7	16.3	16.9
40 – 50	11.4	12.8	14.2	12.8
50 – 60	9.4	9.8	10.1	9.8
60 – 70	7.0	6.1	6.1	6.4
70 – 80	3.8	3.9	2.5	3.4
>80	2.8	6.1	3.0	4.0
total	121.8	239.3	203.2	188.1

* Sample areas of 20.25 ha (trees > 15 cm dbh) and 4.05 ha (trees 5 – 15 cm dbh) per replication

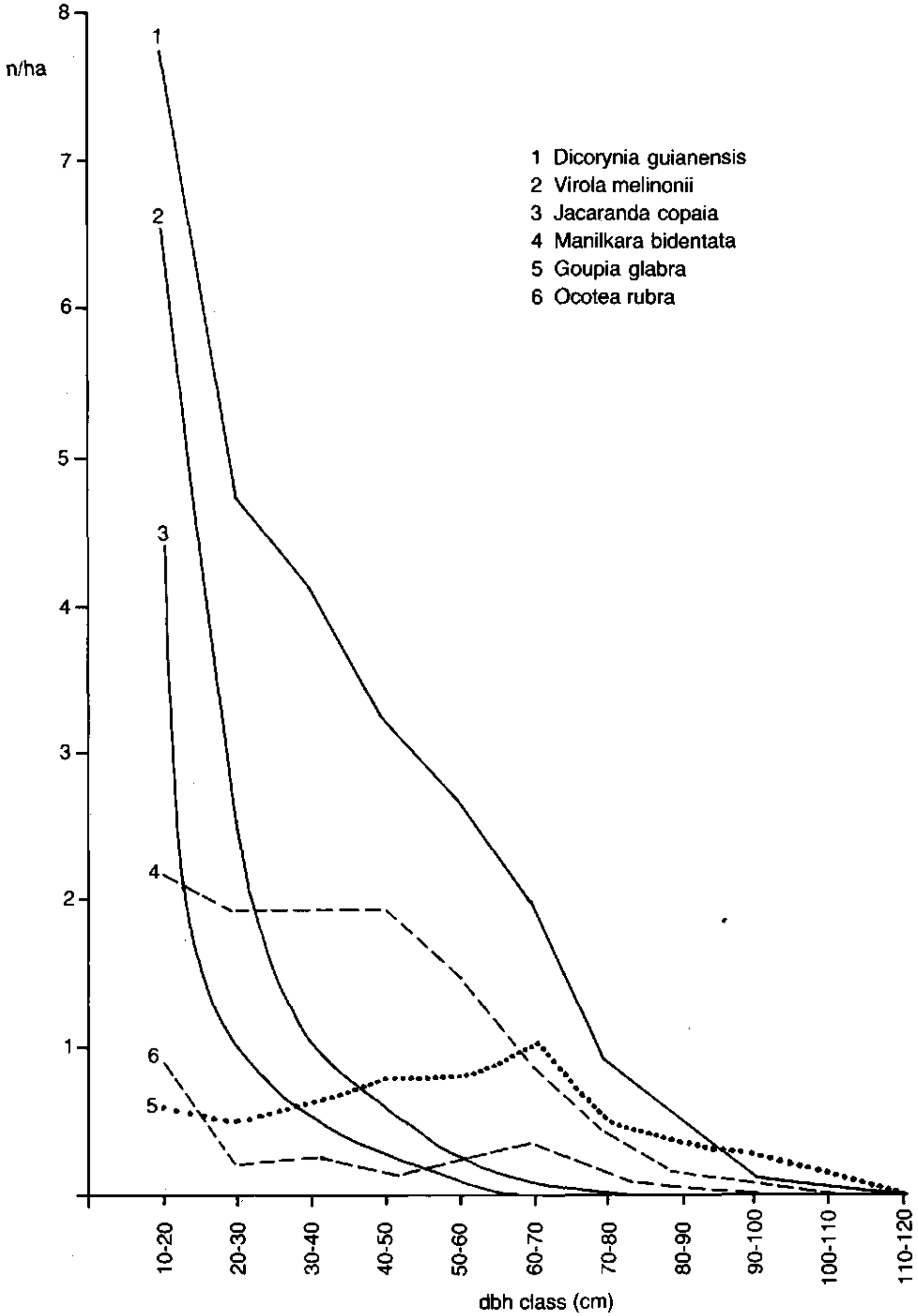


Fig. 4.11 MAIN experiment: size class distributions of six common commercial species

(1974; 1978) described seven types of diameter class distributions, but only four of those apply to species growing to timber size. The most common is the exponential type, which is characteristic for shade tolerant canopy species according to Rollet (for example, basralokus, *Dicorynia guianensis*, in Fig. 4.11) while species with erratic, flattened bell-shaped or approximately linear size class distributions are supposedly light demanding (for example, kopi, *Goupia glabra*, in Fig. 4.11).

Rollet used inventory data from various sources, including Suriname, to support his theory (Table 4.4), and indeed, exponential distributions were found mainly among shade tolerant species, such as basralokus and bergi gronfoeloe (*Qualea rosea*). Most light demanding species, such as kopi, soemaroeba (*Simarouba amara*) and slangenhout (*Loxopterygium sagotii*), had non-exponential distributions. Similar results were obtained in the MAIN experiment (Table 4.5; Fig. 4.11).

There are, however, notable exceptions. Wana (*Ocotea rubra*) is a shade tolerant commercial species which seems to belong to the linear type, and this probably applies also for wanakwari (*Vochysia tomentosa*) and wiswiskwari (*Vochysia guianensis*), while goebaja (*Jacaranda copaia*), a light demanding commercial species, tends to follow the exponential model (Tables 4.4 and 4.5; Fig. 4.11; for light requirements, see Section 5.5). These findings suggest, that light requirement during the initial stages of development is not the only factor determining size class distribution patterns.

Peaks and irregularities in size class distributions are often due to severe disturbance in the past (Rollet, 1974; 1978), and distributions of commercial species provide evidence that such a disturbance has taken place in the MAIN experiment. All species with non-exponential size class distributions show peaks in one of the larger diameter classes (40 – 70 cm dbh), while basralokus and bergi gronfoeloe (*Qualea rosea*), which belong to the exponential type, are slightly over-represented in those classes (Table 4.5; Fig. 4.11). Furthermore, distributions of bolletri (*Manilkara bidentata*) and zwart riemhout (*Micropholis guyanensis var. commixta*),

TABLE 4.4. Mapane region: size class distributions of some commercial species from a survey over 1254 ha

Species	Frequencies (n/ha) per diameter class (cm dbh)							
	25-35	35-45	45-55	55-65	65-75	75-85	85-95	>95
basralokus	1.69	1.42	1.28	0.96	0.60	0.30	0.12	0.05
bolletri	0.44	0.30	0.26	0.22	0.16	0.10	0.07	0.07
goebaja	0.53	0.34	0.11	0.02	0.003	0.00	0.00	0.00
kopi	0.44	0.53	0.56	0.51	0.43	0.32	0.19	0.18
slangenhout	0.16	0.15	0.09	0.06	0.04	0.02	0.002	0.00
wana	0.30	0.26	0.24	0.22	0.16	0.14	0.11	0.15
wanakwari	0.03	0.02	0.02	0.02	0.02	0.03	0.03	0.06
soemaroeba	0.12	0.11	0.12	0.09	0.07	0.05	0.01	0.01

Source: Rollet (1974)

TABLE 4.5. MAIN experiment: diameter class distributions of some commercial species in pristine forest*

Species	Frequencies (n/ha) per diameter class (cm dbh)**									Total
	20-30	30-40	40-50	50-60	60-70	70-80	80-90	90-100	>100	
non-exponential distributions										
slangenhout	0.12	0.16	*0.20*	0.16	0.10	0.02	0.00	0.00	0.00	0.76
kopi	0.51	0.64	0.77	0.81	*0.99*	0.51	0.35	0.28	0.33	5.19
soemaroeba	0.07	0.04	0.08	*0.16*	0.10	0.02	0.05	0.00	0.00	0.52
wiswiskwari	0.15	0.10	*0.18*	0.07	0.02	0.05	0.02	0.00	0.00	0.59
wanakwari	0.03	0.02	0.05	0.03	*0.10*	0.02	0.02	0.00	0.02	0.29
wana	0.16	0.21	0.12	0.20	*0.30*	0.12	0.03	0.02	0.03	1.19
expónential distributions										
goebaja	1.05	0.72	0.33	0.10	0.00	0.00	0.00	0.00	0.00	2.20
okerhout	0.41	0.28	0.10	*0.15*	0.05	0.02	0.00	0.00	0.00	1.01
basralokus	4.70	4.13	3.12	2.65	1.96	0.91	0.49	0.15	0.07	18.18
krapa	1.71	0.79	0.21	0.08	0.00	0.00	0.00	0.00	0.00	2.79
rode sali	1.33	1.21	0.56	0.51	0.15	0.05	0.05	0.00	0.00	3.86
hoogland baboen	2.72	1.02	0.61	0.35	0.05	0.04	0.00	0.00	0.00	4.79
bolletri	1.81	*1.86*	1.83	1.53	0.76	0.44	0.18	0.03	0.05	8.49
zwart riemhout	0.40	*0.51*	0.44	0.35	0.21	0.03	0.02	0.02	0.00	1.98
hoogland gronfoeloe	0.92	0.49	0.25	0.12	*0.23*	0.05	0.05	0.02	0.02	2.15
bergi gronfoeloe	4.51	2.68	2.22	1.70	0.92	0.71	0.58	0.36	0.21	13.89

* Sample area of 60.75 ha (replications 1, 2 and 3)
** Figures in italics indicate peaks in size class distribution

two slow growing Sapotaceae of the exponential type, show flattened peaks in the 30 – 40 cm class.

The most likely explanation for these irregularities is that an exceptionally heavy local storm during the 19th century caused a large number of chablis of various sizes and shapes, and stimulated recruitment of both light demanding and shade tolerant species. Schulz (1960) mentioned the damage caused by a similar storm in the 1950s in the Upper Coesewijne region, about 25 km east of Tonka research area (see also Section 1.1.2). Experience in hurricane areas (see Brown et al., 1983) and results from a study on long-term effects of earthquakes in Panama and Papua New-Guinea (Garwood et al., 1979) show that tropical rain forest is capable of recovery after such disturbance.

Data presented in Table 4.5 and Fig. 4.11 indicate that a heavy storm has a clear and lasting effect upon non-exponential diameter class distributions, while irregularities in exponential distributions are less distinct and tend to gradually fade. This is a result of differences in "survival strategy" between groups of species. Light demanding (non-exponential) species respond to severe disturbance with a marked peak in recruitment, while response of shade tolerant (exponential) species is usually less spectacular. Variation in increment may be relatively small for species with non-exponential distributions and mortality rates are low compared to species of the exponential type. Growth data for wana reported by Schulz (1960) indeed show little variation. Kopi, on the other hand, is highly variable in growth but shows very distinct peaks in recruitment (Schulz, 1960).

These results suggest a hypothesis on patterns in size class distributions of canopy species which differs slightly from Rollet's. Exponential diameter class distributions are found mainly among species able to establish themselves under a comparatively wide range of microclimatic and other environmental conditions, most of which may be characterized as shade tolerant. As most individuals of such species are growing in sub-optimal environments, mortality is relatively high and variation in increment is considerable, resulting in a sharp and fairly regular decline of tree numbers in consecutive size classes. If such a sharp decline is absent, the species concerned requires more specific conditions for its initial development and in most cases, light is probably the limiting factor. After this initial stage, mortality is low and variation in growth rate may be relatively small. The implications for forest management are discussed in Section 4.4.

4.3.3 Spatial variation in tree species composition

The MAIN experiment area is almost homogeneous in soil and physiography (Section 4.1.1), but differences in species composition were nonetheless observed in the field, forming an intriguingly ill-defined pattern. Two ordinations were carried out to detect the origin of such differences, one based on pre-felling frequencies of commercial species in 2.25 ha plots, the other based on post-harvest data of all species in one-hectare plots (for methodology, see Section 3.1.4). In the ordination in selectively logged forest, felled trees were treated as if they were still alive, and the effect of felling on the results is probably small. Logging damage was considered to be of little consequence, firstly because mortality as result of logging was low, and secondly because it probably affected all species in a similar way (see Chapter 5). The ordinations gave more distinct results which indicate that floristic variation in the MAIN experiment is related to abiotic as well as biotic factors. The nature of these factors will be discussed in Section 4.4, together with the results from the Van Leeuwen transect (Section 4.2).

Commercial species. Thirty-seven commercial species were identified among the trees larger than 15 cm dbh in an enumerated area of 67.5 ha, of which basralokus (*Dicorynia guianensis*, 22 trees/ha) and bergi gronfoeloe (*Qualea rosea*, 18 trees/ha) were the most common. The ten other species recorded 100 or more times were, in descending order, bolletri (*Manilkara bidentata*, 9 trees/ha), hoogland baboen (*Virola melinonii*, 7 trees/ha), kopi (*Goupia glabra*, 6 trees/ha), rode sali (*Tetragastris altissima*, 5 trees/ha), krapa (*Carapa procera*, 4 trees/ha), goebaja (*Jacaranda copaia*, 4 trees/ha), hoogland gronfoeloe (*Qualea albiflora*, 3 trees/ha), zwart riem-

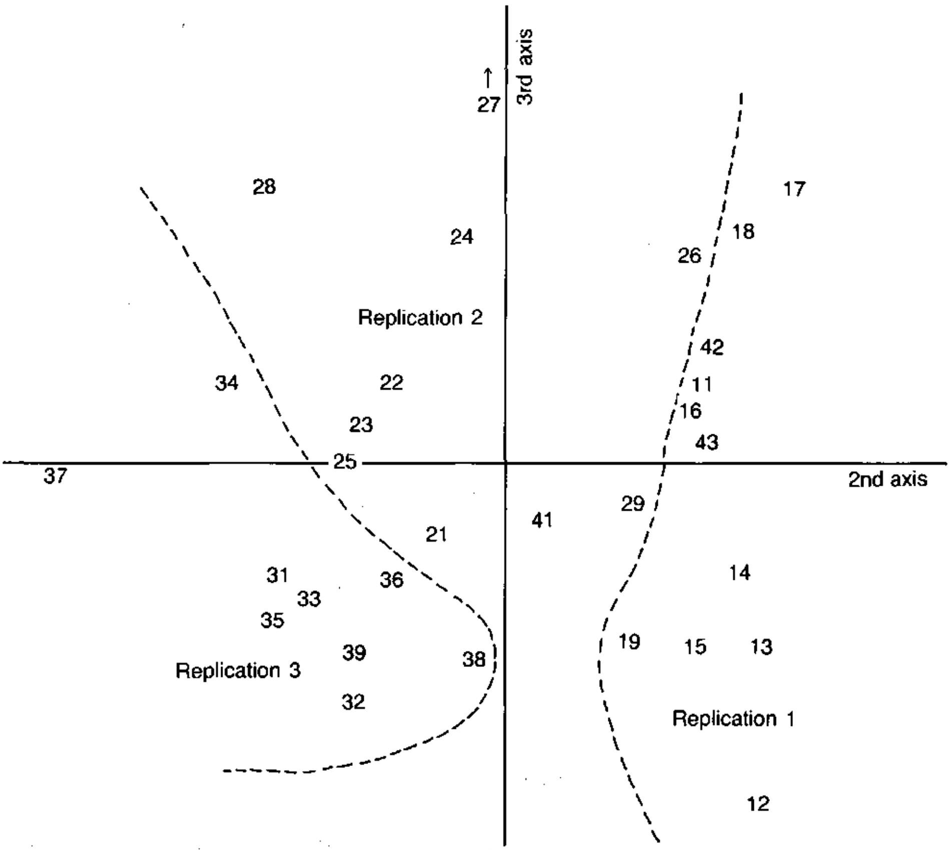


Fig. 4.12a MAIN experiment: ordinated arrangement of plots, based on pre-felling frequencies of commercial species

hout (*Micropholis guyanensis var. commixta,* 2 trees/ha), wana (*Ocotea rubra,* 2 trees/ha) and tingimonisali (*Tetragastris hostmannii,* 2 trees/ha). Okerhout (*Sterculia spp.,* 1.4 trees/ha) was also fairly common. The other 24 species were represented less than once per hectare.

The ordination of plots resulted in a structured arrangement (Fig. 4.12 A). Plots are grouped by replication and the arrangement of replications reflects their geographical positions. Ordinated positions of plots within replications seem less orderly, although it is just possible to identify groupings by slope.

Two sets of plots will be used to illustrate differences indicated by the ordination, the first set being the central plots 15, 25 and 35 in replications 1, 2 and 3. The ordination suggests a small disparity in species composition between plots 25 and 35 and a more marked difference between these two and plot 15. Floristic affinity between plots 25 and 35 was strong indeed (Table 4.6), and although in plot 35 basralokus and kopi were better represented and rode sali notably absent, frequencies

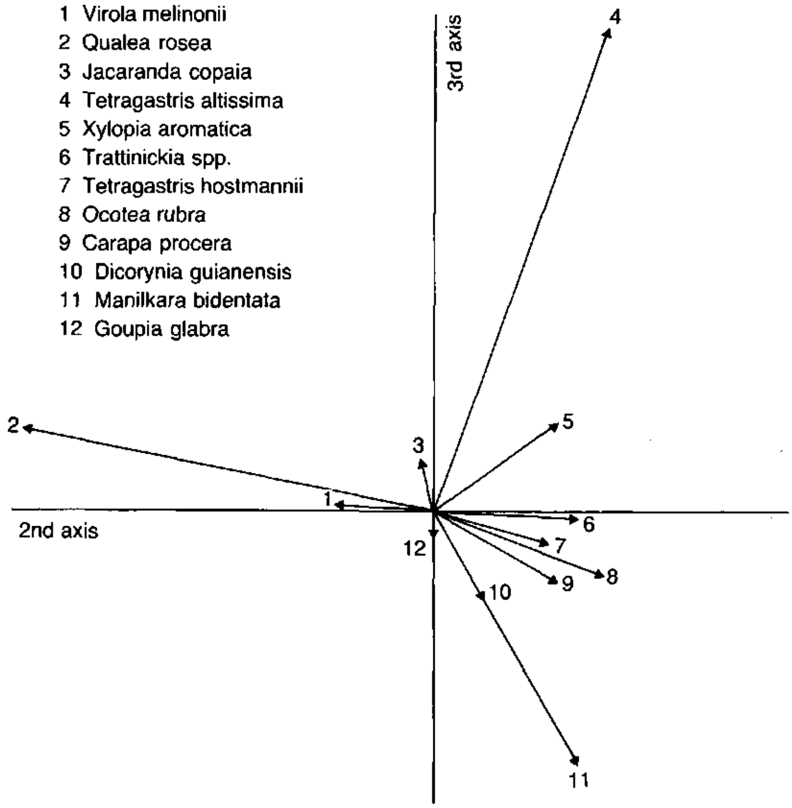


Fig. 4.12b MAIN experiment: approximated impacts of selected species on ordinated arrangement in Fig. 4.12a

of the other species were similar. Differences between these plots and plot 15 were more distinct, the latter being much poorer in commercial trees. This was mainly due to an obvious difference in stocking of bergi gronfoeloe, namely about 30 trees/ha in plots 25 and 35 compared to 2 trees/ha in plot 15 (Table 4.6). Bolletri was markedly more abundant in plot 15 than in the other plots, but variations in stocking of other species were not spectacular.

The second set consists of plots with extreme scores on the ordination axes (plots 12, 27 and 37), whose ordinated positions indicate a maximum in floristic variation. The stand in plot 12 was poorer than those in the other two plots and species composition was distinctly different, particularly the frequencies of bergi gronfoeloe, hoogland baboen, bolletri and wana (Table 4.6). Plot 27 can be described as an outlier, characterized by an exceptionally high frequency of one species, rode sali. High frequencies of bergi gronfoeloe and hoogland baboen and the absence of three common species, including rode sali, were characteristic of the commercial stand in plot 37. Differences in frequencies of species other than these five were not substantially greater than differences between their frequencies in plots 15, 25 and 35.

The two examples illustrate that although floristic variation in the MAIN experiment was small for such a large tract of tropical rain forest, it was by no means

TABLE 4.6. MAIN experiment: pre-felling frequencies of common commercial species in selected 2.25 ha plots

Species	Numbers of trees per hectare					
	Plot 15	Plot 25	Plot 35	Plot 12	Plot 27	Plot 37
basralokus	28.0	26.7	36.9	20.4	20.0	25.3
bergi gronfoeloe	2.2	30.7	28.4	1.8	27.6	40.9
bolletri	14.7	9.3	7.1	23.6	3.6	4.0
hoogland baboen	4.4	6.7	9.8	1.8	6.2	13.8
kopi	6.7	4.9	9.8	4.0	6.7	7.6
rode sali	2.7	4.0	0.0	0.4	26.7	0.0
krapa	3.6	1.3	0.9	4.0	2.2	0.4
goebaja	2.7	4.0	4.4	2.7	4.0	5.3
hoogland gronfoeloe	1.8	3.6	2.2	1.8	3.6	4.4
zwart riemhout	0.9	2.2	2.2	1.3	3.1	0.9
wana	2.7	1.8	0.4	3.1	0.4	0.0
tingimonisali	2.2	1.3	0.9	1.3	0.4	0.0
okerhout	0.9	0.0	1.8	1.8	1.8	0.4
other species	4.2	7.6	5.3	10.7	3.1	11.1
total	77.8	104.0	110.2	78.7	109.3	114.2

negligible, and that the ordinated arrangement of plots is a result of many small and a few large differences in species composition. The contributions of selected individual species to this arrangement are represented by the lengths and directions of the vectors shown in Fig. 4.12 B. That of zwart riemhout, hoogland gronfoeloe and the light demanding species kopi, goebaja and okerhout were small, but the vector lengths of other common species proved more substantial. The ordination technique is such that a species of low average stocking, such as pegrekoepisi (*Xylopia spp.*) and ajawatingimoni (*Trattinickia spp.*), may have a notable influence on the arrangement of plots if it is fairly frequent locally and rare or absent elsewhere (Fig. 4.12 B). Ajawatingimoni was common in replication 1 (2 trees/ha) and rare elsewhere. Pegrekoepisi was found only 13 times in the whole area, in plots 26 and 43 and a few plots of replication 1.

The impact of bergi gronfoeloe, rode sali and bolletri on the ordination of plots is more noticeable than those of other species, the first two species showing marked preferences for certain areas of the experiment. Bergi gronfoeloe was the most abundant commercial species in most plots on the southern plateau, but was relatively infrequent (0 – 10 trees/ha) in replication 1, the south-east corner of replication 2 (plots 26 and 29) and the virgin forest plots 42 and 43. Rode sali was common in most plots of replication 1 and 2 and the virgin forest plots, but was rare in replication 3. Bolletri was well represented throughout the experiment, but was more abundant in plots 12, 15, 32, 38 and 39 than elsewhere.

All species. The MAIN experiment was rich in species, with 193 vernacular names recorded among 7354 trees larger than 15 cm dbh in the 30 one-hectare plots. About 20 commercial species and 55 non-commercial species were recorded per hectare. The total figure of 75 species per hectare is considerably lower than values quoted in Section 1.3, because of the high minimum diameter adopted in the enumeration (see Hladik, 1986). Taking into account that many understorey species seldom reach 15 cm dbh, the total number of tree species per hectare was probably between 100 and 150.

Average frequencies of the 16 most common species, eight of which are commercial and eight non-commercial, are listed in Table 4.7. Frequencies of commercial species were similar to the pre-felling figures of the first ordination. By far the most abundant non-commercial species was rode jakanta (*Dendrobangia boliviana*), a tree which may reach up to 60 cm dbh. Djadidja (*Sclerolobium melinonii*) and boskatoen (*Bombax spp.*) also grow to large sizes. Hoogland oemanbarklak (*Lecythis corrugata*), swietiboontje (*Inga spp.*), fomang (*Chaetocarpus schomburgkianus*), hoogland anaura (*Couepia spp.*) and bergi bebe (*Swartzia benthamiana*) seldom exceed 40 cm dbh, although fomang with large diameters has occasionally been reported (Rollet, 1974). Swietiboontje is a fast growing, light demanding species, but the other non-commercial species listed in Table 4.7 are more shade tolerant.

The 16 species listed in Table 4.7 account for 59% of the total number of trees in the MAIN experiment and all were found in at least 90% of the plots, except rode sali. Kopi, goebaja and boskatoen were fairly evenly distributed and spatial variations in stocking of krapa, hoogland anaura and bergi bebe were also comparatively low (Table 4.7). Frequencies per plot of the other ten species were highly variable.

The ordination resulted in an arrangement of plots similar to that based on commercial species only (Fig. 4.12 A and 4.13 A), except for the positions of plots 27, 38 and 43. The exceptional number of rode sali trees in plot 27, that was mentioned when discussing the first ordination (see Table 4.6), was due to a

TABLE 4.7. MAIN experiment: post-felling average frequencies (n/ha) of common species in one-hectare plots, with standard deviations (SD)*

Species	n/ha	SD	Species	n/ha	SD
commercial			non-commercial		
basralokus	23.8	10.9	rode jakanta	19.5	19.1
bergi gronfoeloe	18.2	15.2	hoogland oemanbarklak	11.3	7.8
bolletri	9.2	4.8	fomang	7.7	4.8
hoogland baboen	7.4	4.3	swietiboontje	7.3	4.4
kopi	6.1	2.5	djadidja	5.9	4.2
rode sali	5.5	5.5	hoogland anaura	5.3	3.5
krapa	4.2	2.9	bergi bebe	5.3	2.7
goebaja	4.2	1.9	boskatoen	3.7	1.8
other species (29)	12.5	n.a.	other species (148)	88.0	n.a.
all commercial species	91.1	n.a.	all non-commercial species	154.0	n.a.

* Trees > 15 cm dbh, including cut stumps, in a sample area of 30 ha

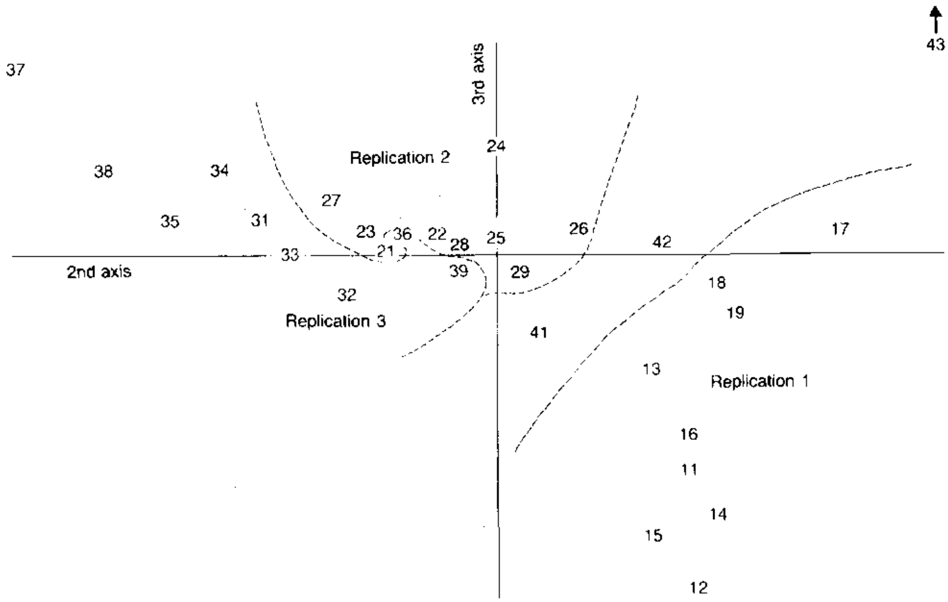


Fig. 4.13a MAIN experiment: ordinated arrangement of plots, based on post-felling frequencies of all tree species

concentration of this species outside the one-hectare plot and does not affect the outcome of this ordination. The somewhat divergent position of plot 38 in Fig. 13 A is a result of a high frequency of rode jakanta (74 trees/ha), whereas the deviation of plot 43 is due to the presence of nine species not found elsewhere in the experimental area.

All common species with distinctly variable spatial distributions (SD > 4 in Table 4.7) had a substantial impact on this arrangement and the analysis revealed their clear preferences for certain parts of the experiment area (Fig. 4.13 B). The two most common non-commercial species seemed to prefer different sites. Rode jakanta was found in very large numbers (44 – 74 trees/ha) west of the water divide in replication 3, but was comparatively poorly represented (less than 10 trees/ha) in replication 1, plot 43 and the central-southeastern area of replication 2. Hoogland oemanbarklak, on the other hand, was almost absent west of the water divide in replication 3 and abundant (21 – 33 trees/ha) in the southern part of replication 1 and plot 43.

The spatial distribution of relatively short-living, light demanding species which require hot and dry conditions for seed germination (pioneer species) also showed a definite pattern. Virtually all these species, such as kromanti kopi (*Aspidosperma album*) and granboesi papaja (*Pourouma spp.*), were locally abundant in replication 1 and the virgin forest plots and almost absent elsewhere, as indicated by the length of their vectors in Fig. 4.13 B. The contrast with the distributions of other light-demanding species is striking. For example, kopi and goebaja were evenly distributed over the experimental area and swietiboontje was more common on the southern

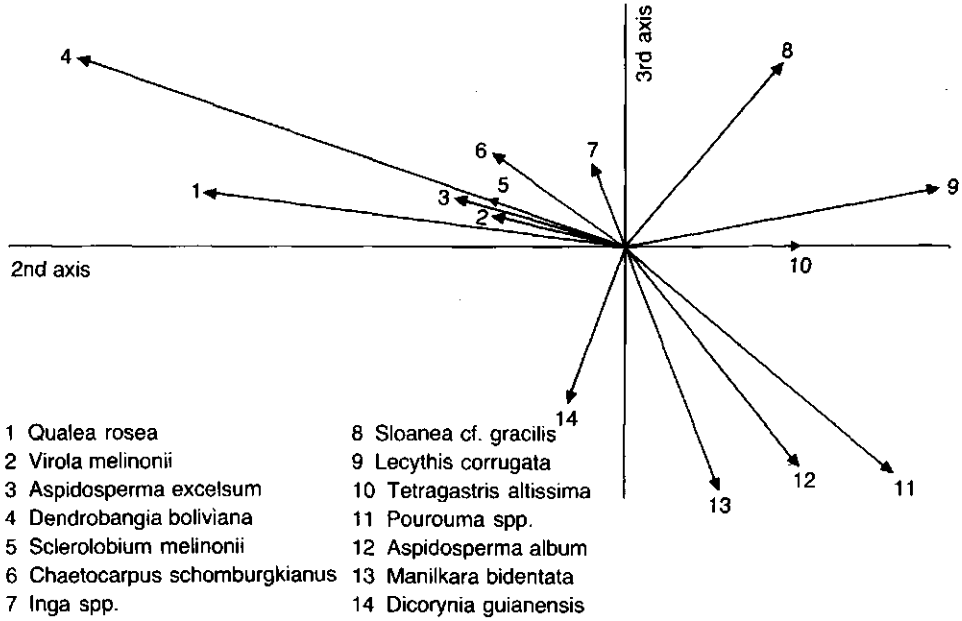


Fig. 4.13b MAIN experiment: approximated impact of selected species on the ordinated arrangement in Fig. 4.13a

plateau than in replication 1. Boskoeswé (*Sloanea cf. gracilis*), a stilt-rooted species which is believed to germinate on decaying fallen stems, was the only pioneer species occurring fairly frequently in replications 2 and 3 (Fig. 4.13 B).

4.3.4 Small-scale patterns in spatial distributions of trees

Spatial distribution patterns within one-hectare plots were analysed with Greig-Smith's χ^2 nested type test (for methodology, see Section 3.1.4). About 300 tests were carried out for various categories of trees to detect clumped and regular patterns in homogeneous physical environments, information which is of silvicultural importance. Refinement aims at improving light conditions and nutrient availability for the commercial stand by poison-girdling non-desirable trees above a specified diameter limit (Section 2.2). Such a treatment functions inadequately if spatial arrangements of commercial and non-commercial trees are distinctly contagious (clumped). Hence, patchy distribution patterns would indicate a need for adjustment of the Celos Silvicultural System, and regular patterns would indicate that no adjustment is necessary where site conditions are favourable. All tests are based on data collected after logging had been completed, including cut stumps in some cases.

Small-scale patterns for all commercial species were studied in all plots of the MAIN experiment, including the virgin forest plots. Significantly contagious distributions were found in only four plots (11, 25, 33 and 39) and significantly

TABLE 4.8. MAIN experiment: spatial distribution of trees of commercial species, using Greig-Smith's χ^2 nested type test*

Item	Mean squares (MS)			Frequency P = 0.05 significance	
	Average	Lowest	Highest	MS > 1	MS < 1
within 4s	0.96	0.60	1.48	1	1
between 4s within 16s	0.96	0.28	1.45	0	1
between 16s	1.46	0.20	6.77	3	1
total	0.97	0.51	1.41	0	0
number of significant tests				4	0

* 27 tests in logged-over forest, 3 tests in pristine forest

regular patterns in none (Table 4.8). The test results therefore suggest neither a clumped nor a regular pattern, but as the averages of MS values are almost unity, they compare to a random Poissonian distribution. Similar results were obtained from tests of individual commercial species (Table IV.2, Appendix IV), and only bergi gronfoeloe (*Qualea rosea*) showed a slight tendency to clumping.

Spatial distribution of non-commercial trees was investigated in the 27 logged-over plots and again, the results do not suggest a contagious or regular pattern. None of the tests gave a significant result (Table 4.9), MS values mostly being less than unity, which suggests a more even distribution than the Poissonian model. Tests for individual non-commercial species do not indicate any tendencies towards clumped or uniform patterns (Table IV.2, Appendix IV), except for swietiboontje (*Inga spp.*) and djadidja (*Sclerolobium melinonii*). These species may be of patchy occurrence, but there is insufficient evidence for definite conclusions.

Spatial patterns among trees within the same diameter class (Table IV.1, Appendix

TABLE 4.9. MAIN experiment: spatial distribution of trees of non-commercial species, using Greig-Smith's χ^2 nested type test*

Item	Mean squares (MS)			Frequency P = 0.05 significance	
	Average	Lowest	Highest	MS > 1	MS < 1
within 4s	0.81	0.46	1.25	0	1
between 4s within 16s	0.87	0.43	1.57	0	0
between 16s	0.79	0.00	2.52	0	3
total	0.82	0.51	1.10	0	2
number of significant tests				0	0

* 27 tests in logged-over forest

IV) were also studied, using separate tests for commercial trees and all trees in four diameter classes. Again, deviations from random expectations were generally not significant, with averages of MS values close to unity.

Small-scale spatial distribution patterns for tree species, species groups and size classes do not, therefore, seem to be contagious or regular in a homogeneous physical environment, but appear to fit a Poissonian distribution, in which trees are located at random distances from randomly selected centres. Spatial arrangement of commercial trees in virgin forest plot 41 is a typical example of such a pattern (Fig. 4.14). The 101 trees were distributed almost exactly according to random

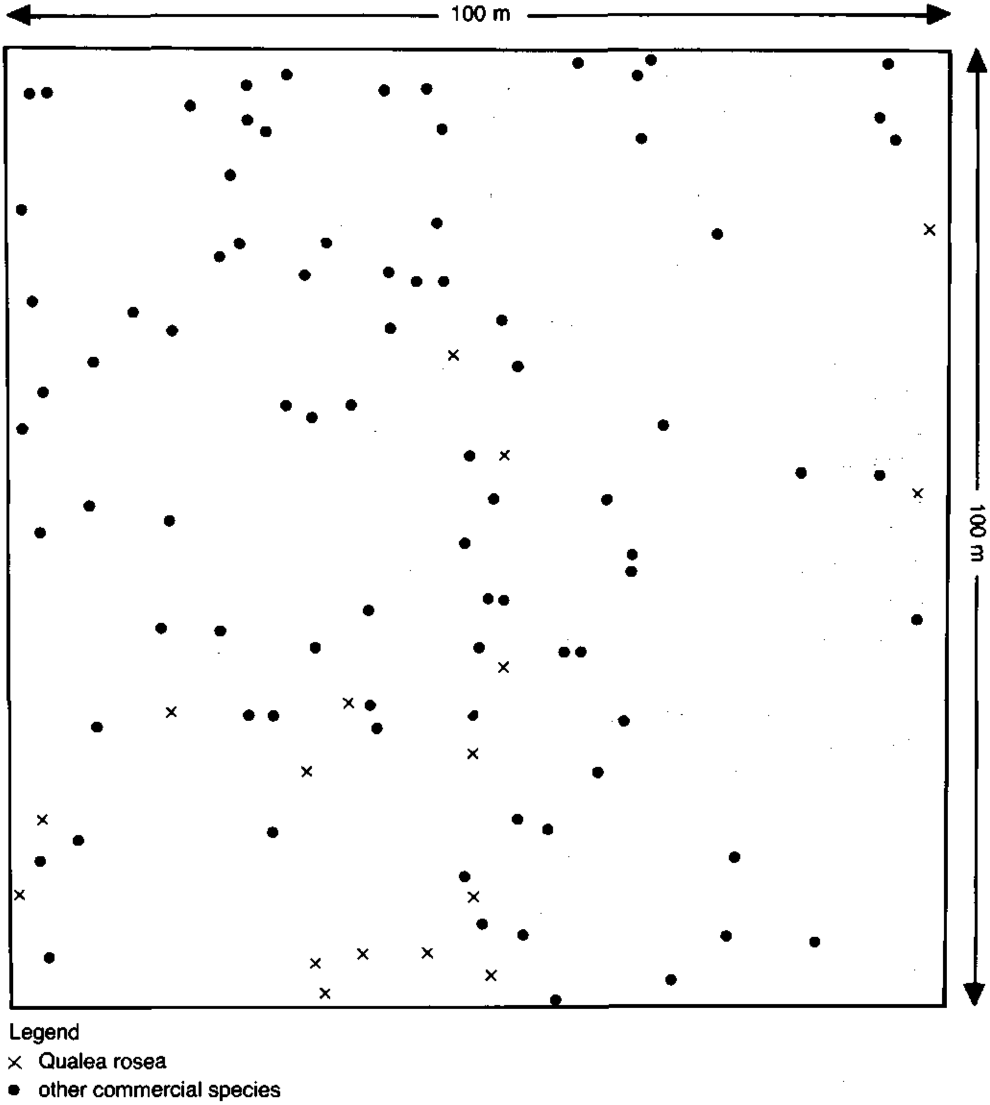


Fig. 4.14 MAIN experiment: spatial distribution of commercial species in plot 41

expectations, which means that areas of high, medium and low density were present. Certain pockets were devoid of commercial trees. Poison-girdling of all non-commercial trees exceeding 20 cm dbh virtually destroys the canopy in such pockets, resulting in dense regrowth of secondary species and severe competition for recruitment of commercial species, but a treatment which leaves part of the canopy intact is likely to permit good growth of commercial regeneration. Fig. 4.14 also shows a significantly contagious distribution of bergi gronfoeloe, which was concentrated in the south-west area.

4.3.5 Spatial distribution of seedlings and saplings

Seedlings and saplings were tallied in small sub-samples within replications 1 and 2, a few years after logging had been completed (Section 3.1.3). More than 20000 seedlings and approximately 2000 saplings were recorded per hectare, including some 5000 seedlings and 300 saplings of commercial species (Table 4.10). It seemed that all commercial species, except bolletri (*Manilkara bidentata*), regenerated well in logged-over forest, an aspect which will be discussed in Section 5.5.

Differences in species composition between replications 1 and 2 are evident (Table 4.10), and mostly correspond with floristic differences between tree populations (see Section 4.3.3). Replication 2 had more seedlings and saplings of commercial species, especially of bergi gronfoeloe (*Qualea rosea*), than replication 1 did. Many young swietiboontje (*Inga spp.*) and other light demanding non-commercial species were found. Swietiboontje, which was more abundant in replication 2 than in replication 1, requires greatly increased illumination for growth but not for germination (see Poncy, 1985). It is known to grow rapidly in refined forest (de Graaf, 1986) and may severely compete with commercial species after silvicultural treatment. Recruitment of pioneer species such as boskoeswé (*Sloanea cf. gracilis*), kromanti kopi (*Aspidosperma album*), granboesi papaja (*Pourouma spp.*), boroma (*Cecropia peltata*) and panga panga (*Palicourea guianensis*), however, was more plentiful in replication 1 than in replication 2, despite more severe logging damage in replication 2 (see Chapter 5).

According to Schulz (1960), "the seeds of most species are dispersed over very short distances only and consequently, there is a great concentration of seeds and seedlings beneath and around the parent trees". If this were true, it would be difficult to regenerate parts of the forest devoid of commercial trees by a natural regeneration technique. The local distribution of commercial tree seedlings was therefore investigated (Section 3.1.4).

In the MAIN experiment, seedlings of commercial species were mostly found at substantial distances from the nearest seed source (Table 4.11). Seed dispersal mechanisms of most commercial species seem very effective, although inter-tree distances for the most common species (basralokus and bergi gronfoeloe) were too small for a meaningful analysis. Krapa (*Carapa procera*) is a notable exception as its large, heavy seeds are dispersed by agoutis and other rodents. Most fallen seeds

TABLE 4.10. MAIN experiment: post-felling frequencies (n/ha) of seedlings* and saplings** of individual species in replications 1 and 2

Species	Seedlings (n/ha)		Saplings (n/ha)	
	Replication 1	Replication 2	Replication 1	Replication 2
commercial				
basralokus	365	313	17	31
bergi gronfoeloe	17	799	8	86
bolletri	0	69	3	22
hoogland baboen	521	556	42	22
kopi	104	399	0	8
rode sali	955	608	6	22
goebaja	295	156	8	6
others	2 101	2 551	167	150
subtotal	4 358	5 451	250	347
non-commercial				
rode jakanta	69	365	6	69
hoogland oemanbarklak	313	278	14	47
swietiboontje	2 656	4 635	153	331
djadidja	868	1 319	17	19
hoogland anaura	69	174	3	28
boskoeswe	260	104	19	22
kromanti kopi	1 718	17	6	6
granboesi papaja	677	139	100	6
boroma	538	35	75	0
panga panga	1 319	208	358	36
others	8 892	9 289	716	1 386
subtotal	17 379	16 563	1 467	1 950
total	21 137	22 014	1 717	2 297

* 0.2 – 2 m total height, in a sample area of 576 m^2 per replication
** 2 m total height – 5 cm dbh, in a sample area of 0.36 ha per replication

are removed from beneath the mother tree within a few hours (Maury-Lechon and Poncy, 1986), but those which survive and germinate are seldom moved over long distances and seedlings were therefore found concentrated within a radius of 15 m from the mother tree.

Another species whose seedlings were often found near potential seed sources was kopi (*Goupia glabra*), but in this case the seed sources were usually felled trees. The seeds are known to be dispersed by spider monkeys and other mammals, which generally swallow the fruits whole and do not digest the seeds (van Roosmalen, 1980; 1985). These dispersal agents forage around kopi trees when the fruits are ripe, and the spatial distribution of seedlings suggests that they deposit their excrement, with kopi seeds in it, near the trees. Kopi is a light demanding species and seeds may remain dormant in the soil for years, only germinating when a large opening is formed. Felling and extraction of kopi trees therefore creates the conditions necessary for the establishment of their offspring (see also Section 5.5).

Seedlings of most other light demanding species, such as slangenhout (*Loxopterygium sagotii*), pegrekoepisi (*Xylopia spp.*) and goebaja (*Jacaranda copaia*), were found nearly always far from the nearest seed source. The same was true for wana (*Ocotea rubra*), a shade tolerant species which may require special conditions for its establishment (see Section 4.3.2).

4.3.6 Palms and lianas

Palms and lianas are of considerable interest to the silviculturist, because they actively compete with tree species for light, space and nutrients. The spatial distributions of these plants were investigated and compared with the distributions of trees (see also Section 4.4). Palms exceeding 1.5 m in total height were tallied shortly before silvicultural treatment (Section 3.1.3). Lianas greater than 5 cm in diameter were sampled after refinement, mainly to assess the efficiency of the liana cutting operation (Section 3.1.3).

Lianas. Woody climbers are very evident in almost all neotropical rain forests, but surprisingly little quantitative information on liana abundance has been published (see Putz, 1983; 1984; Rollet, 1969; 1983; Hladik, 1986). Lianas were numerous in the study area, but very thick individuals were rare (Table 4.12). Approximately 70

TABLE 4.11. MAIN experiment: numbers of seedlings of commercial species in relation to the distance to the nearest seed source

Species	Number of seedlings	Percentage of number of seedlings		
		Distance < 5 m	Distance 5 – 15 m	Distance > 15 m
pegrekoepisi	12	0	0	100
wana	18	0	0	100
slangenhout	42	0	10	90
goebaja	28	0	21	79
tingimonisali	89	7	17	76
kopi*	29	7	55	38
rode sali	89	8	48	44
basralokus	39	3	72	26
bergi gronfoeloe	46	7	78	15
hoogland baboen	62	18	16	66
wiswiskwari	12	25	8	67
krapa	16	13	63	25
others	76	5	16	79
all commercial species	588	6	32	61

* Nearest seed source nearly always a cut stump

TABLE 4.12. MAIN experiment: frequencies of lianas per replication and per diameter class in non-refined plots*

Diameter class (cm)	Numbers per hectare		
	Replication 1	Replication 2	Replication 3
5 – 10	48.3	60.0	76.7
10 – 15	3.3	8.3	5.0
>15	3.3	3.3	5.0
total	55.0	71.6	86.7

* Sample area of 0.6 ha per replication

climbers larger than 5 cm diameter were recorded per hectare, a figure which is comparable to values reported by Putz (1984) for Barro Colorado Island in Panama (84 climbers larger than 4 cm in diameter; 43 climbers larger than 5 cm in diameter), but distinctly higher than estimates published by Rollet (1969) for Venezuelan Guiana (22 climbers larger than 5 cm in diameter). No attempt was made to identify lianas to genus or species, and the sample sizes were too small for a detailed analysis of their spatial distribution. The evidence suggests that there were substantial differences between replications, however, as relatively few lianas were found in replication 1, and higher than average numbers in replication 3 (Table 4.12).

Palms. The abundance of palms is conspicuous in many rain forests in Suriname, and in the MAIN experiment, more than 750 palms of at least 1.5 m total height were counted per hectare (Table 4.13). Most belong to the *Astrocaryum* species boegroemaka (*A. sciophilum*) and paramaka (*A. paramacca*), but koemboe (*Oenocarpus bacaba*), maripa (*Maximiliana maripa*, synonym: *Attalea regia*) and nanaimaka (*Bactris sp.*) were also found frequently. Other species were infrequent. The presence of the swamp species tassi (*Geonoma baculifera*) and pina (*Euterpe oleracea*) on well-drained soils is noteworthy.

Boegroemaka and paramaka are both understorey species which grow very slowly in the shade and hardly seem to respond to improvements in light conditions (see Schmidt, in press). Boegroemaka has large leaves and a short stem, is often gregarious, and tends to form a dense canopy at 5 – 12 m above the ground, while paramaka is a stemless palm with large leaves which may reach heights of about 3 m. It seldom dominates the understorey and seems to be less agressive than boegroemaka.

The configuration of the leaves makes both *Astrocaryum* palms very effective in intercepting falling litter. This qualifies them as "trash-basket plants" (de Granville, 1977; Raich, 1983), and both palms are likely to derive most nutrients from decaying organic debris accumulated at the crown base and around the stem foot. This decomposing litter forms the microhabitat for a variety of litter-dwelling lizards, snakes and other animals of the herpetofauna (Gasc, 1986).

Boegroemaka was recorded in replication 1, the south-east corner of replication 3 and a few patches in replication 2 (Table 4.13). It was distinctly gregarious in replication 1, where as many as 1105 individuals were found per hectare, and where it seemed to suppress effectively the regeneration of trees, other palms and lianas (see also Section 4.4). The same phenonomon was reported by van Roosmalen (1980). Schmidt (in press) estimated the dry weight of boegroemaka leaves in a comparable

TABLE 4.13. MAIN experiment: frequencies of palm species > 1.5 m total height per one hectare plot and per replication

Plot	Frequencies (n/ha) per species						All species (n/ha)
	Boegroemaka	Paramaka	Nanaimaka	Koemboe	Maripa	Other species	
replication 1							
11	1069	38	43	25	86	10	1271
12	1384	58	84	67	4	10	1607
13	1335	38	50	40	27	5	1495
14	651	85	67	46	73	7	929
15	1475	2	29	50	1	15	1572
16	1111	7	54	76	77	10	1335
17	845	13	28	25	48	19	987
18	1090	1	21	39	52	9	1212
19	977	1	23	16	30	4	1051
mean	1105	27	44	43	44	10	1273
replication 2							
21	10	243	30	155	85	1	524
22	90	197	59	113	126	3	588
23	235	154	58	74	80	6	607
24	0	206	61	163	123	6	559
25	0	175	71	88	181	3	518
26	4	212	74	44	112	4	450
27	0	159	47	120	56	2	384
28	0	258	60	112	10	9	449
29	0	180	67	39	90	4	380
mean	38	198	59	101	96	4	495
replication 3							
31	0	435	31	124	71	1	662
32	0	283	67	74	81	2	507
33	1	239	32	37	41	5	355
34	0	163	23	103	2	6	297
35	0	275	13	157	29	1	475
36	224	150	21	37	9	0	441
37	0	243	31	65	3	10	352
38	323	274	22	90	7	12	728
39	659	168	23	64	98	0	1012
mean	134	248	29	83	38	4	537

forest in Kabo research area at 8 t/ha, that is, about half of the total leaf phytomass. The tally of palms did not extend to the virgin forest plots, but this palm was at least as abundant in plots 42 and 43 as in replication 1.

Greig-Smith's χ^2 test, which was used to analyse small-scale distribution patterns of the five most common palms (Section 3.1.4), revealed a significantly contagious pattern for boegroemaka (Table IV.3, Appendix IV; Fig. 4.15), meaning that the boegroemaka canopy was of variable density. Patches of relatively low density included felling gaps and skid trails, where the boegroemaka canopy was still clearly discontinuous three years after logging.

Paramaka was recorded in all 27 plots included in the tally, but was less common in replication 1 than elsewhere (Table 4.13). The boegroemaka and paramaka populations appeared to be almost fully segregated (Table 4.13; Fig. 4.15), which either may indicate that they prefer different sites, or that the stemless paramaka palm is unable to survive under the boegroemaka canopy. Small-scale distribution of paramaka was significantly clumped in nine plots (Table IV.3; Fig. 4.15), suggesting that this palm may impede regeneration of timber species locally. This would, however, have little effect on the future development of the commercial stand.

Nanaimaka is an inconspicuous undergrowth palm, which was found throughout the experiment, with a random or slightly contagious small-scale distribution (Table 4.13; Table IV.3). The species is unlikely to impede growth and regeneration of commercial species significantly (see also de Granville, 1978).

Koemboe and maripa may reach heights of 20 m or more, and compete for light with small and medium-sized trees. Two growth phases are distinguished, the first being an "establishment growth" phase during which the palm is stemless and develops a mature crown and, the second being a phase during which the stem is growing in height and crown size remains fairly constant (see de Granville, 1978). Most individuals recorded in the MAIN experiment were stemless and did not exceed 5 m in total height. Both species were found in all 27 plots, but frequencies per plot varied considerably (Table 4.13). Small-scale distribution of maripa was significantly contagious, although it was not seen to form dense clumps, whereas the distribution of koemboe was only slightly patchy (Table IV.3). Both palms are known to grow taller fairly rapidly when light conditions are favourable (see de Granville, 1978), and they may retard the development of the commercial stand after refinement.

4.4 Discussion

The results presented in this chapter do not indicate the need for any major modifications to the Celos Silvicultural System. Application of CSS is likely to result in attractive sustained yields (see Section 4.3.2), but spatial variation in floristic composition indicates that minor changes in the system are necessary, and there is also a need for regulations to prevent over-cutting.

Spatial variation in tropical rain forest seems to result from ecological processes and from variations in physical site factors. Soil and physiography in the MAIN

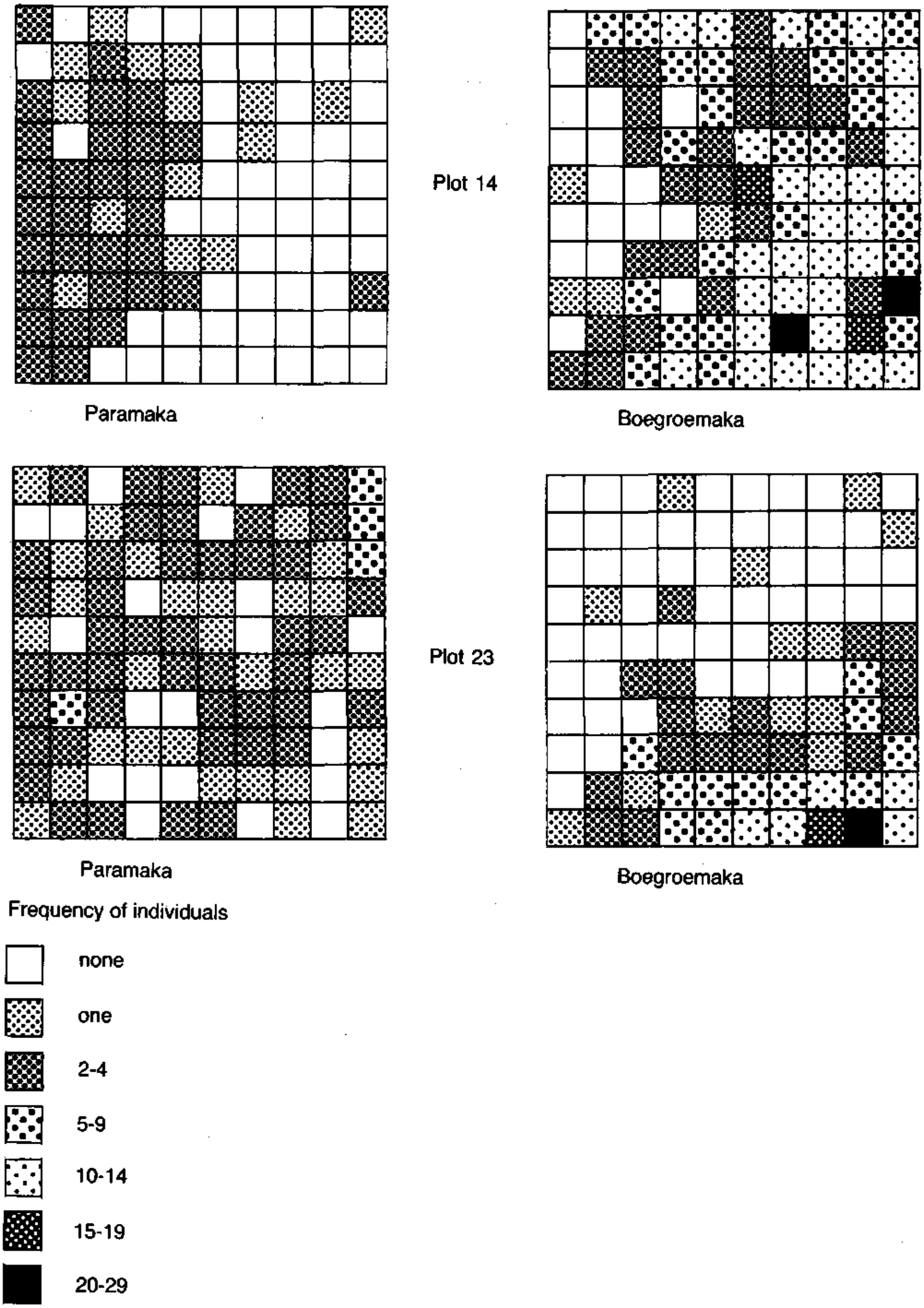


Fig. 4.15 MAIN experiment: spatial distribution of boegroemaka (*Astrocaryus sciophilum*) and paramaka (*A. paramacca*) in plots 14 and 23, each measuring 100×100 m, using frequencies per 10×10 m quadrat

experiment are fairly uniform, but physical factors, such as the depth of the groundwater table, may have been partially responsible for the differences in species composition observed between replications and between plots (see Sections 4.1 and 4.3.3). The effect of site factors was more evident in the Van Leeuwen transect, where there was a marked relationship between species composition and soil properties (see Section 4.2.2).

Unfavourable soil properties may result in a marked deficiency of commercial species in the canopy (Section 4.2). Areas where adverse physical site conditions seem to impede the development of a sound commercial stand were seen in the Van Leeuwen transect and elsewhere in the Tonka research area along creeks and gullies and in shallow depressions. Stands in such areas are unlikely to respond favourably to refinement and are better left untouched.

Sylvigenesis is another source of spatial variation in the stand. Diameter class distribution patterns in the MAIN experiment suggest a gradual change in the floristic composition, started by a heavy storm in the 19th century (Section 4.1.2). Spatial distributions of indicator species, such as kopi (*Goupia glabra*), indicate that this sylvigenetic process was taking place throughout the experimental area before it was disturbed by logging and refinement. The degree of disturbance caused by such storms seems to vary from place to place, as does the subsequent sylvigenetic process set in motion. Sylvigenesis may be partly responsible for the floristic variation within replications, but there is little evidence to support this.

Local shortage of commercial trees is not necessarily a result of poor site conditions, as it was common on good quality soils (Section 4.3.4). Areas without commercial trees on favourable sites seldom exceeded 1000 m^2, and were either composed of mature steady state forest, felling gaps, natural chablis or pockets of young aggrading forest. Regenerating of such areas by means of a natural regeneration technique is possible, since seed dispersal of commercial species is such that adequate recruitment may be expected, provided that dispersal mechanisms remain intact after treatment (Section 4.3.5; see also Section 6.6). The treatment applied in such patches should, however, not eradicate all medium-sized and large trees. Many large gaps contain a few surviving trees, and they should be retained to suppress secondary species and other weeds, provided they do not compete for light with commercial trees. In patches of mature forest without commercial trees, a number of canopy trees should be preserved for the same purpose.

The study also indicates that the boegroemaka palm can have a marked impact on stand development by interfering with the establishment and growth of young trees and other plants in the undergrowth (Section 4.3.6). This may lead to a relatively poor response of commercial recruitment to refinement. The effect of boegroemaka on forest regeneration depends on the density of the palm layer. This effect was hardly noticeable in the Van Leeuwen transect, where the boegroemaka canopy was relatively open, but the consequences were evident in replication 1. Seedlings and saplings of primary species were relatively scarce there (Section 4.3.5), and the paucity of small and medium-sized commercial trees (Section 4.3.2) indicated that few saplings could grow through the boegroemaka layer. Thus, the numerous small openings in the tree canopy (see Fig. 4.10) were probably a direct result of boegroemaka competition.

The presence of a boegroemaka layer may also alter gap regeneration processes. When a large tree falls, it creates an opening in the tree canopy, and also in the palm layer. Some palms die, but others are partially or completely defoliated and survive to form a new boegroemaka canopy after several years. Pioneer species grow fast enough to benefit from such temporary open spaces, and the small openings in the surrounding tree canopy and the sparsity of ground flora also stimulate recruitment and growth of these light demanding trees. This explains why pioneer species were recorded more often in replication 1 and the virgin forest plots than elsewhere in the MAIN experiment (Sections 4.3.3 and 4.3.5). Recruitment of primary species grows less rapidly and is therefore more likely to be overgrown by the recovering boegroemaka canopy. However, individuals which do succeed in growing through this barrier suffer relatively little competition from other trees, and may actually benefit from the presence of boegroemaka. It is likely that some primary species are better adapted to such conditions than others.

Yield regulation is an important aspect of polycyclic management, as sufficient trees should remain after the initial felling to secure future harvests. Medium-sized commercial trees which are likely to grow to large diameters should therefore be retained, and all those belonging to species with non-exponential size class distributions may be regarded as such (see Section 4.3.2). In Suriname, however, concessionaries may take any tree above a minimum felling diameter of 35 cm. This limit is too low for species such as kopi (*Goupia glabra*), wana (*Ocotea rubra*), wiswiskwari (*Vochysia guianensis*) and wanakwari (*Vochysia tomentosa*), also for species which have exponential diameter class distributions and grow to large sizes, such as basralokus (*Dicorynia guianensis*) and bergi gronfoeloe (*Qualea rosea*). A change to two felling limits, 35 cm dbh for species which remain relatively small such as goebaja (*Jacaranda copaia*), krapa (*Carapa procera*), hoogland baboen (*Virola melinonii*), rode sali (*Tetragastris altissima*) and okerhout (*Sterculia spp.*), and about 50 cm for other species, would therefore be an improvement in forest management practice.

5 Effects of logging

Logging in Suriname is carried out by private and state-owned companies, all of whom, except the largest, organize their operations in the simplest way possible (see Hendrison, in press). No plans or maps are prepared in advance and a few large trees, usually 5 – 8/ha, are felled first. This first phase has an effect on the forest comparable to the impact of a heavy storm and several chablis, variable in size and shape, are formed. Microclimatic conditions within chablis are also variable and stimulate regeneration of a wide range of species. Most vegetation in newly formed gaps is destroyed and decays together with the remains of the felled trees, so that nutrients are released and become available to stimulate the development of the residual stand inside and outside the chablis.

The second phase of the logging operation, the extraction of timber, has no natural equivalent. It results in the removal of a substantial part of the phytomass, and the remaining vegetation and soil are further damaged. Heavy equipment, usually a wheeled skidder, collects the logs some time after felling has been completed. The operator makes his own trail through the forest by pushing over trees, palms and other undergrowth in his way. Upon arrival, the driver often finds the log wrongly positioned for extraction and therefore has to push it sidewards with his machine. This manoeuvre partially or completely destroys the vegetation near the stump, which has usually survived felling and plays an important role in sylvigenetic processes. Little further damage is done to the vegetation on the way back because the same trail is used. Skidding damage is not restricted to what is visible above the surface because every movement of the skidder compacts soil and damages tree roots, especially when the soil is moist. When the same trails are used several times, the soil becomes unfit for tree growth for several decades (see Hendrison, in press).

The impact of selective logging on tropical rain forest has received little attention in the literature on South American forestry. The few publications which mention the subject (Lanly, 1982; Estève, 1983; Jonkers and Schmidt, 1984; Boxman et al., 1985; in press; Jonkers and Hendrison, 1986) suggest that extraction rates are generally low and that logging damage in itself is therefore no threat for sustained timber production. In Suriname, timber yields are usually less than 20 m^3/ha and seldom result in severe damage. Nonetheless, any logging damage affects future harvests and it is important for forest management that this impact is understood.

Effects of logging were therefore studied in the MAIN experiment as well as several logging experiments to be discussed in a later publication in this series (Hendrison, in press). Hendrison also suggests improvements in harvesting technique to reduce logging damage, a consideration beyond the scope of the present study. Three harvest intensities were applied in a partially controlled operation in the MAIN experiment, resulting in the extraction of 15, 23 and 46 m^3/ha respectively, and logging methods applied did not differ from what is the normal practice in Suriname, except for a few measures to avoid unnecessary skidding damage (see Section 3.1.2). Logging damage, growth response of the commercial stand and recruitment of commercial species in gaps and on skid trails will be discussed in this chapter.

5.1 Damage to the commercial stand

Selective logging not only reduces the standing stock but also damages the residual stand, because some of the trees not felled are killed or injured. Commercial trees in the MAIN experiment were therefore classified in six categories: felled, destroyed, very severely injured, severely injured, with minor injury and undamaged (for definitions, see Section 3.1.3). The first two categories include all trees which died as result of logging. Very severely injured trees survived exploitation but their chances of full recovery were negligible. The differentiation between severe and minor injury was arbitrary and was ignored in some of the analyses, although severe injury would be more likely than minor injury to be followed by serious decay and would also affect tree growth more.

5.1.1 Damage in relation to felling intensity

The hypothesis that the incidence of each type of damage increases when more trees are being felled was tested by analysis of variance (ANOVA, see Section 3.1.5). Basal areas were computed by damage category and plot and used in four ANOVA tests. Basal area is strongly correlated with trunk volume (Appendix VI) and is therefore an excellent parameter to quantify losses of timber.

Test results for the destroyed and undamaged categories show significant differences between levels of exploitation (Tables V.1 and V.2, Appendix V). It can therefore be concluded, as would be expected, that the incidence of the most severe form of logging damage increases with felling intensity, and the basal area of the undamaged stand decreases with heavier exploitation. The results for those commercial trees which survived with some degree of injury are more interesting. The treatment effect for the very severe injury category was small and statistically insignificant (Table V.3), and a positive correlation between the intensity of logging and incidence of less serious injury was even less evident (Table V.4). Felling more trees therefore did not result in a significant increase in the numbers of injured trees. It is also remarkable that replication effects were statistically significant in two tests (Tables V.2 and V.4), indicating that stand composition has a considerable influence on logging damage. The incidence of damage in replication 1, where small-sized

TABLE 5.1. MAIN experiment: impact of logging on the commercial stand, using basal areas felled (m^2/ha) and proportion of the original stands not felled or surviving logging with specified maxima of injury*

Plot	Basal area felled (m^2/ha)	Percentage of total commercial basal area				
		Not felled	Surviving	Without very severe injury	No or minor injury	No damage
11	1.12	92.1	91.4	91.3	90.3	77.9
12	3.51	71.3	66.0	66.0	62.8	54.9
13	1.41	89.6	86.3	86.1	85.9	73.8
14	2.18	84.5	79.2	75.5	71.8	61.9
15	2.34	84.0	80.7	80.6	78.8	64.0
16	3.98	71.2	64.5	64.2	59.0	46.2
17	3.34	72.8	70.6	70.2	70.1	50.5
18	2.38	80.6	78.2	77.0	73.7	63.4
19	1.19	88.7	88.2	88.1	82.5	74.8
21	2.15	87.7	83.5	83.1	76.9	67.8
22	4.04	72.5	64.3	62.8	57.7	41.6
23	1.52	93.1	89.7	89.6	78.1	71.3
24	4.65	73.5	68.5	68.3	63.1	47.3
25	3.69	81.1	75.1	74.8	73.3	58.5
26	2.74	82.4	79.5	78.6	76.9	58.7
27	2.38	87.8	84.6	83.8	73.9	60.2
28	1.61	91.0	88.3	87.7	85.6	71.1
29	1.19	92.1	88.4	88.2	85.2	69.5
31	4.31	69.4	60.1	55.4	51.8	44.3
32	3.82	75.4	69.7	67.3	65.4	51.7
33	1.70	88.9	84.6	82.3	78.5	68.7
34	1.74	86.1	83.3	80.4	71.4	61.5
35	1.72	89.7	86.2	84.3	81.7	73.5
36	2.28	86.1	83.1	81.7	79.4	67.7
37	1.20	91.7	90.3	90.1	83.4	77.8
38	2.60	78.0	76.0	75.4	70.4	57.3
39	3.36	72.5	69.9	67.6	64.2	58.0

* Sample sizes of 2.25 ha per plot (basal area felled and trees > 15 cm dbh) and 0.45 ha per plot (trees 5 − 15 cm dbh), minimum tree size of 5 cm dbh

commercial trees were relatively scarce (Section 4.3.2), was distinctly less than elsewhere.

The ANOVA results indicated the need for a more detailed analysis. Linear regression analysis (LRA) was therefore used to describe logging damage as a function of harvest intensity. From a silviculturist's point of view it is important to estimate how much of the original stand survives logging without unacceptable damage rather than how much has been lost. A positive approach was therefore adopted, in which each regression equation expressed a functional relation between the proportion of the original stand with less than a specified maximum of damage and the basal area that had been harvested. Five equations (5.1 – 5.5) were derived from the data summarized in Table 5.1.

$$Y_1 = 84.88 - 9.067\,X \qquad (5.1)$$
$$Y_2 = 94.08 - 8.046\,X \qquad (5.2)$$
$$Y_3 = 98.92 - 8.376\,X \qquad (5.3)$$
$$Y_4 = 99.39 - 8.120\,X \qquad (5.4)$$
$$Y_5 = 99.75 - 6.741\,X \qquad (5.5)$$

where:

X = basal area of trees felled (m^2/ha).

Y_1 = percentage of the original basal area of commercial trees which survived logging without damage.

Y_2 = percentage of the original basal area of commercial trees which survived logging without damage or with minor injury.

Y_3 = percentage of the original basal area of commercial trees which survived logging without damage or with minor or severe injury.

Y_4 = percentage of the original basal area of commercial trees which survived logging.

Y_5 = percentage of the original basal area of commercial trees which was not felled.

All the equations fitted data from the MAIN experiment well, with R^2 values ranging from 0.86 to 0.90, except for Equation 5.2, whose correlation was somewhat poorer (R^2 = 0.81).

Fig. 5.1 is a graphical presentation of these equations, in which vertical distances between the various regression lines indicate logging damage. It appears that only a very small proportion of the original stand (about 2 – 5%, depending on logging intensity) was accidentally destroyed, but more of it was injured. The incidence of injury was found to increase slightly; from 13% after a light harvest of 1 m^2/ha to 18% after a fourfold increase in logging intensity, with most injury classified as minor. Thus, logging damage in the MAIN experiment was modest and a yield of 46 m^3/ha (a basal area felled of about 4 m^2/ha) surprisingly caused little more damage than a harvest of 15 m^3/ha.

Data presented in Table 5.2 also indicate that the incidence of damage is not proportional to the volume felled. Harvesting 15 m^3/ha was found to result in the destruction of 6% of the commercial trees larger than 5 cm dbh and to cause injury to another 10% compared with 13% destroyed and 15% injured after a yield of 46 m^3/ha. Higher yields therefore seem to cause less damage per m^3 felled. This result was not entirely unexpected. When felling intensity is low, each felled tree creates a new gap, and an extensive network of skid trails is needed to extract a few scattered logs. An increase in harvest intensity means that crowns of felled trees are more likely to fall into existing gaps, causing little further damage, and skid trails are used more intensively. Additional side tracks are opened up, but most of these

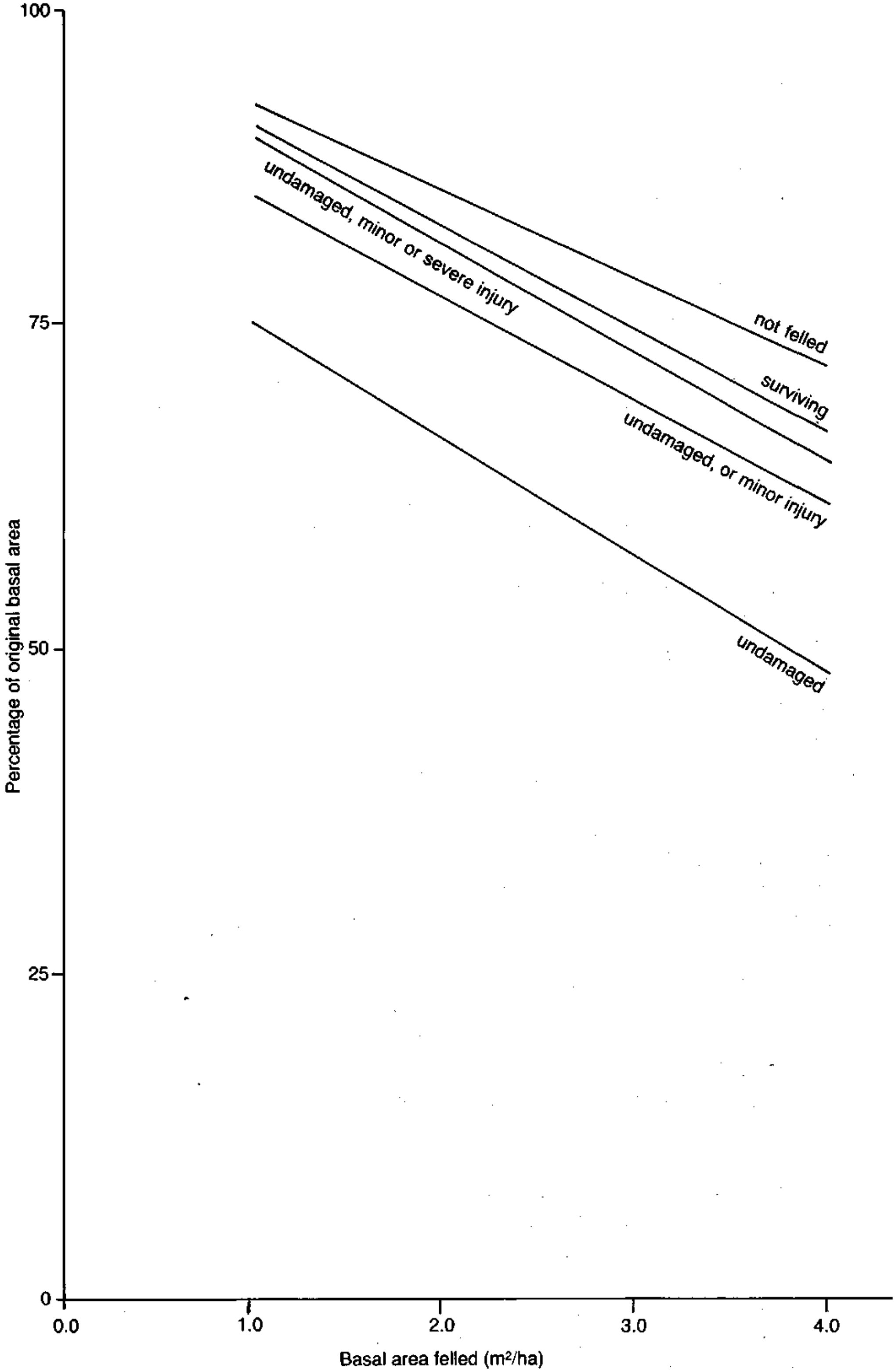


Fig. 5.1 MAIN experiment: logging damage to the commercial stand in relation to felling intensity

are short and they increase the total area under trails only slightly (see Section 5.2).

Most injured trees should not be discounted as a future source of timber, as all but the least vigorous trees will probably recover from minor injury. Trees with severe injury are more susceptible to decay, however, and are less likely to be usable in the future. Trees with very severe injury will probably die or develop into cull trees. Thus, the equation for trees with no more than minor injury (Equation 5.2) is fairly realistic for a residual stand with acceptable damage under conditions comparable to those in the MAIN experiment, while Equations 5.1 and 5.3 provide optimistic and pessimistic estimates. These three equations indicate a sharp decline in timber resources with increasing felling intensity, in spite of the fairly low incidence of damage, mainly because felling a basal area of a few square metres per hectare means harvesting a substantial part of the timber stand (Equation 5.5). In the MAIN experiment, 1 m^2/ha was equivalent to almost 7% of the original commercial basal area and harvesting 4 m^2/ha therefore meant extracting about a quarter of the total commercial stand.

5.1.2 Logging damage and tree size

The probability of trees being destroyed or injured in a selective logging operation are not the same for different size classes. Data presented in Table 5.2 indicate that small trees are much more vulnerable to destruction and very severe injury than larger individuals, but less severe injury was more common among larger trees. This can be explained as follows.

When a tree is felled, its large crown falls through the forest canopy and damages other trees, mostly by colliding with their crowns. Falling trunks seldom hit other trees, and therefore cause little damage. Crowns of nearby medium-sized and large trees will be hit first, but as the rate of fall is still low, most of these are not seriously damaged. Occasionally, a large tree may be uprooted or a hollow trunk may break, but damage is usually restricted to a number of ripped-off twigs and branches. During its fall, the tree gains momentum and any small trees in the way are hit very hard. As the small trees are generally less firmly rooted and snap more readily than larger individuals, many of them either die or survive with very severe injury.

Skidding has a similar effect on the stand. A considerable number of small trees are pushed aside when a skid trail is made, but larger individuals are avoided as collisions would be time consuming and dangerous. The result is a trail which winds slightly around medium-sized and large trees, some of which are injured later because the extracted logs tend to move sidewards when pulled round a bend and scrape off pieces of their bark.

5.2 Felling gaps and skid trails

Damage caused by selective logging is very local, with almost 100% mortality of trees

TABLE 5.2. MAIN experiment: logging damage to commercial trees, frequencies by diameter class and damage category*

Level of exploitation	Dbh class (cm)	n/ha	Percentage in each damage category					
			Felled	Destroyed	Very severe injury	Other injury	No damage	Total
E 15	5 – 15	87	0.0	8.2	4.0	2.6	85.2	100.0
	15 – 35	51	0.0	4.8	2.6	9.9	82.7	100.0
	35 – 65	35	4.4	3.4	0.9	12.8	78.5	100.0
	>65	9	20.4	0.5	0.0	13.5	65.6	100.0
	>5	182	1.9	5.9	2.8	7.1	82.2	100.0
E 23	5 – 15	83	0.0	9.6	3.6	4.8	82.0	100.0
	15 – 35	49	0.0	8.7	2.6	13.2	75.5	100.0
	35 – 65	32	8.1	4.0	1.4	15.9	70.6	100.0
	>65	11	32.6	1.4	0.5	11.3	54.2	100.0
	>5	175	3.5	7.8	2.7	9.6	76.4	100.0
E 46	5 – 15	77	0.0	19.6	5.4	5.8	69.2	100.0
	15 – 35	50	0.0	10.7	3.1	16.5	69.7	100.0
	35 – 65	34	22.7	5.3	2.6	14.6	54.8	100.0
	>65	8	48.5	4.2	0.0	14.2	33.1	100.0
	>5	169	6.9	13.4	3.9	11.1	64.7	100.0

* Sample sizes per exploitation level: 4.05 ha (trees 5 – 15 cm dbh) and 20.25 ha (trees > 15 cm dbh)

in gaps and on skid trails and frequent injury to trees close to them, but damage further away is negligible. The extent of such openings would seem to be a useful indicator of logging damage, so areas of residual forest, gaps and skid trails were recorded in 100×100 m plots in the MAIN experiment (Section 3.1.3), and analysed by ANOVA and LRA (Section 3.1.4).

ANOVA was used to test differences in area by forest class (residual forest, gaps and skid trails) after extraction of 15, 23 and 46 m^3/ha, and the results are summarized in Appendix V (Tables V.4, V.5 and V.6). As anticipated, differences in areas for different logging intensities were significant, showing that harvesting a larger volume results in larger gap and skid trail areas and smaller areas of residual forest.

LRA was applied to generate more information about the relationship between basal area felled and the extent of gaps, trails and residual forest. Equations 5.6, 5.7 and 5.8 were computed from data shown in Table 5.3.

$$Z_1 = 80.92 - 8.92\,X \tag{5.6}$$
$$Z_2 = 18.51 + 4.49\,X \tag{5.7}$$
$$Z_3 = 0.57 + 4.43\,X \tag{5.8}$$

where:

X = basal area felled (m^2/ha).
Z_1 = area of residual forest, expressed as percentage of the total area.
Z_2 = area of gaps, expressed as percentage of the total area.
Z_3 = area of skid trails, expressed as percentage of the total area.

Coefficients of determination for Equation 5.6 (R^2 = 0.67) and Equation 5.8 (R^2 = 0.75) proved acceptable. These equations provide fair estimates for areas under residual forest and skid trails, although some observations deviate substantially from regressed values (Fig. 5.2).

TABLE 5.3. MAIN experiment: areas under residual forest, gaps and skid trails in relation to logging intensity*

Plot	Basal area felled (m^2/ha)	Percentage of total area per plot with			
		Residual forest	Gaps	Skid trails	Total
11	0.95	67	23	10	100
12	2.91	45	47	8	100
13	1.38	70	25	5	100
14	2.04	64	26	10	100
15	2.09	62	32	6	100
16	4.37	30	48	22	100
17	3.77	35	43	22	100
18	1.63	68	29	3	100
19	0.86	75	20	5	100
21	2.25	74	13	13	100
22	3.33	50	35	15	100
23	1.25	68	30	2	100
24	3.37	48	38	14	100
25	3.56	43	35	22	100
26	3.61	63	24	13	100
27	2.11	62	30	8	100
28	0.40	80	15	5	100
29	0.97	76	19	5	100
31	3.11	47	40	13	100
32	4.70	60	19	21	100
33	2.32	62	27	11	100
34	1.13	65	29	6	100
35	1.59	54	35	11	100
36	2.25	63	25	12	100
37	0.99	82	13	5	100
38	2.71	64	24	12	100
39	2.77	51	36	13	100

* Sample size: 1 ha per plot

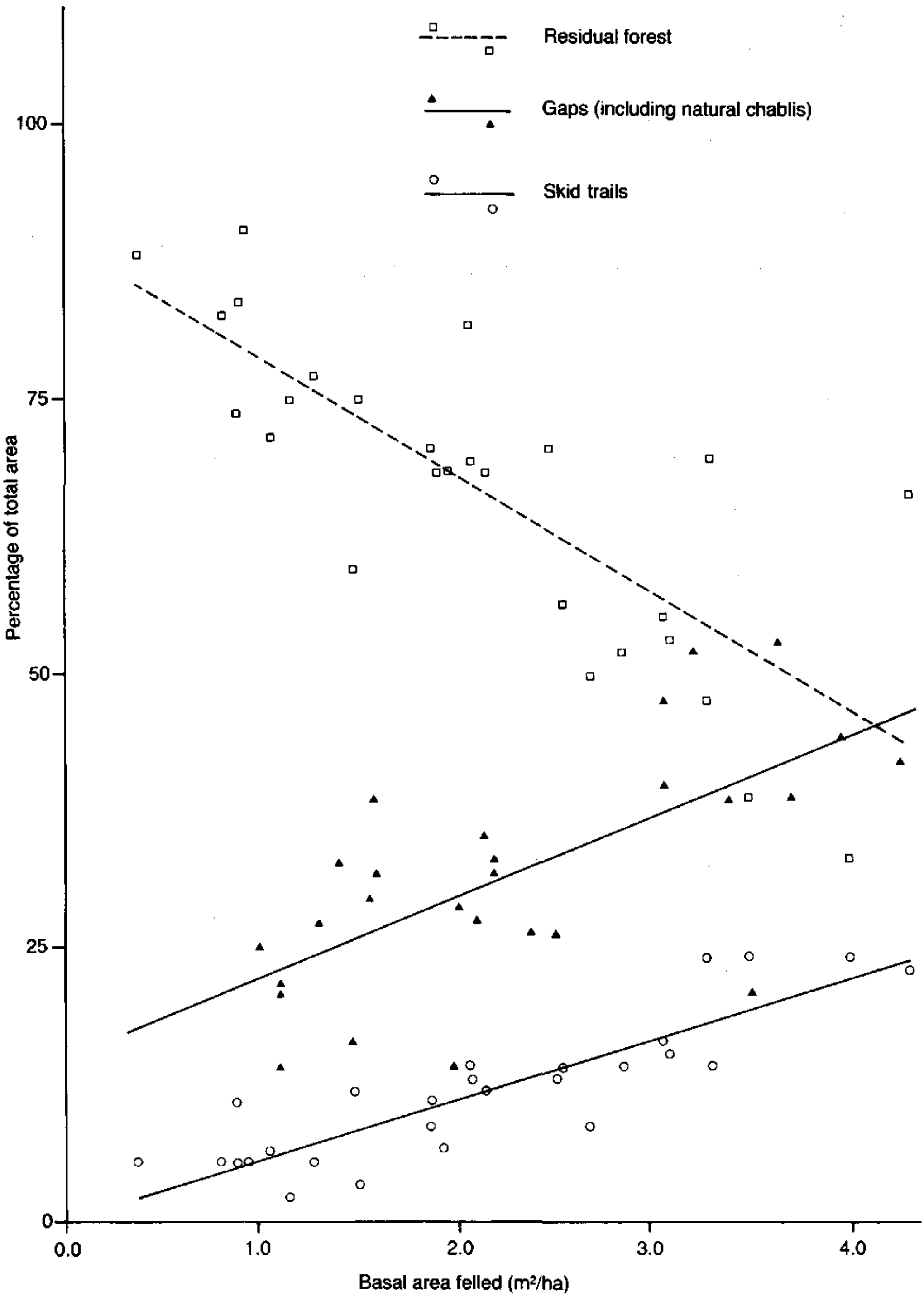


Fig. 5.2 MAIN experiment: graphical presentation of equations 5.6, 5.8 and 5.9, indicating the extent of gaps, skid trails and residual forest in relation to felling intensity

The equation for estimating areas of gaps (Equation 5.7) is less reliable. The coefficient of determination is low ($R^2 = 0.29$) and correlation (R) is barely significantly positive at $P = 0.99$. This low value was not entirely unexpected, however, as it had been impossible to differentiate between felling gaps and natural chablis. Riéra (1983) found that chablis in pristine forest in French Guiana constitute about 6% of the total area, and it is thought that a similar proportion of the MAIN experiment area shortly before logging consisted of natural openings. This percentage varied greatly from plot to plot (see Fig. 4.10), and contributed considerably to unexplained variation.

Boundary effects are another source of variation. Gaps were found where the crowns fell, that is 15 – 45 m from the stumps, so many of the gaps within the 100×100 m assessment plots were due to felling outside the plot boundaries, and some of the gaps caused by felling within the plots were located outside them. Using the basal area felled within 150×150 m plots (Table 5.1) as the argument improved correlation somewhat (Equation 5.9).

$$Z_2 = 14.00 + 5.90\,X'' \qquad (5.9)$$

where:

X'' = basal area felled within 150×150 m plots (m^2/ha).

Z_2 = area of gaps recorded within 100×100 m plots, expressed as percentage of the total area.

Equation 5.9 proved more reliable than Equation 5.7, but correlation remains poor ($R^2 = 0.44$). Fig. 5.2 clearly indicates that areas recorded as gaps tend to deviate considerably from regressed values, and that estimates based on Equation 5.9 merely indicate an order of magnitude.

Selective logging results in extensive areas of skid trails and gaps (Fig. 5.2). After a light harvest of 1 m^2/ha, about 5% of the surface will have become trails and some 20% will have become gaps, whereas felling 4 m^2/ha leads to approximately 18% trails and 38% gaps. These values are very high when compared to estimates for damage to the commercial stand presented in Section 5.1 (see also Fig. 5.1).

This discrepancy is partly because some gaps were natural chablis, but a more important factor is that small trees are more susceptible to fatal damage than larger individuals (Section 5.1.2). Felling gaps and skid trails are therefore concentrated where the basal area was low before exploitation. Furthermore, felling gaps are larger than the actual areas damaged by falling trees. When a felled tree comes down, other trees are hit and exert a substantial reaction force on the falling crown, which is also exposed to aerodynamic pressure. The falling crown is flexible and responds to pressure by reducing and rearranging its volume so that branches bend inwards and backwards, although some may break off. When the tree hits the ground, side pressure ceases and the crown spreads out. Branches swing sideways, thus enlarging the area covered with debris but causing little more damage to the tree stand. An assessment of logging damage based on the extent of openings in logged-over forest therefore seems likely to result in a serious overestimation of the number of trees and the volume of timber lost in the operation.

5.3 Impact on phytomass and nutrient status

Selective logging reduces the phytomass, both by removing part of it from the forest and by killing some more, which is then left to decay on the forest floor. Nutrients stored in extracted timber are lost, but those released from the decaying organic material become available for the residual stand. These changes in phytomass and nutrient status were estimated to determine the extent of the impact (for methodology, see Section 3.1.5). More detailed accounts of the subjects discussed in this section can be found in Schmidt (in press) and Poels (in press).

Dry weights of trees harvested in the MAIN experiment were estimated using Equations 3.2, 3.3 and 3.4 (Section 3.1.5). A yield of 23 m^3/ha was found to be equivalent to felling 47.9 t/ha (Table 5.4), that is, 32.6 t/ha of stemwood and 15.3 t/ha of leaves and branches. Not all stemwood was extracted. The stumps, top ends and defective or poorly formed parts were left, and approximately half (17 t/ha) was taken to the sawmill. According to Jonkers and Schmidt (1984), one tonne of stemwood contains 2.9 kg of nitrogen and 9.3 kg of other nutrients (P, K, Ca and Mg), so that a harvest of 23 m^3/ha results in the loss of about 50 kg/ha of nitrogen and 160 kg/ha of other nutrients from the ecosystem.

These quantities are low compared to the nutrient content of living phytomass in virgin forest, that is about 2 t/ha of nitrogen and 5 t/ha of other nutrients (see Jonkers and Schmidt, 1984; Schmidt, in press). The forest is considered capable of compensating for this slight reduction by taking up nutrients directly from rainfall, from the air by means of nitrogen fixing organisms (Jordan and Herrera, 1981) and from the soil (see Poels, in press; Schmidt, in press; Jonkers and Hendrison, 1986). Harvesting 46 m^3/ha results in a doubling of the loss of nutrients, but it is believed that the ecosystem can cope also with this loss, although full recovery may take longer than the felling cycle of 20 years. Such high yields are exceptional in Suriname and implementation of the felling limits proposed in Section 4.4 will keep losses of nutrients at an acceptable level.

The unextracted parts of felled trees eventually fertilize the residual stand, and so do the remains of other forest components killed in the logging operation. The dry weights of trees killed were estimated to quantify this fertilizing effect of logging, but as pre-felling data were only available for commercial trees (Section 3.1.3), an indirect appraisal of mortality among non-commercial trees had to be made. A relationship between tree size and rate of destruction similar to that found for commercial species (Section 5.1.2) was therefore assumed.

The above ground phytomass of all trees felled or destroyed in obtaining a yield of 15 m^3/ha was estimated at 42 t/ha, of which approximately 30 t/ha remained in the forest as debris. The weight of ripped-off branches of surviving trees and killed root systems has to be added to obtain the total amount of killed phytomass, giving

TABLE 5.4. MAIN experiment: changes in above ground phytomass (t/ha) of commercial (COM) and non-commercial (NON-C) tree species as result of logging*

Level of of exploi- tation		Living phytomass (t/ha) per diameter class and species group														
		5 – 15 cm dbh			15 – 35 cm dbh			35 – 65 cm dbh			> 65 cm dbh			> 15 cm dbh		
		COM	*NON-C*	*total*	*COM*	*NON-C*	*total*	*COM*	*NON-C*	*total*	*COM*	*NON-C*	*total*	*COM*	*NON-C*	*total*
E 15**	before logging	4.0	23.8	27.8	24.5	54.9	79.4	97.9	62.1	160.0	111.3	45.8	157.1	237.7	186.6	424.3
	felled	0.0	0.0	0.0	0.0	0.0	0.0	6.9	0.0	6.9	23.5	0.0	23.5	30.4	0.0	30.4
	destroyed	0.4	2.3	2.7	1.4	3.0	4.4	3.1	0.7	3.8	0.5	0.3	0.8	5.4	6.3	11.7
	after logging	3.6	21.5	25.1	23.1	51.9	75.0	87.9	61.4	149.3	87.3	45.5	132.8	201.9	180.3	382.2
E 23***	before logging	4.0	24.8	28.8	24.1	53.3	77.4	98.9	65.1	164.0	111.6	90.1	201.7	238.6	233.3	471.9
	felled	0.0	0.0	0.0	0.0	0.0	0.0	11.1	0.0	11.1	37.1	0.0	37.1	48.2	0.0	48.2
	destroyed	0.4	2.2	2.6	1.9	4.2	6.1	3.5	2.5	6.0	1.5	1.4	2.9	7.3	10.3	17.6
	after logging	3.7	22.6	26.3	22.2	49.1	71.3	84.3	62.6	146.9	73.0	88.6	161.6	183.2	222.9	406.1
E 46****	before logging	3.9	22.8	26.7	25.2	51.9	77.1	101.1	56.2	157.3	104.0	64.5	168.5	234.2	195.4	429.6
	felled	0.0	0.0	0.0	0.0	0.0	0.0	29.0	0.0	29.0	49.1	0.0	49.1	78.1	0.0	78.1
	destroyed	0.7	4.0	4.7	2.2	4.6	6.8	6.0	3.9	9.9	3.7	3.0	6.7	12.6	15.5	28.1
	after logging	3.2	18.8	22.0	23.0	47.3	70.3	66.1	52.3	118.4	52.2	61.5	113.7	144.5	179.9	324.4

* Sample sizes: 9 ha (trees > 15 cm dbh), 4.05 ha (commercial trees 5 – 15 cm dbh) and 0.24 ha (non-commercial trees 5 – 15 cm dbh) per level of exploitation

** Approximately 12 t/ha extracted

*** Approximately 17 t/ha extracted

**** Approximately 35 t/ha extracted

a figure comparable to the amount of dead phytomass in virgin forest, estimated at 34 t/ha (Jonkers and Schmidt, 1984; Schmidt, in press). Harvesting 46 m^3/ha results in at least 71 t/ha of logging debris, which means an increase in the amount of litter of about 200%. Jonkers and Schmidt (1984) estimated the nutrient content (N, P, K, Ca and Mg) of logging debris at 21 kg per tonne dry weight, so that after yields of 15 m^3/ha and 46 m^3/ha, the amount of nutrients in logging debris is approximately 650 kg/ha and 1550 kg/ha respectively.

More than 90% of logging debris consists of stems and branches, which take many years to decompose completely (Jonkers and Schmidt, 1984). Nutrients are released gradually and estimated quantities made available annually for tree growth are 75 – 175 kg/ha. These values are low compared to the amounts of nutrients released from litter in virgin forest (see Schmidt, in press), but are high enough to have a significant effect on tree growth (see Section 5.4).

5.4 Growth of commercial species in virgin and logged-over forest

Selective logging has a dual effect on tree growth. It results in damage to tree crowns, thus reducing the photosynthethic potential of part of the residual stand, but it also stimulates increment by improving light conditions and nutrient availability.

5.4.1 Growth of medium-sized and large trees

Tree growth in pristine forest is slow. The mean diameter increment for commercial trees larger than 15 cm dbh in the virgin forest plots was only 0.36 cm/yr, a value comparable to results obtained elsewhere in the neotropics (Crow and Weaver, 1977; Murphy, 1970; Pires, 1978; Schulz, 1960). Increment during the first years after refinement was slightly faster, with average rates of 0.43, 0.46 and 0.51 cm/yr recorded in the MAIN experiment after yields of 15, 23 and 46 m^3/ha respectively.

Growth rates in logged stands were analysed by ANOVA (for methodology, see Section 3.1.5) and, considering the small differences between means, gave more conclusive results than expected. The hypothesis of no difference between the various levels of exploitation was rejected at a level of significance of 0.01 (Table V.8, Appendix V), proving that logging has a positive impact on the growth of medium-sized and large commercial trees. Growth rates remain very low the first years after logging and are unlikely to increase in subsequent years (see Section 6.5.2 and de Graaf, 1986). The result therefore has no practical consequences for forest management.

5.4.2 Growth of small-sized trees

The average increment of small commercial trees (5 – 15 cm dbh) in the pristine parts of the MAIN experiment was only 0.11 cm/yr, which is distinctly inferior to rates recorded for larger individuals. Trees in this diameter class are understorey trees measuring 5 – 20 m in total height. Light conditions in the understorey of virgin forest are very poor, except where the death of a larger tree has led to a temporary improvement (see Oldeman, 1974). Most small trees merely survive in the shade of canopy trees and hardly grow, if at all, waiting for better opportunities induced by chablis formation.

Selective logging results in just such an opportunity for many small-sized trees, and the mean diameter increment in recently logged stands was 2 – 3 times that recorded in virgin forest. The results indicate a positive correlation between growth and logging intensity. A relatively high growth rate (0.32 cm/yr) was obtained after a yield of 46 m^3/ha, but mean diameter increment after felling 15 m^3/ha was distinctly poorer (0.21 cm/yr). ANOVA was applied to these results (Section 3.1.5), and showed that the effect of logging intensity on the growth of small commercial trees is significant at $\alpha = 0.005$ (Table V.9). This result illustrates that logging does induce a process of forest recovery, but at a rate too low to be attractive to the forester.

5.4.3 Growth of individual species

Mean diameter increment rates were computed for individual species, using estimates for trees larger than 15 cm dbh and separate calculations for virgin and logged stands. Growth rates in logged-over forest ranged from less than 0.2 cm/yr to more than 1.1 cm/yr, the lowest and highest estimates being for species of infrequent occurrence. Average increments of less than 0.25 cm/yr were recorded for satijnhout (*Brosimum paraënse*, 10 trees), koenatepi (*Platymiscium spp.*, 19 trees), ajawatingimoni (*Trattinickia spp.*, 48 trees) and two species with less than five trees in the whole experimental area. The highest rates, more than 0.75 cm/yr, were for pegrekoepisi (*Xylopia spp.*, 5 trees), agrobigi (*Parkia nitida*, 34 trees), wit riemhout (*Micropholis guyanensis var. guyanensis*, 24 trees), soemaroeba (*Simarouba amara*, 22 trees) and the *Vochysia spp.* wiswiskwari (*V. guianensis*, 35 trees) and wanakwari (*V. tomentosa*, 13 trees). Mean diameter increment rates of wiswiskwari and wanakwari were greater than 1 cm/yr.

Growth rates of the 13 most common commercial species are listed in Table 5.5. Most of them were growing about 0.4 cm/yr in diameter in logged stands, but increment of bolletri (*Manilkara bidentata*) was considerably lower, and relatively high rates were computed for wana (*Ocotea rubra*), basralokus (*Dicorynia guianensis*) and bergi gronfoeloe (*Qualea rosea*). Most growth rates found in virgin forest were lower than rates found in logged-over stands, which indicates that virtually all commercial species respond favourably to the improvements in light conditions and nutrient availability induced by logging.

TABLE 5.5. MAIN experiment: average diameter growth rates of common commercial species > 15 cm dbh in pristine and recently logged stands

Species	Pristine forest		Logged forest	
	Number	Growth (cm/yr)	Number	Growth (cm/yr)
bolletri	50	0.17	540	0.27
tingimonisali	39	0.35	55	0.33
zwart riemhout	11	0.24	122	0.36
kopi*	24	0.21	189	0.38
hoogland baboen	42	0.28	352	0.37
goebaja	24	0.27	191	0.40
okerhout	11	0.35	73	0.40
krapa	32	0.36	233	0.40
hoogland gronfoeloe	11	0.42	153	0.42
rode sali	30	0.42	266	0.48
basralokus	105	0.45	1149	0.54
bergi gronfoeloe	46	0.47	1052	0.55
wana	18	0.50	58	0.54

* Growth rates for kopi are negatively influenced by the presence of many overmature trees in the kopi populations (see Section 4.1)

5.5 Regeneration of commercial species in logged stands

Logging is likely to destroy nearly all regeneration on skid trails, and most saplings in gaps. Seedlings are more flexible and will coppice more readily than saplings and small trees, which suggests that many located in gaps survive logging without lasting damage. Seedlings (0.2 – 2 m total height) and saplings (2 m total height – 5 cm dbh) were tallied approximately three years after felling in small samples from replications 1 and 2 (Section 3.1.3), but as no pre-felling data are available, the loss of recruitment could not be assessed. Data presented in Sections 5.1 and 5.2 suggest, however, that this type of damage tends to be extensive. The extent of gaps and skid trails was such that sapling mortality rates of 20% after a yield of 15 m^3/ha, and 40% after a yield of 46 m^3/ha seem reasonable estimates. Mortality among seedlings was probably slightly less.

The tally indicates that most regeneration destroyed during logging is replaced by new recruits within three years. An adverse effect of logging on stocking of commercial seedlings and saplings was still discernible in replication 2 (Table 5.6). In replication 1, however, abundant regeneration was found in the three plots with the highest felling intensity, while regeneration in other plots was distinctly poorer (Table 5.6). In this replication, a dense palm layer was present which would have suppressed regeneration of tree species (Sections 4.3.6 and 4.4). Logging created openings in this canopy, but only the highest felling intensity apparently resulted in a substantial reduction in palm competition and adequate recruitment of commercial species (see also Section 4.4).

A comparison was made between regeneration of commercial species in residual forest, in gaps and on skid trails (Table 5.6). Seedlings were found slightly less frequently in gaps than in residual forest. This may indicate that it is about three years before the seedling population in gaps is fully restored. Saplings, however, were recorded more often in gaps, which is probably a result of improved growth conditions.

An unexpected finding is that regeneration of commercial species in quadrats classified as skid trails was markedly more abundant than in gaps and residual forest. Seedlings and saplings of primary species were rarely seen on the wheel tracks themselves, which may remain bare for years or become overgrown by herbs and secondary tree species, such as panga panga (*Palicourea guianensis*) and mispel (*Miconia spp.*). The edges of skid trails have become excellent seed beds, however, where the skidder has turned over the topsoil and mixed it with organic debris, and form favourable sites for recruitment of commercial and other primary species.

The species composition of seedling and sapling populations under residual forest was different from that in gaps and on skid trails. The regeneration of light demanding species such as pegrekoepisi (*Xylopia spp.*), kopi (*Goupia glabra*), slangenhout (*Loxopterygium sagotii*) and goebaja (*Jacaranda copaia*) was common in openings and almost absent where the forest cover was still intact (Table 5.7). All these species have effective seed dispersal mechanisms and seedlings were mostly found at large distances from the nearest living seed source (Section 4.3.5). Kopi and pegrekoepisi seem to have a marked preference for disturbed soils along skid trails. Similar soil disturbance may occur in virgin forest when a large tree is uprooted and the soil adhering to its roots is turned over. Riéra (1983; 1985) found kopi and

TABLE 5.6. MAIN experiment: stock of commercial seedlings* and saplings** three years after felling in relation to felling intensity and forest class

	Seedlings (n/m^2)		Saplings (n/ha)	
	Replication 1	Replication 2	Replication 1	Replication 2
per felling intensity				
E 15	0.42	0.59	2.3×10^2	3.6×10^2
E 23	0.32	0.55	1.5×10^2	3.4×10^2
E 46	0.57	0.49	3.7×10^2	3.4×10^2
mean	0.44	0.55	2.5×10^2	3.5×10^2
per forest class				
residual forest	0.40	0.57	1.8×10^2	3.2×10^2
gaps	0.39	0.43	1.9×10^2	3.5×10^2
skid trails	0.68	0.68	5.9×10^2	4.0×10^2

* 0.2 – 2 m total height; sample size 576 m^2 per replication

** 2 m height – 5 cm dbh; sample size 0.36 ha per replication pegrekoepisi seedlings on such tree-fall mounds in French Guiana and although he found that seedlings of these species were at least as abundant elsewhere in the chablis, tree-fall mounds may be important in their regeneration processes. Slangenhout and goebaja were common in felling gaps as well as on skid trails, but goebaja regenerates best in small gaps (Schulz, 1960).

Some species such as basralokus (*Dicorynia guianensis*), bergi gronfoeloe (*Qualea rosea*), wana (*Ocotea rubra*) and hoogland baboen (*Virola melinonii*) seem to have no distinct preference for any forest class (Table 5.7), but may require moderate light

TABLE 5.7. MAIN experiment: numbers of seedlings and saplings of individual commercial species in residual forest, in gaps and on skid trails, three years after logging

Species	n	Percentage of the total number of individuals (n)		
		Residual forest*	Gaps**	Skid trails***
Seedlings****				
pegrekoepisi	12	0	0	100
kopi	29	3	17	79
slangenhout	43	14	47	40
goebaja	26	23	54	23
basralokus	39	44	33	23
bergi gronfoeloe	47	53	32	15
wana	19	61	28	11
hoogland baboen	62	69	21	10
wiswiskwari	13	69	31	0
rode sali	90	72	23	4
krapa	16	81	0	19
tingimonisali	94	82	11	7
Saplings*****				
pegrekoepisi	3	0	0	100
kopi	3	33	33	33
slangenhout	6	33	50	17
goebaja	5	40	60	0
basralokus	17	41	35	24
bergi gronfoeloe	34	62	24	15
wana	5	60	20	20
hoogland baboen	24	58	25	17
wiswiskwari	6	83	0	17
rode sali	9	67	33	0
krapa	5	80	20	0
tingimonisali	9	89	11	0

* 57% of the sample area

** 30% of the sample area

*** 13% of the sample area

**** 0.2 – 2 m total height, in a sample area of 1152 m^2, using only species with more than ten seedlings

***** 2 m height – 5 cm dbh, in a sample area of 0.72 ha conditions for initial development (see Oldeman, 1978).

An unexpected finding is that recruitment of wiswiskwari (*Vochysia guianensis*) was more common in closed forest than in openings (Table 5.7) and that the scarce regeneration of wanakwari (*Vochysia tomentosa*) was found exclusively in residual forest. Both species are commonly considered light demanding because of their fast growth (Section 5.4.3), their non-exponential diameter class distributions (Section 4.3.2) and their frequent occurrence in old secondary forest (see Oldeman and Fundter, 1986). The findings do not support this opinion, and suggest rather that both *Vochysia spp.* require comparatively little light for their initial development. Regeneration of a few other species, such as krapa (*Carapa procera*) and the *Tetragastris spp.* rode sali (*T. altissima*) and tingimonisali (*T. hostmannii*), was also distinctly more abundant under residual forest than elsewhere (Table 5.7). These species are apparently more shade tolerant than most commercial species.

The existence of a relation between light requirements during the initial growing phases and diameter increment in the tree phase was investigated (see also Section 5.4.3). Such a relation is evident when pioneer species (fast growing, extremely light demanding) and primary species (relatively slow growing, more shade tolerant) are compared (Richards, 1952), but is less obvious when a comparison between commercial species is made. Some fast growing species are light demanding in the seedling and sapling phases (pegrekoepisi, agrobigi, soemaroeba), but others seem more shade tolerant (wit riemhout, wiswiskwari, wanakwari). The scarce regeneration of slow growing species such as bolletri (*Manilkara bidentata*), zwart riemhout (*Micropholis guyanensis var. commixta*) and satijnhout (*Brosimum paraënse*) was seen more often in gaps and along skid trails than under residual forest. Ajawatingimoni (*Trattinickia spp.*) is the only slow growing species which seems to regenerate better under residual forest than elsewhere.

5.6 Discussion

Pristine tropical rain forest is fairly easy to penetrate. "On river banks or in gaps where much light reaches the forest floor, there is a dense growth which is often quite impenetrable but in the interior of old undisturbed forest, if one's hand is free to bend a twig here and there, it is not difficult to walk in any direction, though sometimes a detour has to be made to avoid a fallen log or a mass of lianas which have slithered down from above" (Richards, 1952). However, when this forest is logged selectively, access becomes difficult because of logging debris which obstructs passage in almost every direction, and unhindered movement is only possible on skid trails.

The most likely impression of a logged forest is therefore one of great destruction, but findings presented in this chapter indicate that this impression is deceptive. Most debris in the study area consisted of remnants of felled trees (Section 5.3) and damage to the tree stand, although by no means negligible, remained within acceptable limits (Section 5.1), even after a relatively high yield of 46 m^3/ha.

There is therefore no need to limit yields to a maximum of 20 m^3/ha, as was suggested recently by de Graaf (1986) tó avoid damage, although imposing restrictions on sizes of trees to be felled is advisable on other grounds, and the minimum diameter for most commercial species should be about 50 cm rather than the present limit of 35 cm (see Sections 4.4; 5.3 and 6.5.1). A more preferable approach is to improve exploitation techniques to reduce both damage and costs, and Hendrison (in press) shows that this can be achieved by planning logging operations and making a few adjustments to felling and skidding methods (see also Jonkers and Hendrison, 1986). Even the simple control measures applied in the MAIN experiment (Section 3.1.2) seem to have a beneficial effect, but although damage in most commercial operations is more severe than in the study area, the difference is not dramatic.

After logging, conditions for growth and regeneration are more favourable than before because more nutrients are available (Section 5.3) and light conditions are improved. The forest recovers slowly, however, and diameter increment rates were only 0.07 – 0.21 cm/yr higher in logged stands than in virgin forest (Section 5.4). Tree growth stimulated by logging is therefore insufficient and forest management systems based only on such an effect (see Section 2.1) cannot be recommended in Suriname.

Recruitment of commercial species after logging was more encouraging from the forester's point of view (Section 5.5). Open spaces, where vegetation had been destroyed by logging, regenerated well and the increment of seedlings and saplings was stimulated considerably. Seedlings of marketable species growing 0.5 m/yr and more in height were not uncommon in openings and weed problems due to excessive light were exceptional (Section 4.3.5). A more modest improvement in growth may be expected where the canopy is still intact.

Gaps and skid trails occupied a substantial proportion of the forest floor (Section 5.2) but most were partly overtopped by medium-sized and large trees. This is shown clearly on aerial photographs presented in the next chapter (Figs 6.3; 6.4 and 6.5). Seedlings of commercial species in these openings developed adequately but growth could be improved by poison-girdling some overtopping trees. Eradication of too many trees would lead to proliferation of pioneer species, however, and would probably be counterproductive. The extent of openings was such that the creation of more gaps through silvicultural treatment was not necessary and silvicultural operations in recently logged stands should therefore concentrate on improving the increment of the tree stand further, rather than aiming to stimulate seedlings and saplings.

6 Celos Silvicultural System: theory, practice and impact on the stand

The Celos Silvicultural System (CSS), being a method of growing high-quality timber in semi-natural forest (de Graaf, 1986; see Section 2.2 for a brief description), should be implemented only if it is economically feasible, socially acceptable and ecologically justified. CSS as described by de Graaf meets the social and economic requirements because it is inexpensive, easy to implement and may result in job opportunities for some of Suriname's unemployed. Although the response of the commercial stand proved favourable (Section 2.2) and CSS can probably give an attractive sustained yield (Section 4.3.2), there are some ecological constraints and possible improvements that de Graaf did not investigate (Section 2.3). This final chapter therefore not only describes the impact of refinement on stand development, but also evaluates the possibilities for improving CSS.

Modifications in treatment prescriptions described in this chapter, which are intended to reduce refinement costs and lessen undesirable side-effects (Section 2.3), are partly based on the results discussed in Chapters 4 and 5. The evidence presented in Chapter 4 showed that it is ecologically desirable to reduce the intensity of silvicultural treatment in areas poorly stocked with commercial species. Furthermore, eradication of larger individuals of boegroemaka (*Astrocaryum sciophilum*) and other palm species is likely to have a beneficial effect on stand development, but as logging already results in a reduction of palm competition, the need for such a treatment may only arise during the second half of the felling cycle (see also Section 6.6).

It was shown in Chapter 5 that selective logging creates extensive openings where regeneration of commercial species can develop. Further stimulation of commercial recruitment by a poison-girdling treatment does not seem strictly necessary, and such efforts may even be counterproductive in large gaps. Isolated trees in such openings screen the soil from excessive light and poison-girdling them stimulates recruitment of secondary species and weeds rather than the regeneration of commercial species.

Modifications therefore include recommendations to make the first refinement more discriminative by reducing the number of trees poison-girdled where commercial trees are rare or absent (see Section 6.1). This should not noticeably affect the favourable growth response induced by refinement. In addition, improvements in refinement technique are suggested, especially those which diminish the amount of arboricide used (Section 6.2), and the organization of field-work is discussed (Sections 6.3.1 and 6.3.2). Investigations into the need for modification could not include the follow-up treatments, however, because of the premature termination of the project. Suggestions for such improvements are included in the last section of this chapter.

Refinement improves light conditions (see Section 6.1) and makes nutrients available from decomposing killed phytomass (see Section 6.4), thus stimulating the development of the remaining vegetation. The impact of the treatment on growth and recruitment is described in Section 6.5, and the costs involved are discussed in in Section 6.3.3.

6.1 Selection of trees to be eliminated

6.1.1 The choice of diameter limits

Two intensities of refinement were applied in the MAIN experiment (Section 3.1.2), namely a light refinement with a diameter limit of 30 cm for trees to be poison-girdled (treatment SR 18) and a more drastic treatment with a diameter limit of 20 cm (treatment SR 14). The choice of diameter limits applied was based on past experience (see Sections 2.2 and 2.3) and on theoretical considerations summarized below.

The principal aim of refinement is to stimulate growth of commercial trees by killing other trees and lianas, thus reducing competition and making nutrients from killed phytomass available for the remaining vegetation. Nutrient supply is not a major problem in refined forest and there will be an adequate supply even if poison-girdling is restricted to non-commercial species larger than 50 cm dbh. In this instance, there will be approximately 100 t/ha of killed phytomass (see Table 5.3), containing about 1400 kg/ha of nutrients. When the nutrients made available for tree growth by this very light refinement are added to the 650 kg/ha of nutrients in debris left after logging at 15 m^3/ha, or to the 1550 kg/ha left after logging at 46 m^3/ha (see Section 5.3), a figure of 2000 − 3000 kg/ha of nutrients is attained. This is a considerable proportion of the nutrient content of living phytomass in the original virgin forest, estimated at 6400 kg/ha. Competition in refined forest is mainly for light and selected diameter limits should aim to optimize light conditions.

Commercial and other canopy species start to form large reiterated crowns when they are approximately 30 m high, that is, when they have reached a trunk diameter (dbh) of about 30 cm. These "reiterated complexes" (Hallé et al., 1978) compete for light with one another, but the shade from thinner trees, which are generally shorter and have narrower crowns, is of little consequence for their growth. Hence, most non-desirable trees, that is, trees of non-commercial species and trees of commercial species with very serious defects (Section 3.1.2), impede the growth of commercial trees when they are greater than 30 cm dbh, and these trees should be eliminated. Trees less than 20 cm dbh are, however, not expected to reach 30 cm dbh in ten years and poison-girdling such trees during the first refinement is unlikely to improve the diameter increment of mature commercial trees.

Most commercial trees less than 30 cm dbh have not yet reached maximum trunk length and should be encouraged to grow both in height and in diameter. This can be achieved by eradicating overtopping medium-sized and large non-desirable trees and lianas. Competition from small non-desirable trees is likely to stimulate height increment, so they should not be eliminated. Seedlings and saplings of commercial species are also not expected to benefit from the elimination of small trees. Research by Schulz (1960; 1967), Boerboom (1965) and de Graaf (1986) has shown that this leads to excessive light on the forest floor and suppression of the regeneration of commercial species by weeds. It therefore seems unnecessary to poison-girdle non-desirable trees of less than 20 cm or even 30 cm dbh.

6.1.2 Evidence from simulated treatments

Killing all non-desirable trees larger than 20 or 30 cm dbh may lead locally to unfavourable microclimatic conditions, leaching of nutrients and other undesirable side-effects (see Sections 2.3, 4.4 and 5.6). These effects can be diminished or avoided by reducing the intensity of treatment in parts of the forest where such risks exist, that is, where commercial trees are rare or absent. Most trees in such areas hardly compete with commercial trees for light and local reductions in treatment intensity should be possible without affecting the favourable growth response induced by refinement. This means that there is a need for simple criteria to select non-desirable trees which compete for light with medium-sized and large commercial individuals. A simulation study was carried out for this purpose in which 14 treatments were compared, namely treatments SR 14, SR 18 and S 0 (no treatment), elimination of all non-desirable trees (treatment COM) and ten treatments which are described below (for methodology, see Section 3.1.5).

Many non-desirable trees which impede growth of commercial trees can be identified easily in the field, if they overtop one or more commercial trees or if their crowns shade at least one adjacent commercial tree. Two simulated treatments are based on the hypothesis that poison-girdling such obvious impeders leads to an adequate improvement in light conditions. One of these is a modification of treatment SR 14, in which all non-desirable trees of more than 20 cm dbh and seen to be competing for light with commercial trees larger than 20 cm dbh are eliminated (treatment 20-C). The second is a similar modification of treatment SR 18, in which non-desirable trees of more than 30 cm dbh which obviously impede commercial trees larger than 30 cm dbh are killed (treatment 30-C).

Other modified treatments are based on the assumption that impeders are concentrated in the immediate vicinity of commercial trees. Four of these treatments are identical to treatment SR 14, except that poison-girdling is restricted to areas within a radius of 7, 8, 9 or 10 m from commercial stems of more than 20 cm dbh (treatments 20-7, 20-8, 20-9 and 20-10). Four other treatments are similar modifications of treatment SR 18, that is all non-desirable trees of more than 30 cm dbh within distances of 7, 8, 9 or 10 m from the nearest commercial stem larger than 30 cm dbh are eliminated (treatments 30-7, 30-8, 30-9 and 30-10). Treatments 30-C, 30-7, 30-8, 30-9 and 30-10 aim mainly at liberating commercial trees larger than 30 cm dbh, but they should also create acceptable light conditions for smaller commercial trees.

Stands in the simulation study area. The simulation was carried out in three selectively logged plots (central parts of plots 32, 34 and 38; see Section 3.1.5), where the vegetation corresponded to that described for the entire MAIN experiment (see Chapter 4). Nevertheless, differences in stand composition were evident and, although the stands were by no means poor, differences in commercial stocking were substantial (Table 6.1). Spatial distributions of commercial and non-commercial trees deviated little from the Poissonian model (see Section 4.3.4), but a slight tendency towards clumped arrangements was observed in plot 34. Furthermore, the stands were distinctly different from one another in size class distribution and forest architecture, as can be seen on aerial photographs (Fig. 6.5). Each stand is briefly described below.

The forest in plot 32 may be described as predominantly overmature ("degrading growing phase"; Oldeman 1978, 1983) with a large number of commercial trees (100 stems > 20 cm dbh per hectare, see Table 6.1). Three large felling gaps were present, in which a few isolated, small trees and one medium-sized non-commercial tree survived exploitation. Non-desirable trees were less numerous than in plots 34 and 38 (Table 6.1), but some were very large individuals with impressive crowns. As many as 4.7 non-desirable trees per hectare were larger than 95 cm dbh.

The stand in plot 34 consisted of pockets of mature forest ("steady-state growing phase") and overmature forest in a matrix of young forest ("aggrading growing phase") and small chablis. Commercial species were well represented in all size classes (89 stems > 20 cm dbh per hectare, see Table 6.1). The stand contained many small and medium-sized trees with no commercial potential, but there were no non-desirable stems of more than 65 cm dbh (Table 6.1).

TABLE 6.1. MAIN experiment: numbers of desirable stems and non-desirable stems of different diameter classes in the central parts (0.64 ha) of three selectively logged plots

Plot	Category	Numbers per hectare and per diameter class (cm)						
		15-20	20-30	30-40	40-60	60-80	>80	total
32	desirable	17.2	42.2	29.7	21.9	4.7	1.6	117.2
	non-desirable	32.8	37.5	23.4	9.4	4.7	4.7	112.5
	total	50.0	79.7	53.1	31.3	9.4	6.3	229.7
34	desirable	26.6	48.4	17.2	17.2	1.6	4.7	115.6
	non-desirable	70.3	62.5	26.6	15.6	1.6	0.0	176.6
	total	96.9	110.9	43.8	32.8	3.1	4.7	292.2
38	desirable	17.2	25.0	12.5	18.8	7.8	0.0	81.3
	non-desirable	50.0	65.6	26.6	18.8	4.7	3.1	168.7
	total	67.2	90.6	39.1	37.5	12.5	3.1	250.0

The forest in plot 38 may be characterized as an intricate small-scale mosaic of growing phases. It was relatively poor in commercial trees, especially in the size classes from 20 to 40 cm dbh (64 trees > 20 cm dbh per hectare), but there were many non-desirable trees of all diameter classes (Table 6.1). The largest non-desirable tree had a stem of 90 cm in diameter.

Intensities of simulated treatments. The aim of the simulation study was to select treatments better suited than treatment SR 14 to poorly stocked parts of the forest, but equally effective in stimulating the increment of commercial species. Such poorly stocked pockets occurred throughout the MAIN experiment (see Section 4.3.4), and it was therefore expected that at least some non-desirable trees above the diameter limit would be spared when a modified treatment was applied.

This proved to be true for all alternative treatments described above (see Table 6.2). Alternative treatments with 20 cm diameter limits would generally lead to moderate reductions in treatment intensity. Application of treatment 20-10, for instance, would result in poison-girdling 92 trees per hectare, that is just ten trees per hectare less than treatment SR 14. Replacing treatment SR 14 by treatment 20-C means, however, that 46 non-desirable trees would be eliminated per hectare instead of 102, and raising diameter limits from 20 to 30 cm would lead to the preservation of even greater numbers of non-desirable trees. Treatment SR 18 is considerably less drastic than treatment SR 14 and any further restriction would bring the numbers of trees to be poison-girdled down to very modest levels (Table 6.2). Treatment intensity in terms of phytomass is discussed in Section 6.4.2.

Light conditions in treated stands. Changes in light conditions induced by the treatments described above were simulated to allow a comparison between silvicultural treatments, using provisional estimates for average extinction rates per unit of commercial crown space (E_M, see Section 3.1.5). The theoretical range of E_M values is from 0 (each m^3 of commercial crown space exposed to full day-light, no extinction) to 1 (extinction complete, no light reaches the crowns of commercial trees).

The results (Fig. 6.1) indicate that the impact of a treatment on light interception

TABLE 6.2. MAIN experiment: non-desirable stems to be poison-girdled in various refinements in three 0.64 ha plots

Plot	Trees (n/ha) to be poisoned per treatment							
	SR 18	30-C	30-7	30-10	SR 14	20-C	20-7	20-10
32	42.2	25.0	28.1	35.9	79.7	50.0	71.9	78.1
34	43.8	18.8	21.9	29.7	106.3	42.2	65.6	87.5
38	53.1	12.5	10.9	37.5	118.8	46.9	65.6	109.4
mean	46.4	18.8	20.3	34.4	101.6	46.4	67.7	91.7

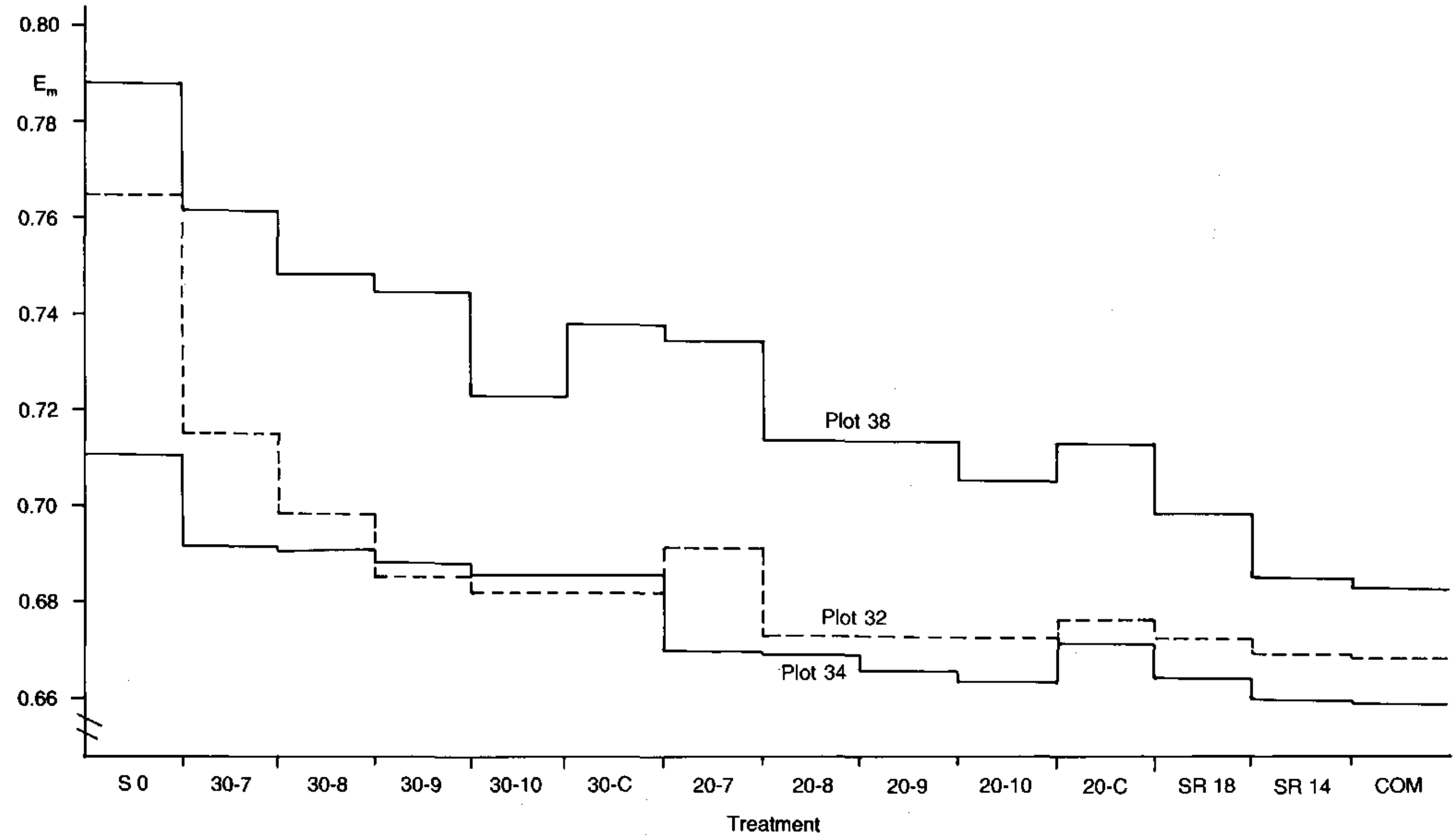


Fig. 6.1 MAIN experiment: simulated light extinction rates (E_M) after various silvicultural treatments in plots 32, 34 and 38. See Section 6.1 for explanation of codes

part of Suriname, and represents the relationship between bole diameters and crown radii of emergent trees.

Trees smaller than 40 cm dbh usually have crown radii of less than 4 m (Fig. 6.2). Some of these crowns may impede the growth of other trees slightly at a distance of more than ten metres, but severe competition over such a distance may only be expected from trees with much larger crowns, mainly in the dbh classes greater than 50 cm. These considerations suggest that poison-girdling should not be restricted to non-desirable trees close to commercial trees, and non-desirable trees likely to grow to 50 cm dbh before the next silvicultural treatment should be eliminated as well.

6.1.4 Conclusions

An alternative treatment (treatment 40/20-10) was formulated according to these principles (Section 6.1.3), in which all lianas thicker than 2 cm should be cut, and in which poison-girdling of non-desirable trees should include all those greater than 40 cm dbh *plus* any of more than 20 cm dbh that are within ten metres of a desirable stem of more than 20 cm dbh. In plot 32, this adjusted treatment would give results identical to those of treatment SR 14. In the other plots, however, small but useful reductions in treatment intensity would be achieved. Treatment 40/20-10 would lead to elimination of 89.1 trees per hectare in plot 34 and 112.5 trees per hectare in plot 38, that is 17.2 and 6.3 trees per hectare less than treatment SR 14 (see Table 6.2). Differences in E_M values achieved with the two treatments proved negligible in all plots. Treatment 40/20-10 is therefore regarded as a good alternative for treatment SR 14. It seems equally effective in stimulating increment of commercial trees, and results in a less drastic opening of the canopy in poorly stocked parts of the stand. This subject will be discussed further in Sections 6.4.2 and 6.6.

6.2 Refinement technique

Techniques to eliminate unwanted trees and lianas should be inexpensive, easy to implement, effective and ecologically acceptable. The aim of most earlier methods developed in Suriname and elsewhere was a great and sudden improvement in light conditions in order to liberate seedlings and saplings of commercial species quickly (for example, Letourneux, 1956; Wyatt-Smith, 1963; Schulz, 1967). This approach may be appropriate in monocyclic systems where most commercial seed trees are killed and very few new recruits may be expected after treatment. A more gradual change in light conditions and nutrient availability is preferable in polycyclic systems, however, because trees need time to adjust to altered environmental conditions (see Section 6.4), and an abrupt transition may lead to undesirable side-effects (see Section 2.3). Moreover, less arboricide may be required if unwanted trees can be killed slowly.

6.2.1 Climber cutting

Climber cutting is not only carried out to reduce competition for light and nutrients, but also to avoid casualties in the commercial stand. Woody climbers are often responsible for binding the crowns of commercial and poisoned trees, resulting in damage when large branches of dead trees fall. Lianas are abundant in the rain forests of Suriname, but most of them are fairly thin and easy to cut with a machete (see Section 4.3.6). This method was used in the MAIN experiment (Section 3.1.2) and proved inexpensive (see Section 6.3.3), but it is only temporarily effective. About 80% of the liana stems treated this way died (Table 6.5) and of the remaining 20% only the stumps survived. These may sprout and grow rapidly in refined forest. Application of arboricide is probably more efficacious in killing lianas, but poisoning all lianas is costly and ecologically undesirable and should only be considered for the few thick woody climbers which are difficult to cut. Improvements in the climber cutting operation are recommended in Section 6.3.2.

6.2.2 Poison-girdling

Methods for eliminating unwanted trees were studied in the MAIN experiment and the arboricide trial. The technique used in the MAIN experiment is a simple one (see also Section 3.1.2), in which trees are poison-girdled with a 5% solution of 2,4,5-T in diesel oil. This is poured into a frill-girdle and on the bark just above it to a height of 10 cm. Occasionally, the frill-girdle may be incomplete on fluted stems, in corners of buttresses or when two stems stand very near to one another. Such uncut sections should receive a 40 cm wide band of arboricide.

The arboricide trial compared the technique used in the MAIN experiment (treatment T-1) with four modified poison-girdling methods which require substantially smaller doses of 2,4,5-T (see Section 3.2). Reductions in arboricide application of between 37% and 69% (Table 6.3) were achieved as follows:

- by applying a 5% solution in the frill-girdle only (treatment T-2);
- by using a 2.5% solution in the frill-girdle and on the bark (treatment T-3);
- by applying a 2.5% solution in the frill-girdle only (treatment T-4);
- by ring-barking regularly shaped trunks twice instead of poison-girdling them (treatment T-5a), and treating irregularly shaped stems and buttressed trees with a 2.5% solution (treatment T-5b, which is analogous to treatment T-3).

The condition of poison-girdled and ring-barked trees was assessed three times during the first two years after treatment. The action of treatment T-1 was slow, although it had been expected that this treatment would kill unwanted trees more rapidly than the other treatments. Some species were highly susceptible to the arboricide and died within a few weeks (for example, Vochysiaceae and *Cecropia spp.*), but most trees were more resistant and perished slowly. About 70% of the

TABLE 6.3. Arboricide trial: quantities of arboricide used in various poison-girdling treatments

Treatment*	Trees to be eliminated		Arboricide used (kg acid equivalent)**	
	Number	Basal area (m^2)	Total	Per m^2 basal area
T-1	100	13.18	0.535	40.6×10^{-3}
T-2	100	12.91	0.331	25.7×10^{-3}
T-3	100	15.08	0.306	20.3×10^{-3}
T-4	100	13.76	0.174	12.6×10^{-3}
T-5a/b	100	13.09	0.163	12.5×10^{-3}

* Treatments: 5% 2,4,5-T solution (T-1 and T-2) or 2.5% solution (T-3, T-4 and T-5b) applied in frill and on bark (T-1, T-3 and T-5b) or in frill only (T-2 and T-4); ring-barking twice (T-5a)

** Volumes of arboricide solution (litres) may be calculated by multiplying by 41.67 for a 5% solution or 83.33 for a 2.5% solution

poison-girdled trees were still alive six months after treatment. The most important direct effect of poison-girdling is that the transportion of assimilates from crown to root system is interrupted because the arboricide rapidly kills cambium and phloem near the frill-girdle and disrupts the defense mechanisms of the tree. In spite of this, the root system may remain active for a year or longer and the impact of poison-girdling on the crown may remain inconspicuous until then. This aspect of the treatment can also be seen on the aerial photographs of the MAIN experiment (Figs 6.3; 6.4 and 6.5).

Another important consideration is that most poison-girdled trees die standing (see also Section 6.4). Observations in the Tonka and Mapane experiments show that branches tend to fall a few years after the tree has died and that most trunks remain standing until they are almost completely decayed. This means that the number of trees killed by falling wood is small.

The highest mortality rates recorded during each enumeration were for treatments T-3 and T-5b. These treatments resulted in 84 and 92% mortality after two years (Table 6.4), indicating that the concentration of 2,4,5-T can be reduced to 2.5% or maybe even less.

Attempts to kill trees by pouring the arboricide into the frill-girdle only (treatments T-2 and T-4) gave inconsistent results. Treatment T-4 was much more successful than treatment T-2 in spite of the lower dosage of arboricide (Tables 6.3 and 6.4). This discrepancy was probably caused by human error and fatigue. Arboricide poured into a frill-girdle is soaked up rapidly by the tree and because it is hard to see which part of the frill-girdle has already been treated, even the most conscientious labourer does not always apply arboricide over the whole circumference of the trunk. A classical solution to this practical problem has been to mix the arboricide with a colouring agent (see Wyatt-Smith, 1963), but this is not effective unless ample amounts of arboricide are administered, causing the frill-girdle to overflow.

TABLE 6.4. Arboricide trial: effects of various poison-girdling treatments on trees to be eliminated, two years after refinement

Effect	Percentage of total number of trees per treatment*					
	T-1	T-2	T-3	T-4	T-5a	T-5b
dead/leafless	75	52	84	81	49	92
almost leafless	9	14	6	4	23	2
no phloem contact	7	6	4	5	28	4
some phloem contact	9	27	5	10	0	2
recovered	0	1	0	0	0	0
tree not found	0	0	1	0	0	0
total	100	100	100	100	100	100

* Treatments: 5% 2,4,5-T solution (T-1 and T-2) or 2.5% solution (T-3, T-4 and T-5b) applied in frill and on bark (T-1, T-3 and T-5b) or in frill only (T-2 and T-4); ring-barking twice (T-5a)

There is very little horizontal diffusion of the poison and any small untreated sections will develop callus formation, thus restoring phloem transportation from crown to root system. This seldom leads to complete recovery (Table 6.4), and although the tree usually survives initially it develops extensive decay near the frill-girdle. When the trunk base has rotted, the living tree may break and fall, thus causing damage to the stand. In order to avoid this, it is recommended that arboricide be applied to the bark as well as in the frill-girdle.

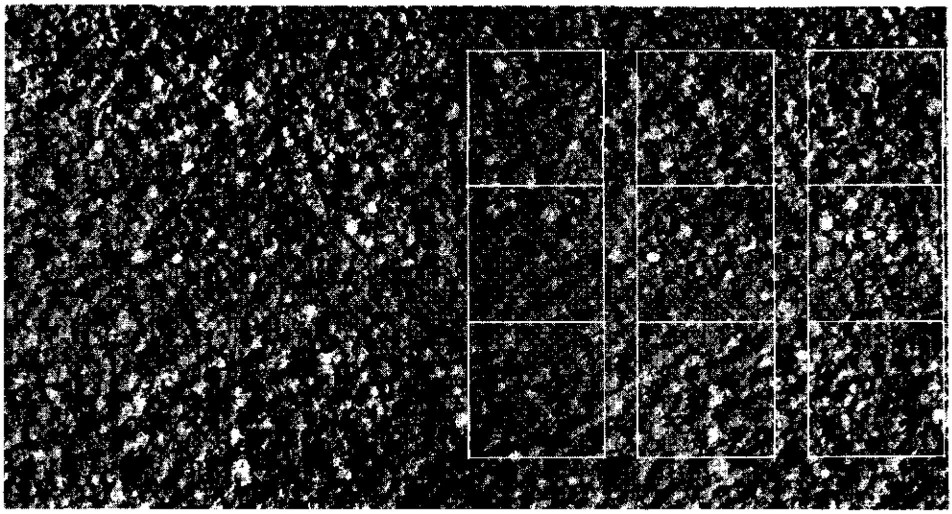


Fig. 6.3 MAIN experiment: aerial photographs of replication 1, taken about four months after refinement. Scale reduced to 1:11 000. Courtesy of Centraal Bureau Luchtkartering, Paramaribo

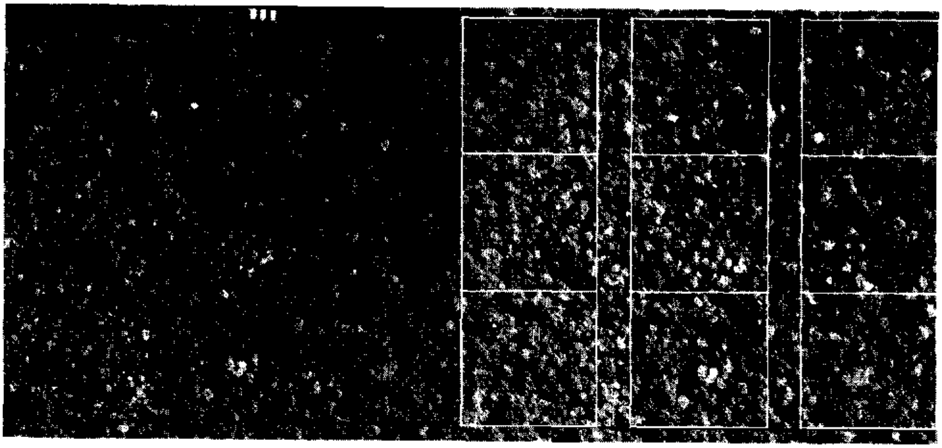


Fig. 6.4 MAIN experiment: aerial photographs of replication 2, taken about six months after refinement. Scale reduced to 1:11 000. Courtesy of Centraal Bureau Luchtkartering, Paramaribo

The results of efforts to eliminate suitable trees by ring-barking (treatment T-5a) were more encouraging. During the first six months after treatment, none of the 53 ring-barked trees died and only two of them had lost virtually all their leaves, but after 15 months, mortality had increased to 32% and another 21% were almost leafless. Two years after treatment, mortality was still increasing steadily and as many as 72% were either dead or dying. No trees had formed callus tissue over both rings (Table 6.4) and extensive stem decay was not observed, so virtually all ring-barked trees will probably die standing.

Treatment T-5a combined with treatment T-5b requires less arboricide than the other refinement techniques (Table 6.3), leads to more gradual changes in light conditions and nutrient availability, and may be equally effective in eliminating unwanted trees. However, the recording period was too short to provide adequate evidence of the effectiveness of ring-barking, so it is premature to recommend this as an alternative to poison-girdling.

6.3 Operations, efficiency and costs

In 1981 and 1982, a refinement was carried out over more than 200 ha of the Tonka research area. The area treated included parts of the MAIN experiment, the arboricide trial, and part of a hydrological experiment in the Ingipipa Creek catchment area (see Poels, in press). This section discusses operational aspects of refinement and is based on experience gained during this exercise.

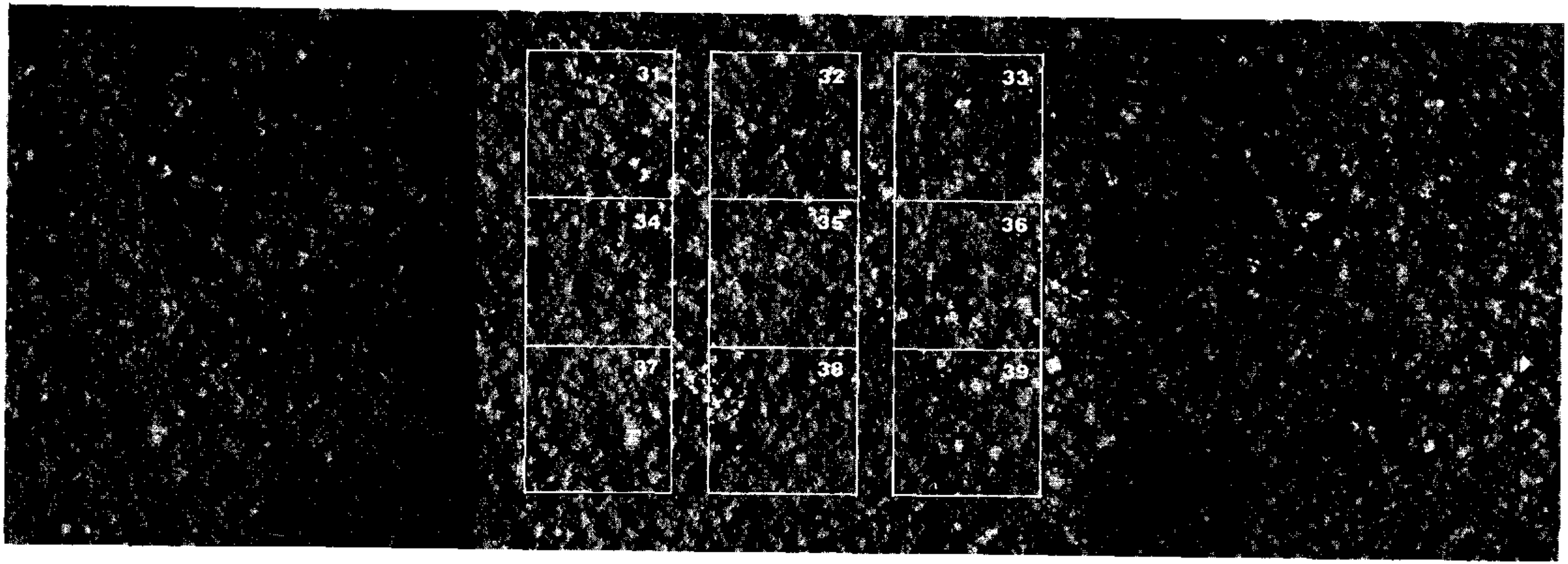


Fig. 6.5 MAIN experiment: aerial photographs of replication 3, taken about nine months after refinement. Scale 1:10000. Courtesy of Centraal Bureau Luchtkartering, Paramaribo

6.3.1 Field organization

De Graaf (1986, p. 47-50) proposed a provisional list of operations for harvesting and first refinement in the Celos Silvicultural System. One of the activities listed, an inventory to determine the diameter limit for refinement, can be omitted if the treatment proposed in Section 6.1.4 is applied (treatment 40/20-10). Furthermore, experience obtained in the Tonka research area indicates that other improvements are possible. This section describes the organization of a refinement operation and supersedes points *g*, *h* and *i* of de Graaf's list. The treatment itself is described elsewhere (Sections 3.1.2 and 6.1).

The first refinement is scheduled for the second year after felling. Treatment immediately after felling is not recommended because access to recently logged forest is obstructed by large amounts of fresh logging debris. It is better to delay the treatment until one year after felling, when passage is easier.

Before the actual treatment starts, parallel lines are cut to facilitate orientation. These lines should be at least one metre wide, approximately 100 m apart and preferably perpendicular to the contour lines. Parties for this work should consist of two men, one who reads the compass and one who cuts the lines. It is advisable to alternate these jobs between the two men. If the stand has been logged according to the Celos Harvesting System, lines cut during the pre-felling enumeration can be used (see Hendrison, in press), but they may have to be re-opened and additional lines may be required.

The refinement operation can start as soon as a few lines have been cut. Tree spotters and liana cutters are sent in first. In the Tonka research area, each tree spotter was accompanied by one liana cutter, but it may be preferable for each party to consist of two tree identifiers and three liana cutters (see Section 6.3.2). These men should stay together and move in a zigzag between the lines. Trees to be eliminated are marked with conspicuously coloured paint, white latex paint mixed with some blue pigment giving very good results. The paint marks indicate which part of the stand has already been worked and should be used for orientation, enabling the crew to work the whole forest systematically, without bypassing parts which then remain untreated.

The poison-girdling gang should follow within a few months. This party consists of three labourers making frill-girdles and two men doing the poisoning. Like the crew before them, these men should stay close together and work the whole stand systematically, moving in a zigzag between the lines. The band of arboricide above the frill-girdle facilitates orientation during this part of the operation and makes supervision easier because it is almost as conspicuous as paint marks, remaining visible for months.

6.3.2 Efficiency in application

Prescriptions for silvicultural treatment should be easy to comprehend by inexperienced labourers (Section 2.3). The instructions given for refinement in the Tonka research area were simple, but that does not necessarily mean that the treatment was carried out properly. In order to detect pitfalls and ensure a smooth operation, the scientists responsible for the experiments participated in the first field work. Despite frequent monitoring of the progress and quality of work, however, there were some discrepancies between actual and prescribed treatments. These are discussed below.

Climber cutting. Woody climbers are numerous, many are fairly inconspicuous and those which are easily seen often grow in intricate tangles in which individual plants are hard to identify. This makes climber cutting a tedious and difficult job. In the MAIN experiment, about 16 thick lianas per hectare had not been cutlassed, approximately one-fifth of the total number present before treatment (Table 6.5). Although this is considered satisfactory (see also Section 6.6), there is room for improvement.

Results would probably have been better if the composition of the scouting and climber cutting party had been more balanced. In the Tonka area, each tree spotter was accompanied by one liana cutter. It was observed that liana cutters often had difficulty keeping pace with the tree identifiers, often lagging behind and moving at a greater speed than was good for the quality of their work. A five-man party consisting of two tree spotters and three liana cutters would therefore be more efficient.

Poison-girdling. Refinement with a 20 cm diameter limit (treatment SR 14) is a radical treatment and as many as 92 trees per hectare should have been poison-girdled in the MAIN experiment, if treatment had been in strict accordance with the prescriptions. Treatment SR 18 is considerably milder and should have resulted in the elimination of 37 trees per hectare. In reality, however, only 73 and 31 poison-girdled trees were recorded per hectare after treatments SR 14 and SR 18 respectively.

Apparently, a considerable number of trees which should have been eliminated

TABLE 6.5. MAIN experiment: analysis of the efficiency of climber cutting, using numbers of thick lianas per hectare in treated and untreated stands

Dbh class (cm)	Lianas in treated stands (n/ha)*			Lianas in untreated stands (n/ha)**
	Cut but alive	Not cut	Total	
5 – 10	9.4	13.3	22.8	61.7
10 – 15	0.6	2.2	2.8	5.5
>15	0.0	0.8	0.8	3.9
total	10.0	16.3	26.3	71.1

* Sample size: 3.6 ha
** Sample size: 1.8 ha

TABLE 6.6. MAIN experiment: analysis of the efficiency of poison-girdling, using numbers of poison-girdled trees and non-desirable trees overlooked during refinement

Treatment	Dbh class (cm)	Non-desirable trees (n/ha)		
		Poisoned trees	Trees not poisoned	Total
SR 14*	15 – 20	0.8	n.a.	n.a.
	20 – 25	13.8	14.6	28.4
	>25	58.6	5.1	63.7
	>20	72.4	19.7	92.1
SR 18**	25 – 30	1.6	n.a.	n.a.
	30 – 35	7.8	5.7	13.5
	>35	21.1	2.7	23.8
	>30	28.9	8.4	37.3

* Diameter limit: 20 cm, sample size: 9 ha per treatment
** Diameter limit: 30 cm, sample size: 9 ha per treatment

were left unpoisoned. Most of these trees were only a few centimetres larger in diameter than the limit set for refinement, but several larger unwanted trees were also overlooked (Table 6.6). In addition, a few trees were poison-girdled unjustly. These were almost exclusively small individuals of non-commercial species (Table 6.6). Commercial trees were seldom poisoned by mistake (0.1 – 0.2 trees per hectare) and refinement did not lead to a substantial reduction in commercial stocking.

It is likely that these errors mostly originate from inaccurate diameter assessment and oversight by the tree spotter, less frequently from faulty species identification and very seldom from oversight by the poison-girdling gang. This means that actual treatments would have complied better with the prescriptions if the diameters of non-desirable stems had been measured more accurately. Such measurements are often necessary to determine whether or not a tree should be poison-girdled and in the Tonka operation, rulers were used because callipers are too large and cumbersome, and tape measurements take too long. However, more accurate measurements do not lead to noticeable improvements in growth response.

Improvements in species identification may be achieved if tree spotters work in pairs. In the Tonka operation, tree identifiers were instructed not to mark a tree for poison-girdling if there was even the slightest doubt that it was a non-commercial species. This rule helps to prevent poisoning of commercial trees, but it also results in the unplanned retention of some non-desirable trees, and the latter will occur less frequently if tree spotters can ask for a second opinion.

6.3.3 Costs

During the refinement operation in the Tonka research area, a day-by-day record was kept showing the composition of parties engaged in silvicultural work, the areas treated and the amounts of arboricide issued to the crews. This record was used to estimate the manpower and arboricide required for an unmodified 20 cm diameter limit refinement. Labour input was expressed in man-days, of approximately six effective working hours per day.

Line cutting was not necessary in Tonka since subdivision lines were available already. According to de Graaf (1986), line cutting takes about two man-days per kilometre. This means that manpower requirements for a completely new set of lines may be estimated at 0.2 man-days per hectare. Climber cutting is an inexpensive treatment. In the Tonka area, only 0.3 man-days per hectare were spent on this activity, but some additional labour may improve its efficiency (Section 6.3.2). Poison-girdling is more expensive. Labour input for frill-girdling and spraying is estimated at 2.2 man-days per hectare (about 13 man-hours per hectare). This figure is similar to the result of an ergonomic study by Staudt (1976), who estimated manpower for these activities to be 14.2 man-hours per hectare. Tree marking takes 0.3 man-days per hectare.

Equipment and supplies consist mainly of arboricide, diesel, and some minor-cost items such as paint, knapsack sprayers, axes and machetes. It was found that 17 litres of a 2,4,5-T solution in diesel oil was enough for a 20 cm limit refinement over one hectare. A 5% solution was used, but a 2.5% concentration proved equally effective (Section 6.2.2). Costs of paint and tools are negligible compared to other inputs and although no record was kept of quantities of paint issued, half a litre per hectare seems a reasonable estimate. Approximately US$ 300 was spent on sprayers, axes and machetes and no effort was made to estimate depreciation because most tools were still serviceable after refinement had been completed.

The total input per hectare for a 20 cm refinement is therefore three man-days, plus 0.4 litres of 2,4,5-T and 16.6 litres of diesel oil, plus overhead costs and some minor expenses. This is substantially less than in previous trials (see Section 2.2) and further cost reductions may be achieved by modifying the treatment prescriptions (see Sections 6.1 and 6.2).

6.4 Impact on phytomass and nutrient status

6.4.1 Actual treatments

An estimate was made of changes in phytomass and nutrient availability in the MAIN experiment after refinement (for methodology; see Section 3.1.5). Reductions in above-ground tree phytomass are summarized in Table 6.7. The dry weight of trunks, branches and leaves of the 73 trees per hectare poisoned in treatment SR 14 (refinement with a 20 cm diameter limit) was estimated at 165 t/ha, more than 40% of the phytomass present before treatment. In addition, comparatively small amounts of root and liana phytomass were killed. Treatment SR 18 (refinement with a 30 cm diameter limit) is milder, but the 31 poisoned trees per hectare still account

TABLE 6.7. MAIN experiment: changes in above-ground phytomass (t/ha) and mortality among poisoned and other trees > 15 cm dbh in the first year after refinement*

Treatments		Dry weight in t/ha						Total
Refinement	Logging	Poisoned trees			Other trees			
		dead	*alive*	*total*	*dead*	*alive*	*total*	
SR 18	E 15	79.8	41.4	121.3	3.9	281.6	285.5	406.8
	E 23	78.6	63.4	142.0	1.9	263.0	264.9	407.0
	E 46	42.9	44.5	87.4	1.6	227.6	229.2	316.6
	all	67.1	49.8	116.9	2.5	257.4	259.9	376.8
SR 14	E 15	94.0	47.6	141.6	12.5	274.8	287.3	428.9
	E 23	151.2	68.7	219.9	1.2	234.1	235.3	455.1
	E 46	64.9	68.6	133.5	4.2	143.6	147.8	281.3
	all	103.4	61.6	165.0	6.0	217.5	223.5	388.4

* Sample size: 3 ha per combination of logging and refinement treatments

for 31% of the pre-treatment phytomass. These figures illustrate once more that refinement is a drastic treatment.

It was found that phytomass reductions in individual one-hectare plots may deviate considerably from the mean values (see Table 6.8) because of natural variation in forest composition and, possibly, of logging. An increase in logging intensity leads to more casualties among non-commercial trees (Section 5.3) and it seems logical that felling a greater volume leaves less trees to be poison-girdled. An attempt was made to find a correlation between logging intensity and phytomass poisoned during refinement, but no evidence of such a relationship was found (Table 6.7).

Decomposing poisoned trees act as fertilizer ("fertilizing effect"; Jonkers and Schmidt, 1984). As one tonne of phytomass contains approximately 14.5 kg of nutrients (4.2 kg N, 0.3 kg P, 3.2 kg K, 6.2 kg Ca and 0.6 kg Mg; Jonkers and Schmidt, 1984), the 117 t/ha of above-ground phytomass poisoned in treatment SR 18 means that about 1.7 t/ha of nutrients were made available for growth of the remaining vegetation. Even larger quantities of nutrients (about 2.4 t/ha of nutrients) may be expected when treatment SR 14 is applied. In addition, relatively small amounts of nutrients were made available from decaying root systems and cutlassed lianas.

The nutrient status after refinement is influenced not only by silvicultural treatment but also by logging. It has been shown in the previous chapter (Section 5.3) that selective logging leaves behind fairly large quantities of dead organic material (30 – 70 t/ha). Amounts of nutrients in logging debris depend on felling intensity and were estimated at 0.65 – 1.55 t/ha (Section 5.3), meaning that some 3 – 4 t/ha of nutrients were made available through selective logging and silvicultural treatment SR 14. This supply is comparable to the nutrient content of the remaining stand and, hypothetically at least, suffices to support the growth of some 200 –

270 t/ha of forest phytomass. Lesser amounts of nutrients are expected to become available after treatment SR 18 (2.3 – 3.3 t/ha).

These nutrients become available gradually because it is several years before virtually all poison-girdled trees are dead (Section 6.2.2 and Table 6.7) and decomposition of dead phytomass is a long-term process (see Schmidt, in press). Thus, logging and silvicultural treatment result in a continuous supply of nutrients over a period of many years. The supply may be larger than necessary for the development of the commercial stand, but there is evidence that the ecosystem is capable of absorbing virtually all nutrients released from decaying phytomass. There may be some accumulation of nutrients in non-exchangeable form in the soil, but losses due to leaching proved negligible (see Jonkers and Schmidt, 1984; Jonkers and Hendrison, 1986; Poels, in press). Recruitment of pioneer species and other fast growing species such as swietiboontje (*Inga spp.*; see Poncy, 1985) is considered important in this context, because they develop rapidly wherever large openings in the canopy appear and may take up substantial amounts of nutrients which might otherwise be lost (see Tjon Lim Sang, in press). More detailed information on phytomass and nutrients in refined forest can be found in Schmidt (in press) and Poels (in press).

6.4.2 Simulated treatments

A simulation study was carried out in plots 32, 34 and 38 to find a treatment less drastic than the 20 cm limit refinement but equally effective in stimulating growth (Section 6.1.2), and estimation of changes in phytomass was part of this exercise. The results are summarized in Table 6.8.

Evidence presented earlier indicates that treatment 40/20-10 is a promising alternative for treatment SR 14, and that treatments SR 18, 20-C and 20-10 are also worth trying (for definitions and discussion: see Sections 6.1.2 and 6.1.4). Treatments SR 18 and 20-C result in relatively small amounts of dead phytomass, but the amounts from treatments 20-10 and 40/20-10 are similar to treatment SR 14 in the well-stocked study area. Reducing the amount of phytomass killed is ecologically desirable (see Section 2.3) and may lead to lower costs, so treatments SR 18 and 20-C may turn out to be more satisfactory than treatments 20-10 and 40/20-10. This subject will be discussed further in Section 6.6.

6.5 Response of the residual stand

Trees of commercial species are known to increase in diameter much more rapidly in response to refinement (de Graaf, 1986; see also Section 2.2), but the response is not instantaneous because it is about two years before the desired improvement in light conditions is fully realized (Section 6.2.2). Moreover, the vegetation needs time to adjust to altered growth conditions. Hydromorphic and mesomorphic shade leaves

TABLE 6.8. MAIN experiment: simulated changes in above-ground phytomass after various silvicultural treatments, using dry weights (t/ha) of remaining trees and poison-girdled trees > 15 cm dbh in three 0.64 ha plots

Treatment*	Phytomass in t/ha					
	Plot 32		Plot 34		Plot 38	
	remaining	*poisoned*	*remaining*	*poisoned*	*remaining*	*poisoned*
reference treatments						
S 0	461	0	316	0	358	0
COM	176	285	185	131	147	211
30 cm diameter limit						
SR 18	203	257	233	84	193	165
30 – C	226	235	277	39	291	67
30 – 7	380	81	275	41	337	21
30 – 8	317	144	274	42	291	67
30 – 9	230	231	258	58	281	77
30 – 10	214	247	255	61	220	138
20 cm diameter limit						
SR 14	183	278	195	121	153	205
20 – C	191	270	253	63	235	123
20 – 7	251	210	232	84	238	120
20 – 8	188	273	226	90	203	155
20 – 9	187	274	215	101	195	163
20 – 10	187	274	211	105	172	186
20 cm and 40 cm diameter limits						
40/20 – 10	183	278	206	110	162	196

* For explanation of codes, see Sections 6.1.2 and 6.1.4

have to be replaced by more xeromorphic sun leaves to upgrade photosynthesis (see Roth, 1984), and dying root systems of poison-girdled trees have to be substituted by newly-formed roots of living plants to prevent leaching of nutrients.

The first one or two years after refinement are therefore a transition period. Data on diameter growth, mortality, flushing, flowering and fruiting during this period were collected in the MAIN experiment (see Section 3.1.3) and are presented below. Information on increment and mortality in subsequent periods is available from the Mapane experiments, described briefly in the introduction of Chapter 3.

6.5.1 Phenological observations

Phenological observations on all trees larger than 15 cm dbh were recorded monthly for 14 months in two 0.25 ha plots (see Section 3.1.3 for methodology). The principal objective of this exercise was to detect differences in phenology between refined forest (plot 21) and untreated forest (plot 22) and the consequences of these findings for CSS are discussed in Section 6.6. Twenty-one trees had been poison-girdled in the refined plot and ten of those were still alive when the first observations were made nine months after treatment. Three poison-girdled trees survived the observation period.

The two sites selected were within a short distance of one another (150 m), and were comparable in stand composition, topography and soils. The stands in plots 21 and 22 both were mostly overmature, with one large felling gap and a few pockets of small and medium-sized trees. Both plots were rich in commercial species, with 28 and 29 commercial trees in plots 21 and 22, respectively. One commercial tree in plot 22 died during the observation period. Non-commercial trees were more numerous in plot 21 than in plot 22, in spite of the refinement, with 27 individuals in plot 21 compared to 22 in plot 22. Eight non-commercial trees died during the observation period, namely one tree in plot 22 and seven poison-girdled trees in plot 21.

Bergi gronfoeloe (*Qualea rosea*) was the most abundant species, with 16 trees in plot 21 and 13 trees in plot 22. Basralokus (*Dicorynia guianensis*) was also common with three trees in plot 21 and five trees in plot 22. The remaining 20 commercial trees belonged to 11 species and five of them were represented in both plots. Alata oedoe (*Minquartia guianensis*) was the most common non-commercial species, with three individuals in each plot. The other 43 non-commercial trees belonged to 26 different species, of which six were found in both plots.

Leaf change. Many observations on leaf change in tropical trees have been published (see Richards, 1952; Longman and Jenik, 1974; Alvim and Alvim, 1978; Schmidt, in press). The average life cycle of the leaves is about 13 – 14 months (Richards, 1952; see also Schmidt, in press) and it is evident that there are widely different types of behaviour. Longman and Jenik (1974) distinguished four "patterns of leafiness":

- Periodic growth, deciduous-type. Leaf fall occurs well before bud break and the tree is leafless for a period varying from a few weeks to several months. A few species in Suriname belong to this type, such as kwatakama (*Parkia pendula*), groenhart (*Tabebuia serratifolia*) and rode lokus (*Hymenaea courbaril*). These species were not represented in plot 21 or 22.
- Periodic growth, leaf-exchanging-type. Leaf fall is associated with bud break and flushing of new leaves starts almost simultaneously with the fall of the old ones. The tree may be leafless for about a week. Canopy trees of basralokus (*Dicorynia guianensis*) and gujavekwari (*Qualea dinizii*) are of this type. Mature and overmature basralokus trees dropped all their leaves after the rains ceased in

August and replaced them almost immediately by new ones. Small individuals of basralokus, however, were evergreen and flushed sparsely at seemingly irregular intervals throughout the year. Both types of behaviour may occur on different reiterations of a single tree, as was observed on one tree in plot 22.

- Periodic growth, evergreen-type. Leaf fall is completed well after bud break and trees produce new leaves in periodic flushes before the old leaves are shed. Virtually all species found in plots 21 and 22 belong to this type. In most canopy species, shoot elongation was discontinuous and was concentrated in, but not entirely restricted to a particular season. Bergi gronfoeloe (*Qualea rosea*), for instance, flushed profusely once a year in August and September, but individual trees may also produce some new leaves at any time of the year. Synchronization of bud break was often less obvious in the understorey, and many small-sized trees were seen to renew only a few leaves during the entire recording period.
- Continuous growth, evergreen-type. Continual production of leaves was not recorded on any trees in plot 21 or 22.

Leaf change in the stand as a whole was distinctly seasonal with peaks in the the long rainy season (March – May) and in the long dry season (August and September) and lows in December and June.

Refinement may slightly affect seasonal rhythms in shoot elongation. Bergi gronfoeloe, for instance, flushed more abundantly and over longer periods in treated forest than in the untreated stand. Furthermore, the results indicate a positive response of the stand to silvicultural treatment, with new leaves on commercial trees recorded 171 times in the treated plot and 137 times in the untreated plot.

Most non-commercial trees which remained in plot 21 after refinement were shade-tolerant understorey species, which did not noticeably respond to the treatment, while the few larger non-commercial trees had all been poison-girdled and did not produce new leaves at all. Non-commercial canopy trees in plot 22 generally renewed their leaves faster than understorey species, and emergence of new leaves on non-commercial trees was observed less frequently in plot 21 (83 times) than in plot 22 (125 times).

Flowering and fruiting. Most information on flowering and fruiting in neotropical rain forest is fairly recent. A few studies on periodicity in reproductive behaviour of tree species have been published (see Sabatier and Puig, 1986; Baker et al., 1983), and many publications on plant-animal interactions also include such information (see van Roosmalen, 1980; Charles-Dominique et al., 1981; Smythe, 1986). Sabatier and Puig (1986) distinguished six patterns of flowering and fruiting in French Guiana: continuous, discontinuous at regular intervals (biannual, annual or biennial), and discontinuous at irregular intervals. Continuous flowering was not observed in plots 21 and 22 and most trees were not seen to blossom more than once. It is therefore impossible to determine periodicity in the flowering of individual species from these data.

Flowering in tropical rain forest generally extends throughout the year and there is no season in which a proportion of the species are not in flower, but even in the least seasonal climates there are maxima of flowering at certain times of the year (Richards, 1952). This is also true in Suriname. In the Tonka research area, the maximum flowering season starts in September or October and lasts until January, and virtually all emergent trees and many medium-sized and small trees were seen to bloom during this period. Bergi gronfoeloe (*Qualea rosea*) started blossoming in October and flowered gregariously for at least one month, and basralokus (*Dicorynia guianensis*) flowered abundantly in December and January. Both species have been observed to flower once every two years (Schulz, 1960; Puig, 1981). Other commercial species seen in bloom during this season were kopi (*Goupia glabra*), hoogland baboen (*Virola melinonii*), harde bast tingimoni (*Protium neglectum*), rode sali (*Tetragastris altissima*) and tingimonisali (*Tetragastris hostmannii*).

The fruits started to grow after pollination and it was several months before they were ripe. Seeds of bergi gronfoeloe, basralokus and many other species fell within a relatively short period in the middle of the long rainy season (late April – early June). Such synchronization in fruiting has been observed in neotropical rain forest by many authors (see Baker et al., 1983). A widely accepted explanation for this phenomenon is that its purpose is to generate a temporary surplus of food for seed predators (see Janzen, 1971; Smythe, 1986). In this way, at least part of the crop is not eaten when still unripe by monkeys, parrots and other arboreal frugivores, or when the seeds fall on the forest floor by terrestrial mammals such as peccaries, agoutis and acouchis (Mittermeier and van Roosmalen, 1980; Hopkins and Hopkins, 1983; Smythe, 1986). This strategy may also be effective against attack by bruchid weevils (Smythe, 1986).

Another plausible explanation for this synchronization is that physical conditions during the long rainy season tend to be more favourable for establishment and growth of seedlings than at other times of the year. Desiccation of germinating seeds is less likely than in less humid periods, and some of the newly established seedlings may benefit from a seasonal peak in chablis formation in the second half of the rainy season. Evidence for a distinct maximum in tree falls during this period is available from both French and Venezuelan Guiana (see Riéra, 1982; 1983; Rollet, 1983).

Only a few commercial trees were seen flowering between February and August 1982. One basralokus tree still had some flowers in February, the only bolletri (*Manilkara bidentata*) in the sample was seen in full bloom in April and produced a few ripe berries in July, and blossoms of krapa (*Carapa procera*) were observed in August. Several non-commercial trees also bloomed during this period. An exceptionally tall individual of hoogland oemanbarklak (*Lecythis corrugata*), a common understorey species (Section 4.3.3), flowered in February and another Lecythidaceae, hoogland konkoni oedoe (*Gustavia hexapetala*), in April. Fruits were seen on both trees until August. All four rode jakanta (*Dendrobangia boliviana*) trees produced blossoms in March and carried fruits until June. A small-sized kaneelpisi tree (*Licaria guianensis*) flowered in June and a large lika oedoe tree (*Antonia ovata*) flowered gregariously in July.

It was found that several commercial species did not reach sexual maturity until they had reached sizes of approximately 30 cm dbh, for example, bergi gronfoeloe (*Qualea rosea*) and basralokus (*Dicorynia guianensis*). Commercial species which seldom grow to large diameters such as krapa (*Carapa procera*) and hoogland baboen (*Virola melinonii*), were observed flowering when still fairly small trees of approximately 20 cm dbh. In the case of basralokus, there was a striking relationship between the "pattern of leafiness" and flowering. Trees which were still evergreen did not produce any flowers, but all larger individuals in the "leaf-exchanging" stage were seen blossoming gregariously. The tree in plot 22 which exhibited both "patterns of leafiness" on different reiterations (see above), flowered and fruited only on the "leaf-exchanging" part of the crown. Basralokus is a popular species on the timber market, and adequate recruitment cannot be expected if loggers are allowed to take any tree larger than the current minimum felling limit of 35 cm dbh. This illustrates once more the importance of increasing the minimum felling diameter for some commercial species (see also Section 4.4).

There is evidence that refinement alters the reproductive behaviour of at least one commercial species, bergi gronfoeloe (*Qualea rosea*), flowering of which was obviously stimulated by the treatment. All emergent trees of this species were seen flowering abundantly in October, that is six trees in plot 21 and six trees in plot 22. In November, the species was still in full bloom in the refined stand, but flowering in the untreated stand had almost ceased. One tree in the refined stand flowered for a second time in January, and fruits in different phases of development were seen on the same branches in subsequent months. *Qualea rosea* fruits are dehiscent capsules, and the ripe fruits open while still on the tree, releasing the winged seeds (see Oldeman and Fundter, 1986). Dehiscence in the untreated plot was virtually complete before the middle of May, but in the refined plot, fruits were observed on all emergent trees until the beginning of June and the tree which had flowered in January carried fruits until July. It may be that reproductive behaviour of other species is also affected by refinement, but the sample was too small to show this.

6.5.2 Growth and mortality of commercial trees

Developments in the first year after treatment. Growth and mortality figures for the first year after treatment are available from the MAIN experiment. As was stated in the introduction to Section 6.5, this was a transition period during which little variation in growth between treatments was expected, and the results confirmed this (Table 6.9). Average growth rates for commercial trees larger than 15 cm dbh increased to about 0.5 cm/yr in treated stands, which is only slightly higher than that found in untreated parts of the experiment. Differences in growth rates between refinement treatments SR 14 (20 cm diameter limit) and SR 18 (30 cm diameter limit) were very small and the impact of logging intensity on diameter increment was even less apparent than before refinement (see also Section 5.4). It was nonetheless considered useful to test variation in growth rates by ANOVA, and statistically significant treatment effects were found both for logging and for refinement (see

TABLE 6.9. MAIN experiment: diameter increment of commercial species in the first year after refinement in relation to level of exploitation and silvicultural treatment

Dbh class (cm)	Silvicultural treatment	Mean diameter growth (cm/yr) level of exploitation			Mean of treatments (cm/yr)
		E 15	E 23	E 46	
5 – 15	S 0	0.17	0.30	0.31	0.26
	SR 18	0.35	0.36	0.45	0.39
	SR 14	0.36	0.42	0.50	0.43
	mean	0.29	0.36	0.42	0.36
>15	S 0	0.40	0.45	0.48	0.44
	SR 18	0.48	0.48	0.58	0.52
	SR 14	0.48	0.51	0.57	0.53
	mean	0.45	0.48	0.54	0.49

Table VII.1, Appendix VII). Diameter growth of small commercial trees (5 – 15 cm dbh) was analysed separately. Although the increment rates were lower than for the larger size classes, a small but statistically significant effect of silvicultural treatment was found (Tables 6.9 and VII.2).

The MAIN experiment was originally designed to test growth in relation to logging and refinement, and results presented here and in the previous chapter (Section 5.4) illustrate that even the existence of very small differences in increment can be shown statistically. That this aspect of the experiment may lead to unexpected results is illustrated by an ANOVA test in Appendix VII (Table VII.1). The analysis resulted in a small but statistically highly significant replication effect, and this needs to be explained.

It is evident from the input data in Table VII.1 that diameter growth figures for replication 1 are low compared to data from the other replications, and that figures for the untreated plots in replication 3 are higher than would be expected if variation was merely random. This is mainly due to seasonal influences. Tree trunks do not only grow in diameter, but also shrink and swell due to changes in moisture availability. Schulz (1960) has shown that moisture stress during a long dry season often leads to a decrease in trunk diameter and similar results have since been reported in other studies (Puig and Prévost, 1986; see also Ashton, 1978). Refinement in replication 1 was carried out in the long rainy season of 1982 and the enumeration was done simultaneously. The next assessment was in the long dry season of 1983 and increment was negatively biased by shrinkage. The untreated plots of replication 3, on the other hand, were assessed in the long dry season of 1981 and again in the long rainy season of 1983 and growth figures for these plots were positively biased.

Mortality among commercial trees was comparable to rates obtained in pristine forest. In areas where the forest had been subjected to no other treatment than selective logging, mortality was somewhat less than 2% per annum, and in the refined plots, slightly more than 2% of the commercial stand died during the first year after refinement. However, this figure includes some defective trees which had been poisoned, and refinement did not lead to a noticeable increase in mortality among trees which had not been poison-girdled (see also Table 6.7).

Growth and mortality in subsequent years. Information on increment and mortality over longer periods is available from two experiments in the Mapane region (Experiment 67/9A and 67/9B). Both Experiment 67/9A ("Mapanebrug") and Experiment 67/9B ("Akintosoela") are described briefly in the introduction of Chapter 3. De Graaf (1986) made an extensive study of stand development in these experiments. The results presented here are partly from his study and partly from internal reports (van der Hout, 1983; Jonkers, 1983).

The forest in the Mapane trials was distinctly different in species composition from stands in the Tonka research area, and the stock of commercial species was poorer than in the MAIN experiment (see Tables 6.10, 6.11 and 4.3). The forest may be characterized as "rode sali forest" since about half the commercial stand was of rode sali (*Tetragastris altissima*). Other common species were hoogland baboen (*Virola melinonii*), krapa (*Carapa procera*) and okerhout (*Sterculia spp.*). These four species seldom grow large (see Section 4.3.2). Commercial species which reach large diameters, such as basralokus (*Dicorynia guianensis*) and bruinhart (*Vouacapoua americana*), were of sporadic occurrence, so commercial trees larger than 60 cm dbh were rare (see Tables 6.10 and 6.11).

The Akintosoela experiment was a 25 ha trial which received a 20 cm refinement in 1975, a similar treatment to that applied in the MAIN experiment (treatment SR 14). The commercial stand responded with greatly increased growth (Table 6.10). In the second and third years after treatment, average diameter growth rates were 0.8 – 0.9 cm/yr. In the next two-year period, the average increment of small trees (5 – 15 cm dbh) started to decline but the growth of larger trees increased to 1.0 cm/yr. In the sixth and seventh years after refinement, growth in the 5 – 15 cm and 15 – 30 cm dbh classes was slightly less than in the previous period, but mean diameter increment of the 30 – 60 cm dbh class increased still further (Table 6.10).

Mortality rates were comparable to figures obtained in refined forest in the MAIN

TABLE 6.10. Experiment 67/9B: temporal changes in diameter growth of commercial species after a refinement with a 20 cm diameter limit (1975)*

Dbh class (cm)	n/ha (1980)	Mean annual increment (cm/yr) per two-year period			
		1976 – 1978	1978 – 1980	1980 – 1982	Mean
5 – 15	118.4	0.8	0.7	0.6	0.7
15 – 30	31.9	0.9	1.0	0.9	0.9
30 – 60	26.0	0.9	1.0	1.1	1.0
>60	1.9	n.a.	n.a.	n.a.	n.a.

Source: van der Hout (1983) and de Graaf (1986)
* Sample size: 2.83 ha (trees 5 – 15 cm dbh) and 16 ha (trees > 15 cm dbh)

experiment. Only 14% of the original commercial stand died during the recording period of six years (van der Hout, 1983), which is equivalent to 2.1% per annum. Mortality among small trees was markedly higher than among the larger ones (see de Graaf, 1986).

According to the treatment schedule proposed by de Graaf (1986), the Akintosoela area should have been treated for the second time eight years after the initial refinement. The results presented here would not justify such action, however, because growth rates were still favourable seven years after the first refinement and there were no indications of a rapid decline in the next few years. Therefore, it was decided to postpone the second refinement for at least two years.

Mapanebrug was the originating experiment for the Celos Silvicultural System (CSS). It was established in 1967 and consisted of 25 assessment plots, each measuring 0.64 ha, in which 16 different treatments were tried. Only three of them are discussed here, namely a control treatment (no silvicultural treatment after selective logging) and two treatment schedules comparable to CSS. One of these treatment schedules is called "treatment 20 + D8", indicating a 20 cm limit refinement followed by 3 cm limit refinement eight years later. Not all non-commercial trees above the diameter limit were poisoned during the second refinement, however, and a few small trees were spared to prevent formation of large open spaces ("filler tree system"; see de Graaf, 1986). The second treatment schedule, "treatment 40 + D8", is identical to treatment 20 + D8, except that the diameter limit of the first refinement is 40 cm.

The control treatment resulted in growth rates which differ very little from those for logged-over forest in the MAIN experiment (Tables 6.9 and 6.11). Increment varied slightly during the observation period. A downward trend is apparent among trees smaller than 20 cm dbh, which is possibly due to increasing competition in the stand. Very few commercial trees died in the control treatment, annual mortality rates being only 1.1% for trees larger than 10 cm dbh and 2.0% for smaller trees.

Mean diameter increment rates after the first refinement once again illustrate the favourable response to treatment (Table 6.11), although the improvements were less marked than in the Akintosoela area. Refinement using a 20 cm diameter limit resulted in higher diameter increment rates than the 40 cm limit treatment, so a 20 cm diameter limit is preferable (see also de Graaf, 1986; and Section 6.1.1). Growth rates after the second refinement were also satisfactory, especially during the first five years after treatment, that is until 1980. In the sixth and seventh years (1980 – 1982), growth in the smallest diameter class (smaller than 10 cm dbh) was poor and increment in the other classes was also less than in the preceding period. Such a decline is to be expected when fast growth leads to more competition in the stand.

Mortality rates for treatments 20 + D8 and 40 + D8 are based on small samples (see Table 6.11) and are therefore not very reliable. Annual mortality for treatment 20 + D8 was relatively high, namely 2.6% for commercial trees larger than 10 cm dbh and 4.7% for smaller individuals. Rates for treatment 40 + D8, on the other hand, were very low, namely 1.4% per annum for commercial trees larger than 10 cm dbh and 1.7% per annum for smaller trees.

TABLE 6.11. Experiment 67/9A: temporal changes in diameter increment of commercial species after various silvicultural treatments

Treatment	Dbh class (cm)	n/ha (1980)	Diameter growth (cm/yr) and standard deviation (SD)*					
			1967 – 1974		1974 – 1980		1980 – 1982	
			Mean	*SD*	*Mean*	*SD*	*Mean*	*SD*
S 0**	5 – 10	115	0.19	0.16	0.15	0.15	0.06	0.14
	10 – 20	46	0.30	0.25	0.25	0.21	0.15	0.17
	20 – 30	13	0.45	0.24	0.48	0.35	0.35	0.30
	30 – 40	10	0.40	0.26	0.47	0.32	0.45	0.42
	40 – 50	6	0.46	0.22	0.48	0.35	0.40	0.39
	50 – 60	6	n.a.	n.a.	(0.56)	0.22	0.44	0.35
	>60	3	n.a.	n.a.	(0.51)	n.a.	0.57	0.41
20 + D8***	5 – 10	109	0.45	0.28	0.71	0.57	0.18	0.24
	10 – 20	70	0.95	0.35	1.10	0.50	0.42	0.45
	20 – 30	39	0.87	0.30	1.06	0.30	0.66	0.57
	30 – 40	20	(0.57)	n.a.	(0.98)	0.17	0.81	0.56
	40 – 50	8	(0.34)	0.04	(0.18)	n.a.	0.74	0.25
	50 – 60	0	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
	>60	0	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
40 + D8****	5 – 10	91	0.29	0.20	0.59	0.41	0.19	0.26
	10 – 20	47	0.56	0.44	0.83	0.41	0.55	0.37
	20 – 30	16	(0.47)	0.25	1.02	0.51	0.60	0.45
	30 – 40	9	0.79	0.31	0.83	0.21	0.86	0.49
	40 – 50	11	0.53	0.21	0.94	0.34	0.79	0.50
	50 – 60	11	n.a.	n.a.	(0.98)	0.01	0.85	0.41
	>60	0	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.

* Growth figures in brackets are based on less than five trees

** No silvicultural treatment, area sampled: 3.20 ha

*** Refinements in 1967 (20 cm diameter limit) and 1975 (3 cm diameter limit), area sampled: 0.64 ha

**** Refinements in 1967 (40 cm diameter limit) and 1975 (3 cm diameter limit), area sampled: 0.64 ha

In de Graaf's treatment schedule (1986), a third treatment was foreseen in the sixteenth year after initial refinement (1983), in order to maintain high growth rates, but the decline in increment recorded in the Mapanebrug experiment was so gradual, that it was decided to delay this treatment by one or two years.

6.6 Discussion

The Celos Silvicultural System in its original form includes three silvicultural treatments within a felling cycle of 20 years (de Graaf, 1986; see also Section 2.2). Each treatment is intended to promote growth and recruitment of timber trees by killing lianas and competing trees with no commercial potential. This should be done judiciously, but the treatments should also be simple and inexpensive (Sections 2.3, 3.1.5, 4.2, 4.3, 4.4 and 6.1). The research discussed in this study focusses on the first years of the felling cycle, but also has implications for the follow-up treatments. Each treatment is therefore discussed in this final section, and additional information from other sources is included to strengthen the theoretical basis for the proposed follow-up treatments. The treatments were designed for dry land forest and should not be applied in swamp forest.

The first refinement should be carried out one to two years after logging (Section 6.3.1). De Graaf (1986) proposed to cutlass all lianas and to poison-girdle all trees without market potential above a diameter limit of approximately 20 cm, the exact limit being derived from inventory data (see also Section 2.2). This approach leads to attractive growth rates (Section 6.5.2), but the treatment tends to be too drastic in poorly stocked parts of the stand (Section 4.4). Various alternatives were compared in an effort to improve the treatment (Section 6.1) of which the most promising is a refinement with two diameter limits, referred to as treatment 40/20-10. The lower diameter limit of 20 cm is to be used in the vicinity of commercial trees larger than 20 cm dbh and the upper limit of 40 cm applies elsewhere (see Section 6.1.4).

This treatment therefore acts as a 20 cm diameter limit refinement (treatment SR 14) in well-stocked forest, but is distinctly less drastic where stocking is poor (see Sections 6.1.4 and 6.4.2). This can be illustrated with an example from the MAIN experiment. Plot 43 was much poorer in commercial trees than any other plot in the experiment (Section 4.3.1), and many non-commercial trees in the range from 20 to 40 cm dbh would not have been poisoned under treatment 40/20-10 because they stood further than 10 m from any medium-sized or large commercial tree (see Fig. 6.6). This modification in refinement prescription is unlikely to affect growth rates noticeably (Section 6.1.4), but it will lower costs compared with a 20 cm limit refinement and an inventory is not necessary.

Treatment 40/20-10 is so similar to the 20 cm limit refinement which has been applied successfully in the Mapanebrug, Akintosoela and MAIN experiments that additional testing is hardly necessary. This is not true, however, for the two other promising alternative treatments, a 30 cm diameter limit refinement (treatment SR 18) and a liberation treatment (treatment 20-C). These treatments are much milder and cheaper than treatment 40/20-10, but may result in somewhat less favourable growth rates (see Sections 6.1.2, 6.4.2 and 6.5.2).

The technique, organization and costs of refinement were discussed in Sections 6.2 and 6.3. Costs were lower than those estimated by de Graaf (1982; 1986), mainly because of improvements in work organization and reductions in the use of arboricide, and further cost reductions may be possible if ring-barking can be applied successfully (see Section 6.2.2). No effort was made to estimate overhead costs, and although some indications are available (see de Graaf, 1986, p. 60), this aspect needs to be investigated further.

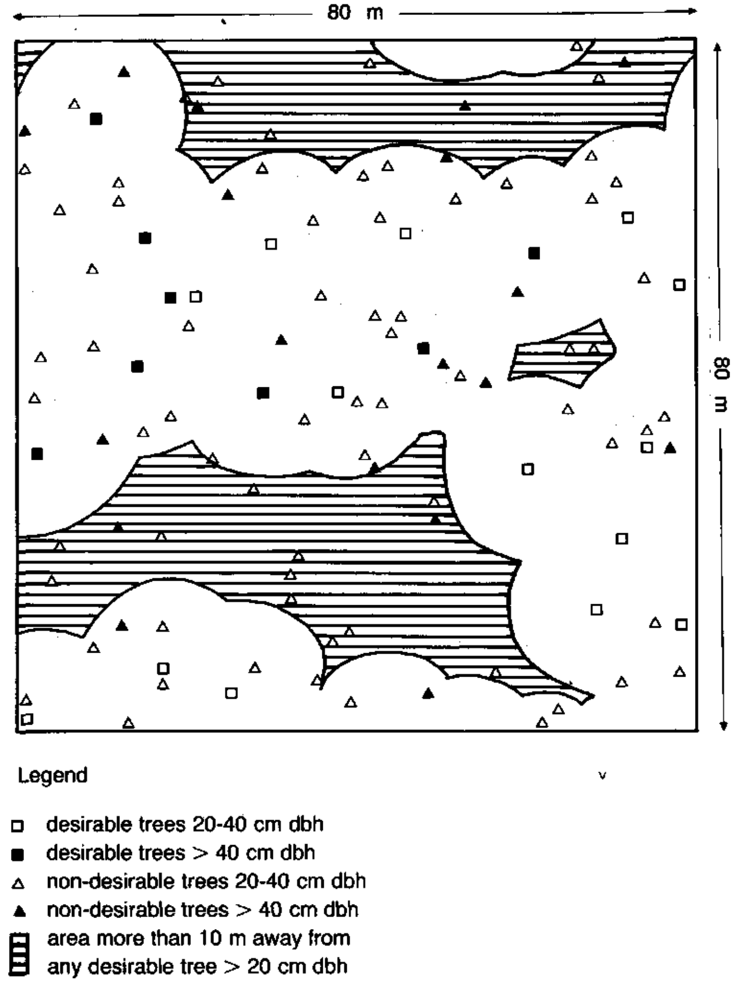


Fig. 6.6 MAIN experiment: spatial distributions of desirable and non-desirable trees in plot 43

The commercial stand responds to first refinement with greatly increased growth and this effect lasts eight to ten years (Section 6.5.2). A second treatment is therefore not required until approximately ten years after logging. Very little information is available on recruitment during this period and although refinement may have a positive effect on the fruiting of commercial species (Section 6.5.1), this is no guarantee of adequate regeneration. An important aspect is the dispersal of seeds, discussed below.

Seed dispersal of commercial species is either by wind (all commercial Anacardiaceae, Bignoniaceae, Vochysiaceae, and a few Leguminosae including basralokus, *Dicorynia guianensis*), by water (ceder, *Cedrela odorata*, and mora, *Mora excelsa*) or by frugivorous animals, particularly birds, monkeys, rodents, tortoises and bats (see van Roosmalen, 1985; Roth, 1987).

Most commercial species are zoochorous (dispersed by animals). Birds and monkeys prefer conspicuously coloured fruits (Cooper et al., 1986), and so do tortoises. Many commercial species produce such fruits (see van Roosmalen, 1985) and depend on these animals for seed dispersal. Spider monkeys, for instance, disperse seeds of a wide variety of species (see van Roosmalen, 1980), including kopi (*Goupia glabra*), soemaroeba (*Simarouba amara*), agrobigi (*Parkia nitida*) and nearly all commercial species of the Burseraceae, Myristicaceae, Guttiferae and Sapotaceae families (see Appendix I).

Agoutis and acouchis hoard large seeds by burying them and are important dispersal agents for many species (see Smythe, 1986; Maury-Lechon and Poncy, 1986; Sabatier and Puig, 1986; Hopkins and Hopkins, 1983; van Roosmalen, 1985). Commercial species which are dispersed by these rodents include krapa (*Carapa procera*), bruinhart (*Vouacapoua americana*), rode lokus (*Hymenaea courbaril*), tonka (*Dipteryx spp.*), rode kabbes (*Andira spp.*) and kwatapatoe (*Lecythis zabucajo*). Some of these (tonka, kwatapatoe) are dispersed by monkeys and bats as well, others are fully dependent on scatter-hoarding animals. Seeds of bruinhart even fail to germinate if they are not buried (Schulz, 1960).

How frugivores survive periods of fruit scarcity (July – September, see Section 6.5.1) is incompletely known, but the information available indicates that zoochorous trees and other plants which fruit during such periods are important for seed dispersers (see van Roosmalen, 1980; Smythe, 1986). This means that such plants should be maintained in forest managed under the Celos Silvicultural System to secure adequate recruitment of zoochorous commercial species. Four zoochorous species which were seen fruiting between July and September are mentioned in Section 6.5.1. Seeds of hoogland konkoni oedoe (*Gustavia hexapetala*) and hoogland oemanbarklak (*Lecythis corrugata*) are dispersed mainly by rodents. Bolletri (*Manilkara bidentata*) and kaneelpisi (*Licaria guianensis*) produce berries which are eaten by birds and monkeys.

Sabatier and Puig (1986) report that small and medium-sized trees, lianas and epiphytes in French Guiana tend to be less seasonal in reproductive behaviour than larger trees. No systematic observations of trees smaller than 15 cm dbh, lianas or epiphytes were made in the MAIN experiment but lianas and small trees were seen flowering and fruiting in the area every month. Similar results were obtained by van Roosmalen (1980), who made phenological observations when studying the feeding strategy of spider monkeys in the Voltzberg region, about 80 km south-west of the Tonka research area. He mentioned that many liana species fruit with no apparent seasonality. Besides the lianas, epiphytes and hemi-epiphytes, 25 zoochorous tree species were recorded as fruiting "out of season" in the Voltzberg area, including three commercial species: kwatapatoe (*Lecythis zabucajo*), purperhart (*Peltogyne venosa*) and riemhout (*Micropholis guyanensis*). Most of the 22 non-commercial species seldom exceed 30 m in height, which corresponds fairly closely with 30 cm dbh, and only five of them may grow large (see van Roosmalen, 1980).

The Celos Silvicultural System should preserve tree species which are vital for seed dispersers. Our present knowledge does not allow us to differentiate between such key species and other zoochorous trees. It is therefore not possible to identify the non-commercial trees which should be spared in silvicultural operations, but in practice there is probably no need to do so, because the information available indicates that most zoochorous trees fruiting between July and September would not qualify for poison-girdling in the first refinement, either because they are too small or belong to commercial species. It may also be important to preserve part of the liana population, and efforts to improve efficiency of climber cutting operations, other than some minor changes in field organization, should therefore not be pursued (see also Sections 6.2.1 and 6.3.1). Hence, there is probably no need to spare more trees and lianas during initial refinement in order to accomodate frugivorous animals. Periodic shortage of food may be more severe shortly after treatment than in the years before, but this is not considered critical for the ecological functioning of commercial species.

The second refinement is best scheduled ten to eleven years after felling and should result in another eight to ten years of good growth. The starting position is more favourable than at initial refinement, so the treatment may be somewhat milder. So far, a second refinement has been applied to two plots in the Mapanebrug experiment (Section 6.5.2). From the results obtained, de Graaf (1982; 1986) proposed a treatment in which all non-commercial trees larger than 5 or 10 cm dbh should be poison-girdled, depending on the outcome of an inventory (see also Section 2.2).

This approach leads to eradication of most non-commercial species and virtually complete elimination of the canopy in poorly stocked parts of the stand and this is considered undesirable. It has been argued above that retaining non-commercial trees may be necessary to secure seed dispersal of many commercial species and, in addition, excessive openings in the canopy should be avoided (see Section 4.4). Moreover, some of these species may become marketable in the future and the system should be flexible enough to accommodate such long-term changes in demand (see also Section 2.3).

Field surveys are necessary for the development of a more acceptable second refinement and these need to form part of follow-up research. The second treatment should preferably be a type of thinning, that is, a refinement similar to the first one except that trees to be poison-girdled should be selected on criteria such as defects, stem form, crown form and growth, if possible, rather than the market potential of the species. This approach aims to stimulate growth, to improve the quality of the timber stand and to minimize the undesirable side-effects mentioned above.

Crooked and defective stems are common in tropical rain forest and their numbers tend to increase after selective felling, as result of logging injury developing into decay and stem deformations. This only happens to some injured trees and it is difficult to predict which trees will recover fully and which will not. Virtually all damaged commercial trees should therefore be retained in the first refinement (see Sections 3.1.2 and 6.1), but ten years after felling, it is easier to identify stems which are too poor to contribute to future yields.

Commercial trees which grow very slowly or not at all are found not only in pristine and logged-over forests, but also in refined stands, a phenomenon indicated by the high standard deviations in Table 6.11 (see also de Graaf, 1986). Medium-sized trees which grow poorly in treated forest are unlikely to contribute to future harvests and do not need to be retained for that purpose. Some preliminary observations were made to identify characteristic features of such trees and it was found that some epiphytes may be useful indicators. The presence of many well developed, undissected lichens on a tree trunk indicates that the bark is shed slowly and that growth is poor. Another indication is the presence of large epiphytic Bromeliaceae on the stem. However, many stagnating trees cannot be identified in this way and more information of this nature is needed if growth is to be used as a criterion in a thinning operation.

The third silvicultural treatment is best scheduled a few years before the second harvest. This light treatment, which has not yet been applied in the experiments, should consist mainly of cutting lianas and other measures to reduce logging damage, and may also include measures to reduce competition of palms (see also Section 4.3.6). Poison-girdling should not be allowed or restricted to palms and small trees for the safety of the loggers.

Growth and mortality rates are such that it is theoretically possible to log the stand again twenty years after the first harvest (see Sections 4.3.2 and 6.5.2; see also de Graaf, 1986; Jonkers and Schmidt, 1984). In practical forest management, however, it is preferable to make allowance for delays in treatment and other eventualities by planning a 25-year felling cycle.

References

ALVIM, P. DE T. AND ALVIM, R., 1978. Relation of climate to growth periodicity in tropical trees. in Tomlinson, P.B. and Zimmermann, M.H. (eds), Tropical trees as living systems. Cambridge University Press, Cambridge, United Kingdom.

ASHTON, P.S., 1978. The natural forest: plant biology, regeneration and tree growth. in UNESCO, Tropical forest ecosystems. (Natural resources research XIV). United Nations Educational, Scientific and Cultural Organization, Paris, France.

AUSTIN, M.P., ASHTON, P.S. AND GREIG-SMITH, P., 1972. The application of quantitative methods to vegetation survey III: a re-examination of rain forest data from Brunei. Journal of Ecology, **60**, 305-324.

BAKER, H.G., BAWA, K.S., FRANKIE, G.W. AND OPLER, P.A., 1983. Reproductive biology of plants in tropical forests. in Golley, F.G. (ed.), Tropical rain forest ecosystems: structure and function. (Ecosystems of the world 14A). Elsevier Scientific Publishing Company, Amsterdam, The Netherlands.

BARTLETT, M.S., 1975. The statistical analysis of spatial pattern. Chapman and Hall, London, United Kingdom.

BAUR, G.N., 1962. The ecological basis of rain forest management. Food and Agriculture Organization of the United Nations, Rome, Italy.

BOERBOOM, J.H.A., 1965. De natuurlijke regeneratie van het surinaamse mesofytische bos na uitkap. Agricultural University, Wageningen, The Netherlands.

BOERBOOM, J.H.A., 1966. Some remarks on the natural regeneration of tropical rain forest, with special reference to a method newly applied in Surinam. in Proceedings 6th World Forestry Congress, Madrid, Spain.

BOURGERON, P.F., 1983. Spatial aspects of vegetation structure. in Golley, F.G. (ed.), Tropical rain forest ecosystems: structure and function. (Ecosystems of the world 14A). Elsevier Scientific Publishing Company, Amsterdam, The Netherlands.

BOXMAN, O., in press. Deterioration of the nutrient store at removal of a rain forest in Suriname. (Ecology and management of tropical rain forests in Suriname). [Provisional title]. Agricultural University, Wageningen, The Netherlands.

BOXMAN, O., GRAAF, N.R. DE, HENDRISON, J., JONKERS, W.B.J., POELS, R.L.H., SCHMIDT, P. AND TJON LIM SANG, R., 1985. Towards sustained timber production from tropical rain forests in Suriname. (Special Paper 9th World Forestry Congress, Mexico City). Netherlands Journal of Agricultural Science, 33, 125-132.

BOXMAN, O., GRAAF, N.R. DE, HENDRISON, J., JONKERS, W.B.J., POELS, R.L.H., SCHMIDT, P. AND TJON LIM SANG, R., in press. Forest land use in Suriname. in Beusekom, C.F. van, Goor, C.P. van and Schmidt, P. (eds), Wise utilization of tropical rain forest lands. (Tropenbos Scientific Series 1). The Tropenbos Programme, Ede, The Netherlands.

BRINKMANN, W.L.F., 1971. Light environment in a tropical rain forest of central Amazonia. Acta Amazonia, 1 (2), 37-49.

Brown, S., Lugo, A.E., Silander, S. and Liegel, L., 1983. Research history and opportunities in the Luquillo experimental forest. (General Technical Report SO-44). US Forest Service, Southern Forest Experiment Station, New Orleans, USA.

Bruijning, C.F.A., Voorhoeve, J. and Gordijn, W. (eds), 1977. Encyclopedie van Suriname. Argus Elsevier, Amsterdam, The Netherlands.

Brünig, E.F., 1983. Vegetation structure and growth. in Golley, F.G. (ed.), Tropical rain forest ecosystems: structure and function. (Ecosystems of the world 14A). Elsevier Scientific Publishing Company, Amsterdam, The Netherlands.

Brünig, E.F., Alder, D. and Smith, J.P., 1979. Vegetation classification and structure. in Adisoemarto, S. and Brünig, E.F. (eds), Transactions of the 2nd international MAB-IUFRO workshop on tropical rainforest research. Chair of World Forestry, Hamburg-Reinbek, Federal Republic of Germany.

Catinot, R., 1965. Sylviculture en forêt dense africaine: première partie. Bois et Forêts des Tropiques, **100**, 5-18.

Charles-Dominique, P., Atramentowicz, M., Charles-Dominique, M., Gérard, H., Hladik, A., Hladik, C.M. and Prévost, M.F., 1981. Les mammifères frugivores arboricoles nocturnes d'une forêt guyanaise: interrelations plantes – animaux. Revue d'Ecologie (Terre et Vie), **35**, 341-435.

Chudnoff, M., 1984. Tropical timbers of the world. (Agriculture handbook 607). US Department of Agriculture, Washington, DC, USA.

Cooper, H.M., Charles-Dominique, P. and Vienot, F., 1986. Signification de la coloration en fonction de la vision des vertébrés consommateurs. in Gasc, J.P. (ed.), Vertébrés et forêts tropicales humides d'Afrique et d'Amerique. Muséum national d'histoire naturelle, Paris, France.

Corsten, L.C.A., 1976. Matrix approximation, a key to application of multivariate methods. in Proceedings of the 9th International Biometric Conference. The Biometric Society, Boston, USA.

Crow, T.R. and Weaver, P.L., 1977. Tree growth in a moist tropical forest of Puerto Rico. (Forest Service Research Paper ITF-22). Institute of Tropical Forestry, Rio Piedras, USA.

Dawkins, H.C., 1958. The management of natural tropical high forest with special reference to Uganda. (IFI Paper 34). Imperial Forestry Institute, Oxford, United Kingdom.

Donis, C., 1958. La forêt dense congolaise et l'état actuel de sa sylviculture. in Haig, I.T., Huderman, M.A. and Aung Din, U. (eds), Tropical silviculture. Food and Agriculture Organization of the United Nations, Rome, Italy.

Estève, J., 1983. La destruction du couvert forestrier consécutive à l'exploration forestière de bois d'oeuvre en forêt tropicale humide africaine ou americaine. Bois et Forêts des Tropiques, **201**, 77-84.

FAO, 1977a. Guidelines for soil profile description. Food and Agriculture Organization of the United Nations, Rome, Italy.

FAO, 1977b. Kuantan forest management unit: forest land use, forest management and operation plans. (Project FAO/MAL/75/012 Technical Report 2). Forestry Department, Kuala Lumpur, Malaysia.

FAO, 1978. A preliminary assessment of the development rates in selectively logged hill dipterocarp forest in the central and east regions of Peninsular Malaysia. (Project FAO/MAL/75/012 Technical Report 3). Forestry Department, Kuala Lumpur, Malaysia.

Freezaillah b. C.Y., 1984. Lesser-known tropical wood species: how bright is their future? Unasylva, **145**, 2-16.

Gauch, H.G., 1982. Multivariate analysis in community ecology. Cambridge University Press, Cambridge, United Kingdom.

Garwood, N.C., Janos, D.J. and Brokaw, N., 1979. Earthquake-caused landslides: a major disturbance to tropical forests. Science, **205**, 997-999.

GASC, J.P., 1986. Le peuplement herpétoloque d'*Astrocaryum paramaca* (Aracacées), un palmier important dans la structure de la forêt en Guyane française. in Gasc, J.P. (ed.), Vertébrés et forêts tropicales humides d'Afrique et d'Amerique. Muséum national d'histoire naturelle, Paris, France.

GOENSE, D., 1987. Mechanized farming in the humid tropics with special reference to soil tillage, workability and timeliness of farm operations: a case study for the Zanderij area of Suriname. (Ph.D. thesis). Agricultural University, Wageningen, The Netherlands.

GOLLEY, F.G. (ED.), 1983. Tropical rain forest ecosystems: structure and function. (Ecosystems of the world 14A). Elsevier Scientific Publishing Company, Amsterdam, The Netherlands.

GONGGRIJP, J.W., 1948. Quelques remarques sur l'emploi d'essences exotiques et indigènes dans la sylviculture tropicale. Bois et Forêts des Tropiques, **5**, 251-257.

GONGGRIJP, J.W. AND BURGER, D., 1948. Bosbouwkundige studiën over Suriname, Veenman, Wageningen, The Netherlands.

GOOR, C.P. VAN AND KARTASUBRATA, J. (EDS), 1982. Indonesian forestry abstracts: Dutch literature until about 1960. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands.

GRAAF, N.R. DE, 1982. Sustained timber production in tropical rainforest of Suriname. in Wienk, J.F. and Wit, H.A. de (eds), Management of low fertility acid soils of the American humid tropics. Inter-American Institute for Co-operation on Agriculture, San José, Costa Rica.

GRAAF, N.R. DE, 1986. A silvicultural system for natural regeneration of tropical rain forest in Suriname. (Ecology and management of tropical rain forests in Suriname 1). Agricultural University, Wageningen, The Netherlands.

GRAAF, N.R. DE AND GEERTS, J.M.P., 1976. Techniek natuurlijke verjonging drooglandbos. (CELOS Rapporten 114). Centrum voor Landbouwkundig Onderzoek in Suriname, Paramaribo, Suriname.

GRANVILLE, J.J. DE, 1977. Notes biologiques sur quelques palmiers guyanais. Cahiers ORSTOM, Série Biologique, **12**, 347-353.

GRANVILLE, J.J. DE, 1978. Recherches sur la flore et la vegetation guyanaise. (Ph.D. thesis). University of Montpellier, Montpellier, France.

GREIG-SMITH, P., 1952. The use of random and contiguous quadrats in the study of the structure of plant communities. Annals of Botany, **16**, 293-316.

GREIG-SMITH, P., 1983. Quantitive plant ecology. 3rd edn, Blackwell Scientific Publications, Oxford, United Kingdom.

HALLÉ, F., OLDEMAN, R.A.A. AND TOMLINSON, P.B., 1978. Tropical trees and forests: an architectural analysis. Springer Verlag, Berlin, Federal Republic of Germany.

HEINSDIJK, D., 1957. The upper storey of tropical forests: part I. Tropical Woods, **107**, 66-83.

HEINSDIJK, D., 1958. The upper storey of tropical forests: part II. Tropical Woods, **108**, 31-45.

HENDRISON, J., in press. Logging operations in managed tropical rain forest in Suriname. (Ecology and management of tropical rain forests in Suriname). [Provisional title]. Agricultural University, Wageningen, The Netherlands.

HEUVELDOP, J., 1977. Die amazonische Caatinga bei San Carlos de Rio Negro, Südvenezuela: relative Beleuchtungsstärken im Bestand. Forstarchiv, **48**, 148-154.

HEUVELDOP, J., 1979. The international MAB rainforest ecosystem pilot project at San Carlos de Rio Negro: micrometeorological studies. in Adisoemarto, S. and Brünig, E.F. (eds), Transactions of the 2nd international MAB-IUFRO workshop on tropical rainforest research. Chair of World Forestry, Hamburg-Reinbek, Federal Republic of Germany.

HLADIK, A., 1986. Données comparatives sur la richesse spécifique et les structures des peuplements des forêts tropicales d'Afrique et d'Amerique. in Gasc, J.P. (ed.), Vertébrés et forêts tropicales humides d'Afrique et d'Amerique. Muséum national d'histoire naturelle, Paris, France.

Hopkins, H.C., and Hopkins, M.J.G., 1983. Fruit and seed biology of the neotropical species of *Parkia*. in Sutton, S.L., Whitmore, T.C. and Chadwick, A.C. (eds), Tropical rain forest: ecology and management. Blackwell Scientific Publications, Oxford, United Kingdom.

Hout, P. van der, 1983. Techniek natuurlijke verjonging: voorlopige evaluatie Experiment 67/9B. (Internal report). Centrum voor Landbouwkundig Onderzoek in Suriname, Paramaribo, Suriname.

Hubbell, S.P. and Foster, R.B., 1983. Diversity of canopy trees in a neotropical forest and implications for conservation. in Sutton, S.L., Whitmore, T.C. and Chadwick, A.C. (eds), Tropical rain forest: ecology and management. Blackwell Scientific Publications, Oxford, United Kingdom.

Hutchinson, I.D., 1982. Sarawak liberation thinning: a practical guide, background and an initial analysis of performance. (Project FAO/MAL/76/008 Field Document 15). Forest Department, Kuching, Malaysia.

Hutchinson, I.D., 1987. Improvement thinnings in natural tropical forests: aspects and institutionalization. in Mergen, F. and Vincent, J.R. (eds), Natural management of tropical moist forests. Yale University, New Haven, USA.

Janzen, D.H., 1971. Seed predation by animals. Annual Review of Ecology and Systematics, 2, 465-492.

Japing, C.H. and Japing, H.W., 1960. Houthandboek surinaamse houtsoorten. Dienst 's Landsbosbeheer, Paramaribo, Suriname.

Jonkers, W.B.J., 1982. Options for silviculture and management of the mixed dipterocarp forest of Sarawak. (Project FAO/MAL/76/008 Working Paper 11). Forest Department, Kuching, Malaysia.

Jonkers, W.B.J., 1983. Houtteelt. in CELOS Kwartaalverslagen 64. Centrum voor Landbouwkundig Onderzoek in Suriname, Paramaribo, Suriname.

Jonkers, W.B.J., 1984. Exploitation, natural regeneration and increment: experiment plan and progress report on experiment 78/5. (CELOS Rapporten 141). Centrum voor Landbouwkundig Onderzoek in Suriname, Paramaribo, Suriname.

Jonkers, W.B.J. and Hendrison, J., 1986. Prospects for sustained yield management of tropical rain forest in Suriname. Paper presented at the Conference on Management of the Forests of Tropical America, San Juan, USA.

Jonkers, W.B.J. and Schmidt, P., 1984. Ecology and timber production in tropical rain forest in Suriname. Interciencia, 9, 290-298.

Jordan, C.F., 1985. Nutrient cycling in tropical forest ecosystems. John Wiley and Sons, Chichester, United Kingdom.

Jordan, C.F. and Herrera, R., 1981. Tropical rain forests: are nutrients really critical? Nature and Resources, 17 (2), 7-13.

Lanly, J.P., 1982. Tropical forest resources. (FAO Forestry Paper 30). Food and Agriculture Organization of the United Nations, Rome, Italy.

Lawson, C.L. and Hanson, R.J., 1974. Solving least squares problems. Prentice-Hall Inc, Englewood Cliffs, USA.

Leersum, G.J.R. van, 1984. Simulation of various silvicultural treatments. (Unpublished M.Sc. thesis). Agricultural University, Wageningen, The Netherlands.

Leeuwen, M.H.W. van, 1983. Relation between soil and vegetation in tropical rain forest in Suriname. (Unpublished M.Sc. thesis). Agricultural University, Wageningen, The Netherlands.

Leigh, E.G., Rand, A.S. and Windsor, D.M. (eds), 1982. The ecology of a tropical rain forest: seasonal rhythms and long-term changes. Smithsonian Institution Press, Washington, DC, USA.

Lescure, J.P., 1981. Quelques données pour l'appréciation du volume des troncs en Guyane française. in L'écosystème forestier guyanais. (Bulletin de liaison ECEREX 3). ORSTOM, Cayenne, French Guiana.

Lescure, J.P. and Boulet, R., 1985. Relationships between soil and vegetation in a tropical rainforest, French Guiana. Biotropica, **17**, 155-164.

Letourneux C., 1956. Les dégagements par annélation et empoissonnement. Bois et Forêts des Tropiques, **46**, 3-10.

Lindeman, J.C. and Mennega, A.M.W., 1963. Bomenboek van Suriname. Dienst 's Landsbosbeheer, Paramaribo, Suriname.

Lindeman, J.C. and Moolenaar, S.P., 1959. Preliminary survey of the vegetation types of northern Suriname. (The vegetation of Suriname I, Part 2). Van Eedenfonds, Amsterdam, The Netherlands.

Livingstone, D.A. and Hammen, T. van der, 1978. Floristic composition and typology. in UNESCO, Tropical forest ecosystems. (Natural resources research XIV). United Nations Educational, Scientific and Cultural Organization, Paris, France.

Longman, K.A. and Jenik, J., 1974. Tropical forest and its environment. Longman, London, United Kingdom.

Longwood, F.R., 1965. Present and potential commercial timbers of the Caribbean with special reference to the West Indies, the Guianas and British Honduras. (Agriculture handbook 207). US Department of Agriculture, Washington, DC, USA.

Maitre, H.F., 1986. Recherches sur la dynamique et la production des peuplements naturels en forêt dense tropicale d'Afrique de l'Ouest. in IUFRO, Proceedings of the 18th IUFRO World Congress. International Union of Forestry Research Organizations, Vienna, Austria.

Maury-Lechon, G. and Poncy, O., 1986. Dynamique forestière sur 6 hectares de forêt dense humide de Guyane française, à partir de quelques espèces de forêt primaire et de cicatrisation. in Gasc, J.P. (ed.), Vertébrés et forêts tropicales humides d'Afrique et d'Amerique. Muséum national d'histoire naturelle, Paris, France.

Mittermeier, A. and Roosmalen, M.G.M. van, 1980. Synecology of Surinam monkeys. in Furtado, J.I. (ed.), Tropical ecology and development: proceedings of the 5th international symposium of tropical ecology. International Society of Tropical Ecology, Kuala Lumpur, Malaysia.

Moerland, J., 1984. Suriname. (Landendocumentatie 1984-1). Koninklijk Instituut voor de Tropen, Amsterdam, The Netherlands.

Murphy, P.G., 1970. Tree growth at El Verde and the effects of ionizing radiation. in Odum, H.T. and Pigeon, R.F. (eds), A tropical rain forest. US Atomic Energy Commission, Oak Ridge, USA.

Myers, N., 1980. Conversion of tropical moist forests. National Academy of Sciences, Washington, DC, USA.

Neil, P.E., 1981. Problems and opportunities in tropical rain forest management. (CFI Occasional Paper 16). University of Oxford, Oxford, United Kingdom.

Oldeman, R.A.A., 1974. L'architecture de la forêt guyanaise. (Ph.D. thesis). University of Montpellier, Montpellier, France.

Oldeman, R.A.A., 1978. Architecture and energy exchange of dicotyledonous trees in the forest. in Tomlinson, P.B. and Zimmerman, M.H. (eds), Tropical trees as living systems. Cambridge University Press, Cambridge, United Kingdom.

Oldeman, R.A.A. (ed.), 1982. Tropical hardwood utilization: practice and prospects. Martinus Nijhoff/Dr W. Junk Publishers, The Hague, The Netherlands.

Oldeman, R.A.A., 1983. Tropical rain forest, architecture, silvigenesis and diversity. in Sutton, S.L., Whitmore, T.C. and Chadwick, A.C. (eds), Tropical rain forest: ecology and management. Blackwell Scientific Publications, Oxford, United Kingdom.

Oldeman, R.A.A. and Boerboom, J.H.A., 1982. Life insurance for tropical hardwood resources. in Oldeman, R.A.A. (ed.), Tropical hardwood utilization: practice and prospects. Martinus Nijhoff/Dr W. Junk Publishers, The Hague, The Netherlands.

OLDEMAN, R.A.A. AND FUNDTER, J.M., 1986. On Diptero-Vochysian tree strategies. in Institut de Botanique, L'arbre. (Naturalia monspeliensia 1986). Languedoc University, Montpellier, France.

ORLOCI, L., 1966. Geometric models in ecology I: the theory and application of some ordination methods. Journal of Ecology, **54**, 193-215.

PIRES, J.M., 1978. The forest ecosystems of the Brazilian Amazon: description, functioning and research needs. in UNESCO, Tropical forest ecosystems. (Natural resources research XIV). United Nations Educational, Scientific and Cultural Organization, Paris, France.

PITT, J., 1961. Report to the government of Brazil on the application of silvicultural methods to some of the forests of the Amazon. Food and Agriculture Organization of the United Nations, Rome, Italy.

POELS, R.L.H., in press. Soils, water and nutrients in a forest ecosystem in Suriname.(Ecology and management of tropical rain forests in Suriname 2). [Provisional title]. Agricultural University, Wageningen, The Netherlands.

PONCY, O., 1985. Le genre *Inga* (Légumineuses, *Mimosoideae*) en Guyane française. Muséum national d'histoire naturelle, Paris, France.

PUIG, H., 1981. Périodicité de floraison et de fructification de quelques arbres de la forêt dense guyanaise. in L'écosystème forestier guyanais. (Bulletin de liaison ECEREX 3). ORSTOM, Cayenne, French Guiana.

PUIG, H. AND PRÉVOST, M. F., 1968. Périodicité de l'accroisement chez quelques arbres de Guyane. in Gasc, J.P. (ed.), Vertébrés et forêts tropicales humides d'Afrique et d'Amerique. Muséum national d'histoire naturelle, Paris, France.

PUTZ, F.E., 1983. Liana biomass and leaf area of a "tierra firme" forest in the Rio Negre basin, Venezuela. Biotropica, **15**, 185-189.

PUTZ, F.E., 1984. The natural history of lianas on Barro Colorado island, Panama. Ecology, **65**, 1713-1724.

QUEENSLAND DEPT. OF FORESTRY, 1983. Rain forest research in North Queensland. Queensland Department of Forestry, Brisbane, Australia.

RAICH, J.W., 1983. Understorey palms as nutrient traps: a hypothesis. Brenesia, **21**, 119-129.

REYES, M.R., 1968. Selective logging, a must tool for continuous production of philippine mahogany in the Philippines. Philippine Forests, **2** (2), 14-21.

RICHARDS, P.W., 1952. The tropical rain forest. Cambridge University Press, Cambridge, United Kingdom.

RIÉRA, B., 1982. Observations sur les chablis, Piste de St. Elie en Guyane. in L'écosystème forestier guyanais. (Bulletin de liaison ECEREX 6). ORSTOM, Cayenne, French Guiana.

RIÉRA, B., 1983. Chablis et cicatrisation en forêt guyanaise. (Thesis). Paul Sabatier University, Toulouse, France.

RIÉRA, B., 1985. Importance des buttes de deracinement dans la régénération forestière en Guyane française. Revue d'Ecologie (Terre et Vie), **40**, 321-329.

ROLLET, B., 1969. La régénération naturelle en forêt dense humide sempervirente de plaine de la Guyane vénézuélienne. Bois et Forêts des Tropiques, **124**, 19-38.

ROLLET, B., 1974. L'architecture des forêts denses humides sempervirentes de plaine. Centre Technique Forestier Tropical, Nogent sur Marne, France.

ROLLET, B., 1978. Organization. in UNESCO, Tropical forest ecosystems. (Natural resources research XIV). United Nations Educational, Scientific and Cultural Organization, Paris, France.

ROLLET, B., 1983. La régénération naturelle dans les trouées. Un processus général de la dynamique des forêts tropicales humides. Bois et Forêts des Tropiques, **201**, 3-35 and **202**, 19-34.

ROOSMALEN, M.G.M. VAN, 1980. Habitat preferences, diet, feeding strategy and social organization of the spider monkey (*Ateles paniscus* Linnaeus 1758) in Surinam. (RIN rapport 80/13). Rijksinstituut voor Natuurbeheer, Leersum, The Netherlands.

Roosmalen, M.G.M. van, 1985. Fruits of the Guianan flora. Utrecht University, Utrecht, The Netherlands.

Roth, I., 1984. Stratification of tropical forests as seen in leaf structure. (Tasks for vegetation science 6). Dr W. Junk Publishers, The Hague, The Netherlands.

Roth. I., 1987. Stratification of a tropical forest as seen in dispersal types. (Tasks for vegetation science 17). Dr W. Junk Publishers, Dordrecht, The Netherlands.

Sabah Forest Department, 1972. Manual of silviculture Sabah for use in the productive forest estate. (Sabah Forest Record 8). Forest Department, Kota Kinabalu, Malaysia.

Sabatier, D. and Puig, H., 1986. Phénologie et saisonnalité de la floraison et de la fructification en forêt dense guyanaise. in Gasc, J.P. (ed.), Vertébrés et forêts tropicales humides d'Afrique et d'Amerique. Muséum national d'histoire naturelle, Paris, France.

Schmidt, P., in press. Ecology of managed tropical rain forest in Suriname. (Ecology and management of tropical rain forests in Suriname). [Provisional title]. Agricultural University, Wageningen, The Netherlands.

Schmidt, R., 1987. Tropical rain forest management: a status report. Unasylva, **156**, 2-17.

Schulz, J.P., 1960. Ecological studies on rain forests in northern Suriname. (The vegetation of Suriname II). Van Eedenfonds, Amsterdam, The Netherlands.

Schulz, J.P., 1967. La regeneracion natural de la selva mesofytica tropical de Surinam despues de su aprovechamiento. (Boletin del Instituto Forestal Latino-Americano de Investigacion y Capitacion 23). IFLAIC, Mérida, Venezuela.

Shepherd, K.R. and Richter, H.V. (eds), 1985. Managing the tropical forest. The Australian National University, Canberra, Australia.

Smythe, N., 1986. The importance of mammals in neotropical forest management. Paper presented at the Conference on Management of the Forests of Tropical America, San Juan, Puerto Rico, USA.

Soe Agnie, E., 1982. The Zanderij soils of Suriname. in Wienk, J.F. and Wit, H.A. de (eds), Management of low fertility acid soils of the American humid tropics. Inter-American Institute for Co-operation on Agriculture, San José, Costa Rica.

Staudt, F.J., 1976. Arbeidskundig onderzoek van werkzaamheden t.b.v. natuurlijke verjonging van het drooglandbos (zuiveringsarbeid). (Internal Report). Agricultural University, Wageningen, The Netherlands.

Steel, R.G.D. and Torrie, J.H., 1980. Principles and procedures of statistics: a biometrical approach. 2nd edn, McGraw-Hill Inc, New York, USA.

Sudiono, J. and Daryadi, L., 1978. Some impacts of the utilization of rain forests in Indonesia. Malaysian Forester, **41**, 121-124.

Synnott, T.J., 1979. A manual of permanent plot procedures for tropical rain forests. (Tropical Forestry Papers 14). Commonwealth Forestry Institute, Oxford, United Kingdom.

Taylor, C.J., 1962. Tropical forestry. Oxford University Press, London, United Kingdom.

Tjon Lim Sang, R., in press. Secondary succession on evergreen seasonal forest in Suriname. (Ecology and management of tropical rain forests in Suriname). [Provisional title]. Agricultural University, Wageningen, The Netherlands.

UNESCO, 1978. Tropical forest ecosystems. (Natural resources research XIV). United Nations Educational, Scientific and Cultural Organization, Paris, France.

USDA, 1975. Soil taxonomy. (Agriculture handbook 436). US Department of Agriculture, Washington, DC, USA.

Vink, A.T., 1970. Forestry in Surinam: a review of policy, planning, projects and progress. Dienst 's Landsbosbeheer, Paramaribo, Suriname.

Vink, A.T., 1977. Surinam timbers. 4th edn, Surtim, Paramaribo, Suriname.

Vooren, A.P., in press. Nature-analogue forestry: ecological framework for rain forest buffer zone management in West Africa. [Provisional title]. (Ph.D. thesis). Agricultural University, Wageningen, The Netherlands.

Wadsworth, F.H., 1947. An approach to silviculture in tropical America and its application in Puerto Rico. Caribbean Forester, **8**, 245-256.

Wadsworth, F.H., 1952. Forest management in the Luquillo Mountains III. Caribbean Forester, **13**, 93-119.

Wadsworth, F.H., 1981. Management of forest lands in the humid tropics under sound ecological principles. in Mergen, F. (ed.), International symposium on tropical forest utilization and conservation. Yale School of Forestry, New Haven, USA.

Weidelt, H.J. and Banaag, V.S., 1982. Aspects of management and silviculture of philippine dipterocarp forest. German Agency for Technical Co-operation, Eschborn, Federal Republic of Germany.

Wood, T.W.W., 1982. Suriname, assistance in forestry development: organization and capacity of the forest service. (Project FAO/SUR/81/004 Working Document 23). Dienst 's Landsbosbeheer, Paramaribo, Suriname.

Wyatt-Smith, J., 1963. Manual of Malayan silviculture for inland forests. (Malayan Forest Record 23). Forestry Department, Kuala Lumpur, Malaysia.

APPENDIX I

CELOS list of commercial species

Family	Scientific name	Vernacular name	Trade name
Anacardiaceae	*Loxopterygium sagotii*	slangenhout	
Annonaceae	*Xylopia aromatica;* *X. nitida*	pegrekoepisi	
Araliaceae	*Schefflera decaphylla* *(syn.: S. paraënsis)*	morototo	
	Schefflera morototoni *(syn.: Didymopanax morototoni)*	kassavehout	morototo
Bignoniaceae	*Jacaranda copaia*	goebaja	futui
	Tabebuia serratifolia	groenhart	tabebuia
Burseraceae	*Protium insigne*	grootbladige tingimoni	kurokai
	Protium neglectum	harde bast tingimoni	kurokai
	Tetragastris altissima	rode sali	
	Tetragastris hostmannii	tingimonisali	
	Trattinickia burserifolia; *T. rhoifolia*	ajawatingimoni	
Goupiaceae	*Goupia glabra*	kopi	goupie
Guttiferae	*Platonia insignis;* *Rheedia benthamiana*	pakoeli	pakuri
	Symphonia globulifera	mataki	manni
Humiriaceae	*Humiria balsamifera*	blakaberi	tauroniro
Lauraceae	*Licaria canella* *(syn.: L. cayennensis)*	kaneelhart	
	Nectandra grandis	zwarte grootbladige pisi	louro preto
	Ocotea globifera	wanapisi	louro preto
	Ocotea glomerata	zwarte kleinbladige pisi	louro preto
	Ocotea petalanthera	witte pisi	louro preto
	Ocotea rubra	wana	red louro

continued

Family	Scientific name	Vernacular name	Trade name
Lecythidaceae	*Lecythis zabucajo (syn.: L. davisii)*	kwatapatoe	
Leguminosae	*Andira coriacea; A. inermis; A. surinamensis*	rode kabbes	angelin
	Dicorynia guianensis	basralokus	angelique
	Diplotropis purpurea	zwarte kabbes	tatabu
	Dipterix odorata; D. punctata	tonka	tonka
	Hymenaea courbaril	rode lokus	courbaril
	Mora excelsa	mora	mora
	Parkia nitida	agrobigi	
	Peltogyne paniculata; P. venosa	purperhart	purpleheart
	Platymiscium trinitatis; P. ulei	koenatepi	
	Vouacapoua americana	bruinhart	wacapou
Meliaceae	*Carapa procera*	krapa	andiroba
	Cedrela odorata	ceder	cedar
Moraceae	*Brosimum paraënse*	satijnhout	satiné
	Brosimum guianense (syn.: Piratinera guianensis)	letterhout	snakewood
Myristicaceae	*Virola melinonii*	hoogland baboen	baboen
	Virola surinamensis	laagland baboen	baboen
Rutaceae	*Fagara pentandra*	pritijari	
Sapotaceae	*Manilkara bidentata*	bolletri	balata
	Micropholis guyanensis var. commixta	zwart riemhout	
	Micropholis guyanensis var. guyanensis	wit riemhout	
Simaroubaceae	*Simarouba amara*	soemaroeba	simarouba
Sterculiaceae	*Sterculia excelsa; S. pruriens*	okerhout	sterculia
Vochysiaceae	*Qualea albiflora*	hoogland gronfoeloe	gronfoeloe
	Qualea coerulea	laagland gronfoeloe	gronfoeloe
	Qualea rosea	bergi gronfoeloe	gronfoeloe
	Vochysia guianensis	wiswiskwari	kwarie
	Vochysia tomentosa	wanakwari	kwarie

Adapted from de Graaf (1986)

APPENDIX II

Description of a soil profile in the MAIN experiment

Site description:
Location: MAIN experiment, centre of plot 25 (Fig. 3.1).
Described by: J.A. de Fretes and R.L.H. Poels on 10th August 1978.
Elevation: approximately 35 m above sea level.
Physiographic position of the site: plain.
Landform of surrounding country: level to undulating.
Microtopography: slightly uneven.
Slope on which profile is sited: one per cent.
Vegetation: undisturbed high dry-land forest.
Climate:
Tropical rain forest climate (Af) with two wet and two drier seasons.
Average precipitation at Coebiti, 30 km to the east: 2385 mm/yr (seven year period).
Average rainfall in driest month (October): 98 mm.
Lowest monthly precipitation record (October 1976): 11 mm.
Parent material: Zanderij sediment of sandy clay loam texture.
Moisture condition: moist throughout.
Depth of groundwater table: not encountered.
Depth of pseudogley or gley: not encountered.
External drainage: slow to medium.
Internal drainage: medium.
Drainage class: well drained.
Presence of surface stones or rock outcrops: none.
Evidence of erosion: none.
Presence of salt or alkali: none.
Human influence: none.

Brief description of the profile:
Very deep well drained profile with a dark brown sandy topsoil and a bright yellowish brown to yellow orange subsoil of sandy clay loam texture. At 113 cm, large quantities of charcoal occur.

Soil horizon description:

Horizon	Depth	Description
A 1.1	0 – 7 cm	Dark brown (7.5 YR 3/3 and 10 YR 3/3) sand; moderately fine and medium crumb structure; loose when moist, non-sticky and non-plastic when wet; many fine and medium pores; abundant fine, common medium and large roots; high organic matter content, partly decomposed; little earthworm activity; few sand pockets; few bleached sand grains; moderately thick (1 – 2 cm) litter layer on surface consisting of 02: virtually undecomposed and 01: partly decomposed litter; clear smooth boundary.
A 1.2	7 – 14 cm	Dark brown (7.5 YR 3/4) loamy sand; moderately fine subangular blocky and fine and medium crumb structure; loose when moist, non-sticky and non-plastic when wet; many fine and medium pores; abundant fine, common medium and large roots; moderate organic matter content, nearly decomposed, often concentrated in little balls (5 mm diameter); few sand pockets; few bleached sand grains; gradual smooth boundary.
A 1.3	14 – 27 cm	Brown (10 YR 4/4) loamy sand; moderately fine and medium subangular blocky structure; very friable when moist, slightly sticky and non-plastic when wet; common fine and medium pores; abundant to many fine, common medium and large roots; common fine charcoal pieces; low organic matter content; some termite activity; few small sand pockets; gradual smooth boundary.
A 3	27 – 49 cm	Dull yellowish-brown (10 YR 5/4) loamy sand; weak coarse and medium subangular blocky structure, subdivided into fine granules; very friable when moist, slightly sticky and slightly plastic when wet; common fine and medium pores; common fine, few medium and large roots; low organic matter content; diffuse smooth boundary.
B 1	49 – 73 cm	Bright yellowish-brown (10 YR 6/6) sandy loam; very weak coarse subangular blocky structure, subdivided into fine granules; very friable when moist, slightly sticky and slightly plastic when wet; many fine pores; common fine and few medium roots; diffuse smooth boundary.
B 2.1	73 – 108 cm	Bright yellowish-brown (10 YR 7/6) sandy loam; very weak coarse subangular blocky structure, subdivided into fine granules; very friable when moist, slightly sticky and slightly plastic when wet; many fine pores; few fine and medium roots; diffuse smooth boundary.
B 2.2	108 – 220 cm	Yellow-orange (7.5 YR 7/8) sandy clay loam; very weak to massive very coarse subangular blocky structure, subdivided into fine granules; friable when moist, sticky and plastic when wet; many fine pores; few fine, very few medium and large roots; few vertical root channels filled with darker material from above; at 113 cm, large quantities of charcoal.

continued

Horizon	Depth	Description
B 3	220 – 300 cm	Yellow-orange (7.5 YR 7/8) sandy clay loam; friable when moist, slightly sticky and slightly plastic when wet; at 280 cm a root channel occurs with a pocket of organic matter.

Classification:

Quartzipsammentic Ultic Haplorthox or, if not classified as oxisol because of textural differences between A and B horizons, Typic Paleudult, with the remark that no evidence of clay illuviation was found in the B horizon.

Remarks:

Description is based on a soil pit (0 – 180 cm) and an augering (180 – 300 cm). Presence of charcoal is atypical for soils in the MAIN experiment.

TABLE II.1. Chemical soil data

Horizon	Depth (cm)	pH		%C	%N	C/N	CEC (me/100 g soil)		Exchangeable cations (me/100 g soil)						P Bray I (ppm)
		H_2O	KCl				at pH = 7	at soil pH	Ca	Mg	K	Na	total bases	Al	
A 1.1	0 – 7	4.0	3.2	2.04	0.13	15.7	6.47	1.38	0.38	0.16	0.07	0.04	0.65	0.73	6.1
A 1.2	7 – 14	3.8	3.3	1.42	0.08	17.8	3.92	1.38	0.08	0.29	0.04	0.04	0.45	0.93	6.8
A 1.3	14 – 27	4.2	3.8	0.83	0.06	13.8	2.67	1.12	0.05	0.08	0.02	0.03	0.18	0.94	4.1
A 3	27 – 49	4.6	3.9	0.47	0.04	11.8	2.12	1.01	0.05	0.09	0.01	0.02	0.17	0.84	2.8
B 1	49 – 73	4.8	3.9	0.28	0.02	14.0	1.31	0.65	0.05	0.12	0.00	0.02	0.19	0.46	0.7
B 2.1	73 – 108	4.8	4.0	0.18	0.02	9.0	1.05	0.44	0.03	0.12	0.00	0.01	0.16	0.28	0.4
B 2.2	108 – 180	4.8	4.0	0.18	0.02	9.0	1.25	0.51	0.03	0.11	0.00	0.01	0.15	0.36	1.1
B 3	220 – 300	5.0	4.2	0.10	0.01	10.0	0.81	0.25	0.03	0.05	0.02	0.01	0.11	0.14	1.1

TABLE II.2. Physical soil data

Horizon	Depth (cm)	Bulk density kg/l	Moisture content (vol %) at pF				pF at sampling	Moisture (vol. %) between pF values		Penetro-meter (kg/cm^2)	Organic matter (%)	Particle density	Total porosity (vol. %)	Air (vol. %) at pF	
			1	2	3.4	4.2		1 and 2	2 and 4.2					1	2
A 1.1	0 – 7	1.23	40.2	15.7	4.7	3.4	2.1	24.5	12.3	0.0	3.52	2.57	52.1	11.9	36.4
A 1.2	7 – 14	1.32	38.7	14.4	5.3	4.4	2.1	24.3	10.0	0.1	2.45	2.59	49.0	10.3	34.6
A 1.3	14 – 27	1.36	38.3	17.6	8.1	6.7	2.1	20.7	10.9	0.6	1.43	2.61	47.9	9.6	30.3
A 3	27 – 49	1.42	36.1	18.9	10.1	8.6	2.0	17.2	10.3	2.0	0.81	2.63	46.0	9.9	27.1
B 1	49 – 73	1.46	33.9	19.2	12.2	10.8	2.0	14.7	8.4	1.4	0.48	2.64	44.7	10.8	25.5
B 2.1	73 – 108	1.43	33.1	16.2	10.1	8.8	2.2	16.9	7.4	1.2	0.31	2.64	45.8	12.7	29.6
B 2.2	108 – 180	1.42	33.8	20.5	14.3	12.7	2.4	13.3	7.8	2.1	0.31	2.64	46.2	12.4	25.7
B 3	220 – 300	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	0.17	2.65	n.a.	n.a.	n.a.

APPENDIX III

Site preferences of some common species

TABLE III.1. Van Leeuwen transect: frequencies of individual species per vegetation unit

Species	Number of trees per vegetation unit								
	unit 1 0.16 ha	unit 2 0.12 ha	unit 4 0.13 ha	unit 6 0.08 ha	unit 8 0.11 ha	unit 11 0.09 ha	unit 13 0.11 ha	unit 14 0.07 ha	unit 17 0.14 ha
preference for clay loam soils (units 1, 2, 4, 6 and 8)*									
rode sali *(Tetragastris altissima)*	4	4	3	1	3	1	0	0	0
hoogland baboen *(Virola melinonii)*	3	1	3	1	1	0	0	0	1
goebaja *(Jacaranda copaia)*	3	3	2	0	0	0	0	1	1
fomang *(Chaetocarpus schomburgkianus)*	0	4	3	4	2	0	0	0	1
ingipipa *(Couratari spp.)*	1	0	3	2	4	0	1	0	1
kleine njamsi oedoe *(Guapira olfersiana)*	4	7	2	0	0	0	0	0	0
preference for (moderately) well drained soils (units 1, 2, 4, 6, 8 and 17)									
basralokus *(Dicorynia guianensis)*	0	2	0	1	1	1	0	0	9
bergi gronfoeloe *(Qualea rosea)***	0	0	2	1	1	0	0	0	5
jakanta *(Dendrobangia boliviana)*	1	1	5	1	0	0	0	0	9
merkitiki *(Tabernaemontana undulata)*	1	2	2	0	1	1	0	0	12
pakiratiki *(Tapura guianensis)*	2	2	1	2	1	1	0	0	15
redi oedoe *(Casearia arborea)*	0	3	0	1	4	0	0	0	2
dwerg oemanbarklak *(Corythophora labriculata)*	1	0	1	4	2	0	0	0	7
preference for sandy soils (units 11, 13, 14 and 17)									
walaba *(Eperua falcata)*	0	0	0	0	0	2	9	9	27
boskoffie *(Coussarea paniculata)*	0	1	0	1	0	7	0	0	13
mispel *(Miconia spp.)*	0	0	0	0	1	3	0	0	4

* Trees of these species occuring on sandy soils are small and in poor condition

** Bergi gronfoeloe trees on sandy soil were small and in poor condition, preference for clay loam soils is not unlikely

APPENDIX IV

Patterns in spatial distributions of trees and palms

TABLE IV.1. MAIN experiment: spatial distribution patterns of trees (including cut stumps) of various size classes: results from Greig-Smith's χ^2 nested type test (analyses for 4×4 blocks)

Dbh class (cm)	Number of tests	Item	Mean squares (MS)			Frequency P = 0.05 significance	
			Average	Lowest	Highest	MS > 1	MS < 1
commercial species							
20 – 30	21	within 4s	1.01	0.48	1.57	0	0
		between 4s	1.16	0.22	3.67	1	0
		total	1.04	0.46	1.65	0	0
		number of significant tests				1	0
30 – 40	13	within 4s	1.24	0.59	1.86	0	0
		between 4s	1.31	0.47	4.40	1	0
		total	1.26	0.78	1.64	0	0
		number of significant tests				1	0
40 – 60	24	within 4s	0.84	0.27	1.44	0	1
		between 4s	1.08	0.04	4.24	1	1
		total	0.89	0.40	2.00	1	1
		number of significant tests				1	0
60 – 90	5	within 4s	0.93	0.65	1.54	0	0
		between 4s	0.98	0.22	1.50	0	0
		total	0.94	0.56	1.47	0	0
		number of significant tests				0	0

TABLE IV.1. Continued.

Dbh class (cm)	Number of tests	Item	Mean squares (MS)			Frequency P = 0.05 significance	
			Average	Lowest	Highest	MS > 1	MS < 1
all species							
20 – 30*	30	within 4s	0.96	0.63	1.24	0	1
		between 4s within 16s	0.86	0.36	1.55	0	0
		between 16s	1.03	0.06	3.40	1	1
		total	0.94	0.63	1.14	0	2
		number of significant tests				1	0
30 – 40	30	within 4s	0.88	0.30	1.42	0	2
		between 4s	1.14	0.04	2.69	0	1
		total	0.93	0.27	1.62	0	1
		number of significant tests				0	0
40 – 60	30	within 4s	0.97	0.25	1.86	0	1
		between 4s	1.02	0.00	4.29	1	3
		total	0.98	0.33	2.04	1	2
		number of significant tests				2	0
60 – 90	10	within 4s	0.94	0.30	1.89	0	1
		between 4s	0.93	0.00	2.83	0	2
		total	0.94	0.48	1.76	0	0
		number of significant tests				0	0

* Analysis for 8 × 8 blocks

TABLE IV.2. MAIN experiment: spatial distribution patterns of individual tree species: results from Greig-Smith's χ^2 nested type test (analyses for 4×4 blocks)

Species	Number of tests	Item	Mean squares (MS)			Frequency P=0.05 significance	
			Average	Lowest	Highest	MS>1	MS<1
rode sali *(Tetragastris altissima)*	2	within 4s	0.72	0.69	0.75	0	0
		between 4s	1.14	0.33	1.94	0	0
		total	0.80	0.67	0.94	0	0
		number of significant tests				0	0
basralokus *(Dicorynia guianensis)*	24	within 4s	1.31	0.44	2.17	3	0
		between 4s	1.39	0.00	3.68	2	6
		total	1.32	0.36	2.35	4	1
		number of significant tests				4	0
hoogland baboen *(Virola melinonii)*	2	within 4s	0.82	0.71	0.92	0	0
		between 4s	1.06	0.50	1.63	0	0
		total	0.86	0.67	1.06	0	0
		number of significant tests				0	0
bolletri *(Manilkara bidentata)*	2	within 4s	0.88	0.38	1.39	0	0
		between 4s	1.63	0.22	3.09	0	0
		total	1.04	0.92	1.16	0	0
		number of significant tests				0	0
bergi gronfoeloe *(Qualea rosea)*	16	within 4s	1.04	0.19	2.23	1	1
		between 16s	3.99	0.19	3.33	8	0
		total	1.63	0.89	3.03	6	0
		number of significant tests				8	0
rode jakanta *(Dendrobangia boliviana)*	11	within 4s	1.13	0.62	2.27	1	0
		between 4s	0.99	0.09	2.30	0	0
		total	1.10	0.58	2.08	1	0
		number of significant tests				1	0
hoogland oemanbarklak *(Lecythis corrugata)*	4	within 4s	0.77	0.41	1.08	0	0
		between 4s	1.50	0.61	3.33	1	0
		total	0.92	0.68	1.07	0	0
		number of significant tests				1	0

TABLE IV.2. continued

Species	Number of tests	Item	Mean squares (MS)			Frequency P = 0.05 significance	
			Average	Lowest	Highest	MS > 1	MS < 1
fomang	1	within 4s	1.07	n.a.	n.a.	0	0
(Chaetocarpus		between 4s	2.15	n.a.	n.a.	0	0
schomburgkianus)		total	1.29	n.a.	n.a.	0	0
		number of significant tests				0	0
swietiboontje	1	within 4s	1.43	n.a.	n.a.	0	0
(Inga spp.)		between 4s	4.61	n.a.	n.a.	1	0
		total	2.07	n.a.	n.a.	1	0
		number of significant tests				1	0
djadidja	1	within 4s	1.25	n.a.	n.a.	0	0
(Sclerolobium		between 4s	4.12	n.a.	n.a.	1	0
melinonii)		total	1.82	n.a.	n.a.	1	0
		number of significant tests				1	0
granboesi papaja	1	within 4s	1.48	n.a.	n.a.	0	0
(Pourouma spp.)		between 4s	1.14	n.a.	n.a.	0	0
		total	1.41	n.a.	n.a.	0	0
		number of significant tests				0	0

TABLE IV.3. MAIN experiment: spatial distribution patterns of individual palm species: results from Greig-Smith's χ^2 nested type test (analyses for 8×8 blocks)

Species	Number of tests	Item	Mean squares (MS)			Frequency P = 0.05 significance	
			Average	Lowest	Highest	MS > 1	MS < 1
paramaka *(Astrocaryum paramaca)*	22	within 4s	0.91	0.60	1.41	0	0
		between 4s					
		within 16s	1.26	0.36	2.32	2	0
		between 16s	3.06	0.09	14.19	7	1
		total	1.08	0.68	1.63	3	0
		number of significant tests				9	0
boegroemaka *(Astrocaryum sciophilum)*	14	within 4s	1.60	1.00	2.52	9	0
		between 4s					
		within 16s	2.57	0.70	4.86	8	0
		between 16s	10.82	1.12	38.85	12	0
		total	2.22	1.10	4.23	13	0
		number of significant tests				14	0
nanaimaka *(Bactris sp.)*	27	within 4s	1.11	0.71	1.77	2	0
		between 4s					
		within 16s	1.15	0.40	2.08	1	0
		between 16s	1.27	0.03	5.17	3	2
		total	1.10	0.04	1.90	3	1
		number of significant tests				5	0
maripa *(Maximiliana maripa)*	21	within 4s	1.64	0.86	4.01	11	0
		between 4s					
		within 16s	3.07	0.80	13.31	17	0
		between 16s	7.32	0.26	21.92	16	0
		total	2.19	0.92	5.01	20	0
		number of significant tests				21	0
koemboe *(Oenocarpus bacaba)*	27	within 4s	1.12	0.52	1.82	3	0
		between 4s					
		within 16s	1.35	0.36	2.53	4	0
		between 16s	1.69	0.05	4.40	4	1
		total	1.19	0.79	1.68	8	0
		number of significant tests				12	0

APPENDIX V

Effects of logging: results from ANOVA tests

ANOVA tests were used to analyse effects of logging. For methodology and discussion, see Section 3.1.4 and Chapter 5. In the tables listed below, asterisks indicate the level of significance: one asterisk (*) means that the null hypothesis is rejected at a level of 0.05, two at a level of 0.01, and three at a level of 0.005.

TABLE V.I. MAIN experiment: damage to the commercial stand, testing basal area (m^2/ha) in the undamaged category with ANOVA

PART I: Input table

Replication	Basal area (m^2/ha) per plot and level of exploitation		
	E 15	E 23	E 46
1A	10.61	8.72	6.73
1B	10.05	9.34	6.38
1C	7.88	7.81	6.19
2A	15.70	11.85	6.13
2B	12.73	9.12	8.31
2C	10.49	11.81	11.38
3A	7.76	10.49	6.23
3B	12.22	11.11	8.01
3C	11.36	6.74	7.07
mean	11.98	9.67	7.38

PART II: Output table

Source	Effect	Degrees of freedom	F-value
replications	48.45	df = 8	F = 2.01
treatment	61.12	df = 2	F = 10.15***
rest	48.16	df = 16	S^2 = 3.01

TABLE V.2. MAIN experiment: damage to the commercial stand, testing basal area (m^2/ha) in the destroyed category with ANOVA

PART I: Input table

Replication	Basal area (m^2/ha) per plot and level of exploitation		
	E 15	E 23	E 46
1A	0.11	0.75	0.66
1B	0.45	0.48	0.92
1C	0.05	0.29	0.24
2A	0.76	0.74	1.21
2B	0.48	0.64	0.88
2C	0.56	0.46	1.16
3A	0.35	0.24	1.31
3B	0.58	0.65	0.88
3C	0.20	0.49	0.32
mean	0.39	0.53	0.84

PART II: Output table

Source	Effect	Degrees of freedom	F-value
replications	11.00	df = 8	F = 2.94*
treatment	9.66	df = 2	F = 10.24***
rest	7.48	df = 16	S^2 = 0.47

TABLE V.3. MAIN experiment: damage to the commercial stand, testing basal area (m^2/ha) in the very severe injury category with ANOVA

PART I: Input table

Replication	Basal area (m^2/ha) per plot and level of exploitation		
	E 15	E 23	E 46
1A	0.02	0.52	0.00
1B	0.03	0.01	0.05
1C	0.02	0.15	0.06
2A	0.02	0.06	0.22
2B	0.12	0.16	0.04
2C	0.03	0.13	0.05
3A	0.36	0.07	0.65
3B	0.32	0.36	0.37
3C	0.04	0.24	0.28
mean	0.11	0.13	0.19

PART II: Output table

Source	Effect	Degrees of freedom	F-value
replications	0.346	df = 8	F = 1.83
treatment	0.041	df = 2	F = 0.88
rest	0.380	df = 16	S^2 = 0.024

TABLE V.4. MAIN experiment: damage to the commercial stand, testing basal area (m^2/ha) in the severe and minor injury categories with ANOVA

PART I: Input table

Replication	Basal area (m^2/ha) per plot and level of exploitation		
	E 15	E 23	E 46
1A	1.90	1.91	1.35
1B	1.68	2.43	2.49
1C	1.40	1.67	2.41
2A	4.02	2.67	3.00
2B	2.97	4.63	3.69
2C	2.83	3.00	3.20
3A	2.39	2.13	1.57
3B	1.80	1.95	2.42
3C	1.79	2.28	1.17
mean	2.31	2.53	2.37

PART II: Output table

Source	Effect	Degrees of freedom	F-value
replications	13.41	df = 8	F = 5.89***
treatment	0.23	df = 2	F = 0.41
rest	4.55	df = 16	$S^2 = 0.28$

TABLE V.5. MAIN experiment: area under residual forest, testing percentage of the total area after logging with ANOVA

PART I: Input table

Replication	Percentage of the total area per plot/level of exploitation		
	E 15	E 23	E 46
1A	67	64	45
1B	70	62	30
1C	75	68	35
2A	68	74	50
2B	80	62	48
2C	76	63	43
3A	65	64	47
3B	54	62	60
3C	82	63	51
mean	70.8	64.7	45.4

PART II: Output table

Source	Effect	Degrees of freedom	F-value
replications	291.0	df = 8	F = 0.55
treatment	3145.9	df = 2	F = 23.86***
rest	1054.8	df = 16	$S^2 = 65.93$

TABLE V.6. MAIN experiment: area under gaps, testing percentage of the total area after logging with ANOVA

PART I: Input table

Replication	Percentage of the total area per plot/level of exploitation		
	E 15	E 23	E 46
1A	23	26	47
1B	25	32	48
1C	20	29	43
2A	30	13	35
2B	15	30	38
2C	19	24	35
3A	29	24	40
3B	35	27	19
3C	13	25	36
mean	23.2	25.6	37.9

PART II: Output table

Source	Effect	Degrees of freedom	F-value
replications	282.7	df = 8	F = 0.58
treatment	1118.0	df = 2	F = 9.22***
rest	970.0	df = 16	$S^2 = 60.63$

TABLE V.7. MAIN experiment: area under skid trails, testing percentage of the total area after logging with ANOVA

PART I: Input table

Replication	Percentage of the total area per plot/level of exploitation		
	E 15	E 23	E 46
1A	10	10	8
1B	5	6	22
1C	5	3	22
2A	2	13	15
2B	5	8	14
2C	5	13	22
3A	6	12	13
3B	11	11	21
3C	5	12	13
mean	6.0	9.8	16.7

PART II: Output table

Source	Effect	Degrees of freedom	F-value
replications	79.4	df = 8	F = 0.54
treatment	526.5	df = 2	F = 14.32***
rest	294.2	df = 16	$S^2 = 18.38$

TABLE V.8. MAIN experiment: diameter growth of commercial trees, testing mean annual increment (cm/yr) of trees larger than 15 cm dbh after logging with ANOVA

PART I: Input table

Replication	Mean increment (cm/yr) per plot and level of exploitation		
	E 15	E 23	E 46
1A	0.40	0.42	0.48
1B	0.43	0.39	0.54
1C	0.45	0.54	0.53
2A	0.47	0.37	0.58
2B	0.39	0.41	0.54
2C	0.39	0.48	0.46
3A	0.50	0.52	0.53
3B	0.41	0.48	0.51
3C	0.43	0.52	0.44
mean	0.43	0.46	0.51

PART II: Output table

Source	Effect	Degrees of freedom	F-value
replications	0.0192	df = 8	F = 0.97
treatment	0.0313	df = 2	F = 6.35**
rest	0.0395	df = 16	$S^2 = 0.0025$

TABLE V.9. MAIN experiment: diameter growth of commercial trees, testing mean annual increment (cm/yr) of trees 5 – 15 cm dbh after logging with ANOVA

PART I: Input table

Replication	Mean increment (cm/yr) per plot and level of exploitation		
	E 15	E 23	E 46
1A	0.19	0.20	0.30
1B	0.39	0.27	0.42
1C	0.16	0.24	0.45
2A	0.20	0.25	0.31
2B	0.17	0.21	0.29
2C	0.27	0.31	0.30
3A	0.22	0.15	0.29
3B	0.22	0.23	0.31
3C	0.11	0.26	0.25
mean	0.21	0.24	0.32

PART II: Output table

Source	Effect	Degrees of freedom	F-value
replications	0.0552	df = 8	F = 2.37
treatment	0.0613	df = 2	F = 10.52***
rest	0.0467	df = 16	S^2 = 0.0029

APPENDIX VI

Stem volume estimation

Measuring trunk volumes in tropical rain forest is difficult and time consuming. Efforts were made to make estimations easier by exploring the functional relationships between stem volume and measurements which are easier to make. Measurements of trunk diameter at breast height (dbh), stem length and stem diameter at crown point were used to compute volumes of individual trees (Section 3.1.4, Equation 3.1). According to Hallé et al. (1978), a tree stem increases in length until the tree changes from a "branched complex" into a "reiterated complex", that is, when apical dominance fades and the vertically oblong crown becomes a more horizontally expanded, often cauliflower or umbrella shaped crown. Most commercial trees reach this point when the dbh is about 30 cm. As stem length is a fairly constant factor and a strong correlation between dbh and stem diameter at crown point may be assumed, it seems logical to seek a functional relationship between the stem volume and the dbh or basal area.

First, a relation between stem volume and basal area was established. Commercial volumes per one-hectare plots were calculated and compared with commercial basal area values, using linear regression analysis (LRA). This resulted in Equation VI.1:

$$Y = -31.82 + 15.53X \qquad \text{(VI.1)}$$

where:
Y = commercial volume (m^3/ha)
X = commercial basal area (m^2/ha)

Equation VI.1 has proved fairly reliable ($R^2 = 0.88$) and it can be used to estimate commercial volume increment per unit area (Equation VI.2):

$$dy = 15.53dx \qquad \text{(VI.2)}$$

where:
dy = change in commercial volume (m^3/ha)
dx = change in commercial basal area (m^2/ha)

It was felt that introducing other variables might yield even more accurate results and equations were therefore developed to convert frequency tables into volume tables. Average stem volumes per 5 cm diameter class were calculated for individual species, as well as for all commercial species combined and analysed with LRA. This resulted in the following equations (VI.3 – VI.15) in which Y = stem volume per tree (m^3) and X = diameter class midpoint (cm):

for slangenhout (*Loxopterygium sagotii*):
$$Y = -0.3484 + (1.223 \times 10^{-3})X^2 \quad \text{(VI.3)}$$
for goebaja (*Jacaranda copaia*):
$$Y = -0.0239 + (1.040 \times 10^{-3})X^2 \quad \text{(VI.4)}$$
for rode sali (*Tetragastris altissima*):
$$Y = -0.0836 + (0.759 \times 10^{-3})X^2 \quad \text{(VI.5)}$$
for tingimonisali (*Tetragastris hostmannii*):
$$Y = -0.2013 + (0.943 \times 10^{-3})X^2 \quad \text{(VI.6)}$$
for kopi (*Goupia glabra*):
$$Y = -0.3152 + (1.020 \times 10^{-3})X^2 \quad \text{(VI.7)}$$
for basralokus (*Dicorynia guianensis*):
$$Y = -0.3232 + (1.208 \times 10^{-3})X^2 \quad \text{(VI.8)}$$
for krapa (*Carapa procera*):
$$Y = -0.1065 + (0.812 \times 10^{-3})X^2 \quad \text{(VI.9)}$$
for hoogland baboen (*Virola melinonii*):
$$Y = -0.2169 + (1.199 \times 10^{-3})X^2 \quad \text{(VI.10)}$$
for bolletri (*Manilkara bidentata*):
$$Y = -0.3018 + (1.133 \times 10^{-3})X^2 \quad \text{(VI.11)}$$
for zwart riemhout (*Micropholis guyanensis var. commixta*):
$$Y = -0.3481 + (1.189 \times 10^{-3})X^2 \quad \text{(VI.12)}$$
for hoogland gronfoeloe (*Qualea albiflora*):
$$Y = -0.4308 + (1.412 \times 10^{-3})X^2 \quad \text{(VI.13)}$$
for bergi gronfoeloe (*Qualea rosea*):
$$Y = -0.1486 + (1.213 \times 10^{-3})X^2 \quad \text{(VI.14)}$$
for all commercial species combined:
$$Y = -0.2335 + (1.125 \times 10^{-3})X^2 \quad \text{(VI.15)}$$

The constants in these equations are remarkably similar to those in a regression equation published by Lescure (1981) for all canopy species in French Guiana (Equation VI.16):

$$Y = -0.274 + (1.247 \times 10^{-3})X^2 \quad \text{(VI.16)}$$

Equations VI.3 – VI.14 (for individual species) proved very reliable with R^2 values ranging from 0.94 (slangenhout) to 0.99 (hoogland baboen, bolletri, bergi gronfoeloe). Equation VI.15 (for all commercial species combined) proved even more accurate with a correlation close to its theoretical maximum ($R^2 = 0.997$).

Regression coefficients in Equations VI.3 – VI.14 indicate stem length. A low coefficient means that the species forms characteristically short stems (rode sali, krapa) or that trunk length is highly variable (tingimonisali, kopi, goebaja). The stems of most canopy trees reach lengths of about 18 m.

APPENDIX VII

Effects of refinement: results from ANOVA tests

ANOVA tests were used to analyse the growth of commercial species after logging (treatment B) and refinement (treatment A). For methodology and discussion, see Sections 3.1.4 and 6.5.2. In the tables listed below, asterisks indicate the level of significance: one asterisk (*) means that the null hypothesis is rejected at a level of 0.05, two at a level of 0.01, and three at a level of 0.005.

TABLE VII.1. MAIN experiment: diameter increment (cm/yr) of commercial trees, larger than 15 cm dbh, in the first year after refinement, tested with ANOVA

PART I: Input table

Replication	Mean annual diameter increment (cm/yr) per plot and per combination of treatments[1]								
	E 15			E 23			E 46		
	S 0	*SR 18*	*SR 14*	*S 0*	*SR 18*	*SR 14*	*S 0*	*SR 18*	*SR 14*
1	0.36	0.51	0.44	0.35	0.37	0.52	0.38	0.55	0.48
2	0.39	0.47	0.55	0.45	0.51	0.50	0.49	0.59	0.54
3	0.45	0.47	0.57	0.56	0.57	0.52	0.56	0.60	0.68
mean	0.40	0.48	0.52	0.45	0.48	0.51	0.48	0.58	0.57

PART II: Output table

Source	Effect	Degrees of freedom	F-value
replications	0.0578	df = 2	F = 11.69***
treatment A	0.0409	df = 2	F = 8.27***
treatment B	0.0269	df = 2	F = 5.43*
interaction A×B	0.0061	df = 4	F = 0.62
rest	0.0396	df = 16	S^2 = 0.0025

[1] E 15: basal area felled approximately 1 m^2/ha
E 23: basal area felled approximately 2 m^2/ha
E 46: basal area felled approximately 4 m^2/ha
S 0: unrefined
SR 18: refinement with 30 cm dbh limit
SR 14: refinement with 20 cm dbh limit

TABLE VII.2. MAIN experiment: diameter increment (cm/yr) of commercial species, 5 – 15 cm dbh, in the first year after refinement, tested with ANOVA

PART I: Input table

Replication	Mean annual diameter increment (cm/yr) per plot and per combination of treatments[1]								
	E 15			E 23			E 46		
	S 0	*SR 18*	*SR 14*	*S 0*	*SR 18*	*SR 14*	*S 0*	*SR 18*	*SR 14*
1	0.14	0.42	0.27	0.25	0.37	0.38	0.39	0.40	0.45
2	0.15	0.34	0.56	0.38	0.31	0.62	0.18	0.46	0.53
3	0.21	0.30	0.25	0.27	0.41	0.25	0.36	0.50	0.53
mean	0.17	0.35	0.36	0.30	0.36	0.42	0.31	0.45	0.50

PART II: Output table

Source	Effect	Degrees of freedom	F-value
replications	0.0153	df = 2	F = 0.70
treatment A	0.1401	df = 2	F = 6.38**
treatment B	0.0748	df = 2	F = 3.41
interaction A×B	0.0131	df = 4	F = 0.30
rest	0.1757	df = 16	$S^2 = 0.0110$

[1] For explanation of codes, see Table VII.1